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SYMPOSIUM

Species Introductions and Their Cascading Impacts on Biotic Interactions in desert riparian ecosystems

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Synopsis Desert riparian ecosystems of North America are hotspots of biodiversity that support many sensitive species, and are in a region experiencing some of the highest rates of climatic alteration in North America. Fremont cottonwood, *Populus fremontii*, is a foundation tree species of this critical habitat, but it is threatened by global warming and regional drying, and by a non-native tree/shrub, *Tamarix* spp., all of which can disrupt the mutualism between *P. fremontii* and its beneficial mycorrhizal fungal communities. Specialist herbivorous leaf beetles (*Diorhabda* spp.) introduced for biocontrol of *Tamarix* are altering the relationship between this shrub and its environment. Repeated episodic feeding on *Tamarix* foliage by *Diorhabda* results in varying rates of dieback and mortality, depending on genetic variation in allocation of resources, growing conditions, and phenological synchrony between herbivore and host plant. In this article, we review the complex interaction between climatic change and species introductions and their combined impacts on *P. fremontii* and their associated communities. We anticipate that (1) certain genotypes of *P. fremontii* will respond more favorably to the presence of *Tamarix* and to climatic change due to varying selection pressures to cope with competition and stress; (2) the ongoing evolution of *Diorhabda’s* life cycle timing will continue to facilitate its expansion in North America, and will over time enhance herbivore impact to *Tamarix*; (3) defoliation by *Diorhabda* will reduce the negative impact of *Tamarix* on *P. fremontii* associations with mycorrhizal fungi; and (4) spatial variability in climate and climatic change will modify the capacity for *Tamarix* to survive episodic defoliation by *Diorhabda*, thereby altering the relationship between *Tamarix* and *P. fremontii*, and its associated mycorrhizal fungal communities. Given the complex biotic/abiotic interactions outlined in this review, conservation biologists and riparian ecosystem managers should strive to identify and conserve the phenotypic traits that underpin tolerance and resistance to stressors such as climate change and species invasion. Such efforts will greatly enhance conservation restoration efficacy for protecting *P. fremontii* forests and their associated communities.

Introduction

The structure of communities is in large part governed by the complex interactions between foundation species and the consumers they support. Foundation species, particularly long-lived foundation tree species, tend to harbor considerable genetic variation that gives rise to the expression of a diverse range in phenotypic traits that in turn support highly diverse biological communities (Whitham et al. 2012). Therefore, a primary goal of conservation biology is to not only protect foundation species, but also the genetic diversity of foundation species that underpin the structure of complex communities (Whitham et al. 2006).

Despite a broad genetic diversity, foundation species can be adapted locally to climate and other environmental characteristics (reviews by Savolainen et al. 2007; Hereford 2009). However, locally-adapted populations may become locally maladapted (O’Neill et al. 2008; Sthultz et al. 2009a; Grady et al. 2011) if they are unable to keep pace with rapid climatic change. As a result, climatic change has become

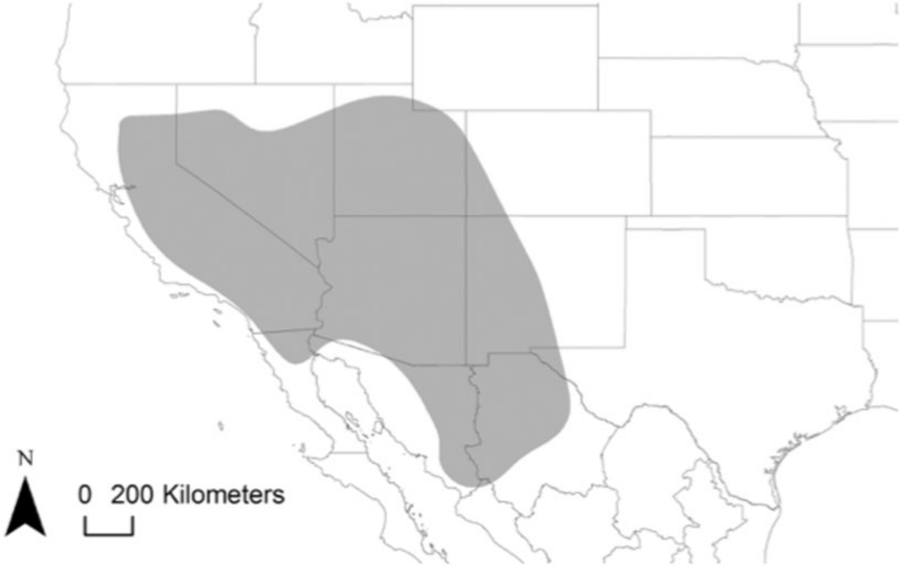

Fig. 1 Map showing where the distribution of *P. fremontii* and *T. chinensis* x *T. ramosissima* overlap in western North America. The polygons were drawn from data provided by Dana Ikeda (Personnel communication).

an amplified agent of selection affecting many foundation species and their community-dependent organisms including mycorrhizal mutualists, insects, annual plants, and birds (e.g., Grant and Grant 2002; Franks et al. 2007; O'Neill et al. 2008; Sthultz et al. 2009a, 2009b). Because different plant genotypes can support different communities and ecosystems (e.g., Johnson and Agrawal 2005; Bailey et al. 2006; Shuster et al. 2006; Schweitzer et al. 2008; Barbour et al. 2009; Keith et al. 2010; Smith et al. 2011), climatic change, as an agent of selection on primary producers, will likely cascade to whole communities. Reduced plant productivity and non-random mortality of specific genotypes resulting from stressful climates, will predictably alter species richness, abundance, and taxonomic composition of communities (Sthultz et al. 2009b; Stone et al. 2010; Kane et al. 2011; Fischer et al. 2013; Ikeda et al. 2013).

Fremont cottonwood (*P. fremontii* Wats.) is one of the most widely distributed and charismatic foundation tree species in the southwestern United States and northwestern Mexico. Their large canopies and vast root systems support a remarkable diversity of organisms. Because *P. fremontii* is a drought-intolerant species that depends on surface flooding for germination, and on contact of its roots with shallow groundwater throughout its life history, its distribution is limited to the margins of streams, rivers, and reservoirs (Stromberg 1993). Thus, the diverse communities that *P. fremontii* supports are also concentrated within these narrow riparian corridors. As with other foundation species of trees, *P. fremontii* tends to be locally adapted to its climate and hydrological conditions, such that shifts either in temperature during the growing season or in hydrologic regime could result in populations becoming locally maladapted (Hultine et al. 2010a; Grady et al. 2011). In other words, climatic change has the potential to cause widespread mortality, extensive reductions in plant productivity, loss in genetic diversity, and a significant reduction in the foundational capacity of populations of *P. fremontii* that are already highly threatened throughout the desert regions in which they occur (Gitlin et al. 2006).

In addition to climatic change, the habitat for *P. fremontii* has been altered by the introduction and spread of the non-native Eurasian tree/shrub tamarisk (*Tamarix* spp.). Several *Tamarix* species (also known as saltcedar) were introduced to North America in the early to mid- 1800s, and two species: *T. chinensis* Lour. and *T. ramossisima* Ledeb., along with their hybrids, *T. chinensis* x *T. ramosissima* have become widely established throughout the western United States and parts of northern Mexico (Gaskin and Schaal 2002; Friedman et al. 2005) with a distribution that overlaps with *P. fremontii* over vast areas of the southwestern United States and northern Mexico (Fig. 1). Establishment of *Tamarix* has been associated with increased frequency of fire (Busch and Smith 1993), reduced biodiversity (Harms and Hiebert 2006), and disruption of mutualisms important to native plants such as *P. fremontii* (Meinhardt and Gehring 2012). Combined with climatic change, *P. fremontii* and its associated communities are likely to experience an ''amplified'' effect of interacting environmental stresses (climate x

Fig. 2 Photographs showing *Tamarix* in southeastern Utah before and after defoliation by *D. carinulata*. The photographs were taken two weeks apart in July 2007.

Tamarix's presence) that may result in critical changes in the structure and function of riparian habitats (Ikeda et al. 2014). If so, the capacity for these ecosystems to serve as hotspots of biodiversity in the desert southwest may be diminished substantially.

Due to the proliferation of *Tamarix* along streams and rivers, and its associated impacts on riparian habitat in the western United States intensive eradication programs have been implemented throughout the region. The most successful, but controversial, approach has been the release of a biological control agent from Eurasia, the northern *Tamarix* leaf beetle, *D. carinulata* Brullê (Dudley 2005; Hultine et al. 2010b), along with other closely related *Diorhabda* sibling species from Eurasia (Tracy and Robbins 2009). The beetle feeds exclusively on *Tamarix* foliage, resulting in periods of complete defoliation that last for several weeks (Dudley 2005; Hultine et al. 2010c; Pattison et al. 2011) (Fig. 2). Infestations of beetles typically result in one to three defoliations per year. These episodic events inevitably reduce carbon storage and in turn reduce the production and growth of leaves, and in some cases lead to the mortality of *Tamarix* (Hudgeons et al. 2007). The rate of mortality, however, can be highly variable across the landscape, depending on a combination of environmental conditions and genetically controlled strategies of resource-allocation by the host plant (Hultine and Dudley 2013; Hultine et al. 2013, 2015; Williams et al. 2014). The extent to which defoliation by *D. carinulata* releases *P. fremontii* and its associated communities from the negative impacts of *Tamarix* is an open question that hinges on several factors, including the geographic distribution of *Diorhabda*, the phenotypic response of *Tamarix* to defoliation, and on the impacts of climatic change on the structure and function of riparian communities.

In this article, we review the interaction among multiple processes of global change with respect to their combined impacts on *P. fremontii* and its capacity to support diverse biological communities. Our review focuses on three primary biotic/abiotic relationships that we anticipate will define the balance between resilience and sensitivity of desert riparian ecosystems to global environmental changes. We start by reviewing the symbiotic relationship between *P. fremontii* and root-associated fungi and the extent to which *Tamarix* may disrupt this important mutualism. We then review the influence of new trophic relationships, specifically herbivory by a specialist herbivore (*Diorhabda* spp.), on the abundance and physiological function of *Tamarix*. Here, we focus on geographical patterns of defoliation, beetle-induced plant mortality, and subsequent impact on co-occurring *P. fremontii* and its root-associated fungal mutualists. Finally, we review how regional climatic change might affect these complex biotic interactions, specifically focusing on alterations in temperature and in the hydrologic cycle that are predicted for the southwestern United States. We pay special attention to the physiological mechanisms that underpin the relationships among component species and their habitat. In this context, we review the inevitable tradeoffs that are associated with resource-allocation, plant productivity, and tolerance of stress to develop a framework for conservation and restoration of valued riparian ecosystems.

Non-native *Tamarix*: a disrupter of root-associated mutualisms

Populus fremontii, like other species in the family Salicaceae, forms important symbiotic associations with mycorrhizal fungi. This association benefits the plant by increasing the absorptive capacity of roots for water and mineral nutrients such as nitrogen and phosphorus whereas the fungi gain carbon in the form of non-structural carbohydrates (NSCs). *Populus fremontii* routinely establishes functional associations with two of the major types of mycorrhizal fungi: ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) fungi (Molina et al. 1992), both of which enhance total surface area in contact with the soil resulting in greater capacity for the uptake of nutrients by the root system. Colonization of the roots of *P. fremontii* by EM and AM fungi is partly governed by genetically controlled root-growth and patterns of carbon-allocation and partly by the local soil environment and by availability of water (Lodge 1989; Smith and Read 1996; Barker et al. 2002; Beauchamp et al. 2005; 2006; Gehring et al. 2006). Therefore, the level of colonization by mycorrhizal fungi can vary among habitats and among populations and genotypes (Lodge 1989; Beauchamp et al. 2006; Gehring et al. 2006).

Tamarix can disrupt the *P. fremontii*/mycorrhizal mutualism, particularly *P. fremontii*/EM association due to its influence on the soil environment (Meinhardt and Gehring 2012, 2013). In field studies from the Verde River in central Arizona, the colonization of the roots of *P. fremontii* by mycorrhizal fungi was 2-fold higher for trees that were neighbored by other *P. fremontii* or willow (*Salix* spp.) than for trees neighbored by *Tamarix* (Meinhardt and Gehring 2012). Although the precise mechanisms that underpin these patterns are unclear, *Tamarix*-induced changes in soil chemistry likely contribute. *Tamarix* alters the salinity of shallow layers of the soil by salt deposition through a combination of leaf exudates and the decomposition of leaf litter (Glenn et al. 2012). In the presence of *Tamarix*, electrical conductivity of the soil (a proxy for salt concentration) was 2.5 fold higher under *P. fremontii* compared to trees occurring with other *P. fremontii* or with willow trees on the Verde River (Meinhardt and Gehring 2012). The combination of the presence of *Tamarix* and the prevention of flooding often results in a steady rise in soil salinity to which many mycorrhizal fungi are highly sensitive (Dixon et al. 1993; Kernaghan et al. 2002). For example, due to upstream regulation of flow in the lower Colorado River and the subsequent absence of overbank flooding, *Tamarix* stands deposited on average 0.16 kg m^{-2} of salts per year, amounting to over 11 kg m^{-2} of salt since flooding ceased in the late 1930s (Glenn et al. 2012).

The tissues of *Tamarix* also contain a host of organic acids and polyphenolic compounds that may reduce mycorrhizal colonization when released to the soil from exudates and/or from the decomposition of litter (Lesica and DeLuca 2004). Chemicals released from *Tamarix* tissues contain several antimicrobial and anti-fungal compounds that could inhibit growth (Meinhardt and Gehring 2013). Alternatively, direct competition with *Tamarix* roots may alter carbon-allocation strategies such that fewer NSCs are available to support growth of root-associated fungi. Importantly, data from field collections and experimental inoculations indicate that *Tamarix* does not form associations with AM or EM fungi in its non-native range (Beauchamp et al. 2005; Meinhardt and Gehring 2012), thereby potentially resulting in reduced mycorrhizal fungal inoculum in *Tamarix*-dominated stands, independent of chemical changes. Given that *Tamarix* negatively affects both AM and EM fungi, potentially through a variety of mechanisms, reductions in mycorrhizal fungal populations are likely to persist as a legacy even after *Tamarix* has been successfully removed.

Regardless of the mechanism that inhibits the colonization and growth of mycorrhizal fungal, the presence of *Tamarix* appears to reduce the physiological performance and productivity of neighboring *P. fremontii*. When greenhouse cuttings were inoculated with either AM or EM fungi, *P. fremontii* had higher overall growth of shoots and greater aboveground biomass allocation when grown with other *P. fremontii* than when grown with *Tamarix* (Meinhardt and Gehring 2012). Although this experiment was relatively short-term, mycorrhizal colonization of inoculated *P. fremontii* roots was dramatically reduced in the presence of *Tamarix*, supporting the results of field studies. In a greenhouse experiment involving only inoculation with AM fungi, the presence of these fungi altered the coexistence ratios of *P. fremontii* and *Tamarix* in favor of *P. fremontii* (Beauchamp et al. 2005). These findings suggest that where *Tamarix* is present, overall productivity and canopy size may be reduced, both of which may have profound impacts on the capacity of *P. fremontii* to support foodwebs, community structure, and biological diversity in riparian habitats.

Biological control of *Tamarix*: the introduction and rapid expansion of *D. carinulata*

Tamarix spp. were introduced to the western United States more than a century ago from Eurasia (Robinson 1965; Brock 1994). It has since spread at rates exceeding 20 km/year and is now a dominant plant on the banks of rivers, streams, springs, and ponds from western Montana to Sonora Mexico, and from eastern Oklahoma to northwestern California (Friedman et al. 2005; Morisette et al. 2006). Along with its potential deleterious impacts on the interaction of *P. fremontii* with the biotic community in the soil, *Tamarix* is considered to have negative impacts on the structure and function of riparian ecosystems, including increased frequency of fires (Busch and Smith 1993; Drus 2013), reduced biodiversity (Harms and Hiebert 2006), reduced habitat quality for wildlife (Rice et al. 1980; Bailey et al. 2001), and reduced ecosystem services as a whole, mostly a consequence of depletion of groundwater via transpiration (Zavaleta 2000; Shafroth et al. 2005). Given these negative impacts, the control of *Tamarix* is now targeted as an important aspect of the control of noxious weeds by local, state, and federal governments. In 2001, the US Department of Agriculture (USDA). Animal and Plant Health Inspection Service (APHIS) approved the open release of the central Asian, northern *Tamarix* leaf beetle (*D. carinulata*), and other closely related *Diorhabda* species as a biocontrol for *Tamarix* in North America. Two *Diorhabda* species are now well established within the range of *P. fremontii*. *D. carinulata* was first released in 2001and has become well established in Nevada, Utah, Colorado, Oregon, Wyoming, Idaho, northern Arizona, and northern New Mexico. The subtropical *Tamarix* beetle, *D. sublineata* was introduced in southern and western Texas where it has become well established along the Rio Grande and has also moved into Mexico along the Rio Conchos, watersheds that are occupied both by *Tamarix* and by *P. fremontii* (Fig. 1).

Currently no *Diorhabda* species has expanded its range into central and southern Arizona, southern California, or Sonora Mexico. However, *D. carinulata* may be poised to do so in the coming years. It originally was collected from Chilik, Kazakhstan, and Fukang, China at latitudes near 45°N and has successfully established at similar North American latitudes (40–45°N), producing two or more generations per season and subsequently entering reproductive diapause in late summer to overwinter in the adult stage (Lewis et al. 2003). Introductions that took place south of *ca.* 37-38°N largely failed (Dudley et al. 2012) owing, in part, to the cue inducing photoperiodic diapause putting the insect out of seasonal synchrony with the host plant. Diapause in *Diorhabda* is triggered by a critical daylength (CDL) (the daylength at which 50% of the population enters diapause) of 14.65 h (Bean et al. 2007). While satisfactory as a developmental cue in northern latitudes, this CDL occurs earlier in the year in southern regions, resulting in a single cohort and premature diapause in the middle of the growing season. Under such conditions, fat reserves are depleted during the long, inactive period before new foliage becomes available the following spring.

Since the initial introductions, natural selection for a shorter CDL has enabled *D. carinulata* to disperse to, and become established at, southern latitudes where it previously did not survive (Bean et al. 2012; Dudley et al. 2012). Specifically, beetles present in southern Utah (37.2°N) have dispersed into northern Arizona and southern Nevada where they now reproduce and overwinter successfully. Continued southward colonization, and anticipated evolution of incrementally later induction of diapause that matches the phenology of *Tamarix*, may ultimately bring the insects through the lower Colorado River to its Delta at the mouth of the Sea of Cortez in Mexico (Dudley and Bean 2012).

A species expanding its range will generally show genetic differences at its leading edge, as compared with the resident population at the center of the distribution. This pattern often is related to founder effects that may or may not be advantageous to dispersing individuals (Baker and Stebbins 1965; Shine et al. 2011). Those individuals dispersing from the main population may then mate selectively, resulting in an enhanced rate of natural selection (Phillips et al. 2008; Price and Sol 2008), and shifts in the induction of diapause with latitude. With the *Diorhabda*/*Tamarix* system, individuals that are less 'latitude-adapted' enter diapause early and overwinter in place at the core of the population. Where late-diapausing individuals remain reproductively active, they engage in flight to potentially unoccupied habitat, and produce another generation along the front of dispersal and colonization (Bean et al. 2007, 2012).

Colonization in southern regions thus presents three ecological gradients that drive the adaptation of *D. carinulata* to environmental conditions (Fig. 3): (1) lower latitudes impose a photoperiodic regime that forces earlier diapause, independent of the seasonal progression of the climate; (2) thermal regimes are generally warmer, with the warm season extended

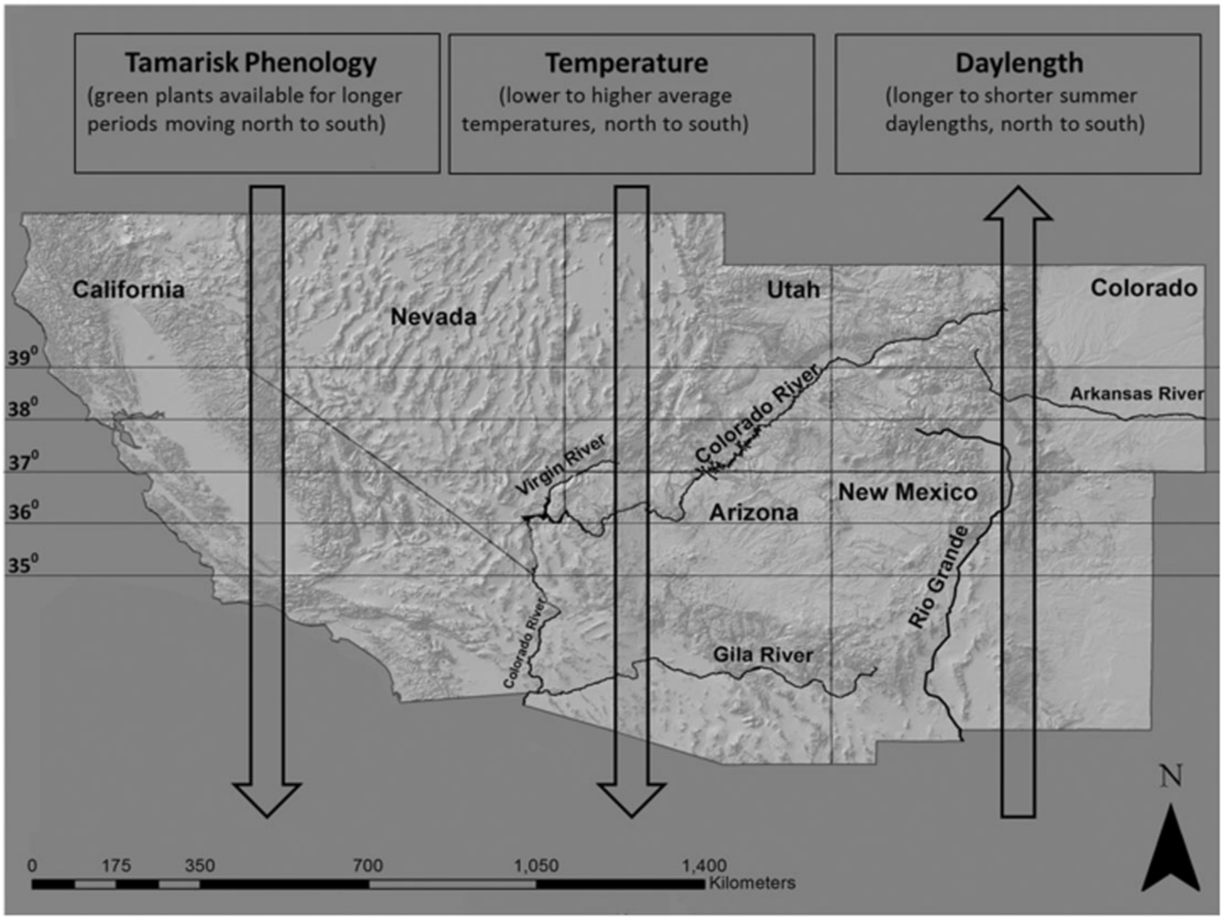

Fig. 3 Ecological gradients encountered by *D. carinulata* as it colonizes from north to south. Daylengths in summer decrease, thereby forcing earlier induction of diapause, in turn causing insects to be increasingly out of synchrony with *Tamarix* that maintains green foliage well into the fall. On the contrary, higher temperatures in southern latitudes permit the development of insects and the growth of plants later in the season.

over a longer period, so that temperatures can have greater influence on the development of diapause (also, growth rates may be accelerated and post-diapause emergence may be influenced by warmer spring conditions); and (3) the longer warm season extends the photosynthetically active period of the host plant both earlier in the spring and later in the fall so that its phenology is less synchronized with its primary herbivore. The third factor has several implications in that premature cessation of feeding while plants remain photosynthetically active allows the host plants to compensate for herbivory by re-building reserves of metabolites that are necessary to avoid mortality (Hudgeons et al. 2007; Hultine and Dudley 2013), thus reducing the effectiveness of the insect as a biocontrol agent. However, an intriguing element of southward the establishment and adaptation of *D. carinulata* is an increase in voltinism; populations that originally produced one generation may yield two or more as they delay diapause and generate additional cohorts (Dalin and Nylin 2012), particularly where relatively mild autumn conditions support continued photosynthetic activity of their host plants (*Tamarix* is only facultatively deciduous). Herbivores' reproductive fitness would, thus, be greatly enhanced (with lower risk of mortality from sudden, unfavorable changes in weather), as would their period and magnitude of impact to host plants (Bean et al. 2013).

The impact of *Diorhabda* on *Tamarix*: Survival versus mortality as a function of resource-allocation

As discussed earlier, *Diorhabda* feeds exclusively on *Tamarix* foliage and photosynthetic bark, and can cause complete defoliation that lasts for several weeks (Fig. 2). When beetle infestations reach outbreak proportions, they typically cause one to three defoliations per year (Pattison et al. 2011). These events reduce carbon storage, leaf production, and stem growth (Hudgeons et al. 2007), in some cases leading to mortality in *Tamarix* (Dudley and Bean 2012; Bean et al. 2013; Hultine et al. 2013). The proportionate mortality, however, is highly variable both within the reaches of a river and across the landscape, and is difficult to predict. Repeated years of defoliation can result in 0–100% mortality (Hultine and Dudley 2013).

Many *Tamarix* species have evolved under intense pressure from herbivores. In its home range, the genus is attacked by over 300 species of host-specific arthropods from 88 genera (Kovalev 1995). This plant-insect co-evolution likely has resulted in a diverse set of defense/tolerance strategies across the range of this genus. Yet defensive mechanisms usually are inadequate to prevent complete herbivory of the foliage by *Diorhabda* (Dudley 2005; Hultine et al. 2010b). Therefore, the survival of *Tamarix* depends on its ability to re-allocate stored metabolites to sustain the production of new photosynthetic tissue after each defoliation. Without doing so, individual *Tamarix* plants become carbon-starved and unable to maintain the minimum level of metabolic activity needed for survival. Repeated defoliation of *Tamarix* by the beetle over a three-year period in northwestern Nevada resulted in a 75% decrease in concentrations of NSCs. This correlated with measurable reductions in total leaf-area (Hudgeons et al. 2007), and substantially decreased radial growth over an eight-year period after the onset of herbivory (Fig. 4). Despite these sharp declines, the mortality of *Tamarix* at this site was only ~40% (Dudley et al. 2006).

Regardless of environmental conditions and the availability of resources, some *Tamarix* populations and genotypes may be better suited to cope with episodic herbivory than are others (Hultine et al. 2013; Williams et al. 2014). Since their introduction, *Tamarix* species have hybridized extensively (Gaskin and Schaal 2002; Gaskin et al. 2006), likely resulting in some novel genotypes that are better adapted to their environment and/or to disturbance than are others. A recent analysis of the annual growth rings of *Tamarix* showed that trees that succumbed to herbivory had higher rates of radial growth before the introduction of *D. carinulata* than did the trees that survived (Hultine et al. 2013). These findings may initially appear counterintuitive because higher growth rates often reflect better availability of resources and greater fitness, which should confer greater resistance to mortality in response to stress. However, in reality these patterns likely reflect various strategies of allocating resources that, in turn, result in important tradeoffs between growth and tolerance to defoliation (Bloom et al. 1985). Specifically, genotypes that have relatively slow growth rates tend to have higher survival rates as a consequence of greater allocation of carbon to the storage-pools of NCSs than to the growth of new tissues (Fig. 5A,B). The reason for this inevitable tradeoff is that the carbon pools of plants are finite and are typically depleted during the growing season (Fig. 5C). In a common garden study, *Tamarix* genotypes from colder climates allocated more biomass to roots than did genotypes from warmer climates (Williams et al. 2014). As a potential consequence of having a higher allocation below ground, and presumably a higher storage of NSCs, genotypes from colder climates were more tolerant of herbivory than were genotypes from lower latitudes (Williams et al. 2014). If this response is ultimately driven by selection for cold tolerance, *Tamarix* plants occurring at higher latitudes or elevations should also display greater allocation of carbon to NSC storage, thereby yielding greater tolerance to episodic defoliation by *Diorhabda*. Therefore, as *Diorhabda* populations

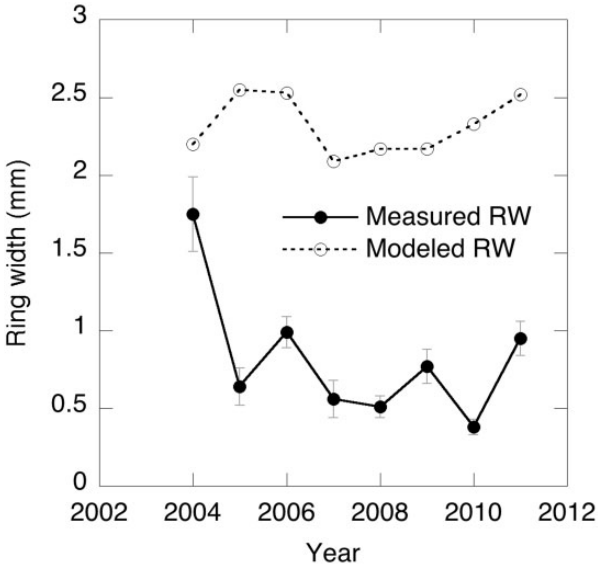

Fig. 4 Measured rates of radial growth compared to predicted growth rates in *Tamarix* trees occurring in western Nevada between 2004 and 2011 ($n = 15$ trees). All of the trees were subjected to herbivory by *D. carinulata* starting in 2004, resulting in a dramatic reduction in radial growth as determined by measuring the width of annual rings. Predicted growth rates during years after *D. carinulata* was introduced were modeled by comparing growth rates during the previous 10 years, before the onset of herbivory, with the regional Palmer Drought Severity Index ($r^2 = 0.75$). Measured rates of annual growth after 2004 were only 25–40% of those predicted on the basis of climate, illustrating the impact that *D. carinulata* has had on this population of *Tamarix*.

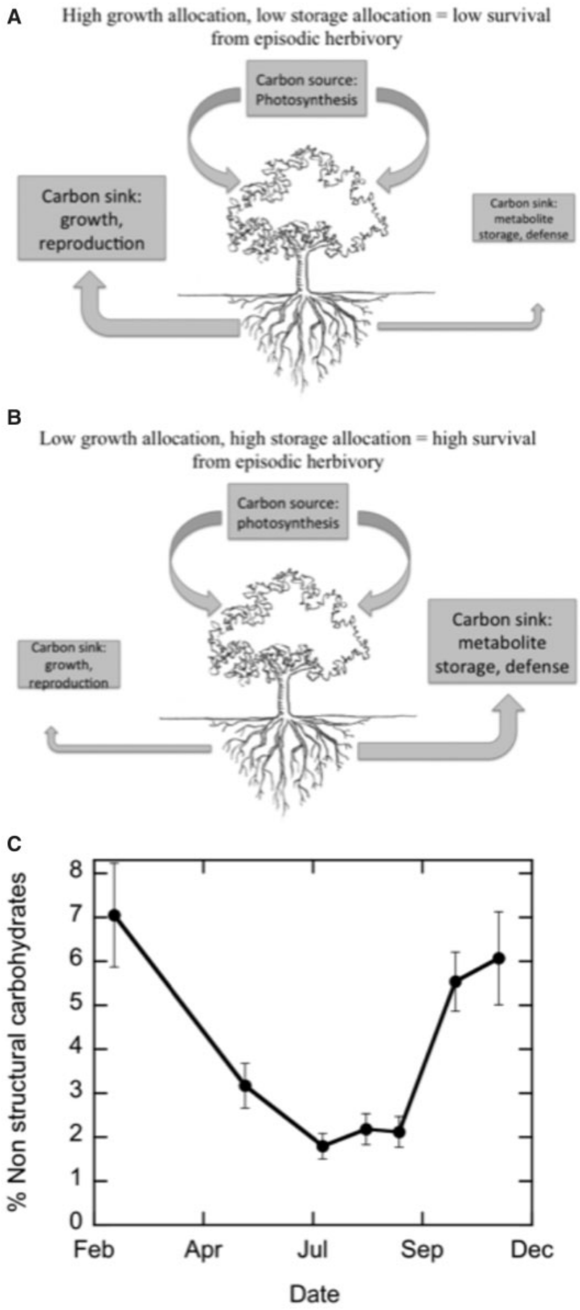

Fig. 5 Tradeoffs associated with various carbon-allocation strategies in mature woody plants. (**A**, **B**) Conceptual diagrams showing resource-allocation tradeoffs associated with plants' carbon budgets. Plants that have large growth (i.e., construction of tissues plus growth respiration) and reproductive sinks relative to storage (i.e., NSC pools and defense) will display relatively low tolerance to episodic herbivory. Therefore, we predict that the tree in the upper panel (**A**) will have higher relative growth rates, but less tolerance to herbivory than will the tree in the lower panel (**B**), and that these disparate strategies for allocating resources among *Tamarix* individuals and populations are genetically fixed. (**C**) Seasonal patterns of concentrations of NSCs in the twigs of mature *Tamarix* trees occurring in southeastern Utah ($n = 20$ trees). The patterns illustrate a reduction of NSC's during the growing season, revealing the competing sinks between growth and storage as shown in panels (**A**) and (**B**).

continue to expand into the warm deserts of the lower Colorado River, rates of mortality and dieback of *Tamarix* there may be amplified relative to *Tamarix* populations occurring in cooler climates.

Independent of temperature and genetics, the capacity for a plant to resist or tolerate disturbance is also a function of its access to local resources. Plants that occur where edaphic conditions are poor could be exposed to low availability of resources such as water and nutrients, either directly or because of high salinity of the soil. Chronic limitation of resources often triggers a ''mortality spiral'' in which the combination of a long-term stressor from poor edaphic conditions and a short-term stressor, such as drought or episodic herbivory, results in a spiraling set of resource deficiencies that ultimately ends with mortality of the plant (Manion 1991). Canopy dieback in *Tamarix* resulting from herbivory by *D. carinulata* increased with salinity of the soil in the Virgin River watershed (Hultine et al. 2015). These findings suggest that stress and limited availability of resources could play an important role in local or landscape patterns of mortality regardless of the number of defoliation events and/or the selection for cold tolerance.

The impact of *Diorhabda* on *Tamarix* soil legacies and root-associated fungi

A primary goal of virtually all *Tamarix* control programs is to improve the habitat quality for native species that usually thrive in riparian areas that are now dominated by *Tamarix* shrublands. Because *P. fremontii* is arguably the most important foundation tree species in the riparian ecosystems of the southwestern United States, successful control of *Tamarix* and subsequent restoration of riparian habitats hinge on whether this species can establish population stability. Among the most important factors that underpin successful reestablishment of *P. fremontii* is the maintenance of its interaction with the soil biota, particularly the mutualistic interaction between the roots of *P. fremontii* and root-associated fungi. An important question is whether repeated defoliation ultimately removes the soil legacy that inhibits the colonization of *P. fremontii* roots by mycorrhizal fungi.

Although the impacts of *Diorhabda* on *Tamarix*'s soil legacies are largely unknown, initial evidence suggests that many defoliation events, and possibly subsequent mortality, may be required to substantially reduce the negative impacts of *Tamarix* on mycorrhizal colonization. For example, a greenhouse study using soils collected from *Tamarix*-infested

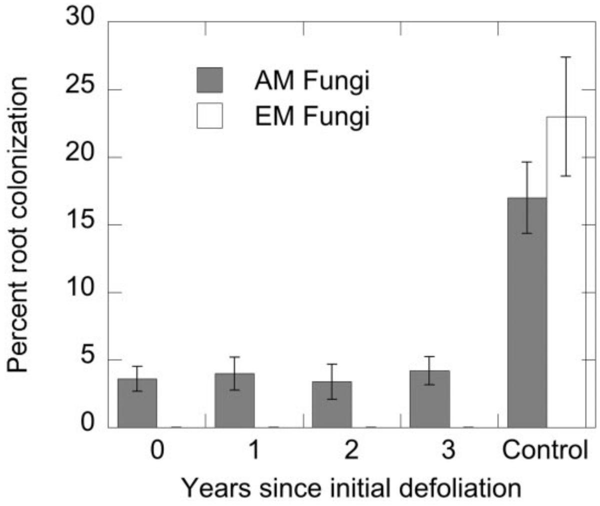

Fig. 6 Mean percent colonization of EM and AM fungi in the roots of *P. fremontii* seedlings grown in soils collected on the banks of the Virgin River in the southwestern United States. Soils labeled "0, 1, 2, 3" were from thick *Tamarix* stands that had experienced 0, 1, 2, and 3 years of defoliation by *D. carinulata*, respectively. The "Control" label indicates *P. fremontii* seedlings grown in soils that lacked a previous *Tamarix* soil legacy. Error bars represent ± the standard error of the mean.

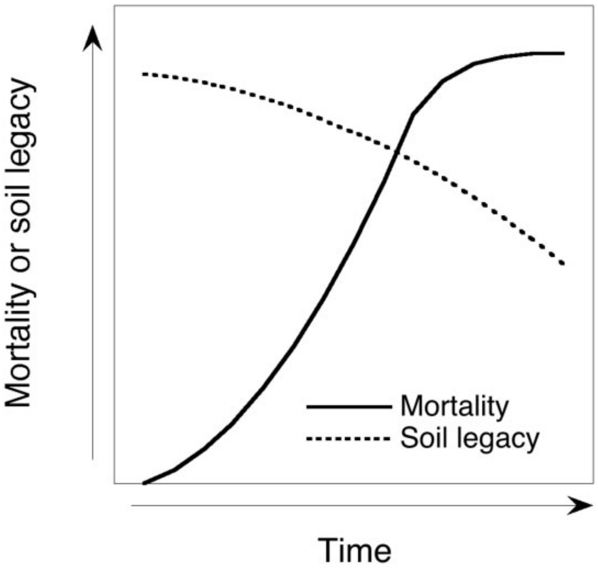

Fig. 7 Relationship between the mortality of *Tamarix* and the residual effect of the legacy on soil biota over multiple years following an initial defoliation by *D. carinulata*. We expect mortality to increase exponentially through time until reaching a plateau as feeding by *D. carinulata* becomes less intense and/or the remaining *Tamarix* plants are those that have a higher tolerance to herbivory (e.g., Fig. 5).

riparian areas along the Virgin River in the southwestern United States appeared to inhibit colonization of *P. fremontii* roots by mycorrhizal fungi, even in soils from sites where *Tamarix* had been defoliated for three consecutive growing seasons (Fig. 6). Specifically, the percentage of roots colonized by AM fungi was about 4% regardless of the number of years with defoliation, compared to 17% in soils with no *Tamarix* legacy (i.e., Control in Fig. 6). These patterns were even more profound for colonization by EM fungi. Virtually none of the *Tamarix* legacy soils from the Virgin River displayed any evidence of the colonization of roots by EM fungi compared to control soils where mean colonization was over 22% (Fig. 6). It should be noted that there was no evidence of mortality or significant canopy dieback in *Tamarix* at any of the stands at the time the soils were collected. Therefore, the deleterious legacy effect of *Tamarix* on mycorrhizal fungi may remain for several years after initial episodic defoliation by *Diorhabda* beetles. However, after the soils were collected, many of the *Tamarix* stands along the Virgin River have experienced extensive mortality with canopy dieback now exceeding 50% in many areas (Hultine et al. 2015); the soil legacy of *Tamarix* may now slowly diminish as mortality increases along the Virgin River (Fig. 7). However, given that AM and EM fungi are obligate and functionally obligate biotrophs, respectively, and that *Tamarix* does not serve as a host plant for these fungi, *Tamarix* legacies may be long-lasting, with restoration of AM and EM fungal assemblages necessary in some areas. As *Tamarix* becomes progressively less dominant in riparian ecosystems, other factors, including species-composition of the flora, quality of the litter, edaphic characteristics, scouring by floods, depositional patterns, and climate will have greater influence on *P. fremontii*/mycorrhizal fungal mutualisms.

Climatic change has impacts on biological interactions in desert riparian forests

According to global circulation models, the western Unites States will experience some of the most profound impacts of climatic change over the next century. These impacts include an increase in air temperature from 1.5°C to 4.5°C, and a reduction in precipitation resulting in greater intensity and duration of droughts (Field et al. 2007; Karl et al. 2009); these events will alter stream-discharge and hydrologic processes in riparian areas (Perry et al. 2012). There is substantial evidence that higher temperatures, higher evaporative demand, and reduced availability of water will all have significant negative impacts on the recruitment, growth, and fitness of *P. fremontii* throughout its range (Stromberg 1993; Horton et al. 2001; Hultine et al. 2010a; Grady et al. 2011). What is less understood is how these projected changes in climate will impact complex biological interactions, foodwebs, and biological communities as a whole in desert riparian forests. We can begin by teasing apart the impacts of climatic change on key biotic interactions (i.e., Fig. 3) to construct testable hypotheses of how changes in climate will ultimately impact the community structure of riparian ecosystems.

Altered environmental conditions due to climatic change are likely to induce changes in plant physiology, soil processes, and relationships between plants and their microbial symbionts. Several previous studies have found that hyphal growth and colonization of roots generally increase with soil temperature in AM fungi and in some species of EM fungi, whereas other studies have reported decreases in growth and colonization or no response to temperature (reviewed by Compant et al. 2010). Patterns of response to climatic warming may be a function of location or biome. In cool climates, increases in temperature may actually stimulate the growth of mycorrhizae and their colonization of roots. Higher temperatures in arctic tundra, for example, increased mycorrhizal growth relative to root biomass (Clemmensen et al. 2006). Because *P. fremontii* primarily occurs in extremely warm climates where temperature at the soil's surface can regularly exceed 50°C, the additional heat-loading predicted for the region will likely have a deleterious impact on its root-associated mutualists. Changes in soil temperature may be partially mitigated by the large canopies and high leaf-area indices (i.e., leaf-area divided by ground-area) of *P. fremontii* trees that buffer soils from direct heat loading. However, the greatest temperature increases are predicted to occur at nighttime hence the interception of direct sunlight by *P. fremontii* canopies may ultimately have only a small impact on changes in soil temperature.

Not surprisingly, drought generally decreases colonization of roots both by AM and EM fungi, although sensitivity to drought can vary among strains (Augé 2001; Shi et al. 2002; Swaty et al. 2004). In *Populus*, AM fungi are favored under dry conditions, whereas the opposite is true for EM fungi (Lodge 1989, Gehring et al. 2006). Mycorrhizal response to drought depends in large part on how the host plant functions during drought. Plants generally allocate a larger percentage of photosynthates below ground during drought, thereby supporting root function, and when drought persists over long periods, the total area of roots tends to increase relative to the area of shoots (Poorter and Nagel 2000). Despite these patterns, plants are often unable to maintain fine roots in dry soils and thus lose the capacity to support mycorrhizal fungi. Some host plants passively reduce the rate of drying of shallow soils through hydraulic lift—the nocturnal efflux of water following transport through roots from deep to shallow layers of the soil (Richards and Caldwell 1987). Likewise, the nocturnal transport of water from plant roots to mycorrhizal fungi has been observed in some host species (Caldwell et al. 1998; Querejeta et al. 2003, 2007). However, there may be physiological barriers that inhibit hydraulic lift and/or direct nocturnal transport of water to root symbionts in *P. fremontii* and other riparian tree species. Woody tissues of *P. fremontii* have a low resistance to drought-induced cavitation of the xylem (Pockman and Sperry 2000), and therefore root systems lose the ability to maintain hydraulic function and conduct hydraulic lift even in moderately dry soils. Moreover, *P. fremontii* and other *Populus* species can achieve high rates of nocturnal transpiration (Snyder et al. 2003; Hultine et al. 2010a). When nocturnal transpiration rates are high, the canopy becomes a competing sink for water with the dry rhizosphere where water efflux from roots would otherwise occur (Hultine et al. 2003). Given these physiological constraints, we anticipate that the decreases in soil moisture expected to occur with climatic change will, in some areas, significantly inhibit *P. fremontii's* relationship with mycorrhizal symbionts. If so, reduced colonization would likely reduce the uptake of plant nutrients that would, in turn, decrease the availability of carbohydrates to support fungal growth, thereby resulting in a feedback spiral toward progressively lower productivity and foundational capacity of *P. fremontii* forests.

In addition to the impacts of climatic change on *P. fremontii*/mycorrhizal mutualisms, climatic change will likely alter the relationship between *Tamarix* and *Diorhabda* throughout the region in western North America where the two species interact. These alterations in the interaction between a specialist herbivore and its host plant should have cascading consequences on the capacity for *Tamarix* to disrupt the relationship between co-occurring *P. fremontii* and its root-associated symbionts.

Climatic change could have direct (temperature) and indirect (impacts on animals that prey on insects and functioning of the host plant) effects on *Diorhabda* in North America. In general, the metabolism and physiology of insects is highly sensitive to temperature with metabolic rates doubling with an increase of 10°C (Gillooly et al. 2001; Clarke and Fraser 2004; Dukes et al. 2009). Therefore, climatic warming tends to accelerate insects' activity, including consumption, development, and movements. In turn, changes in insects' activity can alter population structure and function due to effects on fecundity, generation time, survival, and dispersal (Bale et al. 2002). The metabolic response of *Diorhabda* to temperature follows similar patterns as it does in other insect species (Herrera et al. 2005; Acharya et al. 2013). For example, even small increases in minimum diurnal temperatures result in significant increases in nocturnal feeding on *Tamarix*. At the same time, *Diorhabda* can maintain feeding activity in temperatures approaching 50°C (Acharya et al. 2013). Higher nocturnal temperatures, combined with *Diorhabda's* already high tolerance for extreme heat, could elevate the effectiveness of the biological control of *Tamarix* throughout much of its range. On the contrary, climatic change could increase predation by co-occurring generalist insects that already attack *Diorhabda* given that higher temperatures should also increase the metabolic activity of these co-occurring insects, although there is currently no direct evidence linking climatic warming with efficiency of predation upon *Diorhabda*.

In the absence of stress caused by herbivory from *Diorhabda*, climatic change will most likely have a similar negative impact on *Tamarix* as it does on other woody plant species in desert riparian habitats. The combination of increased evaporative demand (as a consequence of higher temperatures, and reduced availability of water because of lower discharge from streams and its consequent decrease in storage as groundwater) will elevate the water-deficits of plants and reduce rates of photosynthesis. Likewise, climatic warming will increase the carbon demand of living tissues to support mitochondrial respiration (Ryan 1991). A lower supply of photosynthates coupled with a higher respiratory demand will reduce the amount of carbon available for growth, reproduction, defense, and storage of NSCs.

Given that climatic change may amplify the intensity of herbivory by *Diorhabda*, a diminished NSC pool could become especially detrimental and trigger widespread mortality within *Tamarix* stands (Fig. 8). The mortality of *Tamarix* would be especially high in areas where resources are already limited due to poor edaphic conditions or limited availability of water. However, high rates of mortality in *Tamarix* may result in a negative feedback loop that limits episodic defoliation if there is not enough *Tamarix* foliage to maintain substantial populations of *Diorhabda* along riparian reaches. Likewise, surviving *Tamarix* plants would likely be those that have either been selected for tolerance to herbivory, as a function of high allocation of resources toward metabolic storage (Hultine et al. 2013), or that happen to occur in high-resource microsites (Hultine et al. 2015). Thus, climatic change might reset the balance between herbivore and host plant whereby both occur at lower population densities under future climatic conditions.

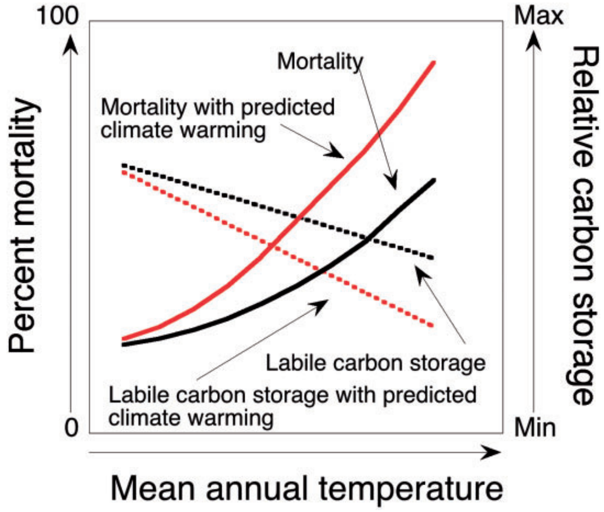

Fig. 8 Relationship between mean annual temperature, relative labile carbon storage, and percent mortality of *Tamarix* with and without the climatic warming predicted for the next century by models of regional climates. Higher temperatures are expected to result in a reduction of stomatal conductance in the canopy, higher rates of maintenance respiration, and an overall reduction in the storage of carbon, resulting in greater mortality relative to the amount of defoliation by *D. carinulata*.

Along rivers and streams where *P. fremontii* and *Tamarix* co-occur, climatic change will likely have both negative and positive effects on *P. fremontii* and its relationship with mycorrhizal symbionts. On one hand, climatic change will directly alter hydrologic processes, increase demand for water, and increase thermal stress on the metabolic activity of *P. fremontii*. Altered hydrology and higher temperatures will concurrently reduce the capacity for mycorrhizal fungi to colonize *P. fremontii*'s roots that in turn will elevate surface contact with the mineral soil and affect subsequent uptake of nutrients and water. On the other hand, climatic change is likely to reduce the relative dominance of *Tamarix* both directly via reduced availability of resources, and indirectly via increased herbivory. If so, the net impact of climatic change on *P. fremontii* populations that co-occur with *Tamarix* may be closer to neutral than those that occur in the absence of *Tamarix*. How these complex biological interactions ultimately play out in the face of climatic change will hinge on the selection of various phenotypic traits that will ultimately govern the structure and function of riparian ecosystems in the future (Whitham et al. 2003, 2006).

Implications for management: conserving phenotypic traits in the face of global change

Populus fremontii forests are considered among the most threatened types of forest in the United States (Stromberg 1993; Webb et al. 2007). The protection of these highly valued forests will require not only the conservation of *P. fremontii*, but also the specific phenotypic traits that buffer their populations from the deleterious effects of global change (i.e., climatic change and invasion by exotic species) and give rise to *P. fremontii*'s foundational status. In other words, genotypes that consist of physiological traits that maximize tolerance to drought and extremely high temperatures, while at the same time provide the foundation for biological diversity, will need to be identified. Likewise, restoration that takes place where *Tamarix*'s soil legacies persist may require the addition of AM and EM inoculum (via soil from areas with healthy cottonwoods) to a small number of trees used for restoration to build up the population of root-associated fungi. To support conservation efforts, research is ongoing to identify genotypes that match current and future environmental conditions and maximize ecosystem services from riparian ecosystems. For example, a network of experimental common gardens are currently being established across broad environmental gradients that will allow researchers to identify specific genotypes that are most, or least, sensitive to environmental change. Once identified, trees with these genotypes can be planted in combination with trees with local genotypes so that restored populations have the appropriate genetic composition and diversity to cope with a broad suite of risks from global change (Grady et al. 2011). Although this concept of assisted migration currently is being debated within the community of restoration ecologists (Kreyling et al. 2011; Frascaria-Lacoste and Fernández-Manjerrés 2012), the careful selection of specific genotypes has the potential to increase the success of foundation species, like *P. fremontii*, given the uncertainties of global environmental change.

It is currently unclear to what extent the biological control of *Tamarix* will improve the environmental conditions for *P. fremontii* and its root-associated mutualists. However, the combination of common-garden studies with technological advances in molecular genomics will provide critical information on the responses of *Tamarix* to climatic change and biological control. As *D. carinulata* continues to advance southward toward the Colorado River Delta while other *Diorhabda* species continue to increase their geographical impact on *Tamarix*, knowledge of how various genotypes respond to multiple stressors will assist managers in prioritizing their efforts in restoration. The advance of *D. carinulata* along the lower Colorado River is particularly relevant, given that the Bureau of Reclamation has already committed over $600 million to riparian restoration in the lower Colorado River Basin. These and other efforts at restoration will benefit greatly from a comprehensive approach that identifies the heritable traits that underpin species' interactions and response to climatic change.

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