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Native shrubs, such as creosote bush, offer tortoises protection and shaded resting sites.

Native forbs, such as desert plantain and many others, are key forage plants for tortoises.

Project title:

DESERT TORTOISE HABITAT RESTORATION LITERATURE REVIEW

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Submitted to: Desert Conservation Program, Clark County

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Natural Resource Conservation LLC provides knowledge services and innovations for effective natural resource management, habitat and species conservation, and ecological restoration. Our company develops adaptive management and scientifically rigorous experiments and monitoring, scientific publications, syntheses of knowledge supporting conservation, and management and conservation plans. We have skills and expertise in vegetation inventories and plant ecology, habitat analysis, fire management, ecological restoration, and monitoring design and analysis.

EXECUTIVE SUMMARY

Habitat restoration has potential for contributing to desert tortoise recovery actions by reversing habitat degradation, replenishing or enhancing habitat resources utilized by tortoises, and limiting further habitat deterioration. To provide a foundation supporting a Mojave desert tortoise habitat restoration workshop, to be held January 24-25, 2022 in Las Vegas, Nevada, this literature review was commissioned by the Clark County Desert Conservation Program to synthesize the status of knowledge of desert tortoise habitat restoration activities. The objectives of the review include: 1) summarizing desert tortoise habitat requirements and indicators of habitat quality, such as availability of protective cover and forage; 2) synthesizing restoration practices and their effectiveness in the Mojave and western Sonoran deserts; 3) providing estimated costs of candidate restoration treatments; and 4) anticipating future restoration and research needs for effective restoration in changing climates and environments.

High-quality desert tortoise habitats can be generalized as providing four features: adequate perennial cover plants, high-quality native food plants, free water for drinking, and safety. Tortoises heavily utilize large shrubs for protection from temperature extremes and predators during daily activities and as burrow-construction locations for longer-term protection. Groups of native annual forbs and certain herbaceous perennials and cacti constitute the most important food plants for meeting tortoise nutritional and energetic requirements. Herbaceous perennials and cacti may have particular significance for sustaining tortoises during dry years with few annuals. Several studies have indicated that non-native annual grasses, now dominating flora across much of desert tortoise habitat, are poor-quality forage and also heighten risk of wildfires that degrade mature shrubland habitat. Safety includes freedom of movement (i.e. habitat connectivity), few or absent subsidized predators, suitable soils with low concentration of toxicants, low or absent infectious disease, limited anthropogenic disturbances (e.g., few roads), low cover of harmful non-native plants, low risk of wildfires, and limited presence of other factors that can kill, injure, or compromise health of tortoises.

Over 50 published restoration studies in the Mojave and western Sonoran deserts have collectively demonstrated that restoration is capable of increasing perennial plant cover and native annual plants, improving soil conditions (e.g., biocrusts), enhancing native seed retention and seed banks, and lowering fire risk. All of these functions would be anticipated to improve habitat conditions for desert tortoises based on tortoise habitat requirements. The review details 11 major restoration treatments (and their numerous variations) evaluated in at least one study and ranging from active revegetation (e.g., outplanting, seeding) to abiotic structural restoration (e.g., vertical mulching) and protection treatments. For example, 16 outplanting studies assessed performance of 46 species and began identifying top-performing species, associated treatments (e.g., protection from herbivory) required to aid plant survival, and potential for outplants to trigger formation of self-sustaining populations. As an example, creosote bush (*Larrea tridentata*), one of the most important shrubs tortoises utilize for cover, has achieved at least 50% survival in five of eight studies in which it was outplanted. Cost estimates and logistics are also presented for the range of restoration treatment options.

The review highlights five main future research and adaptive management needs for advancing tortoise habitat restoration. These needs include: 1) continued development of innovative restoration techniques and bet-hedging approaches to provide managers with "tool boxes" of candidate treatments to deploy in dynamic environmental and management conditions, 2) identifying how to optimize spatial deployment of restoration resources, 3) developing practical techniques for reducing non-native annual grasses across spatial scales, 4) improving linkage between habitat enhancement activities and short- and long-term indicators of tortoise health and population traits, and 5) prioritizing determining if or how habitat restoration activities, such as enhancing availability of nutritional food plants, can play a role in recovering tortoise populations to continue moving from theory to application.

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INTRODUCTION

Ongoing population declines, poor recruitment, and habitat degradation prompted federal listing of the Mojave desert tortoise (*Gopherus agassizii*) population in the Mojave and western Sonoran deserts as threatened in 1990 under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1990). Since then, federal agencies and other conservation organizations have made extensive effort to carry out recovery actions called for in the original and revised recovery plans (U.S. Fish and Wildlife Service 1994a, 2011). The logical, scientifically based recovery actions have included establishing large landscapes as critical habitat recovery units serving as core areas of prime desert tortoise habitat, decommissioning livestock allotments across millions of hectares to avoid potential competition for forage between livestock and tortoises and other habitat changes, implementing range-wide population monitoring, and other conservation measures (Berry and Murphy 2019). Population declines and poor recruitment have continued, however, across most of the range of the desert tortoise and there is concern that many populations are approaching or below viability (Allison and McLuckie 2018, Berry and Murphy 2019). **Reversing these declines is challenging owing to life-history traits of the tortoise (e.g., females requiring approximately 20 years to reach reproductive maturity; Mueller et al. 1998); multi-factor, interactive, and potentially cumulative anthropogenic threats facing tortoises; and the likely possibility that habitat degradation has made tortoises more vulnerable to droughts and other environmental stressors to which tortoise populations may have previously had greater resistance and resilience (Lovich et al. 2014, Barrows et al. 2016, Berry et al. 2020c).** Boarman and Kristan (2006) noted that recovery actions taken after listing are likely to have been necessary actions along a potential pathway to recovery but insufficient thus far given the suites of interacting threats to tortoises. For instance, while designating the critical habitat units could be considered a key first step, degradation of habitat quality within the critical habitats has persisted or even intensified. An example would be wildfires burning hundreds of thousands of hectares of tortoise habitat since 2005, killing some tortoises outright (Kellam 2020), and persistently reducing cover plants required by tortoises and altering forage and soil conditions (Abella et al. 2021). Addressing one threat may be an important step but may not translate into improved measures of tortoise populations if other unabated threats continue limiting tortoise populations, which appears common (Averill-Murray et al. 2012). These observations highlight opportunities to integrate multiple conservation measures including habitat restoration in the next phases of tortoise recovery efforts.

Deteriorating habitat conditions are not the only threat facing desert tortoises, but habitat restoration is consistently ranked as among recovery actions with greatest potential for aiding recovery (e.g, Boarman and Kristan 2006, Reed et al. 2009, Darst et al. 2013, Tuma et al. 2016). This is because habitat improvement has high potential for alleviating several of the likely stressors to tortoises (e.g., lack of protective vegetative cover, malnutrition due to poor forage quality, exposure of tortoises to harmful substances released by eroding soil, lack of connectivity between high-quality habitats such as due to fragmentation from wildfires). Furthermore, improved habitat conditions could enable tortoises to better contend with other stressors. For example, greater availability of native perennial food and succulent plants (e.g., cacti) can potentially serve as "lifelines" improving tortoise survival during droughts when annual food plants are sparse (Medica et al. 1985). Pervasive non-native annual grasses infesting desert tortoise habitat do not provide tortoises with these types of helpful resources, making reducing non-native grasses a top priority for increasing tortoise habitat quality (Drake et al. 2016).

Habitat restoration can be viewed as an activity complementary to other management actions aimed at improving tortoise habitat condition. Activities that would likely be considered separate from restoration, such as management or policy actions to limit tortoise predators subsidized by humans (e.g., common ravens [*Corvus corax*], Boarman 2002) and to limit transmission of disease to natural tortoise populations (Jacobson et al. 2014), may need to occur in tandem with habitat restoration for full benefits to be realized. In this report, habitat restoration follows the Society of Ecological Restoration International (2004) definition of ecological restoration as the repair of habitats that have been degraded or destroyed. Degradation could take many forms, such as loss of key features of habitats (e.g., perennial plants, soil seed banks for promoting plant community resilience, topsoil), alteration of diversity or species composition including replacement of native with non-native species, and disruption of natural ecological processes (e.g., pollination) or introduction of novel disturbances (e.g., frequent, large wildfires in deserts where spreading fires were historically rare; Fig. 1). **Ecological restoration is based on the idea of identifying one or more potential reference conditions (including dynamic references accommodating changing climates and environments) thought to represent high-quality ecosystems appropriate to the environment, pinpointing sources of the degradation and alleviating them (e.g., reintroducing native plants to reinstate the natural processes of pollination and plant recruitment), and monitoring outcomes to enable adjusting restoration approaches as conditions change.** Given that there are often multiple candidate references for restoration, restoration projects can be tailored to emphasize benefits to desert tortoises, such as choosing plant species mixtures specifically offering high-quality forage to tortoises from among the many possible species mixtures that could be used. **Furthermore, restoration is arguably even more relevant during times of rapid climatic change such as the present.** Reducing as many stressors as possible via habitat restoration is likely to provide species with the greatest chance for successfully accommodating environmental change, as compared with species facing these changes in a weakened state in compromised habitat (e.g., DeFalco et al. 2010).

Fig. 1. *Differences in structure between unburned (left) and burned (right) habitat persisting 15 years after the 2005 Loop Fire in southern Nevada. Creosote bush is a major cover plant tortoises utilize for thermal protection and as burrow-construction locations. While some creosote have resprouted in the burned area, they remain smaller and depleted in number by 90% in the burned area.*

Habitat restoration has potential for making three main contributions to desert tortoise conservation: i) enhancing existing habitat generally in good condition but that may be lacking certain features that tortoises could utilize; ii) making degraded, largely unused habitat more useable for tortoises while improving habitat connectivity; and iii) limiting further degradation of tortoise habitat, such as strategically deploying restoration near access points of decommissioned roads to deter further disturbance, or reducing non-native plants to limit potential for wildfires to degrade habitat.

While in some cases after disturbance a "do nothing" approach may be the most ecologically and cost-effective (e.g., if most top-killed native perennials do re-sprout rapidly), a large body of research in the Mojave and Sonoran deserts has shown that plant and soil recovery after disturbance is slow or essentially non-existent without restoration. In a synthesis of 47 published studies in the Mojave and Sonoran deserts, the time estimated for the full reestablishment of perennial plant cover after disturbances (clearing such as for pipeline right of ways, wildfires, and road disturbances) averaged 76 years (Abella 2010). Recovery rate of perennial species richness (number of species per unit area) was highly variable among studies, ranging from full recovery within 3 years to projections of 152 years to full recovery. Recovery of species composition (species present and their relative abundance) to that typical of nearby undisturbed areas was estimated to require an average of at least 215 years, assuming that recovery would continue along a linear trajectory. Recovery of native annual plant species composition may similarly require decades to centuries and be contingent on recovery of native perennials providing nutrient-enriched fertile islands conducive to recruitment of many annual species (Berry et al. 2016a,b).

A recent, separate synthesis of recovery after 32 wildfires dating back to 1980 across a large landscape including tortoise habitat spanning 200 km in the Mojave Desert reported that perennial plant cover required decades to recover while species composition was projected to require centuries at many sites (Abella et al. 2021). Species composition of mature creosote bush (*Larrea tridentata*) communities required an estimated 82 years to full recovery. Blackbrush (*Coleogyne ramosissima*) shrublands required even longer: 550 years to full recovery. In both communities, the time to recovery actually lengthened between measurements made in 2007 and 2016, implying that instead of recovery, species composition of the burned sites was diverging from that of nearby undisturbed communities. **This implied that species composition on burned sites, at least when unassisted by active restoration, may not be capable of recovering to that resembling unburned sites in ambient environmental conditions.**

These long recovery times are significant to desert tortoise conservation efforts for several reasons. First, these types of disturbances (e.g., wildfire) already cover vast areas of tortoise habitats and they are continuing to increase (Brooks et al. 2018). Second, even if some plant recovery occurs (e.g., cover increasing over time), the species may not necessarily be those that were originally present, so their benefit to tortoises may be comparatively lower. A good example is that early colonizing perennial plants tended to be smaller-statured species, too small to cover an adult tortoise, rather than the larger shrubs tortoises favor for cover and burrow-construction locations (Abella et al. 2021). Severe disturbances can become even less hospitable to tortoises if some of the early colonizing perennial forbs that serve as food plants decline after their initial colonization (Drake et al. 2015). Third, the long recovery times imply a cumulatively increasing "recovery debt," whereby increasing portions of the landscape spatially and temporally are not in a mature habitat condition. These observations underscore the potential for restoration to accelerate ecological recovery on existing disturbances while also contributing to efforts to curtail new anthropogenic disturbances.

With few exceptions (Abella et al. 2015c, Devitt et al. 2020), ecological restoration research in the Mojave Desert to date has not occurred specifically with a goal to improve habitat for desert tortoises but rather to advance other goals such as to stabilize soils and to restore biodiversity (e.g., Bainbridge 2007, Scoles-Sciulla et al. 2015, Chiquoine et al. 2016). The goals would often overlap, however. Stabilizing soil, for instance, can simultaneously meet a goal of reversing productivity loss while limiting exposure of tortoises to dust (Rader et al. 2022). Nevertheless, perhaps this literature review and the associated habitat restoration workshop can help foster further integration of habitat restoration research with tortoise conservation research and activities.

This literature review was commissioned by the Desert Conservation Program, Clark County, Nevada, to synthesize the status of knowledge of desert tortoise habitat restoration activities and to provide a foundation for supporting the Mojave desert tortoise habitat restoration workshop, to be held January 24-25, 2022. The objectives of the literature review include: 1) summarizing desert tortoise habitat requirements and indicators of habitat quality, such as availability of protective cover and forage; 2) synthesizing major and emerging restoration practices and their effectiveness in the Mojave and western Sonoran deserts; 3) providing estimated costs of candidate restoration treatments; and 4) anticipating future restoration needs in changing climates and environments and identifying additional research needs for effective habitat restoration. The review fits within the broader contexts of desert tortoise recovery planning (U.S. Fish and Wildlife Service 2011) and other programs such as the Mojave Desert Plant Materials Initiative (an interagency effort led by the Bureau of Land Management), wilderness conservation, invasive plant programs, and fire management. For example, the review identifies plant species thus far most amenable to revegetation, including those providing cover and food plants for tortoises. These types of plants could be prioritized for plant materials development and emphasized in restoration projects. Conversely, species that have performed poorly, but that are important to tortoises, could be prioritized for further research suggested in this review to enable restoration to use these plants.

SUMMARY OF GEOGRAPHIC SCOPE AND DESERT TORTOISE BIOLOGY

This review focuses on habitat ecology, conservation, and restoration within the geographic range of the current federally listed desert tortoise population. This habitat range primarily includes hot desert habitat north and west of the Colorado River. Habitat includes most of the 124,000-km^2 Mojave Desert occupying parts of Arizona, Utah, Nevada, and California, as well as the Colorado Desert Subdivision of the western Sonoran Desert in southeastern California (Figure 1). The Mojave Desert receives much of its rainfall from November through April, during winter and spring (Rowlands et al. 1982). Annual precipitation averages 10-20 cm at low/middle elevations below 1,500 m where most desert tortoise habitat occurs. Topography includes mountain ranges, low hills, washes (ephemeral stream channels), and valleys. Soils include those derived from several rock types (e.g., basalt, limestone) and depositional material from erosion (Rautenstrauch and O'Farrell 1998, Berry et al. 2006, Mack et al. 2015). Geological history and soil age are key factors affecting biota, such as old surfaces of desert pavement compared to young soils in ephemeral stream channels (McDonald et al. 1995).

Dominant vegetation within Mojave desert tortoise habitat is desert shrubland (Rundel and Gibson 1996). Creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) predominate across extensive low elevations, blackbrush (*Coleogyne ramosissma*) and succulent woodlands containing Joshua trees (*Yucca brevifolia*) at mid-elevations from 1,300 to 1,800 m, and coniferous woodlands and forests at the higher elevations. Desert tortoises are most abundant in the low- and mid-elevation creosote bush and mixed shrublands, and are sparse to absent in higher-elevation woodlands and forests (Berry et al. 2006, Rautenstrauch and O'Farrell 1998). In years with sufficient rainfall, most annual plants in the desert shrubland germinate in winter, grow through spring, and senesce by May (Beatley 1974, Smith et al. 2014). The eastern Mojave and western

Sonoran have more summer annuals, stimulated by summer monsoonal storms (Jennings 2002). Annual plants are typically most abundant below canopies of shrubs that form "fertile islands" of shaded, nutrient-enriched soil (Brooks 2009). Some annual species, however, are most abundant in interspaces between shrubs (Abella and Smith 2013). The spatial variation in the distribution of different shrub species and interspaces creates heterogeneity in the annual plant community, which may be important for diversifying the forage available to tortoises (Jennings and Berry 2015). The amount and timing of rainfall are highly variable among years and across the landscape within a year (Hereford et al. 2006). Some years or locations have essentially no annual plants, while others support 50 species of annual plants within a km^2 (Brooks and Berry 2006). Non-native annual grasses are now the predominant component of annual plant communities across much of the desert tortoise's range (Abella et al. 2015d).

The desert tortoise is a long-lived reptile that is both affected by and affects desert habitats. The typical natural life span of desert tortoises is 30-50 years, with maximum life spans exceeding 50-70 years (Medica et al. 2012, Berry and Murphy 2019). The species is distributed at elevations below 1,300 m across much of the Mojave and western Sonoran Desert, except for the Death Valley floor and other low-elevation valleys with minimal rainfall (U.S. Fish and Wildlife Service 1994b). Typical home ranges are 10-20 ha for adult females and 20-50+ ha for adult males during average rainfall years (Harless et al. 2010). Desert tortoises conduct daily and seasonal activities within these home ranges, including foraging, retreating to burrows, and reproduction. Tortoises occasionally travel longer distances, such as 3-7+ km over days to months, for reasons that may relate to mating, foraging, or locating new home ranges (Berry 1986). Desert tortoises spend over 90% of their lives underground in burrows, escaping temperature extremes, lack of moisture, and predators (Nagy and Medica 1986, Mack et al. 2015). All age classes of tortoises are active in spring during the peak spring growing season for winter annual plants. Juveniles can emerge from burrows in February, continue activity through May and June (Berry and Turner 1986), and periodically be active between November and February (Wilson et al. 1999). A second period of heightened activity of adults occurs during the mating season in summer and early fall (Rostal et al. 1994). The species is primarily herbivorous but occasionally eats dead salamanders, caterpillars, bone, and soil material (Esque and Peters 1994, Oftedal et al. 2002, Berry and Murphy 2019). Desert tortoises obtain moisture from succulent, green forage (Nagy et al. 1998) but require free water for drinking from self-constructed catchments or puddles (Minnich 1977, Medica et al. 1980). Most desert tortoises respond to precipitation at any time of year by emerging to drink, unless they are already hydrated (Peterson 1996).

In addition to adding to desert biodiversity, desert tortoises provide several ecological functions in desert ecosystems. For example, dozens, perhaps hundreds, of other faunal species utilize tortoise burrows for protection, such as lizards, snakes, birds, and small mammals (Walde et al. 2009; Berry and Murphy 2019). The digging and burrow excavation activities of tortoises is a bioturbation process that could influence soil nutrient cycling, soil microorganisms, and plant communities while creating soil heterogeneity. Some individual tortoises dig over 10 new burrows annually (Rautenstrauch et al. 2002). It is also possible that tortoises serve as seed dispersers, including for favored native food plants that can be uncommon on the landscape (Lovich et al. 2019).

METHODS AND APPROACH OF THE REVIEW

The review uses the narrative approach for synthesizing tortoise habitat requirements and a systematic review approach for synthesizing ecological restoration data in the Mojave and western Sonoran deserts. To summarize habitat requirements, existing reviews of desert tortoise ecology were synthesized along with reviewing over 350 publications dealing with desert tortoise biology and ecology (peer-reviewed scientific papers, book chapters, conference proceedings including Desert Tortoise Council Symposium proceedings, and agency reports). To obtain restoration literature, systematic searches were performed using the databases AGRICOLA, BioOne, GoogleScholar, JSTOR, Scopus, ScienceDirect, SpringerLink, Web of Science, and Wiley Online Library. Article titles, abstracts, and key words were searched for the following terms: Mojave, Sonoran, restoration, revegetation, rehabilitation, outplanting, seeding, transplanting, propagation, soil, invasive plants, exotic plants, non-native plants, control, treatment, management, and recovery. These searches focused on peer-reviewed journal articles, book chapters, and conference proceedings, collectively the primary holdings of the databases. U.S. Government serial publications (e.g., U.S. Forest Service technical reports, U.S. Geological Survey open-file reports) were then searched. Information on restoration practices from unpublished sources is also included to augment the published information where appropriate. Some of the major previous reviews of desert tortoise ecology and Mojave Desert restoration that the present review builds upon are in Table 1.

Table 1. *Some major reviews of desert tortoise ecology and ecological restoration in the Mojave Desert.*

Reference	Description
Desert tortoise ecology	
Luckenbach 1982	Early review of desert tortoise biology and habitats
Grover and DeFalco 1995	Status of knowledge review of tortoise ecology
Berry and Christopher 2001	Indicators of desert tortoise health
Boarman 2002	Review of threats to desert tortoise populations
Boarman and Kristan 2006	Review of recovery actions and progress toward implementation
Meyer 2008	U.S. Forest Service fire effects information system species account
Nussear et al. 2009	Data synthesis of desert tortoise potential habitat distribution
Averill-Murray et al. 2012	Overview of threats and adaptive management for desert tortoises
Jacobson et al. 2014	Review of diseases of desert tortoises
Abella and Berry 2016	Review of tortoise habitat requirements and habitat enhancement practices
Berry et al. 2016c	Annotated bibliography of desert tortoise 1991-2015 literature
Berry and Murphy 2019	Comprehensive monograph reviewing desert tortoise biology, habitat, and threats
Berry et al. 2020c	Synthesis of 34 years of change in tortoise populations at the DTRNA
Restoration	
Wallace et al. 1980	Early review of Mojave Desert revegetation
Lippitt et al. 1994	Native seed collection, processing, and storage
Roundy et al. 1995	62 papers, Wildland Shrub and Arid Land Restoration Symposium, Las Vegas, 1993
Lovich and Bainbridge 1999	Overview of disturbance history in the Mojave Desert as a basis for restoration
Anderson and Ostler 2002	Review of desert restoration project logistics
Bainbridge 2007	Overview and ideas for desert restoration techniques, strategies and equipment

Abella and Newton 2009	Systematic review of outplanting and seeding in the Mojave Desert
Weigand and Rodgers 2009	Overview of desert restoration practices
Abella 2010	Review of post-disturbance recovery in the Mojave-Sonoran as a basis for restoration

Note:
-DTRNA, Desert Tortoise Research Natural Area.

DESERT TORTOISE LOCAL HABITAT REQUIREMENTS AND INDICATORS OF HABITAT QUALITY

What constitutes high-quality desert tortoise habitat? Research has addressed this using different approaches: i) utilization studies observing how tortoises utilize elements in their habitat relative to the availability of the habitat elements (e.g., which shrub species tortoises choose to construct burrows beneath); ii) correlational studies relating tortoise abundance (or sign) or health with habitat conditions (e.g., correlations between toxicant concentration in soil and tortoise disease prevalence; iii) physiological studies, with one example being determining temperatures lethal to tortoises then measuring variation in temperature across the habitat to identify refugia that remain below lethal temperatures (e.g., availability of cooler microsites below shrubs); iv) experiments that manipulate habitat features or provide tortoises with different conditions in controlled environments and measuring tortoise responses (e.g., offering tortoises different diets and assessing tortoise health); and v) simulation approaches that model potential effects of varying habitat conditions on demographic parameters of tortoise populations. An encouraging sign from this diversity of research is that it has generally arrived at consistent conclusions, leading to a well-supported impression of what constitutes quality tortoise habitat (e.g., Schamberger and Turner 1986, Grover and DeFalco 1995, Boarman and Kristan 2006, Berry et al. 2016c, Tuma et al. 2016).

Fig. 2. *Mojave Desert habitat containing large shrubs as cover plants, diverse annual plant communities including native annual forb food plants with few non-native grasses, native herbaceous perennials and cacti supplying forage during dry years, minimal anthropogenic disturbance to soil and vegetation, and high spatial connectivity. These are all features perceived as contributing to high-quality desert tortoise habitats.*

Sites providing good-quality desert tortoise habitat can be generalized as providing the following four features: cover, food, water, and safety. Cover is needed for both long-term (e.g., hibernation) and short-term (resting) protection of tortoises from environmental stresses (e.g., extreme cold or warm temperatures) and predators (Rautenstrauch et al. 1998, Walde et al. 2009, Mack et al. 2015; Fig. 2). A diversity of high-quality food plants – particularly native annual forbs, herbaceous perennials, and cacti in dry years – is key for tortoise health, growth, survival, and reproduction (e.g., Medica et al. 1985, Nagy et al. 1997, Henen 2002, Hazard et al. 2010, Drake et al. 2016). While tortoises can obtain some moisture from consuming live plants, tortoises require free water for hydration (Nagy and Medica 1986, Peterson 1996, Berry et al. 2002, Esque et al. 2014). Habitat offering safety to tortoises would have minimal presence of threats including: infectious diseases (Jacobson et al. 2014), subsidized predators (Kristan and Boarman 2007), toxicants in the environment (Kim et al. 2014), anthropogenic disturbance (e.g., roads; Nafus et al. 2013), anthropogenic trash that can subsidize predators and also become a digestion hazard (Walde et al. 2007), anthropogenic persecution of tortoises (e.g., shooting, vandalism; Berry 1986), domestic and feral livestock (Berry et al. 2020b), and non-native plants including those that can injure tortoises and fuel wildfires (Drake et al. 2015).

These four main habitat features can interact to produce synergistic and cumulative effects. For example, a habitat could provide adequate cover, food, and water, but hyperpredation by subsidized predators or disease outbreaks could make the otherwise high-quality habitat unsafe for tortoises (Sieg et al. 2015). Conversely, it is poorly understood, but possible, that good-quality conditions of certain habitat features can in part compensate for poorer condition of other features. As one of numerous possible examples, presence of water-supplying cacti could theoretically partly compensate for drier sites with less rainfall or less water retention (Medica et al. 1985). Similarly, sites with high-quality food plants could improve tortoise resistance to disease in some cases (Jacobson et al. 2014). Outcomes of these interactions could hinge on the relative importance of different factors to tortoises and variation in space and time of factors limiting tortoise populations (Tuma et al. 2016).

Each of the four features of cover, food, water, and safety are summarized in the following sections.

COVER

Quality habitats need to offer tortoises protective cover for the time tortoises are inactive (which is most of the year) and as temporary resting sites during active periods when tortoises are traveling for foraging, locating free water, interacting with other tortoises, and exploring home ranges (Berry and Turner 1987, Zimmerman et al. 1994, Rautenstrauch et al. 1998, Hazard and Morafka 2004). Cover can be provided by suitable geological, soil, and shrub availability (Mack et al. 2015). On sites containing suitable geologic material (e.g., caliche), tortoises can seek long-term protection in caves in cliffs or banks of washes, under rock overhangs, or crevices (Woodbury and Hardy 1948). On many sites lacking these geological features, tortoises excavate burrows in soil beneath the canopies of shrubs. Soils optimal for burrow construction are sufficiently friable for digging and sufficiently strong to avoid collapse (Nussear et al. 2009). The most suitable soils are usually in the loamy texture categories (Luckenbach 1982). Tortoises generally select large shrubs below which to construct their burrows, such as creosote bush (*Larrea tridentata*) or catclaw acacia (*Acacia greggii*; Burge 1978, Baxter 1988, Berry and Turner 1987, Wilson et al. 1999). During daily movements, tortoises utilize shrubs sufficiently large for tortoises to excavate a temporary depression (termed a pallet) partially covering a tortoise shell or casting sufficient shade to serve as a resting location (Drake et al. 2015).

Several studies suggest that sites with low density of large shrubs are poor-quality desert tortoise habitat and that disturbances that reduce shrub cover degrade tortoise habitat. For example, in their physiological study, McGinnis and Voigt (1971) showed that when tortoises were deprived of mid-day, shaded retreats during early summer movements, tortoises quickly reached the lower limit (39.5°C) of the lethal deep-body temperature range. At this stage, copious amounts of foaming saliva issued from the mouth and spread down the neck region of tortoises, presumably an attempt at evaporative cooling. Illustrating a high degree of shrub utilization for cover, Rautenstrauch et al. (2002) reported that tortoises individually used an average of 12 burrows annually, including constructing 5 new burrows annually. Studies have further reported correlations between spatial distribution or population changes in tortoises and shrub cover, with few tortoises in areas of low shrub cover (Bury and Luckenbach 2002, Berry et al. 2013, Berry et al. 2020c).

FOOD

An idealized "menu" habitats can provide for tortoises includes a diversity of native annual forbs including key groups (e.g., legumes); certain palatable, herbaceous perennial forbs; some native annual and perennial grasses; and cacti (Burge and Bradley 1976, Turner et al. 1984, Avery and Neibergs 1997, Hazard et al. 2010, Esque et al. 2014). When given a choice, desert tortoises are selective foragers, apparently seeking plants offering particular combinations of digestibility, energy and nutrient content, and minimal contents of potentially toxic substances such as potassium (Nagy et al. 1998, Oftedal et al. 2002, Jennings and Berry 2015). In some cases, tortoises have consumed flowers and leaves of certain shrubs, though shrubs represent only a small portion of diets (Berry and Murphy 2019). Although some non-native forbs can provide nutritional value for tortoises, non-native plants are generally detrimental to site forage quality. Most of the widespread non-native annuals are poor-quality forage and even the non-natives with some forage value can reduce food plant diversity (Schutzenhofer and Valone 2006). **Research has overwhelmingly identified the importance of native annual forbs and certain perennial forbs in meeting tortoise nutritional and energy requirements** (Burge and Bradley 1976, Avery and Neibergs 1997, Jennings 2002, Oftedal et al. 2002, Jennings and Berry 2015). In general, the main families of favored food plants include: Asteraceae, Boraginaceae, Cactaceae, Fabaceae, Malvaceae, Nyctaginaceae, Onagraceae, and Plantaginaceae (Berry and Murphy 2019). Publications synthesizing studies of food plants favored by tortoises and providing plant species lists include Abella and Berry (2016), Berry and Murphy (2019), and Esque et al. (2021).

Within sites, desert tortoise food preferences can vary with tortoise age/size, seasonal progression of plant maturation and phenology, years differing in rainfall and hence moisture and plant availability, and generally on a site's species composition contingent upon site factors (e.g., soil) and disturbance history. Juvenile and adult tortoises can select slightly different sets of species or sizes of plants because the different-sized tortoises can differentially access shorter or taller plants (Morafka and Berry 2002). As the growing season progresses and different plants emerge or mature, tortoise preferences can shift seasonally (Jennings and Berry 2015). For example, as early growing annual plants senesce, tortoises concentrate foraging on annuals maturing later in spring or on herbaceous perennials (Jennings and Berry 2015). During dry years with minimal annual plant germination, herbaceous perennials and cacti may be particularly important to sustaining tortoises (Burge and Bradley 1976, Turner et al. 1984, Medica et al. 1985). Illustrating contingency of tortoise food preferences on site factors, sites with many small ephemeral stream channels can contain food plants uncommon in the habitat overall but highly favored by tortoises (Jennings and Fontenot 1993). Jennings (1997) reported that tortoises focused much of their foraging effort within and on the margins of small washes in a habitat containing only about 10% of its area as washes.

Among sites within a landscape or across the range of desert tortoises, food preferences can also vary with regional species composition. For example, gradients of precipitation quantity across geography or elevation and variation in precipitation seasonality (e.g., proportion of winter to summer) produce different sets of food plants available to tortoises (Esque et al. 2021). Most of the research on tortoise food preferences has been conducted at the site scale, and further studies that compare diet composition regionally may help tailor developing species lists for plant materials development (Murray and Wolf 2013).

Poor nutrition and low-rainfall years with few annual forage plants have correlated with poor tortoise health, underscoring the importance of habitats supplying tortoises with high-quality forage. Two sets of feeding experiments provide examples. In providing tortoises with forb or grass diets, forbs were higher in dry matter and digestible energy than grasses, which provided little nitrogen, and tortoises lost more water than they gained in processing them (Nagy et al. 1998, Hazard et al. 2009, 2010). Juvenile tortoises gained weight rapidly when fed forbs but lost weight and body nitrogen when fed grasses (Hazard et al. 2009). When only grasses were made available, some tortoises consumed them but became ill and died, while other tortoises refused to eat (Hazard et al. 2009, 2010). In another feeding experiment, Drake et al. (2016) offered 100 captive neonate and juvenile tortoises five diets: native forbs (e.g., desert dandelion [*Malacothrix californica*]), the native annual grass six weeks fescue (*Festuca octoflora*), the non-native annual grass red brome (*Bromus rubens*), and native forbs combined with either the native or non-native annual grass. Tortoises fed native forbs had better body condition, growth, immune functions, and higher survival (>95%) than those fed the grass diets. One-third of tortoises fed only grasses died or were removed from the experiment due to poor health. When forbs were at least mixed with grasses, tortoises were generally in good health. Similar to Medica and Eckert (2007), Drake et al. (2016) also found that foraging on red brome, with its pointy inflorescence, could injure tortoises.

Although they may not represent major portions of tortoise diets, non-plant matter may be part of diets. Berry and Murphy (2019) noted that tortoises have consumed soil material at apparent salt licks, bone, dead lizards, and caterpillars. Esque and Peters (1994) hypothesized that tortoises ingested parts of bones and soil and geologic material to maintain gut pH or to obtain nutrients. It is possible that female tortoises consume limestone material to combat calcium stress during the reproductive season (Marlow and Tollestrup 1982). Consuming bone may similarly provide tortoises with calcium (Walde et al. 2007). The potential roles and significance of these non-plant materials in tortoise diets remain poorly understood, but suggest that such resources could be important in habitats. Presence of these items in diets offers another reason why pollution could be a threat to tortoises, such as if they consume toxicants in soil while consuming soil particles (Chaffee and Berry 2006).

WATER

In addition to its effect on forage, precipitation is important for supplying desert tortoises with free water for drinking (Nagy and Medica 1986, Peterson 1996). All else being similar, sites within suitable tortoise habitat that receive consistently greater precipitation could be expected to provide habitat more favorable for tortoises (Schamberger and Turner 1986, Wallis et al. 1999). Tortoises drink from temporary pools during and after rainstorms and also construct shallow catchment basins which hold water for up to six hours (Medica et al. 1980). Tortoises can emerge from shelter at any time of year to drink free water when available (Medica et al. 1980, Nagy and Medica 1986).

Lack of drinking water, perhaps in combination with lack of live forage plants, during dry periods has correlated with numerous problems for individual tortoises and tortoise populations. When free water has been unavailable for too long and tortoises suffer from dehydration, Berry et al. (2002) hypothesized that there can be a "point of no return" at which dehydration is beyond recovery and tortoises at this stage will deterministically die. Tortoises suffering from dehydration in the study weighed 20-40% less than control tortoises and exhibited abnormal behavior, such as not drinking when rain eventually made free water available. During droughts, several studies reported slowed tortoise growth (Christopher et al. 1999, Medica et al. 2012, Nafus et al. 2017) or elevated mortality rates (Turner et al. 1984, Peterson 1994, Henen 2002, Longshore et al. 2003, Lovich et al. 2014). While tortoises may still produce some eggs during short-term droughts (Lovich et al. 2015), protracted, severe drought has corresponded with minimal egg production (Henen 1997).

SAFETY

Numerous factors relate to how safe habitat is for tortoises to avoid injury, premature death, or reproductive failure. Factors that generally increase risk to tortoises include roads, non-native plants that offer poor-quality (or potentially injurious) forage and augment fuels to heighten wildfire hazard, abundant subsidized predators such as common ravens, infectious disease which is often most prevalent near human settlements or where infected tortoises have been released, anthropogenic trash, presence of domestic and feral livestock, and high densities of humans (including for recreation activities) raising risk of illegal collecting or vandalism of tortoises (Grandmaison and Frary 2012). Reviews and syntheses detailing these threats include Boarman (2002), Averill-Murray et al. (2012), Berry et al. (2013, 2015, 2016c, 2020b, 2020c), Darst et al. (2013), Jacobson et al. (2014), and Berry and Murphy (2019), as well as the original (U.S. Fish and Wildlife Service 1994a) and revised desert tortoise recovery plans (U.S. Fish and Wildlife Service 2011). While establishing cause and effect for these individual threats that interact with each other at landscape scales and potentially temporally has been challenging, an accumulating number of studies have shown negative correlations between levels of these threats and measures of tortoise health and population size (e.g., von Seckendorff and Marlow 2002, Kristan and Boarman 2003, Boarman and Sazaki 2006, Berry et al. 2006, 2013, 2015, 2020abc, Keith et al. 2008, Esque et al. 2010, Hughson and Darby 2013, Nafus et al. 2013). These studies support a conclusion that sets of individual threats and their likely synergistic, cumulative effects must be ameliorated to facilitate improvements in tortoise habitat quality (U.S. Fish and Wildlife Service 2011).

Non-native plants are a unique category of threat because they are nearly ubiquitous across tortoise habitat (compared with many other threats that can be spatially cumulative but not necessarily ubiquitous), can trigger landscape-scale habitat change such as via wildfire, and have propagating effects to other threats (e.g., disease) via their influence on tortoise nutrition (Reed et al 2009). **For habitats to be good quality for tortoises, non-native annuals should generally be minimal for several reasons.** First, while certain non-native forbs such as redstem stork's bill (*Erodium cicutarium*) may offer nutritional value (Hazard et al. 2009), other non-native forbs, such as Sahara mustard (*Brassica tournefortii*), are avoided by tortoises (Berry and Murphy 2019). Whether or not they provide nutritional value, non-native annual forb species can form near monocultures, which can limit the diversity of food plants and therefore the nutritional content, variety of plant sizes, and phenological diversity of plants in tortoise habitats (Schutzenhofer and Valone 2006). Second, one of the most ubiquitous invaders in tortoise habitat, the non-native annual grass red brome (*Bromus rubens*), offers poor forage and can also injure tortoises due to the plant's morphology (Medica and Eckert 2007, Drake et al. 2016). Third, non-native annuals benefit from, but harm the growth of, native shrubs that tortoises utilize for cover (Rodríguez-Buriticá and Miriti 2009). Fourth, non-native plants can augment fuels, increasing risk of wildfires that can injure or kill tortoises and persistently alter habitat (Esque et al. 2003, Lovich et al. 2011, Drake et al. 2015, Kellam 2020).

HOME RANGE, CONNECTIVITY, AND OPTIMIZING RESTORATION SPATIALLY

Spatial habitat requirements and quality for desert tortoises can be viewed from multiple perspectives considering different spatial scales, tortoise movements and genetic exchange, and amount of interior compared with edge habitat. At the home range scale of individual tortoises, at least 14 studies assessed variation in home range size (Table 2). Studies defined home ranges as areas in which tortoises conducted daily activities (e.g., foraging) within a year and were usually determined using a polygon method (Harless et al. 2010). On average, home ranges of females are about half the size of those of males. Overall, home ranges of females and males have ranged from 1 (Duda et al. 1999, Freilich et al. 2000) to 410 ha (Hromada et al. 2020). A typical average home range is about 10-50 ha. While there may be exceptions, home ranges generally contract during dry years (Duda et al. 1999, Freilich et al. 2000). **These home range studies are helpful from a restoration perspective in describing the scale at which restoration would need to provide adequate resources (e.g., perennial plant cover, forage) to create potentially viable local home range areas for individual tortoises.**

Table 2. *Summary of published studies examining home range sizes of desert tortoise individuals. Home ranges for females, males, and all (data combined for females and males) are averages, except for Hromada et al. (2020), which are medians. The column titled "range" is the minimum and maximum home range size recorded among individuals.*

Home range (ha)				
Female	Male	All	Range	Reference
15	26	19	3-53	Barrett 1990
21	53	—	8-77	Berry 1986
19	26	23	11-38	Burge 1977
		58	3-315	Drake et al. 2015
1-9	3-26	—	1-44	Duda et al. 1999
7-11	—	—	—	Franks et al. 2011
1-7	5-32	—	1-45	Freilich et al. 2000
16-17	43-49	31-35	5-236	Harless et al. 2010
18	53	33	—	Holt and Rautenstrauch 1996
		12-151	2-410	Hromada et al. 2020
—	—	19	2-73	Medica et al. 1985
9	21	15	6-46	O'Connor et al. 1994

—	—	22	3-89	Turner et al. 1984
—	—	20	4-40	Woodbury and Hardy 1948

Notes:
-If a range is provided in the female, male, and all (females and males combined) columns, this is the range of averages (or the median for Hromada et al. 2020) among study sites.
-(—) notes that the measure was not presented in a study.
-Home range sizes were usually determined using a polygon method based on tracking individual tortoises for various periods of time (typically at least a year to encompass seasonality and sometimes multiple years to encompass variation with annual weather).
-The home ranges are generally for adults, though some studies included some juveniles.

At spatial scales broader than home ranges, habitat connectivity is important for supporting genetic exchange within and among populations (Latch et al. 2011, Averill-Murray et al. 2013), enabling the long-distance travels of 7+ km that tortoises can periodically make over periods of days to years (Berry 1986), and increasing the proportion of interior habitat away from the edges (e.g., near roads) that are generally poor-quality habitat for tortoises (e.g., LaRue 1993, Boarman and Sazaki 2006, Nafus et al. 2013, Berry et al. 2020a). Although minimum sizes of unfragmented habitat required to support viable populations of desert tortoises can be hard to define because of many factors such as variation in habitat quality, the numerous studies showing increased mortality and reduced tortoise density or sign near edges of habitat bordering non-habitat (e.g., roads, urban areas) or anthropogenically disturbed habitat suggest that **patches as large and unfragmented as possible are likely the most high-quality for tortoises** (e.g., Esque et al. 2010, Berry et al. 2013, Carter et al. 2020, Hromada et al. 2020). It is important to note that not all threats necessarily decline in severity in habitat interiors, with cosmopolitan non-native plants being one example (Abella et al. 2009). Rather, there may be fewer (or less severe) threats to contend with in habitat interiors and therefore less cumulative impact (Tuma et al. 2016). Recognizing the importance of interior habitat, 16 large critical habitat recovery units ranging from 17,000-400,000 ha were established as part of tortoise recovery planning (U.S. Fish and Wildlife Service 1994b). Fragmentation is not absent within these units, but they, along with other protected areas, can represent some of the core areas in which conservation and restoration efforts can be focused (Berry et al. 2014a).

Collectively, these observations suggest that management for local-scale habitat connectivity needs to consider connectivity at scale of tens of hectares (typical home range sizes) to kilometers (periodic long-distance travels) to include the range of movements of tortoises reported in the literature (Berry 1986, Harless et al. 2010). What are possible impacts if local habitat connectivity for tortoises is reduced? Limiting access by tortoises to optimal food plants can deleteriously impact their nutrition through inadequate forage quantity or through eating sub-optimal or potentially harmful plant species (Oftedal et al. 2002). Tortoises also drink water from puddles and water catchments, and limiting access to these resources is likely detrimental (Peterson 1996). A well-documented behavior of tortoises is using networks of perennial plants and burrows or other structures (e.g., small caves) as cover, and curtailing a tortoise's ability to move among these resources is inconsistent with the natural behavior tortoises have displayed (Rautenstrauch et al. 2002, Drake et al. 2015). **At the home range scale, habitat area large enough that it offers sufficient perennial plant cover, suitable burrow locations, forage, and drinking water, as well as minimal-risk freedom of movement to access these resources, may be expected to represent good-quality local habitat conditions (Harless et al. 2010).**

Existing research suggests that decommissioning certain backcountry roads could be hypothesized to improve both the connectivity and quality of habitat for desert tortoises. Several studies have reported zones of reduced live tortoise density or indicators of occupancy extending from roadsides. In Mojave National Preserve, for instance, Nafus et al. (2013) found that evidence of tortoise presence was reduced for at least 200 m from two-lane Goffs, Cima, and Morning Star Mine Roads carrying 325-1,089 vehicles/day. Similarly, Boarman and Sazaki (2006) found that density of tortoise evidence was reduced at least 400 m from California State Highway 58 in the western Mojave Desert. Even greater effects were reported along southern Nevada two-lane highways: tortoise sign was reduced 2,000 m or more from roads (von Seckendorff Hoff and Marlow 2002). In that study, the zone of low tortoise evidence increased in width with increasing size and traffic of roads ranging from unpaved desert roads to U.S. Highway 95. The negative correlation between live tortoise density or sign and distance from roads could result from direct mortality via traffic on roads, behavioral alterations where tortoises avoid going near roads (this aversion could result from noise, visual cues, differences in roadside vegetation, or other factors), or a combination of factors (Berry et al. 2006, Boarman and Sazaki 2006, Berry et al. 2013).

Desert tortoise home range, movement, and spatial utilization literature may offer ideas for spatial planning of habitat restoration efforts specifically tailored for tortoises. For example, it is possible that strategically restoring dispersed patches or corridors of perennial cover plants could enable tortoises to better utilize large disturbances otherwise largely devoid of vegetation (Berry et al. 2013, Drake et al. 2015, Gray et al. 2019). Owing to potential heavy utilization of small washes or their margins for foraging (Jennings and Fontenot 1993), prioritizing restoration efforts around these areas or to improve habitat nearby to enhance tortoise access to them could represent a strategic use of restoration resources. Similarly, focusing vegetation restoration efforts away from locations risky to tortoises (such as roadsides) may provide more benefit to tortoises, though there may be other reasons to prioritize restoration locations (such as along roads specifically to deter further disturbance in habitat interiors).

CONTEXT FOR VEGETATION AND SOIL RESTORATION IN DESERT TORTOISE HABITAT

Ecological restoration is not intended to contribute to all recovery actions for the desert tortoise but has high potential to aid overall recovery. For example, instead of restoration, management activities or policies may be most appropriate for limiting tortoise exposure to disease, but restoration activities to enhance forage quality could improve resistance of tortoises to some diseases (Jacobson 1994). Restoration can likely make three main contributions to improving tortoise habitat quality: i) ameliorating or reversing stressors to tortoises, such as poor-quality forage, exposure to toxicants, or lack of cover plants; ii) expanding habitat area useable or favorable to tortoises, such as revegetating denuded areas otherwise avoided by tortoises; and iii) limiting further degradation of tortoise habitat, such as through lowering wildfire risk by reducing non-native plants. Restoration can thus serve as a major tool along with other management and policy activities seeking to contribute to tortoise recovery.

Research has demonstrated that restoration is feasible in the Mojave Desert, even when environmental conditions are adverse, but that it is difficult and restoration projects must generally implement sound practices to be successful in this environment. Typical challenges desert restoration commonly must overcome include limited availability of native plant materials for restoration; low and erratic precipitation and hot, desiccating summers; often intensive levels of herbivory at restoration project sites given limited natural forage (e.g., mammalian herbivores targeting planted species enriched in nutrients from propagation processes in greenhouses); infertile or shallow soils after disturbance; and competition or fire hazards stemming from non-native plants (Bainbridge 2007). Compared to moister regions, these issues are heightened challenges in drylands where plant regeneration even under natural conditions is relatively infrequent, precisely a reason why plant cover in drylands is low naturally. Restoration practices discussed in the remainder of the report can increase chances that restoration projects successfully overcome these limitations.

With few exceptions (Abella et al. 2015c, Devitt et al. 2020), restoration practices and projects in the Mojave Desert to date have been performed under goals not specific to the desert tortoise, although **the restoration goals would often align with tortoise habitat enhancement goals.** For example, many restoration projects reviewed in this report were conducted to revegetate denuded sites to stimulate ecological recovery, increase native plant diversity, ameliorate compacted soils, increase the proportion of native over non-native plants, and to conceal disturbances to deter further anthropogenic impacts. While not necessarily conducted with a specific goal for tortoises, these activities could benefit tortoises by increasing cover plants, enhancing forage conditions, improving soil conditions, and limiting further habitat deterioration (Berry and Murphy 2019). Furthermore, in cases where perennial plants not necessarily utilized by tortoises were restored, these plants could indirectly benefit tortoises through processes such as improving pollinator communities to increase native annuals providing tortoise forage, limiting exposure of tortoises to potentially harmful soil constituents by curtailing erosion, and triggering recruitment of tortoise forage plants via plant-plant facilitation (Abella and Chiquoine 2019, Esque et al. 2021, Rader et al. 2022).

Three of the overarching general restoration goals common in deserts include ameliorating propagule limitations as barriers to plant recruitment, stabilizing and repairing soils to limit further soil degradation, and reestablishing the fertile islands associated with mature perennial plants (Abella 2017b). Fertile islands are shaded, nutrient-enriched soils below the canopies of many mature perennials, usually shrubs (Smith et al. 2014). These fertile islands are hotspots of biological activity for nutrient cycling, soil microorganisms, pollinators and fauna, and recruitment of both annual and new perennial plants. Aside from objectives such as focusing on cacti or perennial forb forage plants or for selecting perennials that may not form fertile islands and instead compete with non-native annuals, re-establishing fertile islands is frequently a major initial step for restoration (Abella et al. 2012b). Eleven major treatments discussed in the following sections can help reintroduce missing propagules of native plants, repair soils, and restore fertile islands.

OVERVIEW OF RESTORATION TREATMENTS

Eleven treatment types in three categories (revegetation, environmental site restoration, and restorative management actions) have been examined in at least one published study in the Mojave and western Sonoran deserts containing desert tortoises (Table 3). Each treatment is detailed in ensuing sections.

Table 3. *Eleven restoration treatments placed in three categories (revegetation, environmental site restoration, and restorative management actions) examined in at least one published study in the Mojave and western Sonoran deserts. Some studies evaluated multiple treatments.*

Treatment	No. of studies
Revegetation	
Outplanting	16
Salvaging and transplanting	3
Cuttings	3
Seeding	13
Assisted natural regeneration	1
Environmental site restoration	
Vertical and horizontal mulching	8
Topsoil salvage and replacement	2
Geomorphic and microtopography treatments	6
Restoring soil features (biocrust, pavement, varnish)	3
Restorative management actions	
Fencing, protection, and herbivory management	3
Reducing non-native plants and fire risk	4

ACTIVE REVEGETATION

OUTPLANTING

Outplanting is planting nursery-propagated seedlings or cuttings at field sites (Fig. 3). A main advantage of outplanting is that by propagating plants in nurseries, it bypasses a need at field sites for seed retention in suitable microsites, successful germination, and early seedling survival, all of which are rare in field settings in deserts (Bean et al. 2004). Compared to seeding, outplanting is intended to represent a greater investment through nursery care in each propagule (seed or cutting) to result in a higher percentage of propagules producing a persistent plant. Outplanting is typically deployed to revegetate small disturbances (e.g., < 10 ha), to strategically establish vegetated islands within large disturbances, or to serve as enrichment plantings diversifying species composition (Hulvey et al. 2017). While the outplants themselves may rapidly provide habitat functions such as shading or floral resources, **reproduction by outplants or facilitation of other species' reproduction could enable outplanting to revegetate larger areas over time than were originally planted (Abella et al. 2012a, Devitt et al. 2020).**

Fig. 3. *Outplants intended to initiate recovery at a disturbed site in Joshua Tree National Park, California. Plants are enclosed in wire cages to deter herbivory.*

Outplanting can produce direct and indirect benefits for ameliorating degraded desert tortoise habitat. Reestablishing native perennials can limit soil erosion, conserving site productivity and limiting exposure of tortoises to fugitive dust potentially containing harmful substances (Grantz et al. 1998d, Jacobson et al. 2014, Kim et al. 2014). Outplanting shrubs may provide protective structures to serve tortoises as resting locations to avoid hot temperatures and as burrow-construction locations (Drake et al. 2015). Outplanting perennial forage species, such as the cactus beavertail pricklypear (*Opuntia basilaris*) and forb desert globemallow (*Sphaeralcea ambigua*), can increase food available to tortoises. Forage-supplying perennials can be particularly important to tortoises during dry years with few annuals (Medica et al. 1985). Indirect benefits of outplanting to tortoises can include enhancing native annual plant forage via formation of fertile islands below perennials and increasing habitat resources needed by other organisms in tortoise habitat (e.g., pollinator communities utilizing floral resources of outplants).

Sixteen published studies in the Mojave Desert have collectively assessed survival of 46 outplanted native perennial species for at least one year after outplanting (Table 4). While many species have not been assessed in more than one study to begin evaluating consistency of their performance, the data do enable identifying nine species exhibiting at least 50% survival in at least two studies. These relatively consistent top performers are shrubs and include: white bursage (*Ambrosia dumosa*), fourwing saltbush (*Atriplex canescens*), cattle saltbush (*Atriplex polycarpa*), Nevada jointfir (*Ephedra nevadensis*), cheesebush (*Hymenoclea salsola*), creosote bush (*Larrea tridentata*), Anderson thornbush (*Lycium andersonii*), honey mesquite (*Prosopis glandulosa*), and Mojave yucca (*Yucca schidigera*).

Table 4. *Summary of survival of 46 perennial species outplanted in the Mojave Desert in 16 published studies that reported and evaluated survival at restoration field sites for at least a year. The last column tabulates the number of studies in which at least 50% of outplants of a species survived. Highlighted species were the best performers with survival of at least 50% in at least two studies. A range of survival percentages is shown if multiple treatments were applied to outplants in a study.*

	Study																	
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**Total**	**≥ 50%**
Grass																		
Achnatherum hymenoides				0-20													**1**	**0**
Achnatherum speciosum				0-0													**1**	**0**
Aristida purpurea	0																**1**	**0**
Distichlis spicata								0-33									**1**	**0**
Muhlenbergia porteri	5																**1**	**0**
Sporobolus airoides	3			50-67				0-2									**3**	**1**
Forb																		
Artemisia ludoviciana															56-75		**1**	**1**
Baileya multiradiata	0																**1**	**0**
Penstemon bicolor	3																**1**	**0**
Salvia sonomensis											0-0						**1**	**0**
Sphaeralcea ambigua	55																**1**	**1**
Stephanomeria pauciflora											0-0						**1**	**0**
Cactus																		
Opuntia basilaris												100					**1**	**1**
Shrub																		
Acacia greggii							88-91					0					**2**	**1**
Ambrosia dumosa	23	0-45	11	50-67		82-90				42-54	33-44	0		8-75	0-50		**10**	**5**
Artemisia cana				0-33													**1**	**0**
Artemisia frigida				0-33													**1**	**0**
Artemisia tridentata				0-33							0-33				17-100		**3**	**1**
Atriplex canescens				100-100						12-28	50-67				0-100	3-100	**5**	**4**
Atriplex confertifolia				80-80													**1**	**1**
Atriplex lentiformis				33-50													**1**	**1**
Atriplex nummularia				50-67													**1**	**1**
Atriplex parryi								0-0									**1**	**0**
Atriplex polycarpa				67-100		44-67				0-31							**3**	**2**
Atriplex torreyi				50-67													**1**	**1**
Baccharis sarathroides				100-100													**1**	**1**
Cleome isomeris						74-81											**1**	**1**
Coleogyne ramosissima											0-100		4				**2**	**1**
Encelia farinosa	0					78-86											**2**	**1**
Encelia virginensis					10-43												**1**	**0**
Ephedra nevadensis				67-100		82-96							61				**3**	**3**
Ephedra viridis				67-100													**1**	**1**
Ericameria nauseosa				67-100											33-33		**2**	**1**
Eriogonum fasciculatum	28			33-50													**2**	**1**
Grayia spinosa				0-0							0-0				8-60		**3**	**1**
Hymenoclea salsola		0-90				64-82											**2**	**2**
Krascheninnikovia lanata			0								0-40				0-67		**3**	**1**
Larrea tridentata	23		2	75-100		89-92				0-12	50-69	92			50-100		**8**	**5**
Lepidospartum squamatum										0-8							**1**	**0**
Lycium andersonii				33-50							20-67				0-33		**3**	**2**
Lycium pallidum											0-0						**1**	**0**
Prosopis glandulosa						33-82			10-62								**2**	**2**
Salazaria mexicana											0-0						**1**	**0**
Sarcobatus vermiculatus								0-22									**1**	**0**
Yucca brevifolia											0-50				29-44		**2**	**1**
Yucca schidigera											0-60				0-67		**2**	**2**
Total	**10**	**2**	**3**	**21**	**1**	**8**	**1**	**4**	**1**	**5**	**14**	**4**	**2**	**1**	**11**	**1**	**46**	**29**

Notes:

-Studies include: (1) Abella et al. 2012a, (2) Bainbridge and MacAller 1996, (3) Brum et al. 1983, (4) Clary and Slayback 1983, (5) Devitt et al. 2020, (6) Edwards et al. 2000, (7) Fidelibus and Bainbridge 1994, (8) Fisher 1984, (9) Grantz et al. 1998c, (10) Graves et al. 1978, (11) Hunter et al. 1980, (12) Newton 2001, (13) Scoles-Sciulla et al. 2015, (14) Walker et al. 2001, (15) Wallace et al. 1980, and (16) Yamashita and Manning 1995.

-Studies evaluated outplant survival for 1-5 years after outplanting among studies.

Many of these top-performing shrubs are favored by tortoises as resting and burrow-construction sites, suggesting that outplanting can enhance availability of these key habitat resources. Furthermore, although many of the studies assessed outplant survival for a relatively short duration (1-3 years after outplanting), the limited number of longer-term studies reported persistence, growth, and flowering of outplants. Clary and Slayback (1983), for example, reported that most outplanted species alive after two years persisted at five years after outplanting in the central Mojave Desert, California. Although not included in Table 1 as the study reported a cover metric rather than survival, Abella (2017a) found that outplants persisted at least six years in a semi-natural environment in the eastern Mojave Desert. Presumably, outplants persisting for these 5-6-year periods would be established in the habitat and then their longer-term survival could be similar to naturally established individuals subject to mortality events from droughts and other factors (Miriti et al. 2007).

In burned desert tortoise habitat, height growth of surviving outplanted shrubs was rapid, with average heights of 49, 42, and 26 cm respectively for eastern Mojave buckwheat (*Eriogonum fasciculatum*), creosote bush, and white bursage three years after outplanting (Abella et al. 2012a). Desert tortoises generally construct burrows beneath larger plants, underscoring the importance of outplant height growth for recovering functions of large shrubs utilized by tortoises for protection (Burge 1978). Highlighting production of floral resources and potential for outplants to reproduce, by three years after outplanting an average of 86% of desert globemallow, 73% of eastern Mojave buckwheat, 33% of creosote bush, and 22% of white bursage flowered (Abella et al. 2012a).

Treatments associated with outplanting can be critical to outplanting success. However, treatments add cost and complexity to outplanting, suggesting that cost-benefit analyses are necessary to compare any treatment-facilitated plant performance increase with an alternative in some cases of simply planting more plants and accepting lower survival. In cases where few seeds are available for propagation or for species difficult to propagate in nurseries, then treatments to maximize survival of each propagule may be appropriate even if treatments are costly. Identifying which treatments are most effective and which species are most reliant on treatments for successful establishment could assist with optimally allocating resources.

Eleven different treatments associated with outplanting have been evaluated in 13 outplanting studies in the Mojave Desert (Table 5). These treatments include: cages for herbivory protection, shelters for microclimate amelioration and herbivory protection, chemical herbivore repellents, irrigation (including different types), constructing water catchments around outplants, fertilization, manipulating fertile islands at planting locations, treating non-native plants to reduce potential competition with outplants, and three treatments associated with outplanting procedures (seedling transport, planting methods, and planting at low or high density). Thus far, it is difficult to extract conclusions from the literature on effectiveness of most treatments because most have been tested in two or fewer studies, results can be highly species- and context-specific, treatments can be contingent and interactive with each other, and numerous variations exist on treatments (e.g., the frequency or amount of water delivered for irrigation) that could further influence their effectiveness. With consideration to this variability and a need for further studies to optimize application of treatments where and when they are most needed, the existing literature offers insight into potential effectiveness of the most commonly applied treatments and ideas for further innovations.

Table 5. *Summary of treatment effectiveness associated with outplanting in the Mojave Desert. Studies assessing one or more treatments and that reported outplant survival percentages for at least a year after outplanting are included. Treatment effects are shown as the ratio of percent survival in the treatment compared to no treatment (or shelter compared to cage for that comparison). Positive effects (+) indicate that a treatment increased survival, whereas negative effects (-) indicate that a treatment reduced survival. The symbols ++ and - - indicate that ratios were not calculated because all outplants died in either the control (++, indicating treatments were crucial to plant survival) or treatment (- -). As an example of the ratios, outplant survival in cages was 40% in Devitt et al. (2020; numbered study 4) compared with 10% survival without cages, resulting in a ratio of +4.0.*

Treatment	Effects (survival ratio)	Study
Protection		
Cage	+4.0, +1.8, +1.8	4, 9, 12
Shelter	+1.9, (++)	1, 2
Shelter : cage	+2.3, +1.5	2, 7
Herbivore repellent	(- -)	2
Moisture enhancement		
Irrigation	+1.9, +1.1, 1.0, 1.0, 1.0, +2.4	1, 3, 4, 8, 10, 13
Water catchment	+1.1	5
Nutrient enhancement		
Fertilization	-1.1	13
Fertile island	+1.4	11
Reduce competition		
Manage non-natives	-1.1, +1.3	10, 13
Planting procedures		
Seedling transport method	1.0	6
Planting method	+2.6	7
Planting density	+1.2	13

Notes:
-Studies are numbered as follows: (1) Abella et al. 2012a, (2) Bainbridge and MacAller 1996, (3) Clary and Slayback 1983, 1984, (4) Devitt et al. 2020, (5) Edwards et al. 2000, (6) Fidelibus and Bainbridge 1994, (7) Grantz et al. 1998c, (8) Graves et al. 1978, (9) Hunter et al. 1980, (10) Scoles-Sciulla et al. 2015, (11) Walker et al. 2001, (12) Wallace et al. 1980, and (13) Yamashita and Manning 1995.
-The fertile island treatment in (11) Walker et al. 2001 tested outplanting in a fertile island microsite where a mature shrub had been removed.
-The seedling transport method in (6) Fidelibus and Bainbridge 1994 compared container with jelly rolled seedlings.
-Planting method in (7) Grantz et al. 1998c compared digging holes with an auger or pick axe.
-Planting density in (13) Yamashita and Manning 1995 compared planting at low or high density.

Some type of physical barrier to mammalian herbivory, either a wire cage or shelter (typically a plastic cone or cylinder; Fig. 4) enclosing outplants, has most consistently enhanced outplant survival among treatments evaluated in at least two studies. **All five studies testing cages or shelters reported that they have at least nearly doubled outplant survival (Table 5).** In one study (Bainbridge and MacAller 1996), no unprotected outplants survived. In two studies of outplant survival in shelters compared with cages, survival was 1.5 (Grantz et al. 1998c) and 2.3× (Bainbridge and MacAller 1996) greater in shelters than in cages. This could be because shelters provided both herbivory protection and ameliorated microclimates, whereas cages mainly only provided herbivory protection. Two of the reasons that some form of herbivory protection has often been key to outplanting success include the intensive levels of herbivory that occur in deserts with naturally low amounts of palatable forage (potentially exacerbated at disturbed sites with little vegetation where outplanting is often performed) and that greenhouse-propagated seedlings may be enriched in nutrients and therefore attractive to herbivores.

Fig. 4. *Outplanted creosote bush that grew to a height of 130 cm and flowered within three years after outplanting to revegetate a burned site in southern Nevada. Shelters protecting outplants in this study doubled outplant survival.*

While it may seem that moisture enhancement via treatments such as irrigation or constructing depressional water catchments around outplants should increase plant survival in deserts, effects of moisture-enhancing treatments on outplant survival have been inconsistent. Three of six studies testing irrigation (either as a slow-release gel or directly introducing water) found that irrigation increased outplant survival. The other three studies found no benefit of irrigation. Similarly, water catchments in Edwards et al. (2000) produced minimal benefit, with 84% outplant survival with catchments and 74% survival without. There could be several reasons for inconsistent benefits of moisture treatments, such as difficulties with delivering sufficient quantities or timing of water to appreciably influence outplant survival or that effects of herbivory can overwhelm influences of moisture availability.

Other treatments may have promise but have not been evaluated for their influence on outplant survival for at least a year in sufficient numbers of studies to date to evaluate their reliability. For example, based on the observation that non-native annual plants reduce fitness of mature shrubs (Rodríguez-Buriticá and Miriti 2009), reducing potential competition experienced by outplants may be expected to enhance outplant survival, particularly at sites with appreciable non-native annuals. Herbicide treatments designed to reduce non-native annuals did enhance outplant survival in one study (Yamashita and Manning 1995) but slightly reduced outplant survival in another (Scoles-Sciulla et al. 2015). Benefits to outplant performance of treating non-native plants could be contingent on factors such as the competitiveness of the particular non-native species at sites, interactions with other treatments, climate, and whether non-native annuals are sufficiently abundant to threaten outplant survival by increasing wildfire risk. Furthermore, there may be potential for selecting native perennials that provide functions for tortoises but that are also competitive with non-native annuals (Abella et al. 2011, 2012b).

Finances and logistics of outplanting vary with factors such as degree of difficulty of obtaining seed, availability of nursery facilities, type and size of containers in which plants are propagated, the number of outplants produced and desired planting density at restoration sites, ease of transporting outplants to field sites, and associated treatments applied to outplants (e.g., shelters, irrigation). Species-specific survival can also be a key factor, though species with lower survival may still be worth outplanting if they provide key functions even if the cost per surviving plant is high. This does highlight, though, how additional research that identifies ways to cost-efficiently enhance propagation techniques and outplant survival in the field has potential to substantially lower restoration costs. **Cost estimates for outplanting and other restoration treatments are presented later in the report.**

SALVAGING AND TRANSPLANTING PLANTS

Transplanting entails moving plants from a donor to a recipient site. It often occurs in the context of salvaging plants before a planned disturbance, then using the salvaged plants to revegetate another site or to revegetate the original donor site in the case of temporary disturbance (McMahon et al. 2008). After plants are salvaged, they may be moved directly to a recipient site or undergo a period of storage and nursery care before redeployment to field sites (Weigand and Rodgers 2009). Transplanting can be viewed as a three-phase "survival budget" including survival of the initial salvage operation, the period of transport or nursery care, and the post-planting period at revegetation sites (Abella et al. 2015b). While each of these phases can result in plant attrition, germination and sprouting of propagules in donor soil associated with salvaged plants can produce additional plants that can be separated and used in restoration. As with the preparation of outplants, the type and size of container to use (including the possibility of bare-root methods) is important for salvaging and caring for plants (Landis et al. 1990). As ongoing research on the numerous potential permutations of containers among species proceeds for propagating Mojave Desert species, a reasonable strategy seems to be balancing salvaging as much root volume as possible with constraints on transport and storage of large volumes of soil and root mass (Smith et al. 2012). Salvaging small- to medium-sized perennials commonly employs 4-L (1-gallon) or 16-L (4-gallon) pots (Abella et al. 2015b). Salvaging the largest perennials, such as Joshua trees (*Yucca brevifolia*), has been done using heavy equipment to move large soil and root volumes in addition to the heavy aboveground material (McMullen 1992).

Three studies in the Mojave Desert demonstrate that salvaging and transplanting native perennials can commonly achieve survival rates exceeding 25-50% cumulatively across all phases of salvage and over 50% specifically after transplants surviving earlier salvage operation phases are placed back in the field at restoration sites (Table 6). **A total of 44 species were evaluated for amenability to transplanting to date and 25 of them achieved at least 50% survival in a study.** Cacti appear particularly amenable to transplanting, as all nine species examined achieved 57-100% cumulative survival. Several shrubs also performed well in at least one study, such as catclaw acacia (*Acacia greggii*), white bursage, creosote bush, desert almond (*Prunus fasciculata*), Mojave yucca, and Joshua tree. Only one of the studies included forbs and found that two forb species eaten by desert tortoises, desert globemallow and wire lettuce (*Stphanomeria pauciflora*; Esque et al. 2021), were among the forbs most amenable to transplanting (Abella et al. 2015b). **Research to date indicates that transplanting is effective for restoring species used by tortoises for cover and food.**

Table 6. *Summary of survival of plants salvaged from sites to be disturbed and transplanted to restoration sites in three studies in the Mojave Desert. Survival is the percentage of transplants placed back out in the field that survived at restoration sites for 2-3 years among studies.*

Species	Study 1	Study 2	Study 3	**Total**	**≥ 50%**
	— Survival % (no. plants transplanted) —				
Grass					
Pleuraphis rigida	14 (29)			**1**	**0**
Forb					
Astragalus preussii	3 (33)			**1**	**0**
Baileya multiradiata	30 (104)			**1**	**0**
Enceliopsis argophylla	17 (18)			**1**	**0**
Eriogonum inflatum	27 (89)			**1**	**0**
Gutierrezia sarothrae	25 (4)			**1**	**0**
Sphaeralcea ambigua	50 (105)			**1**	**1**
Stephanomeria pauciflora	47 (55)			**1**	**0**
Suaeda moquinii	50 (26)			**1**	**1**
Cactus					
Cylindropuntia acanthocarpa	67 (6)			**1**	**1**
Cylindropuntia echinocarpa			49 (332)	**1**	**0**
Cylindropuntia ramosissima			64 (202)	**1**	**1**
Echinocereus engelmannii			57 (7)	**1**	**1**
Echinocereus triglochidiatus			77 (75)	**1**	**1**
Echinomastus johnsonii	100 (8)			**1**	**1**
Ferocactus cylindraceus	100 (5)	85 (20)		**2**	**2**
Grusonia emoryi			70 (27)	**1**	**1**
Opuntia basilaris	93 (103)		83 (23)	**2**	**2**
Shrub					
Acacia greggii	0 (3)		75 (148)	**2**	**1**
Ambrosia dumosa	60 (360)			**1**	**1**
Atriplex canescens			0 (5)	**1**	**0**
Atriplex confertifolia	54 (28)			**1**	**1**
Atriplex hymenelytra	47 (17)			**1**	**0**
Coleogyne ramosissima			29 (94)	**1**	**0**
Encelia farinosa			82 (33)	**1**	**1**
Encelia virginensis	36 (14)			**1**	**0**
Ephedra californica			100 (4)	**1**	**1**
Ephedra nevadensis			57 (60)	**1**	**1**
Ephedra torreyana	36 (22)			**1**	**0**
Eriogonum fasciculatum			61 (23)	**1**	**1**
Grayia spinosa			51 (98)	**1**	**1**
Hymenoclea salsola	19 (21)		100 (5)	**2**	**1**
Isocoma acradenia	38 (16)			**1**	**0**
Larrea tridentata	53 (73)		0 (1)	**2**	**1**
Lycium andersonii			9 (11)	**1**	**0**
Lycium cooperi			10 (10)	**1**	**0**
Prunus fasciculata			79 (34)	**1**	**1**
Psorothamnus fremontii	14 (14)			**1**	**0**
Salazaria mexicana			78 (9)	**1**	**1**
Tetradymia spinosa			0 (3)	**1**	**0**
Yucca schidigera		39 (459)	84 (478)	**2**	**2**
Chilopsis linearis			100 (4)	**1**	**1**
Juniperus californica			0 (1)	**1**	**0**
Yucca brevifolia			54 (782)	**1**	**1**
Total	**23**	**2**	**25**	**44**	**25**

Note: *Studies are numbered as follows: (1) Abella et al. 2015b, (2) McMullen 1992, and (3) Weigand and Rodgers 2009.*

A study in desert tortoise habitat in the eastern Mojave Desert in Lake Mead National Recreation Area illustrated variation in transplant success among species and effects of treatments (Abella et al. 2015b). The study involved salvaging 2105 individuals of 23 perennial species before construction activities that re-routed a park road, storing and caring for the plants for 16 months in a temporary field nursery near the future restoration sites, placing plants at the restoration site after construction activities ceased (with the restoration sites being removed segments of the old road), and monitoring survival for 27 months at the restoration sites (Fig. 5). Immediately after plants were salvaged, several treatments were evaluated for their ability to enhance plant survival: a root-stimulating hormone, a gel polymer added to soil to slowly release water to roots, and soaking roots in water. These post-salvage treatments had no statistically significant effect on plant survival of salvage and the 16 months of nursery residence.

Fig. 5. *Top: temporary field nursery established in a fenced area near a ranger station, which had a water source, in a plant salvage and transplanting project in Lake Mead National Recreation Area. Bottom: transplants placed at one of the restoration sites. All transplants were enclosed in cages to deter herbivory and some were planted on salvaged topsoil and with or without two types of irrigation (hand watering or slow-release gel). Top photo by L.P. Chiquoine.*

Treatments applied to transplants placed back in the field at restoration sites affected transplant survival and interacted with species. Transplants placed on sites receiving salvaged topsoil (upper 20 cm of soil) exhibited 56% survival at 27 months, more than twice as high as the 25% survival of transplants placed on sites without topsoil. **The benefits of planting on salvaged topsoil (without irrigation) were nearly equivalent to irrigating plants** at a 63% augmentation of the site's average rainfall of 16 cm/year. Irrigation increased transplant survival by 1.6×, but the type of irrigation affected species differently. White bursage, for example, responded similarly to hand watering or a slow-release gel affixed near roots in soil. In contrast, for reasons that were unclear, desert globemallow only responded to hand watering. While forbs as a group did not perform as well as shrubs or cacti across the treatments applied, including forbs in salvage operations may be warranted to diversify species composition and provide unique ecological functions.

Published research further has highlighted costs and logistical considerations of transplanting. If salvaged plants can be transported directly to their recipient site and re-planted without nursery care, this may substantially reduce costs but the effects on plant performance remain uncertain (McMahon et al. 2008). A period of nursery care could help plants overcome potential negative effects of the salvage operation, but nursery residence and the additional transport event from the nursery to the restoration site is another opportunity for mortality. Other than Weigand and Rodgers (2009) noting that large Mojave yucca and Joshua tree can cost up to $425 each to salvage, cost estimates of salvaging in the Mojave Desert were not located in the literature. It seems likely that costs are similar to outplanting for small- and medium-sized perennials, as the salvage operation may be similar in cost to seed collection and meeting germination requirements needed to prepare outplants. In terms of logistics, when salvaging cacti, Smith et al. (2012) suggested the potential importance of orienting transplanted cacti in the same direction at restoration sites as they had originally grown. Cactus tissue can become acclimated to the direction of the most intense sunlight. When feasible, salvaging topsoil along with salvaging plants appears beneficial to both provide a substrate for increasing transplant survival at restoration sites and likely other benefits too (e.g., restoring soil microorganisms). The finding in Abella et al. (2015b) that both topsoil and some type of irrigation similarly increased overall transplant survival illustrated a potential tradeoff where salvaging topsoil represents a major up-front effort but may save effort later if less care of transplants is required. Research to date suggests that transplanting can be an effective restoration tool for Mojave Desert perennials when donor sites are available and may be especially important for restoring taller individuals (such as Joshua trees) otherwise requiring decades to grow to maturity.

CUTTINGS

Propagating plants using cuttings from stems, branches, rhizomes, or roots avoids a need for collecting and successfully germinating seed. However, propagating from cuttings requires donor plants and the ability of cuttings to root. **At least four studies have developed techniques for propagating cuttings from material collected from the Mojave or nearby Sonoran Desert for species that occur in the Mojave Desert.**

Using stem cuttings collected in the northern Mojave Desert, Wieland et al. (1971) presented optimal treatments (among combinations of applying concentrations of rooting hormones and greenhouse care techniques) for 16 shrub species (Table 7). With the exceptions of stem cuttings from Utah juniper (*Juniperus osteosperma*) and littleleaf ratany (*Krameria erecta*), which failed to root under any treatment, stem cuttings from 14 species rooted. Applying a root-stimulating hormone (1H-Indole-3-butanoic acid; IBA) enhanced rooting in nine of the species, while five species did not need IBA to stimulate rooting. Further research would be required to evaluate the performance of the rooted cuttings in field settings and how the performance of the cuttings may compare with outplants, transplants, or seedlings originating from seeding.

Table 7. *Summary of treatment results for stimulating rooting of stem cuttings collected from 16 shrub species in the northern Mojave Desert (Wieland et al. 1971).*

Species	**Results**
Ambrosia dumosa	Stem cuttings readily rooted with 0.3% IBA
Atriplex canescens	Stem cuttings from seedlings rooted without IBA
Atriplex confertifolia	Stem cuttings from seedlings or juveniles rooted without IBA
Atriplex hymenelytra	Stem cuttings from seedlings rooted without IBA
Atriplex lentiformis	Stem cuttings rooted with 0.8% IBA
Bassia americana	Stem cuttings rooted without IBA
Ephedra viridis	Stem cuttings from seedlings rooted without IBA
Grayia spinosa	Stem cuttings rooted with 0.3% IBA
Juniperus osteosperma	Stem cuttings failed to root
Krameria erecta	Stem cuttings failed to root
Krascheninnikovia lanata	Vigorous shoots of any age rooted; 0.3% IBA improved rooting
Larrea tridentata	Juvenile plant shoots rooted; 0.8% IBA stimulated rooting
Lycium andersonii	Stem cuttings readily rooted with 0.3% IBA
Lycium pallidum	Juvenile plant shoots rooted; 0.3% or 0.8% IBA stimulated rooting
Lycium shockleyi	Juvenile plant shoots rooted; 0.3% or 0.8% IBA stimulated rooting
Thamnosma montana	Stem cuttings readily rooted; 0.3% or 0.8% IBA stimulated rooting

Note: *IBA is the root-stimulating hormone 1H-Indole-3-butanoic acid.*

Using material collected from near Palm Springs, California, in the Sonoran Desert just south of the Mojave Desert, Chase and Strain (1966) reported that brittlebush (*Encelia farinosa*), cheesebush (*Hymenoclea salsola*), and white bursage (*Ambrosia dumosa*) had at least 33% of their stem cuttings successfully root in at least one treatment. The treatments examined included various rooting hormone solutions, immersion in Hoagland's nutrient solution, and using vermiculite as a rooting medium. In contrast to Wieland et al. (1971), creosote bush (*Larrea tridentata*) cuttings did not root in any treatment. Chase and Strain (1966) further suggested that the ability of cuttings to root could vary among individuals within species. As a result, the authors began randomly selecting individuals from which to obtain cuttings and raised the possibility of identifying traits of individuals potentially most amenable to propagation.

In the Sonoran Desert near the ecotone to the southeastern Mojave Desert, Chiquoine et al. (2021) examined not only rooting ability of plants, but also their subsequent performance in different planting locations at a restoration field site. The study focused on beavertail pricklypear (*Opuntia basilaris*), which provides food for tortoises and is also an important species for pollinators (Esque et al. 2021). Cuttings (single pads) were obtained from a donor site and placed in pots in a greenhouse for root development during six months (83% of pads survived and rooted during this period). At a disturbed field site, cacti were planted either in the open or in the interior of a circle of "nurse rocks" experimentally placed to provide protection to the plants (Fig. 6). In the first 15 months after planting, which had average precipitation, cacti survival did not differ between microsites, but only individuals planted within nurse rocks flowered. Nurse rocks subsequently became even more important during extreme drought. **By 27 months after planting, twice as many cacti survived with nurse rocks compared to without.** Results highlighted the potential importance of selecting or creating favorable microsites for planting locations to increase plant survival and therefore maximize use of plant material. Furthermore, results highlighted that studying plant distributions in reference sites (where pricklypear were largely restricted to growing near rocks) can help guide planting locations and arrangements at restoration sites. The study demonstrated that propagating and planting cuttings in suitable microsites can restore pricklypear populations, even during extreme drought, and that individuals can flower and reproduce vegetatively on site in less than 15 months.

Fig. 6. *Pricklypear, grown from pads propagated in a nursery, enclosed in a "nurse rock" treatment at a restoration site. Plants within nurse rock shelters had higher flowering frequency and greater survival during drought than plants without nurse rocks. Photo by L.P. Chiquoine.*

The three studies above, along with Rowe et al. (2020) who found that most cuttings (pads) of *Cylindropunti*a and *Opuntia* spp. survived for at least five years at restoration sites when moved directly from donor plants in the Sonoran Desert, suggest that propagating species from cuttings is a promising restoration tool. Furthermore, bypassing a need to obtain viable seed for propagating plants, by instead using cuttings, could become increasingly significant if droughts become more severe in coming decades and curtail viable seed production. Further research to advance propagating plant material from cuttings could include screening more species for rooting ability of their different parts (e.g., stems or rhizomes, if present), identifying whether potential variation among individuals in rooting ability is predictable, continuing to test treatments for cost-effectively stimulating rooting either in greenhouse or field settings, examining effects of collecting material from donor plants to minimize potential damage to wild source populations, and assessing the performance of plants derived from cuttings at restoration sites.

SEEDING

Outcomes of seeding have been highly variable among 13 Mojave Desert studies that included a total of 44 native seeded species and monitored plant establishment for at least one year (Table 8). Seeding in some projects failed to result in plant establishment of most or all species, while species, at least in the short term, become established through seeding in other studies.

Table 8. *Summary of seeded species performance in 13 studies in the Mojave Desert that evaluated post-seeding plant establishment for at least a year. Studies used different measures to quantify seedling establishment. Measures of seeded species performance are abbreviated as: seedlings/m^2 (/m^2), % of seeds producing a seedling (% S), and % plant cover (% C).*

	Study													
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**Total**
Species	**/m^2**	**/m^2**	**% S**	**/m^2**	**% C**	**% S**	**/m^2**	**/m^2**	**% S**	**% S**	**/m^2**	**% S**	**/m^2**	
Grass														
Achnatherum hymenoides					10		2.0				1.2		0	4
Achnatherum speciosum					0									1
Aristida purpurea	0													1
Elymus elymoides							1.1							1
Pleuraphis jamesi							<0.4				0.1		0	3
Sporobolus cryptandrus											0.1			1
Forb														
Baileya multiradiata	0											0	2.7	3
Eschscholzia californica					0									1
Linum lewisii													0	1
*Lupinus sparsiflorus**													0	1
Penstemon bicolor	0							9.4				0		3
Penstemon palmeri											1.9		6.7	2
*Phacelia parishii**								3.6						1
*Plantago ovata**		5-48												1
Sphaeralcea ambigua	0	0					<0.4					0	0	5
Sphaeralcea grossulariifolia											0.1			1
Sphaeralcea rusbyi								0.3						1
Xylorhiza tortifolia													0.4	1
Shrub														
Ambrosia dumosa	0		0.5			4				0		0	0.8	6
Artemisia tridentata				0.1										1
Atriplex canescens				0.6	12, 0	62	<0.4				0.2			5
Atriplex confertifolia							0.6							1
Atriplex lentiformis				0.2										1
Atriplex polycarpa				4.2	10, 0	12								3
Atriplex spinifera			1.1											1
Bebbia juncea	0													1
Brickellia incana													0	1
Cleome isomeris				0.8										1
Coleogyne ramosissima									1-22			21		2
Encelia farinosa	0			0.2								0		3
Encelia virginensis													0.1	1
Ephedra nevadensis							0.6							1
Ephedra viridis							<0.4							1
Ericameria nauseosa					0		<0.4							2
Eriogonum fasciculatum	0			0.2	8, 0		<0.4					0		5
Grayia spinosa							<0.4							1
Hymenoclea salsola	0	0					<0.4					0		4
Krascheninnikovia lanata		0	0.3				0.4				0			4
Larrea tridentata	0		0.1		0	0				0		0	0	7
Lepidospartum squamatum						8								1
Lycium andersonii							<0.4							1
Sarcobatus vermiculatus							<0.4							1
Total	**10**	**4**	**4**	**7**	**8**	**5**	**15**	**3**	**1**	**2**	**7**	**9**	**12**	**44**

Notes:

-Studies are numbered as follows: (1) Abella et al. 2012a, (2) Abella et al. 2015c, (3) Brum et al. 1983, (4) Clary and slayback 1983, (5) Grantz et al. 1998a, (6) Graves et al. 1978, (7) Hall and Anderson 1999, (8) Hiatt et al. 1995, (9) Jones et al. 2014, (10) Ostler et al. 2003, Caldwell et al. 2009, (11) Ott et al. 2011, (12) Suazo et al. 2013, and (13) Walker and Powell 1999.

-Species with asterisks are annuals; the rest are perennials.
-In (2) Abella et al. 2015c, the range of seedling densities in different treatments is provided.
-In (5) Grantz et al. 1998a, numbers separated by commas represent plant cover in two separate trials within the study.
-In (11) Ott et al. 2011, data for 1998 (six years after seeding) were used as this year was near peak establishment of seeded species.
-Years after seeding that studies evaluated seeded species establishment were as follows: 1 year: studies 8 and 10; two years: studies 2, 3, 6, 7, 9, 12, and 13; 3-5 years: studies 1, 4, and 5; and 14 years: study 11.

Identifying the consistently best-performing species is difficult because most species were seeded in two or fewer studies, seed viability and seeding rates varied among species, and measures of plant establishment differed among studies. However, some qualitative trends appear evident for species seeded in at least two studies. The perennial grass sand ricegrass (*Achnatherum hymenoides*) became established in three of four studies in which it was seeded, similar to James' galleta (*Pleuraphis jamesii*) which became established in two of three studies. Among forbs, Palmer's penstemon (*Penstemon palmeri*) became established in both studies in which it was seeded, while desert globemallow (*Sphaeralcea ambigua*) became established in only one of five studies. Top-performers to date among shrubs include white bursage (*Ambrosia dumosa*; establishment in three of six studies), fourwing saltbush (*Atriplex canescens*; all five studies), cattle saltbush (*Atriplex polycarpa*; all three studies), eastern Mojave buckwheat (*Eriogonum fasciculatum*; three of five), and winterfat (*Krascheninnikovia lanata*; two of four). *Atriplex* as a whole performed well, as all five species in the various studies in which they were seeded exhibited some establishment in each study. Creosote bush (*Larrea tridentata*) was the poorest-performing shrub species seeded in at least two studies, with establishment in only one of seven studies. Brittlebush (*Encelia farinosa*; establishment in one of three studies) and cheesebush (*Hymenoclea salsola*; establishment in one of four studies) have also performed poorly to date in seeding.

Precipitation exceeded long-term averages in the post-seeding monitoring period in 62% (8 of 13) of studies, which may relate to why at least some seeded species became established in most studies. However, some plant establishment also occurred for at least one seeded species in at least one site in four studies in which precipitation was below average, ranging from 33-85% of average precipitation (Graves et al. 1978, Grantz et al. 1998a, Jones et al. 2014, Suazo et al. 2013). The seeding study occurring in the driest conditions, with 33% of average rainfall, found that seeding failed to result in any plant establishment at most sites, but some species did become established at one of the four study sites (Grantz et al. 1998a).

The longest-term study, monitoring for 14 years (1993-2007) after seeding in the northeastern Mojave Desert for revegetating sand and rock mine sites, portrayed fluctuations in seeded species that correlated with variation in seasonal and multi-year precipitation trends (Ott et al. 2011). For example, the seeded sand ricegrass peaked at a density of 2.2 plants/m^2 in 1997 following multiple wet periods but declined to 0.2 plants/m^2 by 2007 after two years of generally below-average precipitation. In another example, the forb Palmer's penstemon exhibited no or minimal establishment ($\leq$ 0.1 plants/m^2) until four years after seeding. Density was then 2-3 plants/m^2 in 1997-1998 (five and six years post-seeding) during a wet period, dropped to 0.1 plant/m^2 in the dry 2002, increased to 0.7 plants/m^2 in the wet 2005, and was absent in the dry 2007. Four-wing saltbush was consistently present in all study years between 1993 and 2005, but it too disappeared by 2007.

The long-term data of seeded species abundance suggested several conclusions: i) conditions in any particular year of monitoring could have a major influence on perception of seeding effectiveness, ii) establishment in years soon after seeding did not necessarily mean that seeded species became persistent components of the community, iii) there may be "progressions" and "retrogressions" within restoration communities at achieving revegetation goals, and iv) it is possible that seeding (or subsequent reproduction of seeded individuals) can promote seed bank replenishment and thus have beneficial effects even during periods when seeded species are sparse aboveground. Additionally, Ott et al. (2011) highlighted that communities of seeded species on restoration sites may be subject to fluctuations in seedling and mature plant densities with variation in annual and multi-year precipitation periods, similar to mature desert communities.

Twelve studies, including two not in Table 8 that evaluated plant establishment for less than a year, assessed treatments associated with seeding. Results demonstrated mixed success within and among treatments (Table 9). Pelletizing seed, by enclosing seeds in a protective coating, negatively affected seedling emergence for blackbrush (*Coleogyne ramosissima*; Jones et al. 2014). In another study, pelletizing seed of three perennial species did not improve emergence (compared to bare seed) in the first year and failed to result in any live plants by the second year (Abella et al. 2015c). **In contrast, pelletizing seed of desert plantain (*Plantago ovata*), which is favored tortoise forage, tripled the cover of the annual forb through at least two growing seasons after seeding (Abella et al. 2015c).** Protecting seeds from mammalian granivory or herbivory using wire exclusion cages or fences has most consistently enhanced seedling emergence and establishment to date. Four of five studies reported that protection enhanced plant establishment (for at least some species). Only two of six studies found that irrigation improved seedling establishment. In Brum et al. (1983), at least 46 of 47 surviving seedlings across two years were in irrigated plots, but seedling survival was low overall with only 47 of 13,818 seeds (0.3%) producing a seedling after two years. In Hall and Anderson (1999), only a spring irrigation, when combined with seeding on replaced topsoil, improved seedling establishment. Irrigating in both spring and fall or without topsoil did not improve establishment. This was possibly because benefits of irrigation were highly contingent upon conditions at the particular time the irrigation treatment was implemented and that other ecological conditions were not amenable to germination during fall irrigation.

Table 9. *Summary of whether treatments aided establishment of seeded species in 11 studies in the Mojave Desert. Symbols illustrate whether treatments benefited (+), did not affect (0), or negatively affected (--) seedling emergence and establishment. For studies with a treatment with both +,0, outcomes of treatments varied among groups of species or with variations of the treatment.*

Study	Duration (yrs)	Precip. (%)	Pelletize	Protection	Irrigation	Surface	Catchment	Mulch	Tackifier
1	3	103		0	0				
2	2	103	+, 0	+, 0	0				
3	2	146		+	+				
4	0.3	273				+			0
5	3-5	33-76				--			
6	2	76			0				
7	2	167			+, 0				
8	2	85	--	+					
9	1	82						0	
10	2	81		+					

11	0.4	150		0	0	+	0

Notes:
-Studies are numbered as follows: (1) Abella et al. 2012a, (2) Abella et al. 2015c, (3) Brum et al. 1983, (4) DeFalco et al. 2012, (5) Grantz et al. 1998a, (6) Graves et al. 1978, (7) Hall and Anderson 1999, (8) Jones et al. 2014, (9) Ostler et al. 2003, Caldwell et al. 2009, (10) Suazo et al. 2013, and (11) Winkel et al. 1995.
-Duration is how long a study monitored seedling establishment after seeding.
-Surface treatments are treatments such as soil roughening.

Ground surface manipulations and soil amendments implemented with seeding have also displayed mixed success for aiding seedling establishment (Table 9). DeFalco et al. (2012) found that harrowing (implemented before seeding by dragging a metal tine behind a tractor to produce 3-cm wide, 5-cm deep furrows, which were then seeded) improved seedling emergence four months after seeding. Harrowing also increased seed retention on site, enabling potential formation of soil seed banks from seed that did not initially germinate. The only other study finding that a surface or amendment treatment produced a benefit was Winkel et al. (1995). In that study, which examined short-term seedling emergence for five months after seeding, water catchments consisting of sloping areas to collect water enhanced emergence of seeded shrubs. In a study where surface manipulations negatively affected seedling establishment, Grantz et al. (1998a) found that broadcast seeding without soil disturbance was the most effective seeding treatment. This was possibly because this minimal disturbance treatment contained the least cover of competitive non-native annual plants, compared with seeding with ripping and furrowing. Furthermore, drill seeding was generally less effective than broadcast seeding. Mulches (e.g., straw, gravel, or wood bark material) and tackifier (designed to stabilize soil) did not improve seedling establishment in the three studies in which they were tested. While it is possible that ground surface and amendment treatments, such as mulches, could have other benefits beyond aiding seedling establishment, they also increase the cost and complexity of restoration and thus far would likely fail a cost/benefit analysis with respect to improving seeding effectiveness (Table 9).

Seeding rates varied among studies and it seems uncertain whether varying seeding rates could have changed seeding outcomes. For example, seeding local areas at high rates could attract unusually high numbers of granivorous ants, mammals, or birds, but protection treatments could limit seed removal and damage to seedlings. Seeding at high rates did not assure seedling establishment, as instead high seeding rates could simply result in more seeds failing to produce persistent seedlings. For example, Abella et al. (2015c) seeded at a high density of 5000 (cheesebush), 1700 (winterfat), and 13,000 seeds/m^2 (globemallow). However, no seedlings of these three perennials persisted after two years. In contrast, in a study where seedlings did become established, Grantz et al. (1998a) found that doubling the seeding rate approximately doubled the number of seedlings produced.

While complicating identifying general conclusions from the literature to date, the diversity of seeding rates, seeded species, treatments, timeframes of monitoring, and contexts (e.g., precipitation, variability in source genetics and viability of seed) helps illustrate numerous considerations associated with seeding and highlights opportunities for future research. For example, the different timeframes of studies ranging from monitoring seedling establishment for four months to 14 years post-seeding illustrate the significance of differentiating emergence versus persistent seedling establishment. The short-term studies are valuable for ascertaining species and treatments that result in emergence as an initial restoration step, while illustrating that seeding protocols that result in emergence but not seedling establishment can also detrimentally forestall opportunity for soil seed bank formation. If short-term emergence does not occur and viable seeds persist on site, then projects seemingly initially unsuccessful could at least potentially maintain propagule sources if future conditions are more favorable. **It may thus be appropriate to evaluate seeding project effectiveness as three stages consisting of ability to produce emergence, seedling establishment, and either persistent plants or replenished seed banks.**

The existing research further illustrates that project and treatment success is likely contingent on species selection. For example, seeding failed to augment perennial cover plants for tortoises in Abella et al. (2015c) but it did enhance availability of an annual forb food plant. Annual species were rarely included in seed mixtures among studies. Evaluating more annual species is warranted especially given the importance of annual forbs in tortoise diets (Jennings and Berry 2015).

Illustrating how treatments need to be tailored to species-specific needs, pelletizing reduced emergence of blackbrush but enhanced emergence in desert plantain (Jones et al. 2014, Abella et al. 2015c). Various permutations to treatments like irrigation could also affect outcomes, such as Hall and Anderson's (1999) finding that irrigating only in spring provided benefits. Varying the amount and timing of irrigation could affect seeded species differently and in different years varying in precipitation, along with potentially interacting with soil surface conditions.

Continuing to screen a diversity of species for their amenability to seeding, evaluating needs for different treatments (with cost-benefit analyses), and developing tools to match seeding to conditions in which it is most likely to succeed are likely to be productive for generating useful restoration findings. It would also be useful to test seeding using the same sets of species and seed sources but across multiple years to work toward pinpointing the types of years in which different species can be successfully seeded. While it may be assumed that moist years would be most favorable, these years can also have the most competition from non-native plants, and other factors beyond precipitation, such as temperature, also affect seedling emergence (Beatley 1974).

From a practical management perspective, existing research can help identify species amenable to either or both seeding and outplanting, highlights potential in using "bet-hedging" approaches to operational projects, and indicates the utility of protection treatments. *Atriplex* exemplify species that perform well in both seeding and outplanting. White bursage performed at least moderately well in both seeding and outplanting. In contrast, creosote bush and cheesebush performed well in outplanting but poorly in seeding to date. **These observations further suggest that perhaps employing both seeding and outplanting as a bet-hedging approach may be prudent to increase the chance that at least some plants will become established.** Interestingly, protection treatments (e.g., cages or shelters to deter damage to plants) have thus far most consistently aided plant establishment for both outplanting and seeding among all the treatments tested. While cages or fencing may be infeasible, particularly for broad-scale seedings, exploring other procedures for protecting seeds, such as using "decoy seeds" to attract the focus of granivores (Longland and Bateman 1998), may have potential for aiding seeding.

Owing to the usual limitation of availability of native plant seed and to the potential influence of seed source on project outcomes, the question of whether to use locally collected seed (and if so, how local) is commonly raised for restoration projects. This issue is unresolved and the subject of ongoing research. Combined genetics and plant performance analyses are required to determine how successful particular seed sources are in different present and anticipated future environments.

Given frequent local adaptation of plants, the current consensus is that seeds for restoration projects should be collected as locally as possible, unless there are specific reasons to expect that genotypes from elsewhere will perform better (Johnson et al. 2010). In an example of local adaptation in the Mojave Desert, Shryock et al. (2015) identified genetic differentiation in desert globemallow populations along environmental gradients of water stress and temperature seasonality.

ASSISTED NATURAL REGENERATION

Assisted natural regeneration (ANR) is a restoration and management technique for enhancing the natural recruitment of desired species. Unlike outplanting, transplanting, and seeding which assume that humans must reintroduce propagules for successful restoration, **ANR focuses on enhancing recruitment from existing on-site propagules or aiding natural processes to increase propagule availability on site.** This approach has the potential advantages of favoring local genetics, avoiding resource-intensive preparation and transport of plant material, and lowering costs. However, uncertainties in applying ANR include whether restoration can utilize natural regeneration effectively, which methods produce successful ANR, and how ANR compares with active revegetation techniques such as outplanting.

Much of the existing ANR research and application has occurred in forests with tree seedlings, with less focus in drylands. It would seem that ANR may have both challenges and opportunities as a restoration tool in deserts. For example, successful recruitment of desert perennials in natural conditions is generally highly episodic, and while it may not be uncommon for thousands of seedlings to appear at a site some years, few to none of the seedlings survive across multiple years (e.g., Sheps 1973). Thus, while ANR may only be feasible in years with seedlings, techniques that increase survival of seedlings by even small percentages could substantially increase plant recruitment in years with mass germination.

Fig. 7. *Sheltered creosote bush seedling (shown in the inset with the shelter removed) also receiving slow-release irrigation gel in the brown tube in an assisted natural regeneration study in the Dead Mountains Wilderness, California, eastern Mojave Desert. Irrigation gel did not increase survival or growth. Shelters reduced survival but tripled height growth of surviving seedlings.*

To test ANR methods, an initial study in the eastern Mojave Desert located 72 creosote bush (*Larrea tridentata*) seedlings (1-2 years old) in 2017 on a decommissioned road where restoration was desired (Abella et al. 2020). Treatments sought to assist seedlings in overcoming the limitations of herbivory and lack of moisture by enclosing seedlings in plastic tree shelters and providing slow-release irrigation gel (Fig. 7). After two years, and in contrast to expectations, only half as many sheltered as unsheltered seedlings remained alive. However, surviving sheltered seedlings grew 3× faster and taller than surviving unsheltered seedlings. Irrigation gel did not significantly affect survival or growth. Over the longer term, the benefit of the shelter treatment would hinge on whether the taller plants have advantages (e.g., out of reach of some herbivores, more rapid flowering) and whether the treatment was worth the cost. The shelters cost $3 each. Labor equated to 15 minutes/plant and included transporting shelters on foot 1.5 km to the project site in a wilderness setting, installing and checking shelters, and removing them at the end of the experiment. As the lower foliage on seedlings within shelters died, problems with shelters could have been excessive heat buildup, too little sunlight, or inadequate gas exchange (Oliet et al. 2019). Further research would be needed to test different colors or types of shelters which can function differently, making ventilation holes in shelters, or other materials and designs.

While results were mixed for this initial ANR Mojave Desert study, they highlighted that further research exploring other species and other techniques may be warranted to determine whether potential benefits of ANR could be realized for ANR to become another potential habitat restoration tool. The study also highlighted a possible contrast, where the treatments of irrigation gel and shelters did not improve survival in ANR but have substantially increased survival of greenhouse-grown creosote bush seedlings in outplanting. It is possible that treatments aiding outplants are not the same as those that could aid natural seedlings in ANR.

ENVIRONMENTAL SITE RESTORATION

ABIOTIC STRUCTURAL RESTORATION: VERTICAL AND HORIZONTAL MULCH

There is considerable interest in ascertaining to what extent abiotic structures can provide ecological functions similar to live perennial plants because abiotic structural restoration could be cheaper and logistically easier than active revegetation (Li et al. 2017, Chiquoine et al. 2022). Moreover, restoration of abiotic structures would be less time sensitive and less contingent upon variable precipitation compared with timing of seeding and outplanting. The abiotic structures, once restored, would be present and available to assist with recovery across years varying in precipitation (Grantz et al. 1998b). While abiotic structures would not be expected to produce litterfall (contributing to fertile island formation) and all the functions of live plants, abiotic structures could partly or fully provide some of the functions such as shading, slowing wind speeds and trapping soil and seed particles, accumulating soil nutrients, facilitating recruitment of plants, and potentially even serving as resting or burrow-construction locations for desert tortoises.

Fig. 8. *Vertical mulch structures, shown in the bottom right of the photo and in the center-right (to the left of the top of the wilderness sign), as part of restoration on a decommissioned road in the Dead Mountains Wilderness Area, southeastern California, eastern Mojave Desert. The vertical mulch was constructed from collecting dead branches of creosote bush and arranging them vertically in the soil to mimic structure of a creosote bush shrub (albeit without live foliage).*

A main abiotic structure for restoration is vertical mulch, consisting of dead plant material (e.g., branches) placed upright in the ground (Fig. 8; Bainbridge 1996). To evaluate whether vertical mulch could serve as "nurse objects" that facilitate recruitment of plants for restoration in Joshua Tree National Park, a recent study compared plant communities over nine years among outplants, vertical mulch, and interspaces (Abella and Chiquoine 2019). In general, across years, plant cover around and below vertical mulch structures was intermediate between that below outplants and in interspaces. **This suggested that vertical mulch could benefit native plant communities, including annual forbs that are important forage species for tortoises.** However, non-native annual grasses also benefited from vertical mulch. The study suggested that treatments targeting non-native plants may need to be paired with vertical mulching (as well as outplanting) to enable native plants to receive more of the benefits of vertical mulching. Additionally, the study indicated that while some vertical mulch structures could degrade or be knocked over (such as by humans potentially), most structures persisted through the nine-year study. Wood decomposition studies suggest that, owing to aridity, wood decomposition is slow in southwestern deserts and vertical mulch is likely capable of persisting for decades (Ebert and Ebert 2006).

Another recent study, in the Sonoran Desert along the ecotone to the Mojave Desert and near the Chuckwalla Critical Habitat Unit for desert tortoises, **illustrated how abiotic structural**

restoration could succeed and serve as a bet-hedging restoration approach during severe drought when active revegetation failed (Rader et al. 2022). Along a disturbed energy transmission line corridor, the initial growing season (2018) after outplanting was implemented was the driest of the last 47 years and 100% of outplants died despite some irrigation and plant care. As outplanting failed, vertical mulch increased native shrub seedling cover at the driest restoration site and reversed soil erosion across sites by increasing the soil accumulation rate by 6× to 2 cm/year. These restoration benefits of the abiotic treatments occurred across two years despite the record drought conditions. The study illustrated a key point in that while it may be possible to conduct phased outplantings (or seedings) across years to bet hedge that at least one year will have favorable precipitation, it can be logistically difficult to propagate or store plant materials across multiple years and to mobilize resources to implement active revegetation annually. However, the one-time treatment of establishing the abiotic structures enabled them to be present for stimulating restoration benefits. Including some abiotic structural treatments along with active revegetation may be a prudent bet-hedging strategy in case active revegetation fails.

Mulch, such as straw, wood materials, or gravel, placed horizontally and often covering more of sites than vertical mulch, has had inconsistent and generally limited restoration effects to date in the Mojave Desert. As detailed in the outplanting and seeding sections of this report, mulch applied in combination with active revegetation has had inconsistent and minimal benefit. Ostler et al. (2003) found that three mulches (gravel, cellulose fiber, or wood bark material), but not straw mulch, enhanced early emergence of seeded species, but no mulch type resulted in seedlings persisting the second year (Caldwell et al. 2009). In that study, the bark and cellulose fiber mulches reduced soil moisture, possibly because the materials absorbed water, making it unavailable to seeds and plants (Caldwell et al. 2009). Winkel et al. (1995) concluded that wheat straw mulch crimped into soil did not benefit early seedling emergence. When applied around outplants, Grantz et al. (1998b) reported that straw and bark mulch did not improve plant vigor. In other studies, Walker and Powell (2001), in examining mining disturbances, found that when applied to mining waste heaps, rock mulch improved soil water retention but not when applied to an abandoned road. For restoration of former road locations, Chiquoine et al. (2016) reported that wood shavings incorporated into soil did not improve lichen and moss recovery as components of biocrust but did increase cyanobacteria density and soil fertility.

More broadly, results from other deserts have similarly reported inconsistent benefits of mulching, such as results from the Sonoran Desert. For example, bark mulch did not improve survival or growth of outplanted honey mesquite (*Prosopis glandulosa*; Bainbridge et al. 2001). Similarly, wheat straw mulch did not enhance establishment of seeded plant species (Banerjee et al. 2006). In contrast, Beggy and Fehmi (2016) did find that wheat straw increased seeded species establishment and tempered soil erosion. Using rock mulch, Fehmi (2018) found that plant cover was 12× lower in mulched plots, indicating highly detrimental effects of mulch. Also indicative of potential negative effects, grass mulch did not increase seeded species establishment and instead appeared to increase non-native grass cover (Woods et al. 2012).

An overall appraisal of the science to date suggests that vertical mulch has benefited native plant recruitment (though potential benefits to non-natives as well is a concern), while horizontal mulch has rarely benefited native plants and in some cases has had negative effects. There are indications that the type (e.g., various organic sources, rock) and perhaps thickness (Fehmi 2018) of the mulch material can influence effects of horizontal mulch (Kay 1978). Further exploring these types of variables, as well as further examining whether horizontal mulch could produce benefits (e.g., slowing soil erosion, replenishing soil organic matter over time, possibly trapping naturally dispersing seeds) beyond those associated with active revegetation (Bainbridge 2007), is likely warranted to further understand whether horizontal mulch has restoration benefits relative to costs.

TOPSOIL SALVAGE AND REPLACEMENT

While information is limited for the Mojave Desert, re-applying topsoil is likely to be among the most ecologically effective strategies for restoration where salvaging topsoil is feasible and appropriate (Allen 1995, Abella et al. 2015b; Fig. 9). This conclusion is based on three lines of evidence: ecological studies of soil properties and biota, limited but highly successful examples of restoring topsoil in the Mojave Desert, and more extensive research with topsoil salvage in other deserts. While soil nutrient pools and root matter can be held in deep (e.g., > 50 cm) soil layers in some desert soils, generally organic matter and nutrients are most concentrated in upper soil layers (e.g., upper 5-30 cm; Koyama et al. 2019). Most seeds, often at least ~90% of the total, occur in the upper 5 cm of desert soil (Guo et al. 1998). Soil biota, including constituents of biocrust, are also often concentrated in surface soil (Williams et al. 2012). These observations suggest that salvaging the upper 5 cm of soil has potential to encompass much of an ecosystem's stored plant propagules and soil resources. In one of the few studies of influences of salvaging topsoil for Mojave Desert restoration, planting salvaged native perennials on salvaged topsoil doubled survival compared with planting on non-topsoil surfaces (Abella et al. 2015b). The benefit of topsoil (without irrigation) to plants was nearly equivalent to irrigating them. More extensive research in other drylands, such as in Australia, has highlighted that re-applying topsoil can speed ecological recovery while retaining local genetics and species composition if donor and recipient sites are matched well (Waryszak et al. 2021).

Fig. 9. *Plant recovery on an area receiving salvaged topsoil (right side of gray line) after disturbance from re-alignment of Northshore Road, Lake Mead National Recreation Area, eastern Mojave Desert. The photo was taken four years after disturbance.*

To maximize benefits of topsoil for restoration, careful planning can aid salvage operations (e.g., Ghose 2001, Scoles-Sciulla and DeFalco 2009, Abella et al. 2015b). Present knowledge suggests that ideal salvage procedures for Mojave Desert soils include: 1) avoiding areas infested by non-native plants or soil contaminants; 2) consistently salvaging the upper 5-10 cm when a goal is to maximize soil seed bank density; and 3) timing salvage to occur in summer from May through September (and later into fall if it is a dry year) to capture winter annual seeds dispersed the previous spring, but before seedlings emerge in fall/winter. Illustrating how mixing subsoil with topsoil can dilute seed bank resources, Scoles-Sciulla and DeFalco (2009) found that germinable seed density was reduced by 86% for the upper 4 cm of soil (the most important for seedling emergence) when salvaging the upper 30 cm of soil (Fig. 10). Further research could examine benefits of strategically salvaging "fertile island" soil below the canopy driplines of shrubs to increase efficiency of nutrient and seed capture, thereby reducing space required to store soil (Abella et al. 2015b). Salvaging some interspace soil could also be wise to ensure capture of seeds of annual plants primarily growing in the open (Guo et al. 1998).

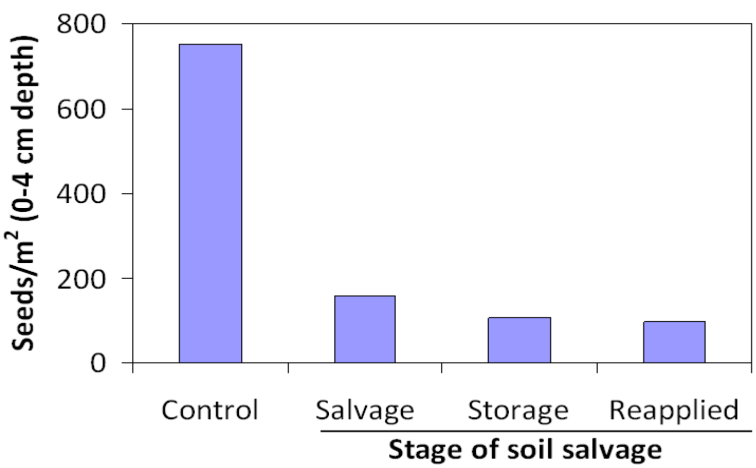

Fig. 10. *Loss of germinable seed during three stages of topsoil salvage, relative to the 0-4 cm soil layer of undisturbed desert, in the eastern Mojave Desert. Most (79%) of the seed loss occurred during the salvage operation itself, likely because subsoil (to a depth of 30 cm) was mixed with topsoil. The topsoil was stored for 4 months. Data from Scoles-Sciulla and Defalco (2009).*

If topsoil cannot be transferred directly from donor to recipient sites, topsoil needs to be stored carefully to maximize biotic and nutrient retention. **Topsoil should be stored as briefly as possible before reapplication.** Practical constraints typically result in some storage being required, and this unavoidably creates some loss of biotic components (Fig. 11). If soils must be stored, storage time ideally would not exceed 6-12 months (Ghose 2001, Scoles-Sciulla and DeFalco 2009). For long storage durations, treatments could potentially extend longevity of biotic components. Some possible treatments may include transplanting vegetation (such as native cactus pads) on top of the piles to potentially enhance longevity of soil microorganisms. These types of treatments have not been tested extensively and should be considered experimental. Also, the height of stockpiles should be as short as possible, preferably no more than 45-60 cm tall, because the deeper the pile, the more likely biotic components will be lost. If storage space limitations require deeper piles, consider periodically turning the soil. Stored soil should be protected, such as via tackifier, from wind erosion or other damage.

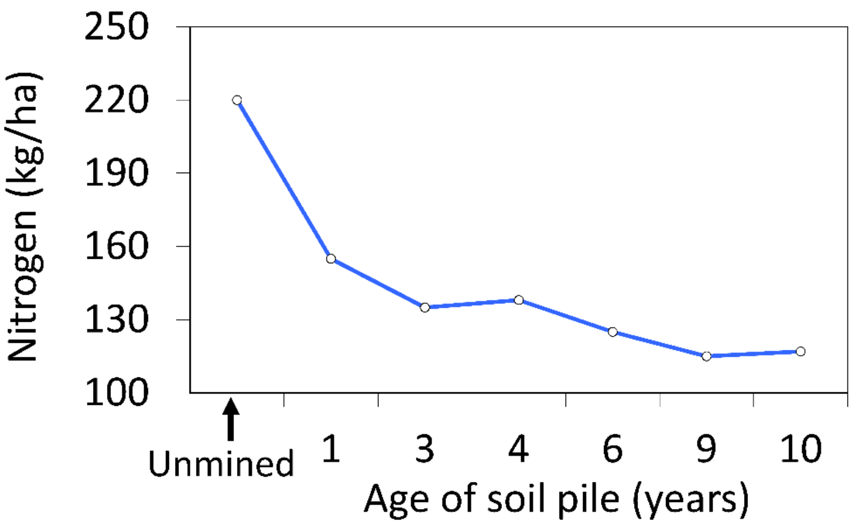

Fig. 11. *Loss of nitrogen in stockpiled topsoil stored for 1 to 10 years, relative to undisturbed soil. Data from Ghose (2001) in coal mining areas of arid land in India. Performing further research on procedures for storing salvaged biotic and abiotic components in the Mojave Desert could aid restoration efforts.*

GEOMORPHIC AND MICROTOPOGRAPHY TREATMENTS

On disturbed sites targeted for restoration, land surface shaping and soil roughening treatments have potential to deter soil erosion from water and wind, retain seeds and biotic material, and to improve favorability of soil conditions for plant colonization by concentrating soil resources and offering regeneration niches (Weigand and Rodgers 2009, Fick et al. 2016). Bainbridge (2007) discussed numerous possible surface treatments, such as roughening (e.g., pitting, imprinting, ripping; Fig. 12), water catchments, constructing check dams and fences, fabrics or organic mats, and horizontal and vertical mulches presented in previous sections of this report. Not all of these treatments and their variations (e.g., different materials of organic mats or spatial configurations) have yet been extensively tested for their effectiveness at improving site conditions or for cost-benefit assessments.

Some of the treatments were evaluated in a limited number of studies in the Mojave Desert and ecotone with the Sonoran Desert or are currently being tested. On eroding, abandoned agricultural land in the western Mojave Desert, constructing a network of parallel wind fences (10 m between fences) perpendicular to prevailing winds reduced fugitive dust emissions by 64% from a height of 0.2-2 m above ground (Grantz et al. 1998c). Plastic cones (61 cm tall) and wire cages (91 cm tall) distributed at a density of 460 structures/ha across the site reduced dust emissions by 6-fold at a height of 0.2 m above the ground and by 25% at a height of 1 m (Grantz et al. 1998c). Revegetation generally reduced dust emissions more (91-99% at a height of 1 m) than fences or distributed smaller structures, but revegetation was not successful every year (Grantz et al. 1998a). With additional examples discussed in the outplanting and seeding sections for how surface treatments can benefit or not affect revegetation, DeFalco et al. (2012) illustrated how harrowing (3-cm wide, 5-cm deep furrows created by dragging a device behind a tractor) increased soil seed bank formation by 55% after seeding in the central Mojave Desert. Soil pitting, producing a rough soil surface with many depressions, has retained moisture, trapped seeds, and increased survival of outplants (Bainbridge 2000). While ripping can de-compact soils, Caldwell et al. (2006) cautioned that additional research be directed toward developing ripping techniques for reducing soil compaction, to avoid undesirable effects like raising salts from subsoils into the rooting zone.

Fig. 12. *Left: Imprinting intended to roughen the surface of compacted soil to deter erosion, retain nutrients and biotic resources, and create favorable conditions for native plant establishment (photo courtesy of D.A. Bainbridge). Right: Ripped road designed to de-compact soil and promote plant establishment.*

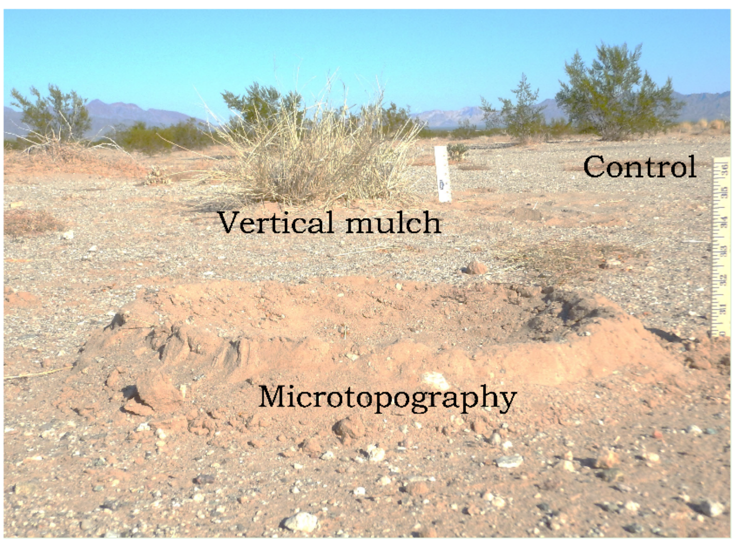

Fig. 13. *An experiment near the Chuckwalla Critical Habitat Unit for the desert tortoise examined how constructing microtopography structures (50-cm outer diameter, 10 cm tall) with vertical mulch and control (no treatment) influenced plant recruitment and soil properties on a disturbed site along an energy transmission corridor (Rader et al. 2022). The photo was taken just after treatments were implemented.*

Current studies are evaluating minimal-input techniques for constructing pits/catchments and distributed roughening treatments in desert tortoise habitat, with mixed success. Rader et al. (2022) found that constructing depressions using hand tools undesirably increased cover of non-native grasses (while not benefiting natives; Fig. 13). However, the depressions did result in some soil accumulation (0.1 cm/year) compared to a loss of 0.4 cm/year of soil without treatment. Creating distributed patches of roughened soil enhanced native annual plant cover and species richness in the patches (Chiquoine et al. 2022; Fig. 14). **In addition to significantly reducing soil compaction, the roughening treatments nearly doubled soil moisture content from 2% to 3.5%, likely partly via increasing water infiltration.**

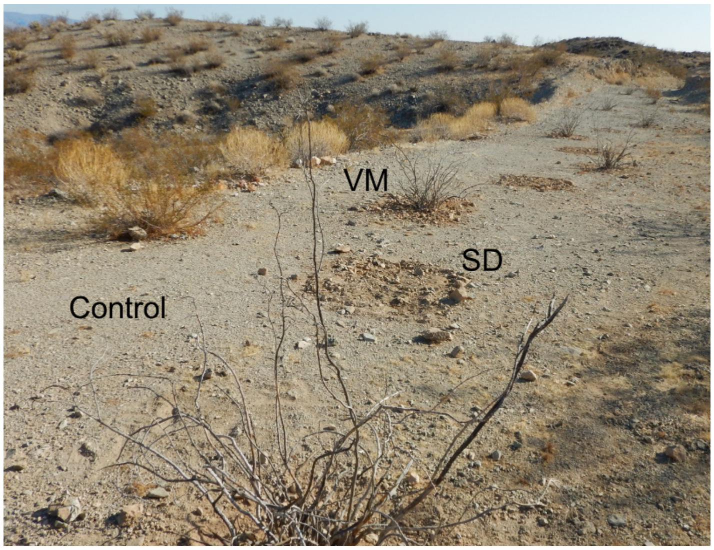

Fig. 14. *An experiment examined influences of distributed surface de-compaction (SD) compared with vertical mulch (VM) and control (no manipulation) treatments on an abandoned road in a wilderness setting in the eastern Mojave Desert (Chiquoine et al. 2022). The SD treatment entailed de-compacting the upper 5-10 cm of soil using rock hammers and hand rakes in 1 m × 1 m patches. The photo was taken in December 2017 when treatments were implemented.*

Restoring Soil Features: Biocrust, Desert Pavement, and Desert Varnish

Biocrusts, defined as soil surface layers including bacteria, cyanobacteria, algae, mosses, liverworts, fungi, or lichens, can be major components of undisturbed desert ecosystems on sites suitable for biocrust establishment (Belnap et al. 2001). In addition to adding diversity via their own species constituents, functions that biocrusts provide include limiting soil erosion, increasing accumulation of soil organic matter and nutrients, and interacting (positively or negatively) with vascular plants (Bowker 2007). Biocrust functions can vary with the constituent of biocrust (e.g., lichen- compared with cyanobacteria-dominated crust), amount of coverage or abundance of biocrust, structure and thickness of biocrust layers, variation in precipitation, and other components of habits such as vascular plant composition (Pietrasiak et al. 2013). Well-developed biocrust layers can require decades to recover after severe disturbance (Kidron et al. 2020).

Research on biocrust restoration techniques has been expanding across drylands globally particularly in the last 10-15 years, including in the Mojave Desert, but is still considered in the early stages (e.g., Antoninka et al. 2020). Bowker (2007) outlined three main stages for restoring biocrusts: i) stabilizing soil to enable favorable surfaces for biocrust colonization and growth; ii) resource manipulations such as changing water or nutrient availability to favor biocrust growth; and iii) inoculation-based techniques, such as salvaging or propagating biocrust organisms and re-applying them as dry powders, slurries, or outplants similar to outplanting vascular plants.

Most of these treatment variations have not been tested extensively in the Mojave Desert, but **two studies evaluated potential for salvaging and transplanting biocrust material.** Cole et al. (2010) evaluated transplanting of the dominant biocrust moss *Syntrichia caninervis*. While moss cover declined 20-52% (relative to initial cover) and shoot density declined 26%, all transplanted sections of moss survived after 27 months. The authors suggested avoiding transplanting source material derived from shaded (below shrub) microsites to an open site, similar to recommendations to matching orientation toward the sun when transplanting cacti (Smith et al. 2012).

To restore severely disturbed decommissioned road sites in the eastern Mojave Desert, Chiquoine et al. (2016) tested effects of applying biocrust inoculation (salvaged and stored dry for two years), salvaged topsoil, an abiotic soil amendment (wood shavings), and outplanting white bursage (*Ambrosia dumosa*). **Eighteen months after treatment, only plots receiving biocrust inoculation contained lichen and moss cover.** Plots receiving inoculation further recovered 43% of the cyanobacteria density found on undisturbed controls. In addition to inoculation, applying salvaged topsoil also increased cyanobacteria density. Wood shavings and white bursage plants had no influence on lichen and moss recovery but did influence cyanobacteria composition and soil fertility. Plots receiving biocrust inoculation also had enhanced soil stability, likely important to retain biotic material and reduce soil erosion. The study concluded that while it may not always be possible to salvage (or store) biocrust material, being able to do so can accelerate recovery of biocrust. Moreover, the study suggested that if even small amounts of donor biocrust material is available, it can serve as inoculation sources to enhance biocrust recovery over time.

Ongoing research generally with biocrust and in other deserts has further illustrated potential for biocrust restoration, such as by establishing greenhouse production facilities to grow biocrust material (e.g., Antoninka et al. 2016). It is possible that lichens and mosses can be propagated in greenhouses, then outplanted to restoration sites not unlike the process for vascular plants (Ballesteros et al. 2017). Cyanobacteria inoculation could similarly be prepared and re-introduced to restoration sites accompanied by treatments to potentially enhance growth.

Desert pavement is a stone-covered geomorphic surface, consisting of angular or rounded, densely packed stones, usually one or two layers thick and set in or overlaying a matrix of fine-grained soil material, on generally flat terrain in arid regions (Haff and Werner 1996). Desert pavements are typically ancient surfaces, commonly exceeding 10,000-100,000 years old (Seong et al. 2016). Desert pavements cover appreciable area within the range of desert tortoises, including the generally flat valleys representing extensive tortoise habitat (Wood et al. 2005). While plant cover on desert pavement is sparse, a frequent dominant native annual (desert plantain, *Plantago ovata*) of pavement is a forb tortoises favor as forage (Musick 1975). Additionally, because water infiltration is minimal on pavements and thus runoff is high, desert washes and drainages in pavement landscapes can contain abundant vegetation, including forage plants along washes (Musick 1975).

Desert pavements take many millennia to form but can be readily disrupted or destroyed via disturbances such as off-road vehicles (Elvidge and Iverson 1983). An experiment in the western Mojave Desert found that small disturbances "healed" naturally through repositioning of displaced stones over time (Haff and Werner 1996). Small 10-cm^2 disturbed plots became "repaved" at a rate of 10% per year, resulting in recovery in a decade. Recovery of larger but still small plots declined sharply, with a "repaving" rate of 1% per year on 40-cm^2 plots. In retrospectively assessing 40-year-old displaced boulder locations, Haff and Werner (1996) found that the locations had filled with material but the infilled stones were half the diameter (1 cm compared with 2 cm) of stones found on nearby desert pavement. These observations suggest that natural processes can repair small disturbances in desert pavement, but that larger disturbances are likely to require decades to many centuries (or even millennia) for the pavement surfaces to heal (Haff and Werner 1996).

Restoration techniques are not well developed for desert pavements and are complicated by the fact that pavements represent an integrated geomorphic landform of both the surface stone layer and underlying vesicular soil horizon of fine-grained material which forms on millennia time scales. However, it is possible that treatments such as applying stones (or re-arranging stones such as through raking), salvaged or synthesized fine soil material, or applying adhesives (e.g., to conglomerate rocks or bind them to soil) could begin to at least **provide some of the functions of pavement surfaces** or to conceal the disturbance (Abella et al. 2007; Fig. 15).

Fig. 15. *Disturbed area without (left) and with restoration (right) in Lake Mead National Recreation Area, eastern Mojave Desert. Restoration involved outplanting creosote bush and raking and applying coloring treatments to simulate desert pavement and desert varnish. The disturbance occurred in 1998 and the photo was taken in 2006, nine years after restoration. Before disturbance, the site contained a mature creosote bush shrubland with extensive desert pavement.*

Desert varnish is often associated with desert pavement and can be disturbed with disruption of pavement surfaces or rocks in other topographic settings, such as hillslopes. Desert varnish is a thin brownish, orange to black coating on rock surfaces in arid regions and consists of manganese, iron, clay particles, and various trace elements such as magnesium (Dorn and Oberlander 1982). Varnishing processes require millennia to create well-developed desert varnish, which can be quickly disrupted when rocks are scraped, dislodged (exposing non-varnished surfaces), or removed (Haff and Werner 1996). Aesthetics is a main reason to mitigate damage to desert varnish for visual restoration, including to attempt to limit further disturbance. However, while poorly understood, it is possible that **mitigating damage to desert varnish could also have ecological influences** such as with light reflectance and soil temperatures, potentially affecting biota (Abella et al. 2007). Little formal testing to evaluate ecological effects has been performed with techniques for damage mitigation to desert varnish, but techniques such as raking to adjust rock configuration and applying artificial coloring amendments to simulate the chemical composition and appearance of varnish may have potential (Abella et al. 2007).

RESTORATIVE MANAGEMENT ACTIONS

FENCING AND PROTECTION TO LIMIT DISTURBANCE

Fencing and other practices to limit disturbance can benefit desert tortoises through improving required habitat features (e.g., forage quality and quantity) and potentially through reducing stressors such as subsidized predators and vandalism by humans (Berry et al. 2020c). Strategically deploying fenced exclosures to limit access by domestic or feral animals (or otherwise removing the animals) has improved forage conditions and plant cover for tortoises (Brooks 1995). There is considerable overlap in forage preferences among desert tortoises and domestic livestock (cattle and sheep) and feral burro, particularly in the forb component heavily utilized by all the animal groups (Nicholson and Humphreys 1981, Avery and Neibergs 1997, Jennings and Berry 2015). In seven studies across the Mojave Desert, for example, the native annual desert plantain (*Plantago ovata*) comprised the greatest percentage (11%) of feral burro diets (Abella 2008). Based on bite counts of juvenile desert tortoises, this forb also formed 23% of tortoise diets in the central Mojave Desert (Oftedal et al. 2002). Constructing exclosures and removing feral burros has led to (Abella 2008) or correlated with (Abella et al. 2019) increases in native plants.

Long-term research at the 8-km^2 Desert Tortoise Research Natural Area provides an example of the potential benefits of fencing or protection. During a 34-year study of habitat conditions and tortoise populations inside the fenced natural area (with tortoises able to pass beneath the fence) compared with conditions outside the fence, perennial cover plants and native food plants were more abundant inside the fence (Brooks 1995, Berry et al. 2020c; Figure 16). Common raven density was lower inside the fence several years (Berry et al. 2020c). By the end of the study in 2012 after 34 years of protection, **tortoise densities were 2.5× greater inside the fence** compared with outside (Berry et al. 2020c). Thus, protection appeared to enhance cover plants utilized by tortoises for protection and to increase forage quality and quantity. These and potentially other habitat improvements (e.g., limiting fragmentation) correlated with higher densities of tortoises. Limiting anthropogenic impacts, whether via fencing or other management strategies, appears to significantly alleviate some of the threats facing tortoises and may begin reversing habitat deterioration (Brooks 1995, Berry et al. 2014a, Berry et al. 2020c). It is possible that strategically deploying restoration or non-native plant treatments could accelerate or accentuate these benefits.

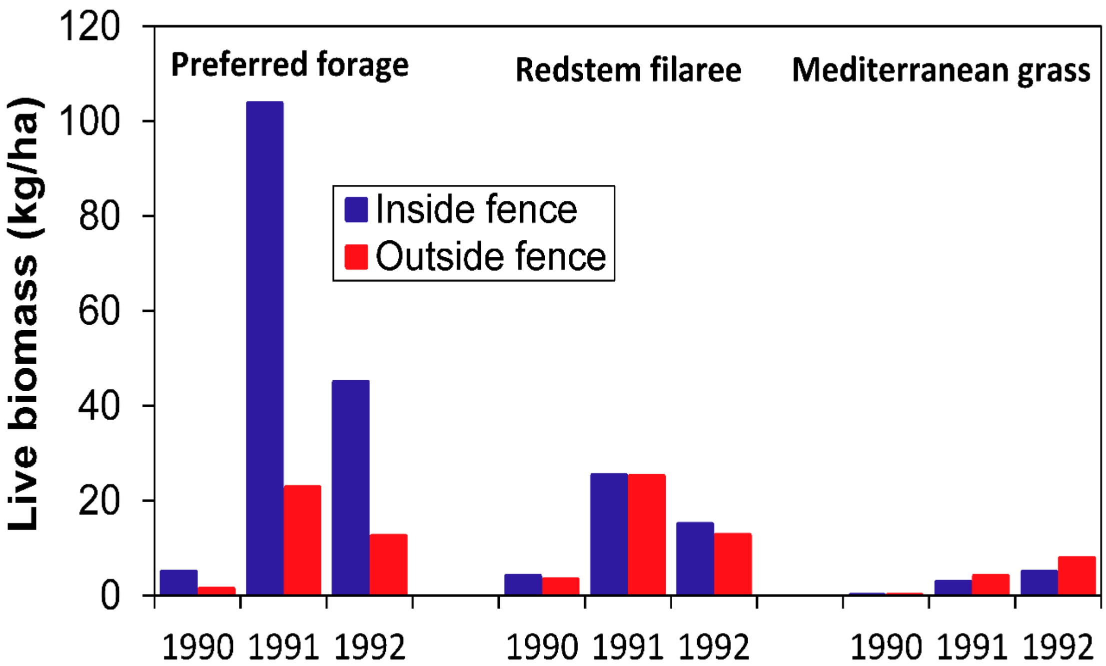

Fig. 16. *Biomass of preferred forage plants and non-native redstem filaree (generally better forage than non-native grasses but less preferred by tortoises than some native forbs) and non-preferred Mediterranean grass (a non-native annual) inside and outside fencing at the Desert Tortoise Natural Area. Data, from Brooks (1995), are shown for three years varying in rainfall.*

Reducing Non-Native Plants and Fire Risk

Non-native plants, particularly annual grasses, can degrade habitat for desert tortoises in two main ways: reducing quality of the annual plant community (lowering forage quality and quantity available to tortoises) and heightening risk of wildfire that can harm tortoises directly (Berry and Murphy 2019) and reduce large-statured native perennials for at least decades to centuries (Abella et al. 2021). Fire risk in invaded desert habitats is considered correlated with the amount and continuity of non-native annual grass biomass (Brooks 1999, Rao et al. 2010, Abella 2020). Non-native annual grasses, such as Mediterranean grass (*Schismus* spp.) and red brome (*Bromus rubens*), compete with native perennial species tortoises utilize for cover and with native annual forage plants (Holzapfel and Mahall 1999, Brooks 2000, Rodríguez-Buriticá and Miriti 2009). **When non-native annuals are reduced, native annuals, including high-quality tortoise food plants, have generally responded positively.** For example, Brooks (2000) found that thinning *Schismus* via cutting doubled density of native annuals in a wet year. Some of the increasing natives were bristly fiddleneck (*Amsinckia tessellata*) and other forb species that Jennings and Berry (2015) identified as forage favored by tortoises. Native annuals also remained green two weeks later in spring on *Schismus*-thinned plots, which could allow tortoises to forage longer (Brooks 2000).

Carefully timed herbicide applications have reduced non-native plants while increasing native annuals. On a burned site in the western Mojave Desert, Steers and Allen (2010) found that applying the post-emergent herbicide Fusilade early in the growing season reduced non-native grasses as well as the non-native forb redstem filaree (*Erodium cicutarium*). Species richness and cover of native annuals were up to 3× greater in treated compared to untreated areas. Glyphosate and some other herbicides were effective in reducing or eliminating germination of another non-native annual forb, Sahara mustard (*Brassica tournefortii*; Abella et al. 2013a). These studies further illustrate that many nuances related to treatment application, such as timing, weather any given year, treatment type, secondary invasion by non-target species, and differential responses among native plants can influence outcomes, necessitating further work to identify treatment strategies effective in a range of conditions.

Effects of herbicide on the desert tortoise are unclear, but early timed herbicide applications, exploiting the accelerated phenology of non-native compared to native plant species (Marushia et al. 2010), could generally occur when tortoises are inactive (Esque et al. 2014). For example, Steers and Allen (2010) applied herbicide in January. Adult tortoises remain in underground burrows until at least mid-February in some years (Burge 1977, Rautenstrauch et al. 1998), although juveniles may be active from November through February when local temperatures are warm (Wilson et al. 1999). The California Invasive Plant Council (2015) published best-management practices to reduce non-target effects of herbicides to fauna, while controlling non-native plants damaging to wildlife populations, that may be useful in desert tortoise habitats. Potential negatives of non-native plant treatments must be balanced against the positives of curtailing deterioration of tortoise habitats by non-native plants and the threat wildfires pose to tortoises.

In addition to established non-native plants such as red brome, new invasions of harmful plants are an omnipresent threat to tortoise habitat particularly given increasing disturbance and vectors for species introductions. A central tenet of invasive species science is that the early detection and removal of new invaders is cheaper and more effective than attempted eradication of established infestations (Davis 2009). Roads and trails can be main introduction locations for non-native plants to invade habitat interiors (Brooks 2009; Berry et al. 2014b). An example of surveying for and treating incipient populations of non-native plants in desert tortoise habitat was the "Weed Sentry" program collaboratively performed by the National Park Service and University of Nevada Las Vegas (Abella et al. 2009). **This early detection program surveyed 3,300 km of roads between 2009 and 2011 in the eastern Mojave Desert, including in desert tortoise habitat, and removed over 37,000 non-native plants in incipient populations, potentially forestalling invasions (Abella et al. 2009).** It should be noted that in addition to new invaders, surveying for expanding populations in habitat interiors of regionally established non-native species may also help conserve high-quality native species habitats (Abella et al. 2009). As a result, roads should be incorporated into broader landscape strategies for non-native plant management, because many firmly established non-native plants are not, or at least are no longer, distributed only along roadsides (Craig et al. 2010). For example, perhaps washes should also be part of landscape-scale detection programs, as washes in particular facilitate the spread of Sahara mustard, a species tortoises avoid eating (Berry et al. 2014b, Berry and Murphy 2019). Decommissioning un-needed backcountry roads would be expected to reduce vectors for non-native plant spread, in addition to reducing fragmentation of tortoise habitat (DeFalco and Scoles-Sciulla 2011).

Non-native plants pose a top threat to sustainability of desert tortoise habitat (Esque et al. 2002, Brooks and Matchett 2006). Further research exploring potential improvements in habitat quality from treating non-native plants, developing effective treatment strategies to optimize benefits while minimizing negative tradeoffs, and identifying techniques and monitoring effectiveness across scales (e.g., strategically treating fuel breaks in priority locations to landscape-scale treatments) is warranted and a likely top research priority for working toward tortoise recovery goals (Reed et al. 2009, Darst et al. 2013, Tuma et al. 2016).

Exemplifying the type of work needed to identify treatment strategies and tradeoffs, Chiquoine et al. (2020) recently found that carbon addition in the form of sucrose, designed as an alternative to herbicide, successfully reduced non-native plants but had the previously unreported negative tradeoff of severely damaging soil biocrust in tortoise habitat in the eastern Mojave Desert. Whether other forms of carbon can help ameliorate nitrogen enrichment from atmospheric pollution (Brooks 2003) to reduce non-native plants without undesirable tradeoffs or be able to be applied at meaningful spatial scales remains unclear (Steers et al. 2011). Controlled experiments and operational adaptive management projects with monitoring could help assess a range of treatment scenarios with goals of reducing fire risk, protecting and promoting growth of perennial cover plants for tortoises, and enhancing quality of native annual plant communities for meeting tortoise nutritional needs.

FINANCES AND LOGISTICS OF DESERT HABITAT RESTORATION

Estimated costs for restoring desert habitats vary primarily with the severity of the disturbance coupled with factors such as accessibility of sites (influencing transportation costs) and site factors including the diversity of vegetation that was lost. **Estimated costs for restoring damaged desert plant communities, including topographic and soil restoration where necessary as a first step to enable plant establishment, are summarized in Table 10.** Published cost estimates in Table 10 include those typical across North American deserts (Bainbridge 2007) and as project-specific estimates illustrating some of the variation in costs among site conditions and restoration goals. There is considerable overlap in restoration cost estimates among projects and regions. This is not surprising because the general restoration practices (e.g., outplanting) are similar and fixed-costs are generally similar among projects. For example, the cost of outplanting is generally similar across regions because outplanting in all regions similarly involves the costs of collecting seed, propagating seedlings in nurseries, transporting plants to field sites, and the activities of planting and maintaining plants. One of the standard pot sizes for propagating seedlings of desert perennials in nurseries is 1 gallon, which can be ordered for similar cost across the United States. In general, project-specific costs, such as disturbance severity or how far restoration sites are from main access roads and the resulting transportation costs, may be anticipated to produce as much or more variability in costs within regions as there is among regions.

Table 10. *Summary of published cost estimates for at least partially restoring damaged or destroyed desert habitats generally in the Southwest and specifically for the Mojave and Sonoran deserts.*

Region	Cost per hectare	Context	Reference
General	\$49,420-123,550	Intensive restoration	Bainbridge 2007
General	\$12,355-49,420	Moderate-intensity restoration	Bainbridge 2007
General	\$7,413-12,355	Low-intensity restoration	Bainbridge 2007
General	\$2,471	Minimal-input restoration	Bainbridge 2007
Mojave	\$9,225	Includes seeding, outplanting, and irrigation	Brum et al. 1983
Mojave	\$12,355-24,710	Includes site preparation, soil amendment, outplanting	McMahon et al. 2008
Mojave	\$1,651	Outplanting, protection, irrigation; \$34-55 per surviving plant	Devitt et al. 2020
Sonoran	\$26,834	Outplanting and plant care; \$64 per surviving plant	Abella et al. 2015a
Sonoran	\$4,430	Includes site preparation, outplanting, irrigation	Bean et al. 2004

Notes:

-The general costs for restoration of damaged desert habitats in Bainbridge (2007) span a gradient of restoration intensity from the highest and costliest including activities such as salvaging soil and

plants, amending soils, and performing both outplanting and seeding with species-rich mixtures, to low-intensity, cheaper restoration including limited site recontouring and low-diversity, minimal seeding and outplanting. Note that these are generalized activities and costs, and not all activities may be appropriate or necessary depending on site conditions, disturbance severity, and restoration resources available.
-Protection in Devitt et al. (2020) consisted of caging outplants to deter herbivory.

Bainbridge (2007) presented cost estimates for restoration of severe disturbance in hot deserts based on four tiers of restoration intensity. Intensive restoration cost an estimated $49,420 to $123,550/ha. Moderate-intensity restoration cost $12,355 to $49,420/ha. Low-intensity restoration cost $7,413 to $12,355/ha. The least intensive restoration, using minimal-input techniques, cost an estimated $2,471/ha. The most expensive, intensive restoration included salvaging soils and plants and re-applying them later to that or another restoration site, recontouring sites (e.g., ripping soils to ameliorate de-compaction), amending soils (e.g., applying mulch or inoculating them with biocrust organisms), seeding at least 10 species, intensive outplanting at a density of 25,000 plants/ha, caring for outplants such as through supplemental watering, and maintaining and monitoring sites such as treating non-native plants. Moderate-intensity restoration included site recontouring, seeding 3-10 species, outplanting at a lower density of 2500 plants/ha, caring for outplants, and limited maintenance and monitoring. Low-intensity restoration included limited site recontouring (e.g., erosion control structures), some seeding with a low-diversity mixture (e.g., ≤ 3 species), a limited outplanting at a low density of 500 plants/ha including some plant protection and irrigation, and some maintenance of the site (e.g., continuing to water surviving outplants). The least expensive tier, a minimal-input approach, included a simple site recontouring (e.g., ripping), applying an abiotic surface treatment such as vertical mulch in lieu of major active revegetation, and application of a minor revegetation technique such as a simple seed mixture.

Other restoration projects in the Mojave and Sonoran Desert that reported cost estimates are near or within the range of the Bainbridge (2007) generalized estimates. Using outplanting, seeding, and irrigation to revegetate disturbed powerline right-of-ways, Brum (1983) provided a cost of $9,225/ha. To restore native desert plants to Mojave Desert sites disturbed by construction activities (which altered surface soils and removed vegetation), McMahon et al. (2008) provided costs of $12,355 to $24,710/ha. Restoration activities in the McMahon et al. (2008) study included salvaging topsoil, recontouring, planting perennials, seeding, and managing sites to limit damage by unauthorized off-road vehicle use. To revegetate a burned site in the Mojave Desert through outplanting, Devitt et al. (2020) estimated a cost of $1,651/ha, or $34-55 per surviving plant. These costs included greenhouse plant propagation, the activity of outplanting, and providing herbivory protection (wire cages around each plant) and supplemental irrigation across two years. In the Sonoran Desert, Bean et al. (2004) estimated a cost of $4,430/ha to restore denuded sites using outplanting. Bean et al.'s (2004) detailed budget included activities such as installing temporary irrigation on site, treatments for non-native plants, and the cost of outplanting. Also in the Sonoran Desert, Abella et al. (2015a) provided an estimated cost of $26,834/ha to revegetate roadside sites disturbed by construction activities. This cost included outplanting and plant care activities and totaled $64 per surviving plant. Revegetation sites in the Abella et al. (2015a) study were small and widely dispersed, which may be more costly in aggregate to have to restore than a single larger site such as in Bean et al. (2004). Numerous small, dispersed sites could incur high travel costs and have limited "economy of scale" compared to fewer, larger sites.

Another approach to estimating restoration costs is using prices for native plants available from nurseries. In national park or other settings where using in-park genetic sources is usually important, the nurseries would need to propagate seeds made available from parks. An example cost estimate is available from the Nevada Division of Forestry state nursery (9600 Tule Springs Road, Las Vegas, NV 89131), which offers a variety of native shrub and perennial forb species growing in desert tortoise habitat. A typical cost of a 1-gallon plant is $7. Cost estimates of transporting the plants, planting them, applying any amendments, and plant care would then need to be calculated. Any additional soil or site restoration practices needed to prepare sites for restoration would also require computation, such as using the Bainbridge (2007) four-tiered estimates.

Treating non-native plants is often required as part of desert restoration activities to ensure native species are the beneficiaries or to ensure restoration efforts are not negated by wildfires facilitated by non-native plants. Moreover, treating non-native annuals is likely to generally improve forage conditions for desert tortoises if native forbs respond positively (Brooks 2000, Steers and Allen 2010). Two hot desert studies provided similar cost estimates for treating non-native plants. In the Mojave Desert, Brooks et al. (2006) reported that treating the non-native annual forb Sahara mustard (*Brassica tournefortii*) cost $811/ha/year using mechanical treatment (hand tools) and $384/ha/year using herbicide. Brooks et al. (2006) noted that treatments would need to continue for several years to deplete the soil seed bank and to remove any newly germinated seedlings. To encompass multiple wet years with appreciable germination, treatments may need to span a 5-10 year period. Outside of desert tortoise habitat but likely representing typical costs for treating upland perennial invaders, treating the perennial buffelgrass (*Pennisetum ciliare*) in the Sonoran Desert using mechanical and herbicide techniques typically costs $500/ha (Abella et al. 2013b). Treatments for buffelgrass often occur for at least five consecutive years to remove any new seedlings, with these types of follow-up treatments likely necessary to successfully reduce many invasive perennials within tortoise habitat (Abella et al. 2013b).

ANTICIPATED EFFECTS OF CHANGING LANDSCAPE CONDITIONS AND CLIMATES

Three of the several ongoing or anticipated habitat changes include continued disturbance and/or fragmentation, non-native plant invasions, and climatic changes. Wildfires and non-native plants were covered elsewhere in the report, and another ongoing disturbance anticipated to continue affecting tortoise habitat is renewable energy development (solar and wind). Reviewing effects of renewable energy developments on tortoise habitat is beyond the scope of this review and in summary, ongoing energy developments have been replacing and fragmenting tortoise habitat (Lovich and Ennen 2011, Hernandez et al 2015). Energy developments can also alter nearby habitat, such as by changing microclimates or correlating with invasive plant abundance (Moore-O'Leary et al. 2017). Although some energy developments have retained some vegetation and supported a tortoise population, the long-term viability of such populations is uncertain and the developments contribute to cumulative anthropogenic disturbance and fragmentation (Lovich et al. 2014, 2018).

The climate changes projected for desert tortoise habitat in upcoming decades include warmer temperatures and increased frequency, duration, or severity of droughts (Lovich et al. 2014, Guida and Abella 2020). The lower average precipitation could also be accompanied by shifts in the timing, frequency, or amount of rainfall per event (Knapp et al. 2008). While predicting the future is difficult and these climate projections (especially for precipitation variables) have uncertainty, one way to view current and potential future climate changes is through a precautionary principle assuming that future climates may be less favorable for tortoises than recent past climates (e.g., Wallis et al. 1999, Nagy et al. 2002, Medica et al. 2012, Lovich et al. 2015, Abella et al. 2019). **Furthermore, both the declining population of the tortoise and unfavorable habitat changes may make tortoises more vulnerable to climatic fluctuations than they normally would be.** For example, clearly tortoise populations persisted through past droughts in the last several thousand years but conditions did not include today's pervasive anthropogenic alterations to habitat such as fragmentation and conversion to non-native annual vegetation (Morafka and Berry 2002).

Changing climates could affect tortoises by interacting with tortoise physiology, habitat distribution, resource availability, and other species that affect tortoises. For example, the lower lethal deep body temperature of 39.5°C for tortoises is already reached on hot days if tortoises do not have shelter and are exposed to full sun (McGinnis and Voigt 1971). Continued climatic warming could induce changes in daily and seasonal activity of tortoises, such as reducing activity periods in hot months while increasing them in cooler months. This also underscores that having suitable perennial plants may become even more important in the future warmer climate for offering thermal protection to tortoises. It is possible that tortoise spatial distributions could shift as well, such as tracking cooler and moister climates and vegetation distribution (Barrows and Murphy 2011). To what extent this can or will actually occur is uncertain, however, due to fragmentation limiting tortoise movement and the fact that cooler, moister, upper elevations are generally not considered tortoise habitat (Averill-Murray et al. 2013, Barrows et al. 2016). Tortoise distribution could largely remain *in situ* but tortoises could focus even more of their activity in areas such as small washes receiving supplemental moisture and containing forage plants (Jennings and Fontenot 1993). The key habitat resource of free water for drinking could also be affected in several climate scenarios. Increased evaporation, changes in water retention if rainfall amount per event changes, or shifts in seasonality or frequency of water availability could all change (Knapp et al. 2008). One positive feature of tortoise life history for adapting to potential rainfall timing changes is that tortoises have been observed emerging from shelter at any time of year to drink free water, suggesting a possibility that tortoises could still flexibly utilize rainfall events (Medica et al. 1980, Peterson 1996). How climate will affect annual communities, which is virtually unknown, could have profound effects on tortoises by influencing food quality and quantity and fire activity. Drought years with little forage and drinking water have correlated with elevated mortality of tortoises and decreasing indicators of tortoise health (Henen 2002, Longshore et al. 2003, Medica et al. 2012). Presumably, more severe shortages of food plants would accentuate these deleterious trends. Reduced precipitation and warming temperatures could increase, decrease, or have minimal influence on fire activity. Drought could curtail fuel production and therefore fire activity. Conversely, fire activity could increase if periodic wet years with copious fuel production are followed by severe fire weather conditions.

From a vegetation habitat perspective, two of the main ways restoration has potential to assist tortoises in contending with potentially warmer and drier climates is conserving/enhancing perennial cover for thermal protection and restoring native annual and herbaceous perennial food plants while reducing non-native annual grasses. A major concern is that many non-native annuals may now disproportionately benefit from rain events by occupying the most favorable microsites (i.e. nutrient-enriched, shaded locations below shrubs; Abella and Smith 2013). This could become a positive feedback reinforcing the trend whereby non-natives preferentially reproduce and replenish seed banks while natives do not. Reducing non-native plants to enable natives to better utilize rainfall and to offer tortoises appreciable forage in more years (including some forage in climatically marginal years) is likely to be a priority.

RESEARCH AND ADAPTIVE MANAGEMENT NEEDS

While there are numerous research priorities in habitat restoration, this review suggests five strategic, programmatic areas to advance vegetation and soil aspects of tortoise habitat restoration.

1) To build on the few dozen existing Mojave Desert restoration studies, testing should continue on species performance and treatments for cost- and ecologically effective revegetation and soil restoration techniques and on how to integrate treatments to maximize bet-hedging in variable environments. As this review has shown, existing studies have begun identifying top-performing plant species and the types of treatments required to enable successful revegetation. However, only dozens of native perennials and fewer annuals have yet been examined in even one study for their revegetation potential, whereas tortoises may collectively utilize at least 250 plant species for cover and forage (Esque et al. 2021). Furthermore, several studies with priority plant species may be needed to develop reliable propagation and restoration procedures to make the species viable for restoration in tortoise habitats. There is a need to avoid a potential misconception that conducting multiple studies focused on similar goals represents a wasteful, duplication of effort. **Instead, testing variations to different candidate restoration practices in different conditions can help provide practitioners with information on expected treatment reliability, a "tool box" of potential treatments to choose among to deploy, and improved matching of treatments to conditions in which they are expected to provide the greatest chance for success.**

2) **Research on how to most effectively deploy restoration resources spatially is likely to be beneficial.** For example, if managers have funds for 3,000 outplants to revegetate a disturbance, how are the outplants best deployed? Should they be evenly spaced to potentially stimulate recovery into coalescing patches? Or, should they be planted in clusters as revegetated islands that could expand while serving as thermal refugia, enabling tortoises to move through and utilize a recovering habitat sooner?

3) A major research program is needed to develop local and landscape-scale approaches to **improve the condition of the annual plant community by reducing non-native annual grasses** (in turn reducing hazardous fuels) while promoting native herbaceous food plants.

4) **Research that improves the linkage between habitat enhancement activities and short- and long-term indicators of desert tortoise health and population traits is likely to be beneficial.** This represents a next step from previous research that correlated extant environmental features with tortoise health (e.g., correlating tortoise growth with forage availability; Medica et al. 2012) and in studies advocating for the potential that habitat restoration may have for improving tortoise health (Reed et al. 2009, Darst et al. 2013). The opportunities in this realm for collaborations between tortoise biologists and plant ecologists/restoration ecologists seem extensive. There is an existing supportive literature outlining tortoise health indicators that could be assessed for evaluating changes in tortoise health during and after restoration activities (Berry and Christopher 2001, Nagy et al. 2002).

5) The literature has extensively described that multiple threats face tortoises and that these threats can interact with each other, be cumulative spatially and temporally, and that addressing only one or a few threats may not improve tortoise well-being if other threats continue unabated. **A research priority is exploring whether comprehensive habitat restoration is actually capable of reversing declining short-term indicators of tortoise health and longer-term population declines.** Perhaps this could be examined within a protected, test landscape (*sensu* Berry et al. 2020c) as an adaptive management experiment. With as many other threats (e.g., anthropogenic disturbance, subsidized predators, presence of disease) as possible minimized or eliminated, comprehensive restoration could be implemented (including but not limited to enhancing perennial cover plant availability, reducing non-native plants and promoting high-quality native forb forage plants, and reconstructing hydrology as needed) across years and short- and long-term indicators of tortoise response measured. Until the type of research in priorities #4 and #5 is implemented, it will likely be difficult to accurately understand the potential role that habitat restoration could have in aiding tortoise recovery efforts. This adaptive management research opportunity may offer insight into both the fundamental ecology of the desert tortoise and the potential benefits and challenges of habitat restoration as a recovery action.

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