The good with the bad: when ecological restoration facilitates native and non-native species

Running head: facilitating native and non-native species

Scott R. Abella[1,2], Lindsay P. Chiquoine[1]

[1]University of Nevada Las Vegas, School of Life Sciences, Las Vegas, NV 89154-4004, U.S.A.

[2]Address correspondence to S.R. Abella, email scott.abella@unlv.edu

Author contributions: SRA conceived and designed the research, with LPC designing supplemental 2017 sampling; SRA, LPC collected the data; SRA analyzed the data; SRA wrote and edited the manuscript; LPC edited the manuscript.

Organisms interact with each other along a spectrum ranging from competition to facilitation. A theme in restoration ecology is tipping the balance of these interactions to favor desired species and site conditions, exemplified by restoring fertile islands and their nurse plant effects to encourage plant recruitment. We tested the effectiveness of outplanting nursery-grown native perennials and vertical mulching (placing dead plant material upright in soil) for stimulating annual plant recruitment in a disturbed Mojave Desert shrubland in Joshua Tree National Park, California, U.S.A. Over nine years, differences in annual species richness and cover between interspaces and below outplants and vertical mulch varied among years, potentially via inter-annual fluctuations in precipitation or maturation of restoration sites. In the ninth year, which was the wettest, both native and non-native cover averaged 3× higher below outplants than in interspaces. Overall among years at the microsite scale, non-native annual plants more consistently exploited environments provided by outplants and vertical mulch structures than did native annuals. However, these restoration structures were important for native annual diversity. At the 40-m^2 plot scale, disturbed plots that received outplanting supported greater richness of

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/rec.12874

native annual species than disturbed unrestored plots. By facilitating both non-native and native plants, reestablishing fertile islands to restore dryland ecosystems is a conundrum for restoration. Treatments reducing non-native plants may need to accompany fertile island restoration to tip the balance of facilitative plant interactions in favor of native species.

Key words: exotic species, fertile island, invasibility, outplanting, positive plant interactions, vertical mulch

Implications for Practice

- Outplanting native perennials can facilitate recruitment of both native and non-native annual plants, creating a tradeoff for using outplanting to restore fertile islands.
- Placing vertical mulch in the soil can be used to produce effects on annual plant communities that are intermediate between those of outplants and interspaces.
- Restoring structure required by native species but that also benefits non-natives is a conundrum. Fertile island restoration should be accompanied by consideration of potential facilitative effects to non-native plants.
- Reducing non-native annuals could enable native annuals to more fully utilize the facilitative benefits provided by restored fertile islands.

Introduction

Interactions among and between native and non-native species range from competitive to facilitative (Holmgren et al. 1997; Holzapfel & Mahall 1999; Rodríguez-Buriticá & Miriti 2009). One of restoration ecology's goals is tipping the balance of competitive-facilitative interactions to favor native species (El-Bana et al. 2003; Steers & Allen 2010; Cordell et al. 2016). In drylands, reestablishing fertile islands to facilitate desirable biota is often considered a first step in restoration (Hulvey et al. 2017). Fertile islands structure the spatial heterogeneity in many drylands and are defined as spatial concentrations of resources and/or biological activity below the canopies of perennial plants (Mudrak et al. 2014). Relative to interspaces between perennial plants, increased biological activity in fertile islands can be triggered by several mechanisms. These include shading and ameliorated microclimates below perennial plants, greater soil moisture, concentrated soil nutrients, trapping of seeds, and animal-plant interactions (El-Bana et al. 2003; Schneider & Allen 2012; Li et al. 2014). Nurse plant effects often accompany fertile islands, whereby the fertile island-forming perennial serves as a “nurse” facilitating the recruitment and growth of other plant species. Nurse plants often benefit annual plants, creating spatial heterogeneity between interspaces and fertile islands (Abella & Smith 2013). While perennial-annual plant relationships can change among years differing in rainfall, site conditions, and species of plants, fertile islands are generally fundamental to plant recruitment and diversity in drylands (Brooks 1999; El-Bana et al. 2003; Craig et al. 2010).

Outplanting nursery-grown seedlings is a main method for restoring perennial plants to potentially reestablish fertile islands to degraded drylands. While seeding and outplanting both have advantages and disadvantages, outplanting is often more reliable than seeding for reestablishing perennial plants to priority sites in drylands (e.g., Commander et al. 2013; Li et al. 2014; Rathore et al. 2015). This is because outplanting bypasses the need for germination and survival of vulnerable young seedlings at restoration sites subject to limited and unpredictable precipitation. To achieve outplant survival, treatments such as irrigation and initially protecting plants from herbivory are often needed (Scoles-Sciulla et al. 2014).

While the ability to establish perennials through outplanting and the importance of fertile islands in natural desert ecosystems are appreciated, little research has tracked whether outplants in restoration are actually accompanied by the formation of nurse plant effects facilitating annuals as in undisturbed reference ecosystems. Annual plants are key components of desert ecosystems, driving ecological processes as diverse as soil nutrient cycles and food web dynamics during intense periods of biological activity (Facelli & Temby 2002; Vamstad & Rotenberry 2010). Annual plant communities in many contemporary drylands now have a component of non-native species, creating uncertainty for which annual plant groups might benefit from nurse plant effects (Rodríguez-Buriticá & Miriti 2009).

Does restoring live or dead perennial plants facilitate annual plant communities, and if so, are native or non-native annuals the beneficiaries? We examined this question by comparing annual plant communities over a nine-year period among restoration treatments including outplanting and vertical mulch consisting of dead plant material (e.g., branches) placed upright in the ground. By being cheaper and not requiring survival of a plant, vertical mulch is sometimes used as a surrogate to outplanting (Bainbridge 1996). We tested the following null hypotheses at two spatial scales: 1) at the microsite scale, there is no difference in species richness and cover of native and non-native annual species among restored perennial plant structures (outplants and vertical mulch) relative to interspaces and naturally established perennials in undisturbed reference ecosystems; and 2) annual plant measures do not differ at the plot scale (40 m^2) among disturbed plots receiving or not receiving outplanting and vertical mulch and compared with undisturbed reference plots. Findings contribute to a broad topic in restoration ecology of improving understanding of tradeoffs in ecological responses to restoration, and how these tradeoffs might be managed to favor native species.

Methods

Study Area

We performed this study in Joshua Tree National Park, California, U.S.A., in the southern Mojave Desert. The study area was along Keys View Road, with elevations ranging from 1292-1542 m on a broad alluvial fan. Soils were derived from granitic and gneissic rocks and classified as Torripsamments and Haplargids of the Morongo, Jumborox, and Pinecity series (Houdeshell et al. 2013). Vegetation physiognomy of mature sites consisted of desert shrubland, with the tallest plants being *Yucca brevifolia* (Joshua tree), with a variety of smaller shrubs, perennial grasses such as *Pleuraphis rigida* (big galleta grass), and perennial forbs. Depending on weather any given year, suites of annual forbs and grasses inhabited interspaces and below perennial plants. Typifying contemporary Mojave Desert ecosystems, the ephemeral plants included mixtures of native and non-native species, with predominant non-natives including the annual grasses *Bromus rubens* (red brome), *Bromus tectorum* (cheatgrass), and *Schismus* spp. (Mediterranean grass), and the annual forb *Erodium cicutarium* (redstem stork's bill; Schneider & Allen 2012). In addition to competing with native annuals, non-native annuals augment fuel loads that sustain unnaturally severe fires, threatening mature shrublands (Rao et al. 2010). Livestock grazing was not permitted, but numerous mammal and invertebrate herbivores inhabit the area (Vamstad & Rotenberry 2010). A weather station 20 km northeast of the study area in Twentynine Palms, California, at an elevation of 604 m (lower than the study area), reported the following 1935 through 2017 averages: 11 cm/year of precipitation (range: 1-31 cm/year), January daily low temperature of 2.5°C, and July daily high temperature of 40.6°C (Fig. S1; Western Regional Climate Center, Reno, Nevada, U.S.A.).

Restoration Activities

Along a 6-km section of Keys View Road, 60 sites (each 100-150 m^2) were disturbed by road maintenance activities in 2007-2008 to widen, resurface, and provide concrete berms (20 cm high) for the road (Fig. 1). The disturbed sites were adjacent to the resurfaced road, which was completed by 2008. Disturbances were created via heavy equipment work areas and where the old road infrastructure was removed. Disturbed sites were denuded and re-contoured when restoration commenced. A restoration treatment of planting 800 native perennial plants was implemented at the sites in February 2008 by the National Park Service. The nine species used were common in the study area's mature shrublands (Table S1). Seed for these plants was locally collected (within 8 km of the restoration sites), and the seedlings were grown for a year in the park nursery. Seedlings were grown in tall pots (15 cm in diameter × 40 cm tall) filled with a 2:1:2 sand:organic mulch:perlite mixture. Planting at a density averaging 1 plant/10 m^2 was done by hand using shovels. Plants were given 8 L of water when planted and 8 L/month in a monthly watering for the first two years, after which watering was discontinued. To deter mammalian herbivory, each outplant was enclosed in a 1 m tall, wire mesh cage (5 mm openings) buried and affixed to the ground using rebar. Cages were removed after 2011 after outplants had established. Vertical mulch was created in spring 2008 by collecting dead plant material (branches and stems, which were not differentiated by species) from mature shrublands and placing the material upright in the soil at a density averaging 1 piece/4 m^2 (Fig. 1). Vertical mulch was intended to partially provide functions of living plants such as shading, concentrating materials, promoting native annuals, and visually restoring areas to limit further disturbance (Bainbridge 1996).

Data Collection and Analysis

Along the road corridor from the pool of 60 disturbed sites, we randomly selected six sites each of the following four treatments: unrestored (control), vertical mulch only, outplanting only, and vertical mulch + outplanting (Fig. 2). In the center of each site parallel to the road, we established a 2-m × 20-m plot, sized to fit within the rectangular-shaped sites. In April or the first week of May at the peak of winter annual plant biomass in 2009-2011 (1-3 growing seasons after restoration) and 2017 (ninth growing season after restoration), we measured the annual plant community within disturbed plots at two spatial scales. These scales were microsites (below perennial plants or vertical mulch and in interspaces) and whole plots (40 m^2). At the microsite scale in a 0.5-m × 0.5-m (0.25 m^2) quadrat centered on each outplant within plots, we categorized the areal percent cover of each annual species using cover classes: 1 = 0-1%, 2 = 1-2%, 3 = 2-5%, 4 = 5-10%, 5 = 10-25%, 6 = 25-50%, 7 = 50-75%, 8 = 75-95%, and 9 = > 95% (modified from Peet et al. [1998]). We selected this quadrat size to fit snugly around the canopy of typical outplants. Outplants were individually tagged. We sampled the same individuals each year, except that we sampled only individuals with visible, live foliage to ensure they were alive. On average, 3.7 outplants (range 2-7) were available to sample per plot. On plots with vertical mulch, we collected the same data as for outplants for five vertical mulch structures (with a 0.25-m^2 quadrat centered on each structure) within each plot, systematically selecting structures closest to the center of the plot at 2, 5, 9, 13, and 17 m along the 20-m plot axis. On each disturbed plot, we sampled an interspace (≥ 1 m from the canopy edge of a live perennial plant or vertical mulch structure) nearest to 3, 7, 11, 15, and 19 m (five interspaces total per plot) using a 0.25-m^2 quadrat.

To scale up cover from the microsite to the 40-m^2 plot scale, we calculated the proportion of the plot area that each microsite (perennial plant, vertical mulch, or interspace) occupied and multiplied this proportion by the average cover an annual species had in the microsites. We also surveyed entire plots for species not already recorded in microsites and used the same cover classes as for microsites to categorize cover of these species at the plot scale.

Using randomly selected geographic coordinates, we further selected six roadside sites containing undisturbed, mature shrubland to serve as undisturbed reference sites. We sampled these sites using the same size of plots at the same time and years (2009, 2010, 2011, and 2017) as the disturbed plots. We measured the annual plant community using the same cover classes in five, 0.25-m^2 quadrats centered along the same coordinates (3, 7, 11, 15, and 19 m) as for interspace sampling in the disturbed plots. Owing to the greater and more continuous shrub cover on undisturbed plots, we measured the proportion of quadrat areas covered by perennials and interspaces and scaled cover of annual plants to the 40-m^2 plot scale using this proportion of perennial cover and corresponding area of interspaces. Using the same methods as for disturbed plots, we surveyed entire areas of undisturbed plots for species not already recorded in quadrats and categorized cover of these species. In 2017, we additionally measured annuals within undisturbed perennial plant microsites with the same cover classes used throughout the study within five 0.5 m × 0.5 m (0.25 m^2) quadrats per undisturbed plot. These quadrats were centered on the largest perennial plant nearest the plot centerline at 2, 5, 9, 13, and 17 m along the 20-m plot axis.

In 2017, we were only able to sample a randomly selected three of the six plots of each of the four treatment types on disturbed sites (including disturbed/unrestored controls), which included 23 outplants in total on plots. To keep the total number of outplants sampled nearly constant per year (38-45 outplants), we collected an additional microsite data set in 2017 for 21 off-plot outplants that were also along the roadsides and nearest (usually within 50 m) to plots.

We sampled annuals below these outplants and in a paired interspace (≥ 1 m from the canopy edge of an outplant) using the same methods as for on-plot outplants. We also randomly selected three of the six undisturbed, reference plots for sampling in 2017. Taxonomic nomenclature followed Natural Resources Conservation Service (2018).

We conducted statistical analyses at two spatial scales: the 40-m^2 plot scale and microsite scale. The response variables included species richness (per 40 m^2 for the plot scale and per 0.25 m^2 for the microsite scale) and cover of native and non-native annual plants (scaled to 40 m^2 at the plot scale and average percent cover by microsite at the microsite scale). For the plot scale, we analyzed each response variable using a mixed-model, repeated measures analysis of variance including treatment (disturbed/unrestored, vertical mulch, outplanting, vertical mulch + outplanting, and undisturbed/unrestored) and year (2009, 2010, 2011, and 2017) as fixed effects and plot as a random effect. We performed a sensitivity analysis for potential influences of sampling only three of six plots per treatment in 2017 by conducting analyses with only the three replicate plots sampled all years compared to the full data set. Conclusions did not qualitatively differ, so we report results using all available data.

For the microsite scale, we used the three whole-plot treatments that included a restoration action (vertical mulch, outplanting, vertical mulch + outplanting) as a framework to compare the vertical mulch, outplant, and interspace microsites within whole plots. To test a null hypothesis of no difference between or among microsites, separately for each whole-plot treatment and response variable, we performed a mixed-model, split-plot, repeated measures analysis of variance including plot as a random effect and year, microsite nested within plot, and the year × microsite interaction as fixed effects. To accommodate the random effects, we used PROC GLIMMIX in SAS 9.3 for whole-plot and microsite analyses (SAS Institute 2009).

Accepted Article

For overall models significant at $P < 0.10$ for the plot and microsite analyses, we compared means at the appropriate interaction or main effect using Tukey-Kramer adjustments for multiple comparisons at $P < 0.10$. We set P at 0.10 for all statistical analyses as a compromise between Type I and Type II errors. For our null hypothesis, falsely inferring that restoration does not affect non-native plants, when it actually does, would be as much of a concern as would falsely inferring restoration effects. For the additional microsite data collected in 2017, we compared means of each of the four response variables between outplant/interspace and undisturbed perennial/interspace pairs using paired *t* tests set at $P < 0.10$.

Results

Plot Scale

At the 40-m^2 plot scale, disturbance and restoration treatments significantly influenced native annual species richness, while non-native annual species cover was influenced by interactions between disturbance and year (Fig. 3, Table S2). Species richness of native annuals in disturbed plots receiving outplanting was higher than in disturbed unrestored plots, but lower than in undisturbed reference plots. The cover of non-native annuals was at least 3× greater in undisturbed reference plots than in any disturbed plot (with or without restoration) from 2009 through 2011 (1-3 years after restoration). In 2017 (9 years after restoration), however, cover did not differ among treatments.

Microsite Scale

At the microsite scale around individual vertical mulch structures, outplants, and interspaces, the species richness and cover of non-native and native annuals varied through year × microsite interactions or main effects across years (Table S3). Restoration treatments frequently had influences on both non-native and native richness and individual species that changed through time (Fig. 4a-c, Table S4). For example, 2-3 years after restoration in 2010-2011, native richness was often lower in vertical mulch and outplant microsites compared to interspaces. However, nine years after restoration in 2017, native richness was higher below outplants than in interspaces within vertical mulch + outplanting plots. Vertical mulch and outplants generally increased non-native cover above that of interspaces (Fig. 4d-f). Native species cover was lower and less responsive to treatments than non-native cover, but did display a year × microsite interaction where cover patterns below outplants shifted through time (Fig. 4e).

The additional microsites sampled in 2017 supported results of microsite effects from restoration plots and provided comparisons between microsites in undisturbed reference ecosystems and microsites in restoration sites (Fig. 5). Species richness of native annuals was not higher below perennial plants compared to interspaces in undisturbed sites, but was 38% higher below outplants compared to interspaces in restoration sites. Cover for both non-native and native annual species was nearly identical between below-perennial and interspace microsites in undisturbed sites. At restoration sites, however, cover for both species groups was over 3× greater below outplants compared to in interspaces.

Discussion

Climate Interactions with Restoration

Some authors have hypothesized that nurse plant effects are strongest in dry years, presumably because benefits provided by nurses, such as shading, are most needed by beneficiary plants when precipitation is sparse (e.g., Tielbörger & Kadmon 2000; Facelli & Temby 2002). However, data have not consistently supported that hypothesis (Tielbörger & Kadmon 2000; Abella & Smith 2013). In fact, some species might best exploit the nutrient-rich soils of fertile islands in wet years when moisture is less limiting (Brooks 1999). Data in our study would also not unequivocally support a hypothesis that nurse plant effects are strongest in dry years. If anything, annual plant cover was highest below outplants (relative to interspaces) in the moistest years of 2010 and 2017 for both non-native and native species (Fig. S1). Species richness was generally similar or lower below outplants and vertical mulch compared to interspaces early in the study (2009-2011), but tended to be highest below outplants and vertical mulch by 2017. This ninth year of the study was the wettest, but outplants and vertical mulch structures were also oldest by then. Further monitoring is needed across wet and dry years to pinpoint if or how precipitation any given year interacts with outplant and restoration age.

Restoration Effect Across Spatial Scales

The effects of outplanting and vertical mulch on annuals were generally stronger at a local spatial scale (i.e. near and below outplanted individuals or emplaced vertical mulch) than at the 40-m^2 plot scale. To have a large effect on annuals at the plot scale, it would seem that outplanting or vertical mulch would need to either: 1) occur at a high density so that their localized effects comprise a large proportion of the plot area to more greatly influence the plot as a whole, 2) influence plants in interspaces which occupy most of the plot area, or 3) trigger the establishment of naturally recruiting perennials that convert interspaces to fertile islands or hotspots of annual plant recruitment. Given the high survival of outplants and persistence of vertical mulch, the first mechanism would seem to be the most certain – but also the most expensive – way to influence annuals at the plot scale. The second mechanism seems to conflict with the fundamental premise of fertile island formation. By definition, fertile islands form below the canopies of perennial plants, not in interspaces (Mudrak et al. 2014). As a result, we may not expect outplanting to increase annual plants in interspaces, and in fact, outplanting could reduce annuals in interspaces if the outplants harvest water and nutrients from them (Thompson et al. 2005). It is possible, however, that outplanting and vertical mulch could increase annuals in interspaces in as yet poorly understood ways, such as somehow changing wind patterns or animal utilization that could influence seed dispersal and plant establishment. The third mechanism seems plausible, but would be contingent on the recruitment and persistence of perennial species that influence annuals. In deserts and specifically in Joshua Tree National Park, cohorts of seedlings of perennial species often appear then die within a few years, meaning that the establishment of persistent perennial cover that can influence annuals might only occur every few decades (Miriti et al. 2007). While we observed some natural establishment of perennial species such as *Sphaeralcea ambigua* (desert globemallow), perennial cover on restoration plots continued to be mostly supplied by outplants throughout the study, perhaps because dry conditions limited natural recruitment of perennials.

Potential Influences of Time and Composite Outplanting Effects

How long it takes fertile islands to form and nurse plant effects to appear is largely uncertain in natural ecosystems and those undergoing restoration. In our study, nurse plant effects appeared within the first year below outplants. Whether this fast expression of nurse plant effects during restoration resulted from outplants quickly ameliorating microclimates, trapping seeds, enhancing soil fertility or other mechanisms of fertile island formation is unclear, as are the possible legacy influences of planting and plant care activities. In one of the few studies of fertile island development below outplants, Rathore et al. (2015) found that numerous soil properties differed below seven-year-old shrub outplants compared to interspaces in the Thar Desert in India. In that study, outplants had been grown in the greenhouse in soil from the site and cages were not needed to protect outplants, so these differences likely represent “pure” effects of shrubs and suggest that fertile islands formed within seven years.

Our study likely represents the composite influence of an outplanting treatment including excavating soil to house a plant and nursery soil around its roots, installing a protective cage, and irrigating for the first two years. Nurse plant effects remained evident in 2017, after cages were removed, irrigation had been stopped for seven years, and the central stem of many outplants had expanded to cover (and thereby exclude annuals from) the original area of planted nursey soil. These observations suggest that while we cannot rule out the potential legacy influences of the outplanting treatment on observed nurse plant effects, we can hypothesize that the 2017 results represent "pure" nurse plant effects provided by outplants or at least sustained nurse-plant-like effects. Future experiments could partition the potential influences of composite outplanting treatments by having several different controls, such as installing only cages and nursery soil or concurrently irrigating both outplants and interspaces. Such information could help identify tradeoffs in planting and stewardship practices including considerations such as cost, survival rates of outplants, and influences on nurse plant effects.

Intermediate Effects of Vertical Mulch and Longevity

In general, annual plant species richness and cover near vertical mulch were intermediate between those around interspaces and outplants. This raises a question as to whether vertical mulch provides only some of the benefits of live nurse plants, a question not yet resolved in the literature by experiments seeking to partition fertile island effects into physical and biotic influences of perennial plants. After three years, artificial plants (plastic shrub-like structures) emplaced in the Negev Desert in Israel did not display organic matter-enriched soils like live shrubs did, but neither artificial plants nor live shrubs served as nurse plants (Berg & Steinberger 2012). In the Arabian Desert of the United Arab Emirates, dead shrubs and grasses better facilitated annual plants than did live shrubs and grasses (El-Keblawy et al. 2016). In the

Mojave Desert, Holzapfel & Mahall (1999) found that killing a shrub that had formed an existing fertile island and affixing the dead shrub canopy back on the fertile soil resulted in effects to annual plants equivalent to below live shrubs. However, killing a shrub and not placing the dead canopy back on the fertile soil reduced annual plants compared to below live shrubs. Combined with our results of placing dead plant material in an interspace, these studies highlight that much is yet to be learned regarding the relative importance of soil fertility, perennial plant canopies, and other potential mechanisms driving nurse plant effects.

In addition to potentially enhancing plant recruitment, vertical mulch is suggested to curtail soil erosion and provide visual restoration to limit further disturbance (Bainbridge 1996). However, it is unclear how long vertical mulch may persist to provide these benefits or whether tradeoffs with non-native plants exist. During fieldwork, we noted that some vertical mulch structures had broken or fallen over, but many structures persisted and remained upright after nine years. The longevity of properly anchored vertical mulch may thus hinge on wood decomposition rates. In the arid (18 cm of precipitation/year) South African Karoo, dead shrubs lying on the ground lost 50% of their dry weight in 9-18 years (Milton & Dean 1996). In the U.S. Sonoran Desert (10 cm/year precipitation), 10-50 cm long pieces of *Fouquieria splendens* (ocotillo) wood lost half their weight after 30 years and would completely disintegrate within an estimated 114 years (Ebert & Ebert 2006). These studies and our observations suggest that vertical mulch can provide visual restoration benefits for at least decades, but a concern is that vertical mulch generally benefitted non-native plants more than natives.

Should Fertile Islands be Restored and can They Facilitate Native Species?

In earlier studies (Abella et al. 2011, 2012; Abella & Smith 2013), we began questioning the restoration of fertile islands as the dominant initial goal in much of desert restoration, due to the apparent paradox of restoring the same structure of undisturbed drylands pervasively infested by non-native plants. These concerns were based on studying perennial-annual plant relationships in undisturbed, reference sites. Results from restoration treatments in the present study reinforce these concerns. Our study's main finding was that restoring perennial plants facilitated the recruitment of native annuals in some circumstances, but benefited non-native annuals more consistently. This conundrum raises questions about restoring fertile islands without further treatments to favor native species.

To address this conundrum, we suggest pursuing two complementary approaches: 1) shifting focus to restoring perennial species that do not necessarily form fertile islands, and 2) pairing restoring fertile island-forming species with treatments to reduce non-native species. While most native perennial species facilitate non-native annuals in North American hot deserts, a small subset of native perennials have neutral or even competitive effects on non-native annuals (Brooks 2009; Abella et al. 2011). These perennials appear to have relatively short average life spans (less than a few decades), frequently colonize disturbed sites, and may have combinations of traits averse to forming well-developed fertile islands and nurse plant effects (Abella et al. 2011, 2012). *Sphaeralcea ambigua* and *Bebbia juncea* (sweetbush) exemplify these sorts of native perennial species and have supported the fewest non-native annuals in reference ecosystems and invasibility experiments (Brooks 2009; Abella & Smith 2013). Further exploring the restoration potential of these types of perennial species is warranted because they could provide restoration with functional benefits (e.g., covering soils, providing forage for wildlife), without facilitating non-native plants. But precisely because they may not serve as nurse plants, a shortcoming could be lack of facilitation of native plants. This drawback likely renders non-fertile island-forming species only a partial solution for desert restoration. Limited research on the success of herbicide and other treatments at reducing non-native annuals in naturally established desert shrublands (e.g., Brooks 2000; Schutzenhofer & Valone 2006; Steers & Allen 2010) suggests that the second option – pairing outplanting with treatments to reduce non-native annuals – warrants further study for ensuring that native species are the beneficiaries of restored fertile islands.

Acknowledgements

Restoration activities were organized between the Federal Highways Administration and National Park Service, with Katy Matthews, Lamp Truitt, Scott Szabo, Maggie Brown, and many other individuals with Joshua Tree National Park (JTNP) participating in implementing restoration. We thank Alice Miller for organizing a cooperative agreement between JTNP and the University of Nevada Las Vegas (UNLV) to fund initial research in 2009-2011; Cayenne Engel (UNLV) who was instrumental in sampling design and data collection in 2009-2011; Joslyn Curtis (UNLV) for helping with data collection in 2011; Neil Frakes and Michael Vamstad (JTNP) for supporting the research and facilitating permits; and Sharon Altman (UNLV) for formatting Fig. 3. The 2017 remeasurement was supported by the California Fire Science Consortium (Desert Region) of the Joint Fire Science Program. We appreciate reviews by the coordinating editor and two anonymous reviewers that improved the manuscript.

LITERATURE CITED

Abella SR, Craig DJ, Chiquoine LP, Prengaman KA, Schmid SM, Embrey TM (2011) Relationships of native desert plants with red brome (*Bromus rubens*): toward identifying invasion-reducing species. Invasive Plant Science and Management 4:115-124

Abella SR, Craig DJ, Smith SD, Newton AC (2012) Identifying native vegetation for reducing exotic species during the restoration of desert ecosystems. Restoration Ecology 20:781-

787

Abella SR, Smith SD (2013) Annual-perennial plant relationships and species selection for desert restoration. Journal of Arid Land 5:298-309

Bainbridge DA (1996) Vertical mulch controls erosion, aids revegetation (California). Restoration and Management Notes 14:82

Berg N, Steinberger Y (2012) The role of perennial plants in preserving annual plant complexity in a desert ecosystem. Geoderma 185-186:6-11

Brooks ML (1999) Habitat invasibility and dominance by alien annual plants in the western Mojave Desert. Biological Invasions 1:325-337

Brooks ML (2000) Competition between alien annual grasses and native annual plants in the Mojave Desert. American Midland Naturalist 144:92-108

Brooks ML (2009) Spatial and temporal distribution of non-native plants in upland areas of the Mojave Desert. Pages 101-124 In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, Miller DM (eds) The Mojave Desert: ecosystem processes and sustainability. University of Nevada Press, Reno

Commander LE, Rokich DP, Renton M, Dixon KW, Merritt DJ (2013) Optimising seed broadcasting and greenstock planting for restoration in the Australian arid zone. Journal of Arid Environments 88:226-235

Cordell S, Ostertag R, Michaud J, Warman L (2016) Quandaries of a decade-long restoration experiment trying to reduce invasive species: beat them, join them, give up, or start over? Restoration Ecology 24:139-144

Craig DJ, Craig JE, Abella SR, Vanier CH (2010) Factors affecting exotic annual plant cover and richness along roadsides in the eastern Mojave Desert, USA. Journal of Arid

Environments 74:702-707

Ebert TA, Ebert TA (2006) Decomposition rate of ocotillo (*Fouquieria splendens*) wood in the desert of southern California and its use in estimating adult survival by life-cycle graph analysis. Plant Ecology 186:177-187

El-Bana MI, Nijs I, Khedr AA (2003) The importance of phytogenic mounds (nebkhas) for restoration of arid degraded rangelands in northern Sinai. Restoration Ecology 11:317-324

El-Keblawy A, Kafhaga T, Navarro T (2016) Live and dead shrubs and grasses have different facilitative and interfering effects on associated plants in arid Arabian deserts. Journal of Arid Environments 125:127-135

Facelli JM, Temby AM (2002) Multiple effects of shrubs on annual plant communities in arid lands of South Australia. Austral Ecology 27:422-432

Holmgren M, Scheffer M, Huston MA (1997) The interplay of facilitation and competition in plant communities. Ecology 78:1966-1975

Holzapfel C, Mahall BE (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. Ecology 80:1747-1761

Houdeshell C, Fahnestock P, Roecker S, Meirik E, Munnecke M, Miller A (2013) Soil survey of Joshua Tree National Park, California. United States Department of Agriculture, Natural Resources Conservation Service, and United States Department of the Interior, National Park Service, Washington, D.C.

Hulvey KB, Leger EA, Porensky LM, Roche LM, Veblen KE, Fund A, Shaw J, Gornish ES (2017) Restoration islands: a tool for efficiently restoring dryland ecosystems? Restoration Ecology 25:S124-S134

Li X, Jiang D, Zhou Q, Oshida T (2014) Soil seed bank characteristics beneath an age sequence of *Caragana microphylla* shrubs in the Horqin sandy land region of northeastern China. Land Degradation and Development 25:236-243

Milton SJ, Dean WRJ (1996) Rates of wood and dung disintegration in arid South African rangelands. African Journal of Range and Forage Science 13:89-93

Mudrak EL, Schafer JL, Fuentes-Ramirez A, Holzapfel C, Moloney KA (2014) Predictive modeling of spatial patterns of soil nutrients related to fertility islands. Landscape Ecology 29:491-505

Natural Resources Conservation Service (2018) The PLANTS database. National Plant Data Center http://plantsusdagov (accessed 24 February 2018)

Peet RK, Wentworth TR, White PS (1998) A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63:262-274

Rao LE, Allen EB, Meixner T (2010) Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts. Ecological Applications 20:1320-1335

Rathore VS, Singh JP, Bhardwaj S, Nathawat NS, Kumar M, Roy MM (2015) Potential of native shrubs *Haloxylon salicornicum* and *Calligonum polygonoides* for restoration of degraded lands in arid western Rajasthan, India. Environmental Management 55:205-216

Rodríguez-Buriticá S, Miriti MN (2009) Biting the hand that feeds: the invasive grass *Schismus barbatus* (Poaceae) is facilitated by, but reduces establishment of, the native shrub *Ambrosia dumosa* (Asteraceae). Journal of Vegetation Science 20:241-250

SAS Institute (2009) SAS/STAT 92 user’s guide. SAS Institute, Inc., Cary, North Carolina

Schneider HE, Allen EB (2012) Effects of elevated nitrogen and exotic plant invasion on soil seed bank composition in Joshua Tree National Park. Plant Ecology 213:1277-1287

Schutzenhofer MR, Valone TJ (2006) Positive and negative effects of exotic *Erodium cicutarium* on an arid ecosystem. Biological Conservation 132:376-381

Scoles-Sciulla SJ, DeFalco LA, Esque TC (2014) Contrasting long-term survival of two outplanted Mojave Desert perennials for post-fire revegetation. Arid Land Research and Management 29:110-124

Steers RJ, Allen EB (2010) Post-fire control of invasive plants promotes native recovery in a burned desert shrubland. Restoration Ecology 18:334-343

Thompson DB, Walker LR, Landau FH, Stark LR (2005) The influence of elevation, shrub species, and biological soil crust on fertile islands in the Mojave Desert, USA. Journal of Arid Environments 61:609-629

Tielbörger K, Kadmon R (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. Ecology 81:1544-1553

Vamstad MS, Rotenberry JT (2010) Effects of fire on vegetation and small mammal communities in a Joshua tree woodland. Journal of Arid Environments 74:1309-1318

Figure 1. Example sites from a restoration project along Keys View Road, Joshua Tree National Park, California, U.S.A. Top: paired photos of a 2-m × 20-m outplanting plot in 2010 (two years after restoration) and 2017. Middle: examples in 2017 of a vertical mulch + outplanting plot (left photo) and development of a large *Eriogonum fasciculatum* (California buckwheat; deep greenish flowering plant extending over the road berm on the right side of the plot) outplanted nine years earlier (right photo). Bottom: examples in 2017 of the abundant non-native annuals *Schismus* spp., *Bromus rubens* (red brome), and *Bromus tectorum* (cheatgrass) below a shrub canopy on a vertical mulch and outplanting plot (left photo) and view of an undisturbed reference ecosystem (right photo). Photos by E.C. Engel (top left) and S.R. Abella (all others).

Figure 2. Layout of one example replicate illustrating treatments to study the effects of vertical mulch and outplanting on soils disturbed by road construction, Joshua Tree National Park, California, U.S.A. Within whole plots, the species richness and cover of annual plants were

measured in microsites (e.g., below outplants, in interspaces) sampled with 0.25-m^2 quadrats centered on microsites. Annuals were also measured at the 40-m^2 plot scale.

Figure 3. Species richness and cover at the whole-plot scale (40 m^2) for non-native and native annual plants during a nine-year study period on soils disturbed by road construction and receiving outplanting or vertical mulch restoration treatments, Joshua Tree National Park, California, U.S.A. Values are means and error bars stand for +1 SE. Data are shown at the appropriate level of statistical resolution according to the main effects of year or treatment or the year × treatment interaction. No factors were significant for native annuals (d), so data are displayed across the year-treatment combination for descriptive purposes. Within a panel or inset graph, means without shared letters differ at $P < 0.1$ (Tukey-Kramer adjustments for multiple comparisons). The associated analysis of variance statistics are in Table S2.

Figure 4. Variation in non-native and native species richness and cover for annual plants among microsites (interspace, vertical mulch, and outplant) within whole-plot restoration treatments during a nine-year study on disturbed soils in Joshua Tree National Park, California, U.S.A. Values are means and error bars stand for +1 SE. Data are shown at the appropriate levels of statistical resolution depending on whether year × microsite or main effects of year and microsite were significant in overall models. Insets show comparisons across microsites when main effects (year and microsite) were significant. Within a panel or inset separately for non-native and native species, means without shared letters differ at $P < 0.1$ (Tukey-Kramer adjustments for multiple comparisons). The associated analysis of variance statistics are in Table S3.

Figure 5. Mean species richness and cover of annual plants compared between interspaces paired with either below perennial plants in undisturbed reference ecosystems or below outplants after restoration, Joshua Tree National Park, California, U.S.A. Data are for 2017, representing

nine-year-old outplants. Error bars stand for +1 SE. Within a panel separately for non-native and native species, paired means with the same symbol differ at P < 0.1 (paired *t* test, 20 degrees of freedom for each test). The undisturbed category represents average values below individual perennial plants in undisturbed, reference sites. The outplant category represents average values below individual outplants in disturbed sites receiving restoration outplanting.

Figure 1

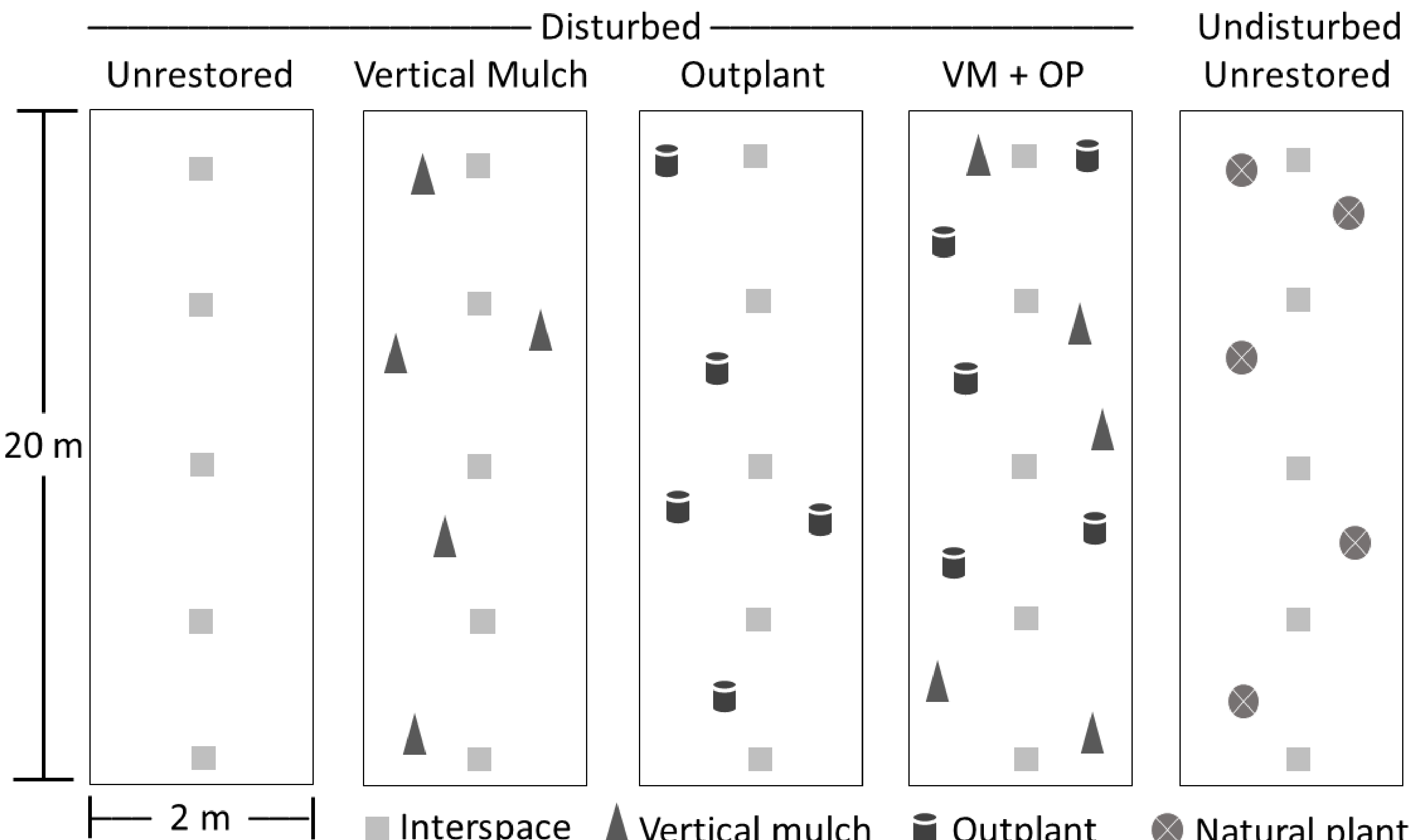
Disturbed
Undisturbed
Unrestored
Vertical Mulch
Outplant
VM + OP
Unrestored
20 m
2 m
Interspace
Vertical mulch
Outplant
Natural plant

Figure 2

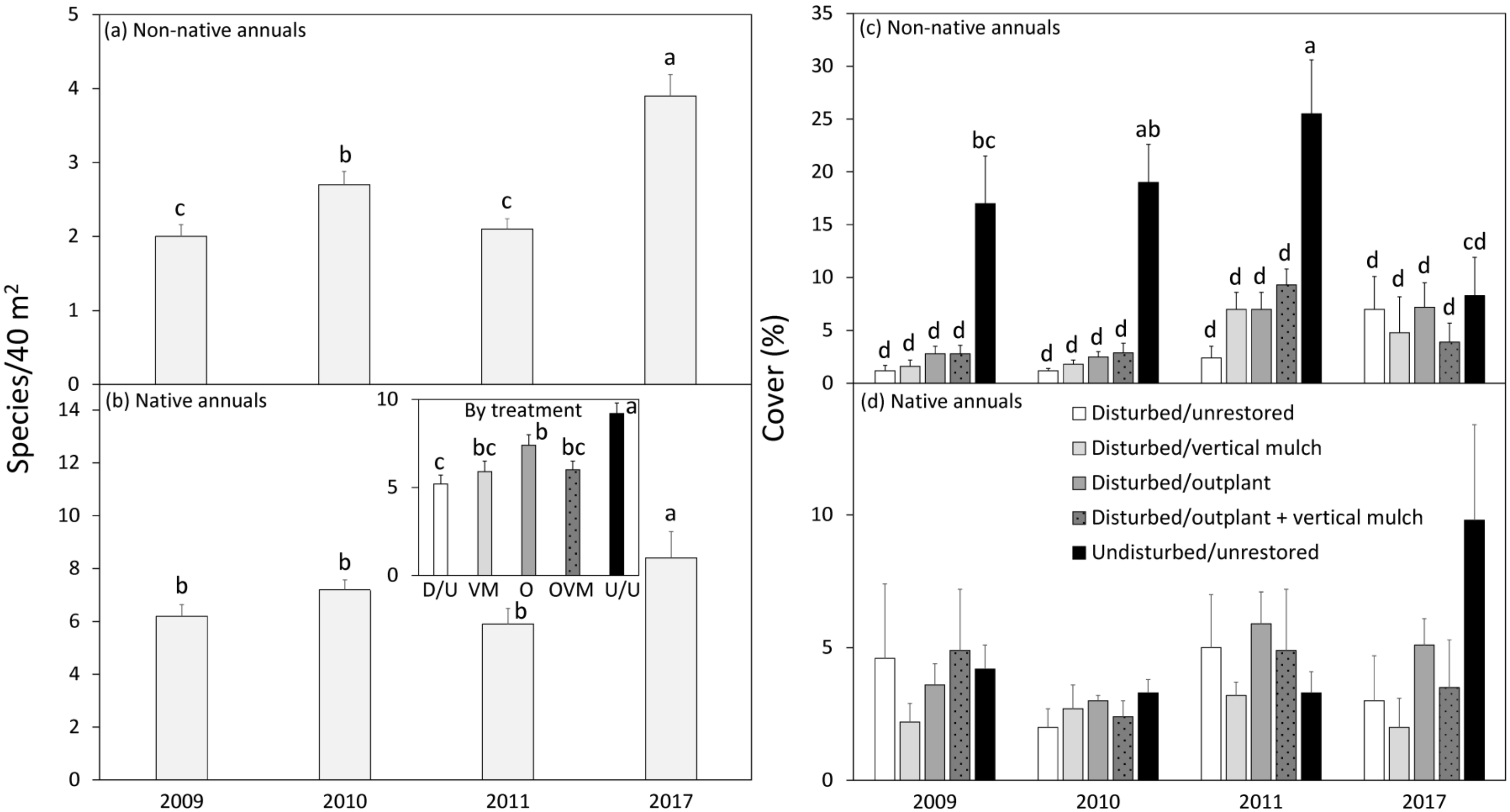
(a) Non-native annuals
(b) Native annuals
By treatment
D/U
VM
O
OVM
U/U
Species/40 m²
2009
2010
2011
2017
(c) Non-native annuals
(d) Native annuals
Cover (%)
Disturbed/unrestored
Disturbed/vertical mulch
Disturbed/outplant
Disturbed/outplant + vertical mulch
Undisturbed/unrestored

Figure 3

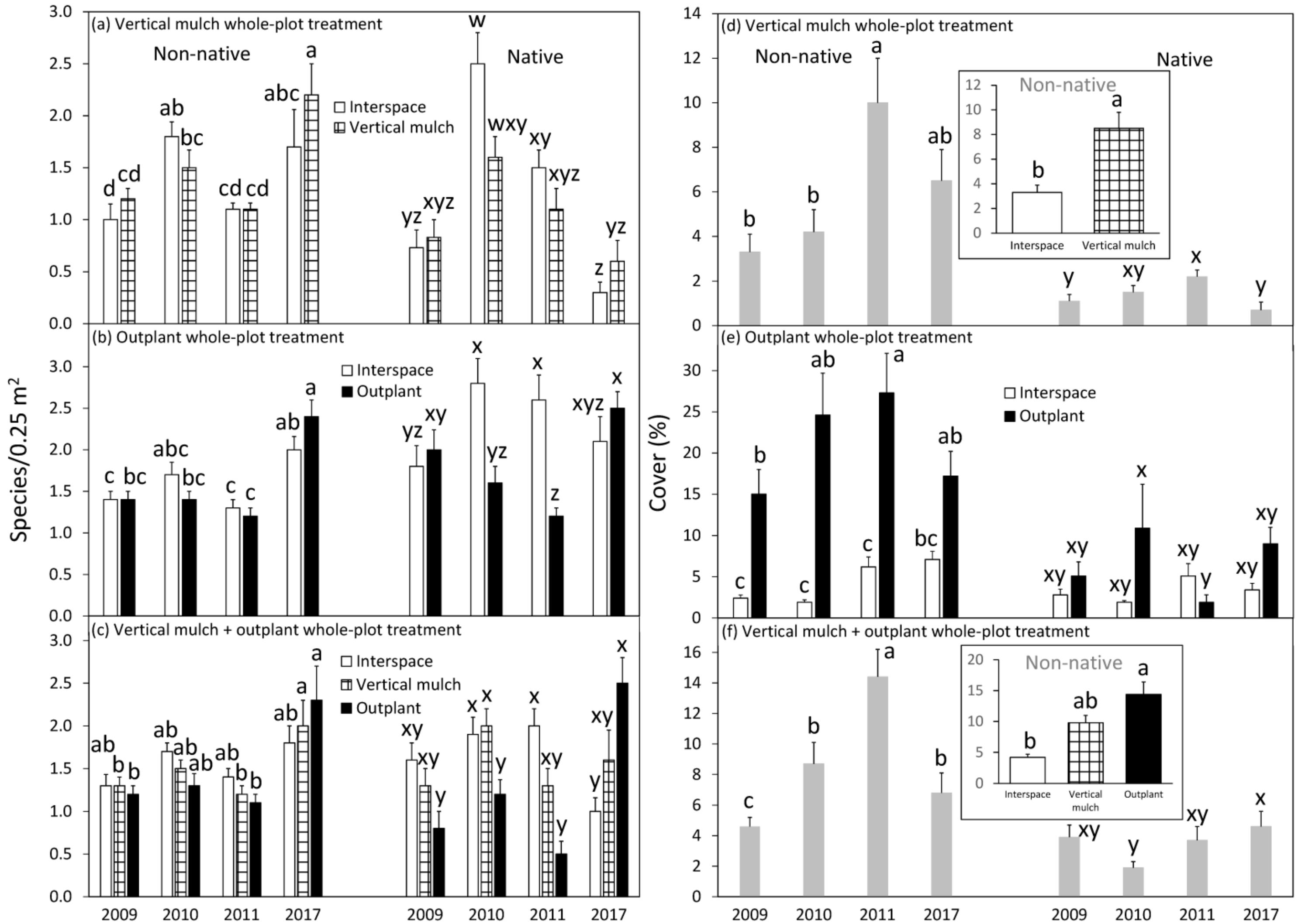
(a) Vertical mulch whole-plot treatment
Non-native
Native
Interspace
Vertical mulch
(b) Outplant whole-plot treatment
Interspace
Outplant
(c) Vertical mulch + outplant whole-plot treatment
Interspace
Vertical mulch
Outplant
Species/0.25 m²
(d) Vertical mulch whole-plot treatment
Non-native
Native
(e) Outplant whole-plot treatment
Interspace
Outplant
(f) Vertical mulch + outplant whole-plot treatment
Cover (%)
2009
2010
2011
2017

Figure 4

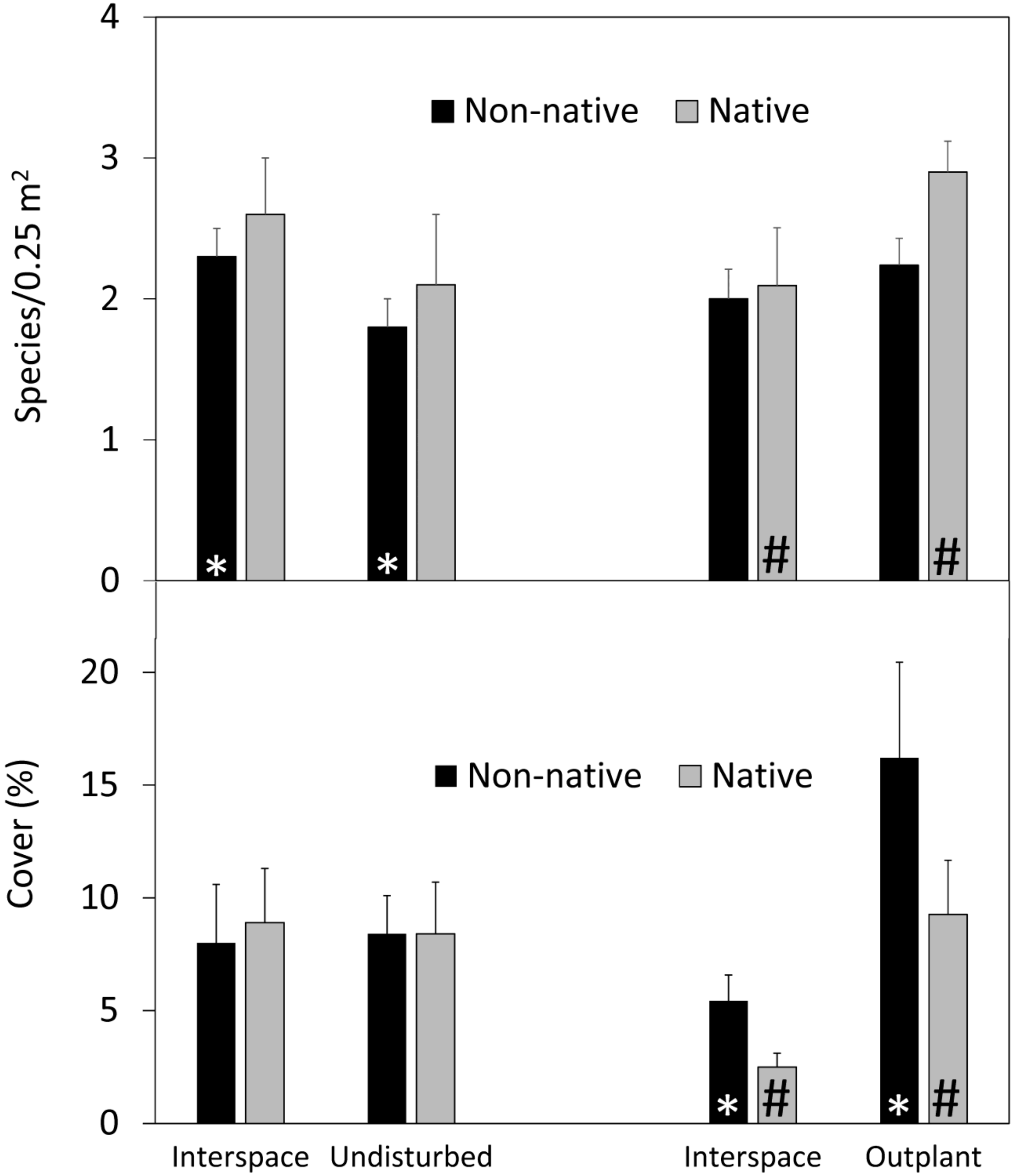
Non-native
Native
Species/0.25 m²
4
3
2
1
0
*
*
#
#
Cover (%)
20
15
10
5
0
*
#
*
#
Interspace
Undisturbed
Interspace
Outplant

Figure 5