



Increasing global aridity destabilizes shrub facilitation of exotic but not native plant species

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ABSTRACT

Earth's dryland (hyper-arid, arid, semi-arid, and dry sub-humid) ecosystems face increasing aridity and invasion by exotic plant species. In concert, these global changes threaten the biodiversity, ecosystem functioning, and economic viability of drylands worldwide, with critical implications for environmental quality and human wellbeing. Positive interactions (facilitation) from shrubs can buffer native plant communities against increasing aridity, but this could backfire if exotic species are facilitated more than natives. Thus, understanding how native and exotic plant species respond to shrub facilitation along aridity gradients is essential for predicting the ecological consequences of concomitant aridification and exotic plant invasion in changing drylands. Here, we performed meta-analyses using 152 independent studies to compare the positive effects of shrubs on native vs. exotic plant species across Earth's dryland ecosystems that vary in aridity. Globally, shrubs facilitate the abundance, diversity, reproduction, and survival of native plant species but do not consistently facilitate any measure of exotic plant performance. As aridity increases, shrub effects on native species do not change, but shrub effects on exotic species become more negative. Thus, across dryland ecosystems globally, shrubs facilitate more measures of native plant performance than exotic plant performance, and as aridity increases, shrub facilitation remains stable for native species but transitions towards resistance for exotic species. At the global scale, dryland aridification may pose a greater threat to exotic species than native species, inasmuch as shrubs and their interactions remain intact.

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1. Introduction

Drylands (hyper-arid, arid, semi-arid, and dry sub-humid ecosystems; Phillips et al., 2022) help sustain humankind. Drylands cover over 40% of the earth's land surface, comprise 44% of the world's arable land, support more than 50% of the world's livestock, and are home to over two billion people (Millennium Ecosystem Assessment, 2005). Drylands are also ecologically important, supporting high levels of endemism and therefore contributing substantially to global biodiversity (Davies et al., 2012). However, abiotic and biotic global changes are rapidly and severely degrading dryland ecosystems (Millennium Ecosystem Assessment, 2005; Huang et al., 2020; Phillips et al., 2022), including increasing aridity (aridification) (Huang et al., 2016) and accelerating biological invasions by exotic plant species (DiTomaso et al., 2010). Increasing aridity degrades drylands by exacerbating water scarcity, reducing the quality and quantity of primary productivity, reducing forage availability for livestock and wildlife, increasing susceptibility to erosion and soil loss, and accelerating the encroachment of invasive woody plant species (Havstad et al., 2018; Huang et al., 2020). Exotic plant invasions degrade drylands by displacing native plant and animal species, altering disturbance regimes, and drastically shifting patterns of biodiversity, nutrient cycling, and energy flow (D'Antonio and Vitousek, 1992; DiTomaso et al., 2010; Lucero et al., 2015). In concert, increasing aridity and exotic plant invasion endanger the biodiversity, ecosystem functioning, and economic viability of drylands worldwide (Garbowski et al., 2021; Ravi et al., 2021), with critical implications for environmental quality and human wellbeing (Reynolds et al., 2007; Muñoz et al., 2019; Hoover et al., 2020).

Positive interactions among species (facilitation) can mediate the ecological effects of aridification and exotic plant invasion in changing drylands. Facilitative interactions enhance biodiversity, ecosystem functioning, and multispecies coexistence in biological communities globally, but particularly in drylands (Callaway, 2007). Importantly, the stress-gradient hypothesis (SGH) asserts that facilitation is most important where environmental stress is greatest (Bertness and Callaway, 1994). In this context, positive interactions have the potential to buffer dryland communities against increasing abiotic stress associated with aridification (Armas et al., 2011). However, the community-level outcomes of positive interactions depend upon which species are facilitated most. For instance, native and exotic plant species in the same communities can respond very differently to positive interactions (Filazzola et al., 2020; Lucero et al., 2019, 2020). Theoretical (Northfield et al., 2018) and empirical (Cavieres, 2021; Lucero et al., 2021; Lortie et al., 2021) studies show that strong facilitation of invasive species relative to natives can accelerate biodiversity loss by increasing the abundance and competitive impacts of invaders. However, there remains considerable opportunity to investigate the predictability of these interactions along aridity gradients. This knowledge gap is significant because increasing aridity in drylands (Huang et al., 2016) is expected to shift biotic interactions away from competition and towards facilitation (He et al., 2013), potentially exacerbating the ecological disruptions of exotic and invasive species that capitalize on positive interactions (Garbowski et al., 2021). Thus, understanding how native and exotic plant species respond to positive interactions along aridity gradients is essential for predicting the ecological consequences of concomitant aridification and exotic plant invasion in changing dryland ecosystems.

Facilitation by shrubs is a useful framework for examining these global change issues. Across drylands globally, shrubs are a dominant and increasing vegetation class that have major effects on ecosystem functioning (Naito and Cairns, 2011; Eldridge et al., 2011). Shrubs often facilitate the biodiversity of dryland communities by creating favorable microsites that ameliorate environmental extremes and increase soil water and nutrients (Filazzola and Lortie, 2014). Species provenance (native or exotic status) and environmental severity influence the intensity of shrub facilitation (Armas et al., 2011; Lucero et al., 2019; Filazzola et al., 2020), but we do not understand these effects at the global scale. Our objective was to use meta-analysis of the literature to compare the intensity of shrub facilitation on native vs. exotic plant species along an aridity gradient spanning Earth's hyper-arid, arid, semi-arid, and dry sub-humid ecosystems. We hypothesized that 1) dryland shrubs affect the performance of native and exotic plant species differently, and 2) the intensity of shrub facilitation becomes more positive as relative aridity increases for both native and exotic plant species, consistent with the SGH.

2. Materials and methods

2.1. Systematic review process and data extraction

We performed a meta-analysis of the literature to compare the intensity of shrub facilitation on native and exotic plant species across Earth's dryland ecosystems. Here, we define exotic as a plant species that has been anthropogenically translocated from a distant native range to a novel non-native range, usually from one continent to another. We did not differentiate between exotic and invasive species because estimates of local impacts (i.e., community-level effects of exotic species) could not be extracted from primary articles. Importantly, we are unaware of any evidence that invasive species respond differently to shrub facilitation than exotic species as a whole. We did not delineate shrubs as primary (i.e., climax) or secondary (i.e., colonizing) vegetation because these designations are not necessarily species-specific, and because the disturbance history of study areas was seldom reported in primary articles. In April 2021, we queried the Web of Science using the terms 'shrub AND facilitat* AND positive'. Our search returned 642 peer-reviewed studies published between 1991 and 2021 in 150 different journals. Each of these studies were screened to meet the following criteria: 1) primary research article (i.e., no reviews, meta-analyses, or conference reports), 2) examined plant-plant interactions, 3) the facilitator species was a shrub, 4) study was conducted in a(n) hyper-arid, arid, semi-arid, or sub-humid ecosystem (cutoff criteria given below), 5) provenance of the beneficiary species was reported or able to be extracted, and 6) response data was available or able to be extracted. We identified 152 studies that met these criteria, resulting in 708 unique shrub-open contrasts ("instances") for the meta-analysis. When primary studies did not report the local provenance of beneficiary species, we extracted this information using the Plants of the World Online database (POWO, 2021). Further details of the review process and data extraction are shown in a PRISMA

figure (Fig. S1) (Moher et al., 2009).

Response measures of the plant community included plant abundance, diversity, growth, reproduction, and survival (see Fig. S2 for a histogram). Abundance was the density of plants per unit area. Diversity measures estimated species richness, evenness (Ruwanza, 2019), or indices of diversity such as the Shannon–Wiener (Khosravi Mashizi and Sharafatmandrad, 2020). Growth measures estimated plant biomass, root/shoot length, relative growth rates, or leaf area. Reproduction measures estimated recruitment directly or via proxies such as flower, fruit, cone, vegetative stem, or seed production. Survival measures estimated absolute or proportional plant survival over the study period. Extractable response data were defined as mean values for each shrub and open microsite, an estimate of variance, and specific sample size.

We extracted precipitation and temperature values in order to calculate an aridity index for all sites where unique instances occurred. Using the geospatial coordinates reported by the authors of each primary study, we extracted mean annual precipitation (mm) and temperature values (°C) for each study site from a $0.5 \times 0.5^\circ$ grid of downscaled climate data provided by the Climatic Research Unit of East Anglia (CRU, 2021). The mean was calculated using a 30-year average between 1990 and 2020, inclusively. This timeframe was selected because it represents the contemporary climate conditions of the study sites. We used these values to calculate a modified deMartonne aridity score for each instance (Eq.1). To assist in interpretation so that high aridity scores denoted highly arid conditions, we subtracted the classical deMartonne aridity index (deMartonne, 1920) from the maximum aridity score from our dataset (40). Therefore, values closer to zero represent dry sub-humid environments and values closer to 40 represent hyper-arid environments (Eq 1).

$$\text{Aridityscore} = 40 - \frac{\text{Totalannualprecipitation}}{(\text{Meanannualtemperature} + 10)}$$

Study sites with classical deMartonne aridity scores > 40 were not considered drylands (Pellicone et al., 2019) and were thus excluded from our synthesis.

We calculated the log response ratio (LRR) effect size metric for each instance (using the function ‘escalr’ in package metafor) by taking the natural log of the quotient of the shrub plot divided by the open plot. We used LRR because it produces effect estimates that are symmetrical around zero and sampling distributions that closely resemble a normal distribution (Viechtbauer, 2017). A LRR value of 0 would be no shrub effect on beneficiary species, positive values would be facilitative shrub effects, and negative values would be

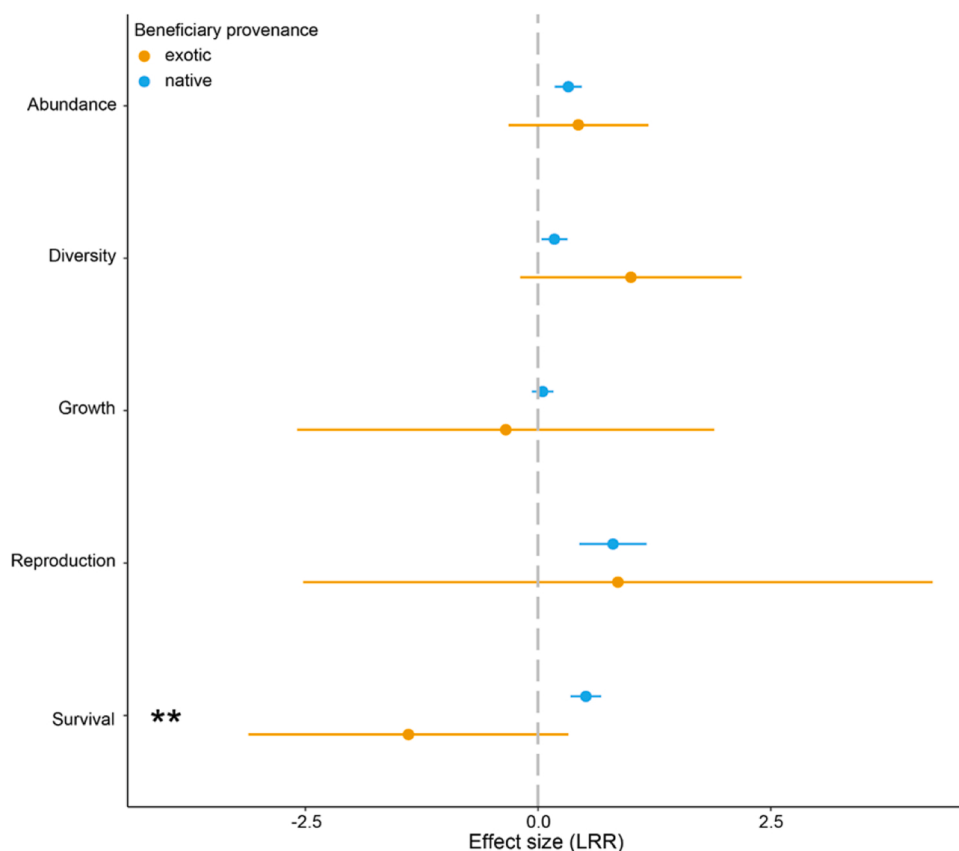


Fig. 1. Shrub effects (LRR) ($\pm$ 95%CI) on measures of native and exotic plant performance. Positive LRRs indicate positive effects, negative LRRs indicate negative effects. Asterisks indicate different ($p < 0.05$) effects on natives vs. exotics.

antagonistic shrub effects.

2.2. Meta-analyses

We conducted meta-analyses in R version 4.0.3 (R Development Core Team, 2020) using the package metafor (Purssell, 2015; Viechtbauer, 2017). To test whether shrubs had different effects on measures of native and exotic plant performance, we fit independent meta-analytic mixed models for native ($n = 673$) and exotic ($n = 35$) subsets of the dataset with LRR as the response variable, the study as a random effect, and response measure as a moderator. Confidence intervals were calculated using Wald-type intervals to determine whether LRRs differed significantly from zero.

To test whether aridity influenced the intensity of shrub effects on native and exotic plant species, we fit a meta-analytic mixed model with LRR for each instance as the response variable; the study as a random effect; and aridity score, beneficiary provenance, and their interaction as moderators. This model did not differentiate among response measures (abundance, diversity, growth, reproduction, survival). As there was a significant aridity score $\times$ provenance interaction, we fit separate meta-analytic mixed models for the native ($n = 673$) and exotic ($n = 35$) subsets of the dataset with LRR as the response variable, study as a random effect, and aridity score as a moderator.

For each meta-analytic mixed model, we evaluated heterogeneity and the potential for publication bias across studies. To assess heterogeneity, we conducted Q-tests and calculated heterogeneity test statistics (I^2). Significant ($p < 0.05$) Q-values and large I^2 statistics suggest meaningful interstudy heterogeneity. We assessed the potential for publication bias with funnel plots using function ‘funnel’ in R package metafor. Symmetrical funnel plots suggest no meaningful publication bias (Figs. S3-4). All statistical models were calculated using restricted maximum-likelihood estimates, as this approach is relatively robust to potentially biased estimates of population heterogeneity (Viechtbauer, 2017). Pairwise contrasts comparing plant response measures between native and exotic species was accomplished with general linear hypothesis testing using function glht in R package multcomp (Hothorn et al., 2008).

3. Results

Across Earth's dryland environments, shrubs facilitate more measures of native plant performance than exotic plant performance (Fig. 1). Across drylands, shrubs facilitate the abundance, diversity, reproduction, and survival of native plant species but do not consistently facilitate any measure of exotic plant performance (Table S1). Strikingly, across drylands globally, shrub effects on plant survival are more positive for native species than exotic species (Fig. 1, Table S2).

Increasing aridity differentially influences shrub effects on native and exotic species (Table 1). As aridity increases, shrub effects on native species do not change, but shrub effects on exotic species becomes less positive and more negative (Table S3). Said differently, as drylands become more arid, shrub facilitation of native species remains stable, but shrub facilitation of exotic species breaks down and transitions toward resistance (Fig. 2) – the opposite pattern predicted by the SGH. We detected significant heterogeneity across studies (Table 1, S3) but no publication bias (Figs. S3-4).

4. Discussion

Dryland shrubs and their interactions have considerable potential to buffer native plant species against the synergistic effects of aridification and exotic plant invasion. Increasing aridity is the leading cause of land degradation in drylands (Geist and Lambin, 2004), and drylands are expected to become more arid as our planet warms (Huang et al., 2016). Bioclimatic modeling shows that aridification and exotic plant invasion can synergistically degrade dryland ecosystems (Ravi et al., 2021), though it is clear that not all dryland systems are equally vulnerable to invasion, and not all exotic species will respond equally to climate change (Thuiller et al., 2008; Bradley et al., 2010; Catford et al., 2011; Bellard et al., 2013). Nonetheless, because shrubs consistently facilitate more measures of native plant performance than exotic plant performance (Fig. 1), and because shrubs increase resistance against exotics as aridity increases (Fig. 2), dryland aridification may ultimately pose a greater threat to exotic species than native species, inasmuch as shrubs and their biotic interactions remain intact. Of course, this does not overshadow the importance of species-specific responses at finer spatial scales (Filazzola et al., 2020).

Our synthesis enriches our understanding of the species-specificity of positive interactions. We have long known that not all species are facilitated equally (Callaway, 1998), but only more recently have we begun to understand the ecological implications of

Table 1

Results of a meta-analytic mixed model with LRR as the response variable; modified deMartone aridity score (Aridity), beneficiary provenance (Provenance), and their interaction (Aridity $\times$ Provenance) as moderators; and study as a random effect (not shown). Results of the corresponding interstudy heterogeneity analysis are also given.

Term	Meta-analysis				Heterogeneity		
	Estimate	SE	z-value	p-value	I^2	Q_E	p-value
Intercept	1.090	0.310	3.450	< 0.001	99.13%	4,0267.3	< 0.001
Aridity	-0.049	0.017	-2.860	0.004	99.13%	4,0267.3	< 0.001
Provenance	-90.910	0.330	-2.740	0.006	99.13%	4,0267.3	< 0.001
Aridity $\times$ Provenance	0.054	0.018	2.950	0.003	99.13%	4,0267.3	< 0.001

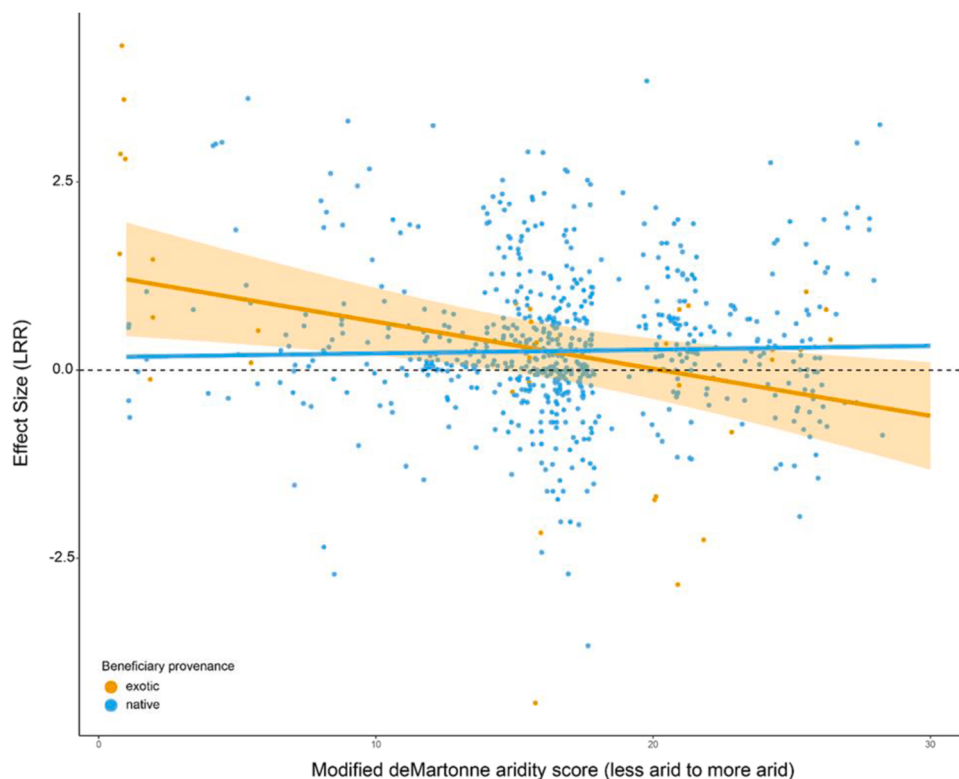


Fig. 2. Shrub effects (LRR) meta-regressed against aridity for native and exotic beneficiary species. The significant regression (for exotic species) is shown with a 95% confidence band. Positive LRRs indicate positive effects of shrubs, negative LRRs indicate negative effects of shrubs.

provenance-specific facilitation (Northfield et al., 2018). Strong facilitation of exotic and invasive species relative to natives can accelerate the degradation of plant communities both directly (Cavieres, 2021) and indirectly (Lortie et al., 2021). Recent studies at local (Lucero et al., 2019) and regional (Lucero et al., 2021) scales have reported that dryland shrubs facilitate exotic species more strongly than natives at the provenance level. However, our synthesis suggests that this is not the case globally.

It is not necessarily surprising that, at the global scale, increasing aridity destabilizes shrub facilitation of exotic but not native plant species. Positive interactions influence the evolution of ecological niches (Verdú et al., 2021), and native species presumably share a longer co-evolutionary history with one another than with their exotic counterparts. Thus, it is not unexpected that positive interactions should be more stable between native shrubs and native neighbors than between native shrubs and exotic neighbors. To this point, we emphasize that practically all primary studies relevant to our synthesis evaluated the effects of *native* shrub species.

Our findings underscore a rich literature showing that environmental context mediates the intensity of species interactions, though not always as predicted by the SGH. Meta-analyses across taxa and biomes have returned broad support for the SGH (Lortie and Callaway, 2006; Dohn et al., 2013; He et al., 2013; Dangles et al., 2018). However, support for the SGH along aridity gradients is more nuanced (Michalet et al., 2014; Filazzola et al., 2020), with some studies indicating that the SGH does not always “hold water” in drylands (Butterfield et al., 2016). In this context, we found no support for the SGH for either native or exotic plant species. This differs from the synthesis of He et al. (2013), which found that increasing environmental stress mediated global shifts towards positive interactions for both natives and exotics (also see Lortie and Callaway, 2006; Dohn et al., 2013). However, our synthesis focused on the effects of shrubs, whereas He et al. (2013) did not focus on any particular group of potential facilitators. Rather, our results are consistent with Filazzola et al. (2020), who found that dryland shrubs facilitated exotic plant species most where relative aridity was lowest, suggesting that the risk of shrub-facilitated invasion was greatest under the most mesic conditions. This matches theory and experimentation that invasion success is greatest where abiotic resources are relatively plentiful (Davis and Pelsor, 2008).

Why might native and exotic plant species respond differently to shrubs as aridity increases? We propose that natives and exotics respond differently to covariation in water and nutrient availability near shrubs. Perennial facilitators often increase nitrogen and other soil nutrients under their canopies (reviewed by Callaway, 2007; Filazzola and Lortie, 2014), and increased nutrients tend to disproportionately benefit exotic and invasive species relative to natives (Levine et al., 2004; Davis and Pelsor, 2008; Besaw et al., 2011). However, nitrogen availability decreases substantially when soil water is low (Plett et al., 2020) – a condition that native species may tolerate better than exotics (Besaw et al., 2011; Shivega and Aldrich-Wolfe, 2017). In this context, we suggest that in relatively mesic (i.e., dry sub-humid) dryland conditions, where soil water is less limiting, exotic species readily capitalize on the islands of fertility associated with shrubs (Schlesinger et al., 1996), perhaps even better than natives (Lucero et al., 2019). However, we suggest that this advantage wanes as aridity increases due to drier soils that make the nitrogen within islands of fertility less available.

As aridity increases, competition for limited water may also intensify. Several studies have reported increasing interspecific competition for water at the driest end of water gradients (reviewed by Michalet et al., 2014). Antagonistic effects of native shrubs on exotic species (biotic resistance) could increase with aridity if established shrubs are generally stronger competitors for limited water than exotic neighbors, which is well documented in mixed shrub-herbaceous communities (Ryel et al., 2010; Zhang et al., 2016). In this context, an exciting next step would be to experimentally quantify the competitive effects of native shrubs on herbaceous native and exotic neighbors along mixed water and soil nutrient gradients.

Our understanding of the global impacts of shrub facilitation on exotic species is based on limited information. Our synthesis included 708 independent shrub-open microsite contrasts, but of these, only 35 examined the potential for shrubs to facilitate exotic species (Fig. S2). This relatively small sample size helps explain why error estimates for LRRs specific to exotic species were far larger than those for native species (Fig. 1) and suggests that many more studies are needed for more precise comparisons of shrub facilitation on native and exotic beneficiaries along stress gradients. In this context, our statistical contrasts of shrub effects on native vs. exotic species could potentially be viewed as conservative (i.e., susceptible to false negatives at the $\alpha = 0.05$ level). Shrub facilitation is a driving force in the organization of dryland plant communities (Callaway, 2007), but our synthesis reveals that the potential for shrubs to influence the performance of exotic species, and therefore the trajectory of plant invasions, has been understudied in dryland ecosystems.

Our results suggest a cautious approach for managing shrub encroachment. Many studies have found that shrub encroachment into dryland herbaceous plant communities can reduce landscape-level productivity and alter economically important ecosystem services (Eldridge et al., 2011). Mitigating these effects has been a major focus of land management efforts globally (Pilliod et al., 2017; Davies et al., 2012). However, we find that dryland shrubs consistently increase the abundance, diversity, reproduction, and survival of native plant species, and in the most arid environments, can potentially resist exotic invaders. Shrub encroachment is not always desirable, but management actions that conserve dryland shrubs and their biotic interactions may help secure vital ecosystem services supplied by native plant species in changing drylands (see also Maestre et al., 2009).

5. Conclusions

At the global scale, shrub facilitation of exotic species has attracted far less empirical attention than shrub facilitation of native species. Nonetheless, we found that across drylands globally, shrubs facilitate more measures of native plant performance than exotic plant performance, and shrub effects on plant survival are more positive for native species than exotic species. As drylands become more arid, shrub facilitation of native species remains stable, but shrub facilitation of exotic species breaks down and transitions toward resistance. Thus, at the global scale, dryland aridification may pose a greater threat to exotic species than native species, inasmuch as shrubs and their interactions remain intact.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

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Author contributions

JEL, CJL, AF, and RMC conceived the study; AF, CJL, and JEL designed the methodology; JEL, AF, JB, NG, SH, MFM, MO, MS, MZ, and CJL screened the primary articles and entered the data; AF performed the meta-analyses and data visualizations; JEL wrote the manuscript; RMC, AF, MS, and CJL led the editing and revision. All authors contributed substantially to the article.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02345](https://doi.org/10.1016/j.gecco.2022.e02345).

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