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Drivers of seedling establishment success in dryland restoration efforts

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Restoration of degraded drylands is urgently needed to mitigate climate change, reverse desertification and secure livelihoods for the two billion people who live in these areas. Bold global targets have been set for dryland restoration to restore millions of hectares of degraded land. These targets have been questioned as overly ambitious, but without a global evaluation of successes and failures it is impossible to gauge feasibility. Here we examine restoration seeding outcomes across 174 sites on six continents, encompassing 594,065 observations of 671 plant species. Our findings suggest reasons for optimism. Seeding had a positive impact on species presence: in almost a third of all treatments, 100% of species seeded were growing at first monitoring. However, dryland restoration is risky: 17% of projects failed, with no establishment of any seeded species, and consistent declines were found in seeded species as projects matured. Across projects, higher seeding rates and larger seed sizes resulted in a greater probability of recruitment, with further influences on species success including site aridity, taxonomic identity and species life form. Our findings suggest that investigations examining these predictive factors will yield more effective and informed restoration decision-making.

Restoration ecology is rapidly advancing in response to the ever-expanding global decline in ecosystem integrity and its associated socio-economic repercussions[1–4]. Nowhere are these dynamics more evident than in drylands, which help sustain 39% of the world's human population[5] but remain some of the most difficult areas to restore[6,7]. Restoration of degraded dryland ecosystems is frequently constrained by low and variable precipitation, extreme temperatures, relatively low soil fertility, seed quality and availability and a prevalence of invasive species[8–11]. As a result, successful establishment of seeded species in dryland restoration projects may be as low as 1%[12,13]. Despite these challenges, only a small fraction of terrestrial ecology (6%)[14] and restoration studies (<5%)[15] are conducted in drylands.

Dryland ecosystems are ecologically distinct[16,17], increasing in global extent under shifting climates[18–20] and have been recognized as degraded in over 50% of their range[21]. Depending on the severity of degradation, vegetation recovery of depleted and denuded dryland landscapes through natural succession processes is very slow, if not impossible[22]. Passive restoration methods (for example reducing livestock and wildlife grazing) are often ineffective alone, as degraded dryland environments can show stability and resilience in undesired states[11]. Resource-intensive methods such as seedling

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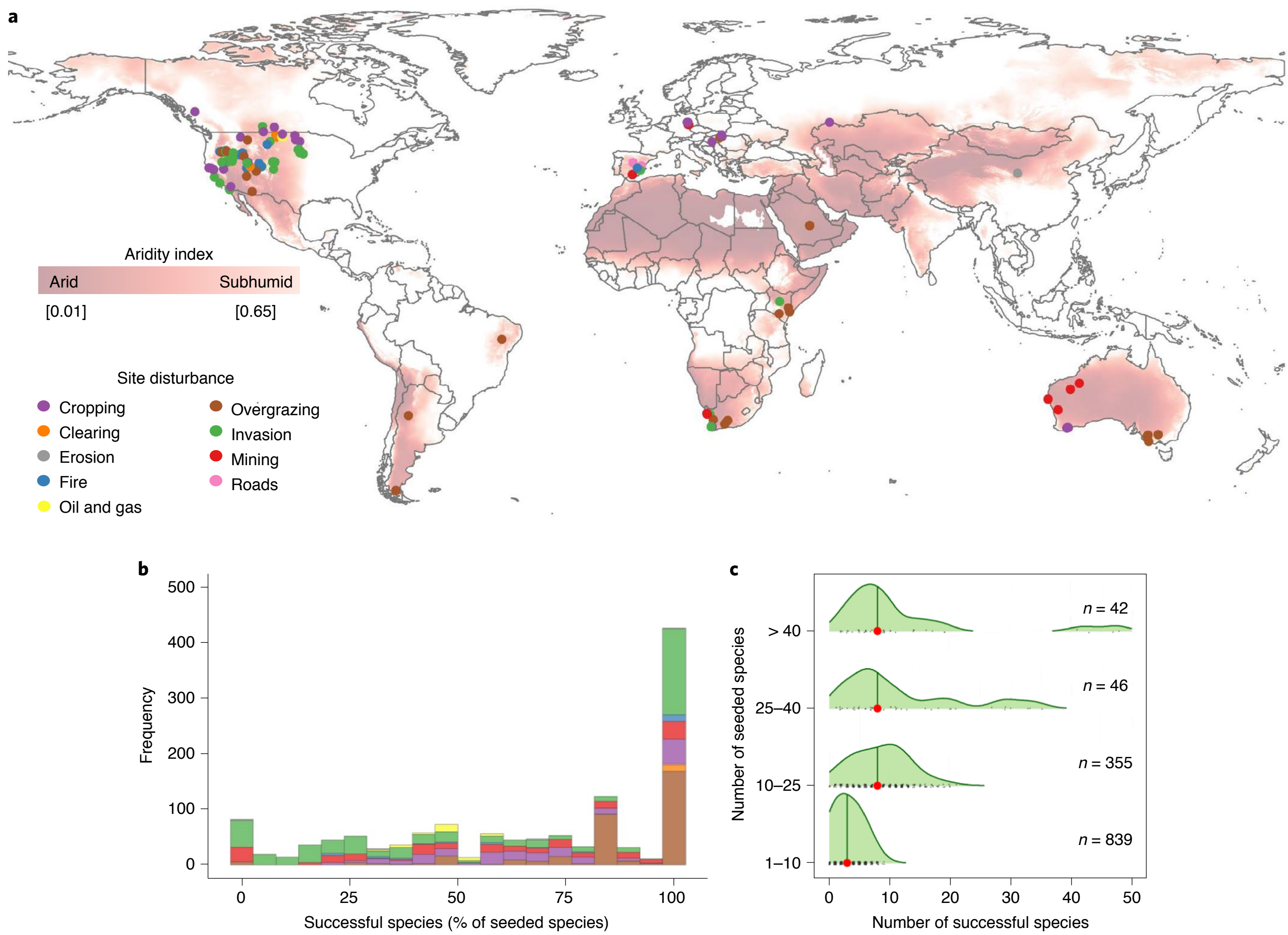

Fig. 1 | Restoration seeding in drylands globally showed limited but promising success. a,**b**, The distribution of restoration sites spans drylands globally, with restoration seeding triggered by a variety of anthropogenic disturbances (as shown in **b**). Note that a single point in **a** covers a diameter of >250 km due to the mapping scale; if project sites are closer than that distance, a single point represents more than one project. **b**, We found evidence that a portion of projects had a high proportion of successfully seeded species. For instance, in 30% of projects, all seeded species were recorded during monitoring. We also found that dryland restoration seeding is somewhat of a gamble, with none of the seeded species recorded in 17% of projects. **c**, While seeding more species would be expected to lead to greater species richness, there was a limit to this increase. Rarely did a project record more than 10–15 successful species, regardless of the number of species seeded.

transplants or prescribed fire can be used for dryland restoration, but often logistical challenges or expense limit the widespread application of these techniques[23–25]. Consequently, seeding is a widely used approach for dryland restoration[26,27], generally because it is an intuitive and spatially feasible strategy to reintroduce desired species[28]. It is clear that seeding in dryland ecosystems is challenging, with most projects exhibiting low germination and establishment success[29], and high mortality in the development from seedling to adult plant[13]. Yet seeding remains one of the only viable methods of reintroducing or enhancing populations of native species at large scales in natural settings. Thus, it is essential to understand what elements contribute to overall seeding success.

Here we present a large-scale assessment of restoration seeding in drylands. Well-documented restoration seeding trials and controlled experiments allowed us to compare restoration outcomes over a range of biotic and abiotic conditions[30]. This is important because restoration trajectories are driven by a series of ecological assembly filters[31]—processes that sort and narrow the pool of potentially establishing species based on the intersection of site conditions, exogenous factors and species' traits[32]. In restoration, filter models have most commonly focused on abiotic constraints, such as resource availability; external factors, such as disturbance type or limitations in propagule sources; and biotic constraints, such as priority effects and competition from resident species. Large data synthesis allows many of these factors to be assessed in a single framework over wide ranges of each potential variable. We sought to elucidate general drivers in dryland restoration seeding efforts, as well as identify whether there are key sources of unexplained variability. While the ultimate goals of restoration vary among projects (such as increasing habitat value, reducing erosion, reducing fire risk and so on), we focused on a response variable common to all types of seed-based restoration efforts: whether projects were able to establish target species. A small number of restoration trials included seeding exotic species, either as desired species for key ecological functions or as experimental treatments to understand effective control methods. Our analysis included any seeded species and we assessed species success without distinction based on origin to understand general drivers of species-level outcomes. We measured species-level seeding success based on species occurrence (density or cover >0) at the sampling unit level, so that our final response variable was the probability that a species was present in an individual replicate, also referred to here as 'species success' or,

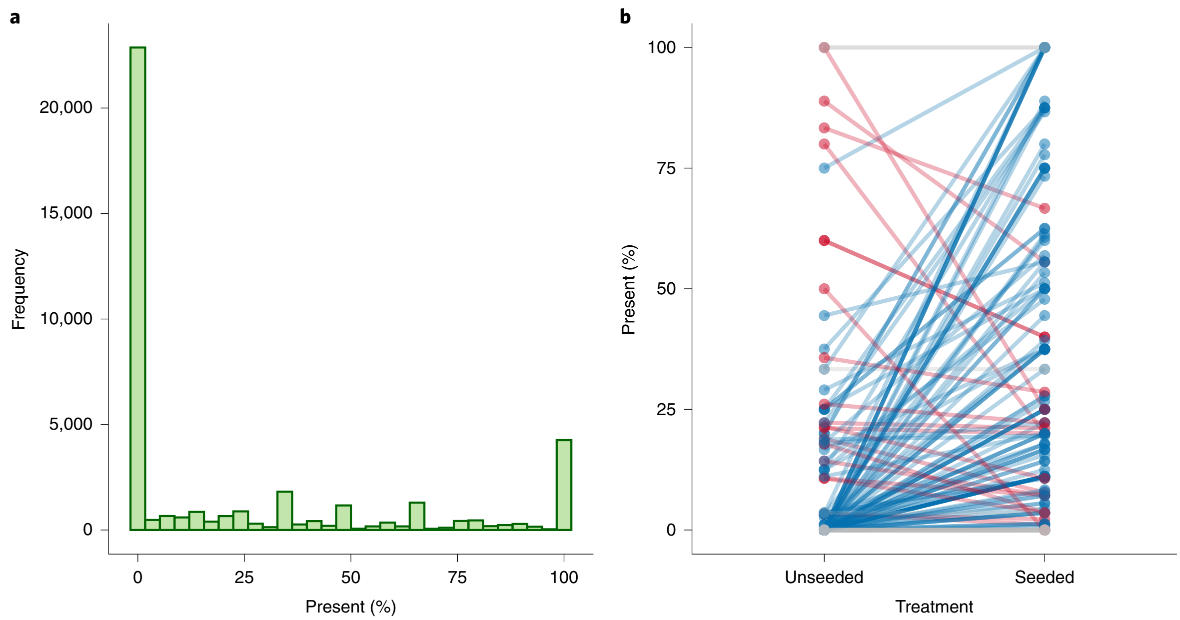

Fig. 2 | Individual species failed often, but seeding still resulted in significantly increased success for target species. a, Within a restoration treatment, individual species success (defined as the probability of a species being present during monitoring) was relatively low, with 57% of species failing to recruit when seeded. **b**, Seeding did, however, clearly increase success in seeded treatments compared with unseeded controls, with each line in **b** representing the difference in success of one species in an unseeded and seeded treatment pair. Blue lines indicate greater success in seeded treatments and red lines indicate greater success in unseeded controls. The prevalence of lower success of target species in control treatments emphasizes the role of propagule limitation in these systems. The same methods were used for measuring success in unseeded controls and seeded treatments.

more generally, 'success'. It is important to note that, as with any synthesis effort, some biases exist in the database. The most influential in this analysis are probably caused by the geographic prevalence of western regions, specifically North America, and the predominance of experimental studies at relatively small scales.

Results and discussion

Our database reflected widespread patterns of dryland degradation (Fig. 1a), where restoration seeding projects were implemented in response to a variety of disturbances that ranged from mining and road construction to erosion and fire. Overall, plant invasion was the most reported disturbance and it often accompanied cropping, grazing and fire, which probably led to positive feedbacks between degradation pressures[33,34]. In almost a third of projects, all seeded species had some individuals that established (Fig. 1b). The inherent risk of seeding in drylands was also apparent: in a distinct set of projects (17%), seeded species were not detected during the monitoring period. Most projects seeded fewer than ten species and the number of species present did not consistently increase with the number of seeded species (Fig. 1c); only rarely (12%) were more than ten seeded species present during the first sampling period in a given treatment.

As a result, the success of an individual species was low, aligning with other studies of dryland seedling recruitment[12,13]. In 57% of the individual species records, the species failed to recruit in any surveyed replicate across time (Fig. 2a) and on average species were successful—that is, recorded—in only 24% of replicates within a treatment. Seeding was key for a successful outcome: the majority of targeted species were more common after seeding, with almost a doubling of overall species success (Fig. 2b). There were a small number of instances where the seeded species was more likely to be found in unseeded controls than in seeded treatments (6% of studies). This could be due to seed sourcing, for example if the provenance of seed used for treatments was not appropriate for the region[35], while unseeded controls may have had an in situ seed bank of locally adapted seed that allow for passive recovery. Alternatively, incorporation of highly competitive species in seeded areas may reduce the success of competitively inferior species and could lead to greater success of these species in unseeded controls[36].

Given these overall patterns, we then explored the most generalizable predictors that could characterize the presence of a target species after seeding efforts. We focused our analysis on three factors that could be critical determinants of successful dryland restoration seeding projects, reflecting different aspects of potential ecological filters. First, the rate of seeding is the primary method of overcoming propagule limitations, and it varied in these projects from 1 seed m^{-2} to over 7,000 seeds m^{-2}. Second, abiotic filters in drylands are most closely linked to water limitation, captured in our data using the global aridity index (annual precipitation/annual potential evapotranspiration)[37]. Third, a prominent biotic filter was considered: the competitive effects of other species. Management of competitive effects in restoration commonly focuses on controlling weed invasion—that is, reducing the abundance of species viewed as barriers to restoration goals. This was reflected in our database; weed control was the most commonly used management tool in drylands, occurring in 46% of treatments. Thus, controlling weed invasion was used to assess the role of biotic filter management (that is, reducing competition) in restoration outcomes. We considered three factors that may affect how seeded species respond to these ecological filters. First, the influence of species characteristics that drive seedling growth patterns and longevity, here captured as a factor combining life form and lifespan; second, seed size, which can interact with the environment to influence restoration success[38]; and third, taxonomic identity, which probably represents unmeasured phenotypic traits.

As would be predicted in the dynamics of seed-limited populations, adding greater numbers of seed was an important predictor of success (Fig. 3a). On average, the predicted probability of success increased sharply with increased seeding rate. This high

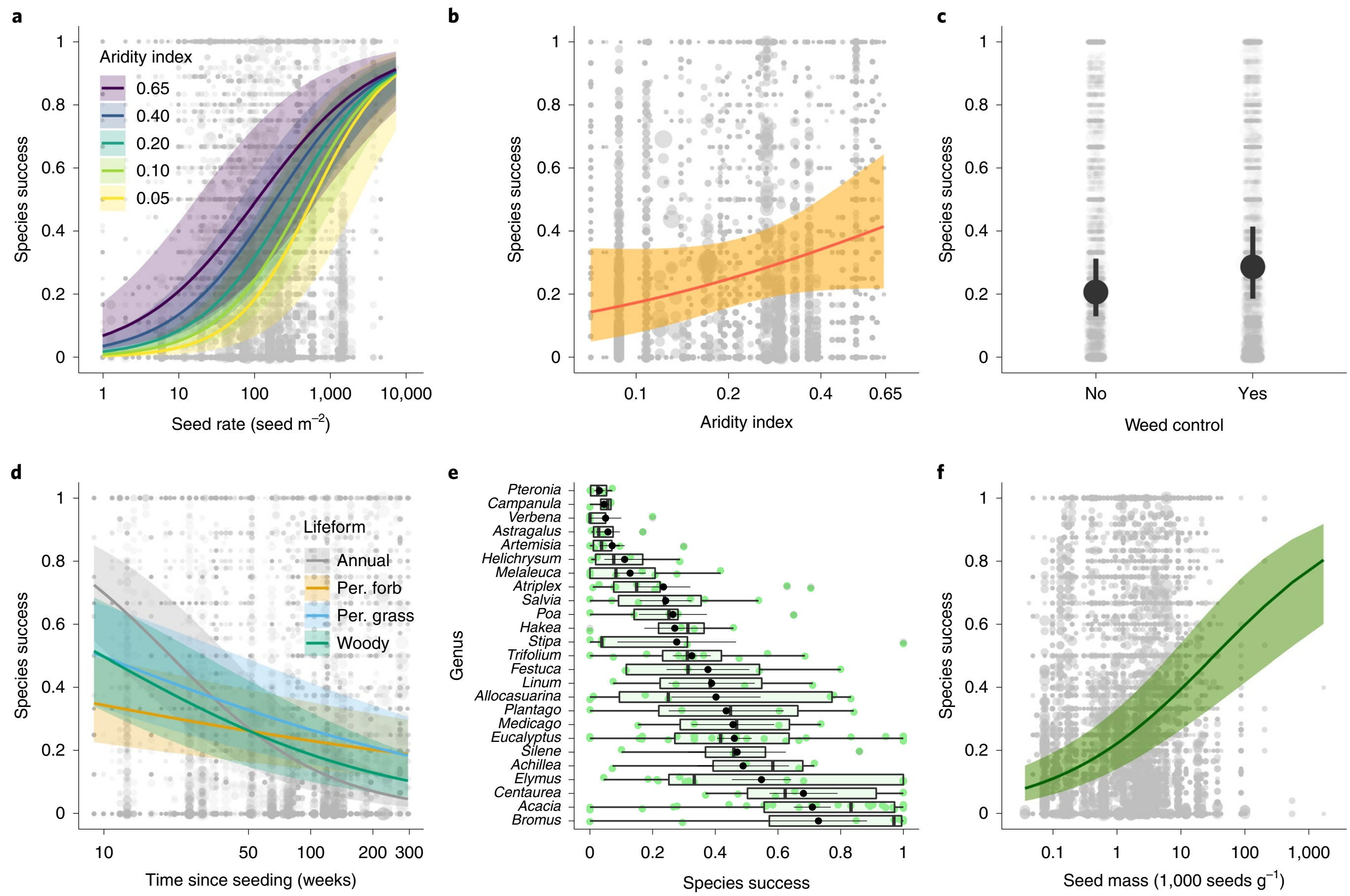

Fig. 3 | There were clear predictors of seeding success. **a**, Success is influenced by ecological filters and species characteristics including propagule limitation, where increasing seed rates lead to dramatically higher rates of species success. This relationship was mediated by site aridity, with more mesic sites benefiting less from additional seed inputs. The main effect of aridity emphasizes the importance of abiotic filters (**b**), where aridity (that is, values close to zero) depresses the probability of restored species success. **c**, Managing competitive effects with weed control led to modest gains in species success. **d**–**f**, Intrinsic species characteristics such as plant functional type (**d**), taxonomic grouping (**e**) and seed mass (**f**) affect species success, with the strategies that characterize annual species leading to initially high success followed by more rapid declines over the first six years of monitoring; some genera have higher probabilities of success than others and seed size has an overall positive influence on species success. Solid lines (**a**,**b**,**d**,**f**) and dots (**c**) indicate population-level predictions (that is, marginal means) conditioned on the fixed effects. Confidence bands and error bars represent 95% confidence intervals (CI).

seeding rate is likely to be well outside the resources available for most restoration seeding projects, as seed is an expensive component of restoration projects. Thus, while increasing seeding rates may lead to higher success rates, it can be limited by financial and biological resources[31].

It would be tempting to increase seeding rates by increasing application of less expensive seed, but it is important to note that our study assessed seeding rates on a per species basis. That is, the likelihood of a given species recruiting at a site increased only when its own seeding rate was elevated, and we did not analyse effects of seeding rates of other species. Mixes are often dominated by species that have less expensive seed and higher overall likelihood of recruitment[39]. Increasing seeding rates uniformly over such a mix would be likely to increase competitive pressure on less competitive species[40]. This common seeding practice may influence our results through a form of sampling bias, as many of the species with the highest seeding rates are also likely to be species that are more financially and biologically available and may therefore also be easier to recruit. We note, however, that although the optimal seeding rate may be difficult to implement, our data suggest that for seeding rates below the optimum, any additional seed inputs should have strong and immediate impacts on restoration seeding success.

Influence of seed rate was mediated by site-level aridity. Overall, arid sites showed much lower probabilities of a species being present under similar seed rates (that is, 32% lower success in drier sites with 100 seeds m^{-2}). However, the benefits of adding additional seeds led to more rapid increases in success in arid sites (Fig. 3a), up to the extremely high seed rates where success was high regardless of climate. On more mesic sites, fewer seeds may be needed to enhance species success because of the increased success of individual seeds in wetter regions. Although this is an important finding for planning project-level seed rates in the most arid sites, it is important to recognize the generally depressed rates of species success at the majority of seeding rates in arid sites (Fig. 3b), emphasizing the strength of abiotic constraints in these systems. As sites become increasingly arid, the predicted success rate fell from about 42% [CI 22–64] to 14% [CI 5–35], with the decline being strongest at the dry end of the gradient. These patterns were slightly different when considering North America only, where, notably, the most arid sites benefited from the addition of more seeds, but never quite reached the levels of success observed in the full database (see Supplementary Note 3 for the full North American results). Thus, the expense of increasing seed rates in arid sites comes with an increasing cost of unsuccessful seed inputs. This finding quantifies the well-established fact that water availability is a key constraint for seedling establishment and survival[41]. While we assessed average long-term site aridity here, it is likely that other factors such as extreme weather events following seeding or the site-level pattern of rainfall received within the first season after seeding[29], as well as landscape and soil characteristics, also play a role in influencing restoration seeding success in arid sites[42,43]. Indeed, nearly a third of the variance in success metrics was due to site-level random effects that were unmeasured in our study, emphasizing the need to incorporate factors such as other sources of environmental variation (for example topographic and edaphic factors) in assessing restoration seeding outcomes.

While weed control positively influenced the probability of restoration seeding success over time, the effect size was surprisingly small: weed control only resulted in an 8% increase in probability of species success over time (Fig. 3c). Since many disturbance types in arid environments typically promote the proliferation of weed species, we expected that weed control would be an important action to reduce competition and enhance the probability of species success[44]. Within our database, however, invasion was most common in specific regions (North America and Europe) or after particular disturbance types (cropping, grazing and fire). Thus, many projects that did not apply weed control were in regions that did not report invasion as a problem, or in disturbances such as mining or erosion, where abiotic factors outweigh biotic competition. As our database continues to develop, these patterns of management outcomes may be more comprehensively assessed. In our analysis of North America only, for example, where invasion is a commonly cited restoration motivator, there was a slightly greater positive impact of weed control, with an increase of 9% as opposed to 8% in the full database.

Probability of species success decreased significantly over time, contingent on plant functional type. Seeded annual species had the highest predicted initial success (~72%) relative to other plant functional types, with a nonlinear decline through time to reach a probability of ~5% after six years (Fig. 3d). Although they were not frequently seeded and sometimes represented seedings of non-native species, patterns of recruitment and decline in annual species are consistent with their life history strategy[45]. Disturbance-oriented native annuals have shown promise as competitors with invasive species in drylands[44,46], and these results highlight that annual plants could play an important role in initial site stabilization. While initially high, annuals had the lowest predicted success at the end of our time window, and although their seeds can remain dormant for decades and may return years after initial establishment[47,48], their life history strategies may represent a barrier to long-term retention in restoration projects. Perennial forbs had the lowest initial success of the four plant functional types analysed, but increased to have probabilities of species success similar to those of perennial grasses after six years. Perennial forbs are known to have a diversity of dormancy characteristics and germination requirements[49] that could delay germination, possibly contributing to low initial presence but increased species success over time.

By its nature, our database contains many unidentified variables that differ among studies but almost certainly contribute to species success in projects, resulting in high variation despite overall trends (Fig. 3). For example, we cannot identify species that are particularly effective for use in restoration seeding projects, as they would differ by region and project. However, we note that in our models, species identity accounted for 50% of explained variance of random effects and 30% of all variation in success. This might reflect differential success of species belonging to taxonomic groups which share traits that influence plant growth and survival in arid ecosystems (that is, reduce water loss or increase resource acquisition). For example, in our database, species from the genus *Bromus* (Poaceae), *Acacia* (Fabaceae) and *Centaurea* (Asteraceae) showed high average success across species (Fig. 3e). This result highlights that careful species selection is a key step to increase success of seed-based restoration projects[50]. Finally, we found that seed mass had an overall positive influence on the presence of individual species (Fig. 3f), although again there was high variation surrounding this overall trend (see Supplementary Note 4 for further details on the database taxonomic composition). Thus, our results indicate that dryland restoration trials which test the efficacy of seeding multiple species at different seeding rates, as well as efforts to understand barriers to establishment for genera with lower average success and further investigation of the role of seed size on successful establishment, would be excellent areas of research.

To our knowledge, our database is the largest collation and analysis of restoration projects from any ecosystem type, and we aim to increase participation and contributions as we move the vast majority of the database into the public domain. The database has continued to grow since the analysis began and we welcome any additions (www.drylandrestore.com). In particular, we have few datasets from arid regions in Asia, the Eurasian dry grassland belt and adjacent desert and semidesert regions, and dryland areas of North Africa. Thus, our results under-report restoration efforts from these regions and results may be biased by areas with larger samples, such as western North America. Additionally, other factors, such as the amount and timing of precipitation in the year of seeding, seeding timing and seeding methods, are all known to affect outcomes in some species, and almost certainly contribute to the variation observed among studies; the variation observed among our datasets indicates many possible explanatory factors that have yet to be explored. Increasing the breadth and depth of this resource will allow deeper assessment of predictor and response metrics, as well as the ability to study interactions among causal factors; such additions would help translate our observations of overall trends into specific recommendations for restoration practice. Finally, future restoration needs to account for possible climate change scenarios and land-use policies, carefully selecting species that can persist in a changing world. The need is great for restoration science to make rapid advances in the next decade, especially in global drylands, and we can only meet that need by synthesizing our shared knowledge to provide guidelines and recommendations for practitioners and land managers.

Methods

GAZP database. The Global Arid Zone Project (GAZP) is an international collaboration aimed at developing a spatially extensive, long-term and continually expanding database. The curated primary datasets included in GAZP meet the following criteria: they describe a restoration project (that is, a project aimed at 'assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed'[51]) located in drylands (that is, an area receiving less than 600 mm of precipitation per year, with an aridity index at or below 0.65) and included seeding a minimum of three species. Single species monoculture treatments were accepted where multiple monocultures were implemented in the same project.

All data were collected directly from researchers or practitioners and then processed into a set database structure. Data collection began in January 2018 and is ongoing. For the purposes of this analysis, we used data collected up until August 2019, reflecting a total of 20 months of active collection and processing time. As of this analysis, the database encompassed 89 independent studies covering 174 individual sites, 1,632 treatments and 594,065 observations from 671 species (see Supplementary Note 1 for details). Seeded species represent a wide range of taxonomic groups and phylogenetic lineages, including plant species from 29 orders, 66 families and 339 genera (see Supplementary Note 4 for a breakdown of the database phylogeny). The data include species outcomes for any seeded species, regardless of whether they were native or exotic to the restoration site.

Species terminology and measurement units were standardized across datasets. Plant names were standardized after The Plant List v1.1 database[52] (see Supplementary Note 1 for full protocol details). All spatial measurements were converted to m or m^2, all coordinates were converted to decimal degrees, volumetric measurements were converted to mL and temperature to °C, and all seeding rates were transformed to estimated seeds per m^2. Many datasets were provided in weight of seeds per area and these were transformed using seed weight averages from the Seed Information Database[53]. This allowed all datasets to include the same treatment structure of seeds/area, which could be linked to at least a subset of the response data in plants/area.

We acquired site-level data for each project to evaluate environmental drivers of restoration success. Data included coarse topography, historical climate and land cover class information. We also collected species-level trait data, primarily from the TRY database[54] (see Supplementary Note 1 for the full methods and details of the database). Site preparation data were noted where available in our database, but few studies conducted site preparation work and as such we were limited in how it could be incorporated into our analyses. Similarly, soil information was infrequently available for studies in our database, and at present there are no consistent soil classification maps available at a global scale that match the site-level scale of the database. Similarly, a global dataset on ecologically relevant climatic and weather pattern data is currently unavailable, although efforts to create such databases are currently underway (SoilTemp, https://soiltemp.weebly.com/).

Restoration success. We measured success based on occurrence (density or cover >0), a criterion that meets the minimal requirement for restoration seeding success. For each sampling unit within a treatment, we recorded a target species as either present or absent. Thus, the final response variable was the probability that a species was present in a single sample point across a whole treatment, referred to throughout the text as the 'probability of species success' or just 'success'. We assessed the influence that seeding had on success in the first monitoring point for each project that contained an unseeded control. The same metrics were used to quantify unseeded controls and seeded treatments. Additionally, we assessed trends through time for all projects in the database, with or without unseeded controls, by modelling success across all time points up to six years, with the number of weeks since seeding as an additional predictor. While a simple presence score may seem like a low bar for success, and may not work for categorizing restoration outcomes in regions with more favourable conditions, we found that there was considerable spread and many failures using this response variable, indicating that it can be a meaningful measure of restoration outcomes in dryland systems.

Predictor variables. We focused on three external predictors of species success. These included biotic and abiotic filters including species inputs (seeding rate, dispersal filter), site conditions (site aridity, abiotic) and site treatments (weed control, biotic). We also considered three factors that may affect how seeded species respond to these ecological filters. First, the influence of species characteristics that drive seedling growth patterns and longevity, here captured as a factor combining life form and lifespan; second, seed size, which can interact with environment to influence restoration success; third, taxonomic identity, which probably represents unmeasured phenotypic traits. Seeding rate was included as seeds per m^2, and was log-transformed then centred and standardized with a z-score transformation[50]. To maintain a relatively continuous distribution of seeding rate, we excluded any data that seeded at rates higher than 10,000 seeds per m^2 (see Supplementary Note 2 for detailed statistical protocols). This resulted in the exclusion of 0.03% of the total dataset.

Life form was included as a categorical predictor. This was determined for each species as each dataset was processed and was assigned as either annual, perennial graminoid, perennial forb or woody species. The assignment per species combined data from TRY on lifespan and Raunkiaer on life form, the contributor's data if included and online sources such as the USDA Plants Database[55] and the Western Australian Florabase[56]. Seed mass was extracted on a per species basis from the Seed Information Database[53] and was log-transformed, centred and standardized with a z-score transformation. Species identity was included as a random predictor and then residuals were explored against species, genus and family classifications. We calculated an aridity index for each site by dividing the site-level mean annual precipitation[57] by mean annual potential evapotranspiration[37,58,59]. Here, increasing positive values of the aridity index correspond to increasing site moisture. This value was log-transformed, centred and standardized with a z-score transformation. Last, we included a binary variable for whether the treatment included weed control efforts. We were able to include this variable because application of some form of weed control was the most common treatment across the database and had global spatial coverage. Other management treatments were not possible to include in analysis due to uneven spatial coverage but, nonetheless, general trends are discussed in the results section.

Model structure and validation. To model the probability of success, we used zero-inflated generalized linear mixed effect models (ZIGLMM) implemented using the R package 'glmmTMB' v1.01 (ref. [60]) in R v4.0.2 (ref. [61]). We created models for two types of responses: initial success comparing unseeded controls and seeded treatments, and trends through time excluding records for unseeded controls. For both model types, we assumed a binomial distribution with a logit link function, and the number of replicates (that is, binomial denominator) was included as a weighting variable in each model[62]. To control for the excess of zeros in the data, both models were fitted with zero-inflation[63] (see Supplementary Note 2 for full statistical protocol details).

The first model, testing the role of seeding on success in initial recruitment, included only one predictor: a yes/no treatment factor for whether a species was seeded. We modelled initial recruitment across all species using only the first monitoring time point in each study, and we used only those data that had both an unseeded and seeded treatment for direct comparison. We initially used a nested random intercept structure of treatment within site, within project and a crossed random variable for species ID, because some species were seeded in multiple studies. However, because the dataset was limited to one time point per treatment, the random treatment variable prevented model convergence and was dropped. During model checking protocols (see Supplementary Note 2 for protocols and Supplementary Note 3 for diagnostic plots), the inclusion of species ID in the random structure of this reduced dataset was found to cause outliers and was also removed. Thus, the final model had a random structure of site within project.

To determine the stability of success trends through time, we analysed all time points in each study but restricted data to a minimum of two months postseeding and a maximum of six years postseeding. Although restoration trajectories can be longer than six years, long-term restoration monitoring is rare[57] and this was reflected in the GAZP database. We included time since seeding (weeks) as an additional predictor, log-transformed and standardized using a z-transformation. Given the differences in temporal patterns of different life forms, we also included the interaction between time since seeding and life form. We included the nested random structure of treatment within site, within project and a crossed random variable for species ID. Less than a third of the treatments (28.9%) had more than three sampling times, so temporal autocorrelation was not incorporated within individual treatments beyond the fixed effect of time and the nested random structure.

We used Q–Q plots of random effects to visually check for clear patterns in residuals. Additionally, we visually checked residuals for deviations in uniformity, zero-inflation and model overdispersion (see Supplementary Note 3 for details on model validation, results and extended results). We acknowledge that modelled relationships with time are log-linear, with interaction terms that alter only the rate and intercept of the relationship based on life form. This probably misses important nonlinearities that may vary uniquely with each life form. There is inherent computational complexity in modelling a database of this kind, and although there are important signals in the consistent declines in success through time and the differences between life forms, there is still much to explore as the database continues to grow.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data housed in the GAZP database is a compilation of primary research data from active projects worldwide. The database is being launched as a publicly available tool, with some datasets requiring authorization by the individual contributor for full release due to internal data use agreements. To make it findable, accessible, interoperable and reusable (FAIR), the database requires extensive documentation and clear curation, which will be an ongoing effort as the project develops. The data used for this analysis that have been approved for release will be available, with clear metadata included, through github (https://github.com/paternogbc/ms_global_dryland-restoration, https://doi.org/10.5281/zenodo.5062861). For the full subset of data used for this analysis, including the restricted data, please contact the corresponding author.

Code availability

Code for all statistical models and plots is available on github (https://github.com/paternogbc/ms_global_dryland-restoration, https://doi.org/10.5281/zenodo.5062861). Note that the data housed publicly are not the full data set used in this analysis. To execute the code exactly as conducted here, please contact the corresponding author for the dataset used in the analysis.

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Author contributions
N. Shackelford conceived the work, conducted data collection, processing, analysis and writing. G.B.P. conducted processing, analysis, writing and compilation of supplementary material. D.E.W, K.L. Suding and T.E.E. conceived the work, assisted with data collection and guided the manuscript development and editing. E.A.L. and L.N.S. wrote, compiled and extensively edited the work. M.F.B., A.M.F. and P.A.H. assisted with data collection and edited the work. M.F.C., Q.G., A.K., D.J.L., K.Z.M., S.M.M., L.M.P., R.E.Q., P.T. and C.E.W. contributed to writing the work and providing feedback. A.A., M.A.B., E.A.B., N.B., O.W.B., C.B., M.E.L.B., C.S.B., C.M.B., P.J.B., E.C., P.J.C., A.C., C.D.C., K.W.D., B.D., J.D., S.D., J.E., E.E., H.L.F., S.E.F., M.G., E.G.R., P.J.G., P.A.G., B.H., P.M.H., J.J.J., J.J.-B., R.K., A.T.K., J.E.L., J.L., C.E.M., L.M.-M., T.M., S.J.M., T.A.M., A.M.M., J.A.N.-C., M.W.P., P.L.P., M.L.P., M.J.R., N. Saayman, M.C.S., T.P., E.W.S., K.L. Stuble, S.M.U., O.V., K.V., S.W., M.W. and Z.X. contributed data to the work.

Competing interests
The authors declare no competing interests.

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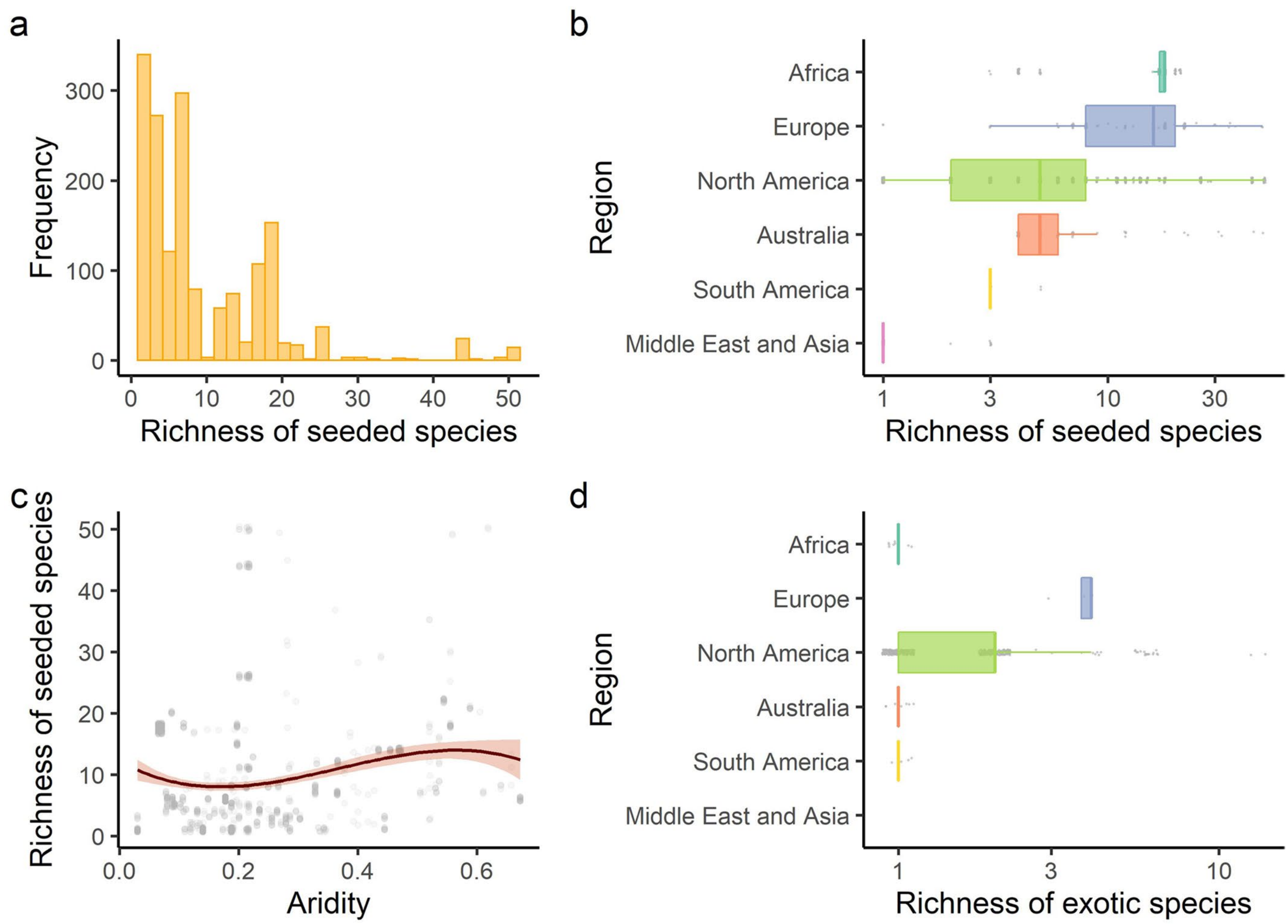
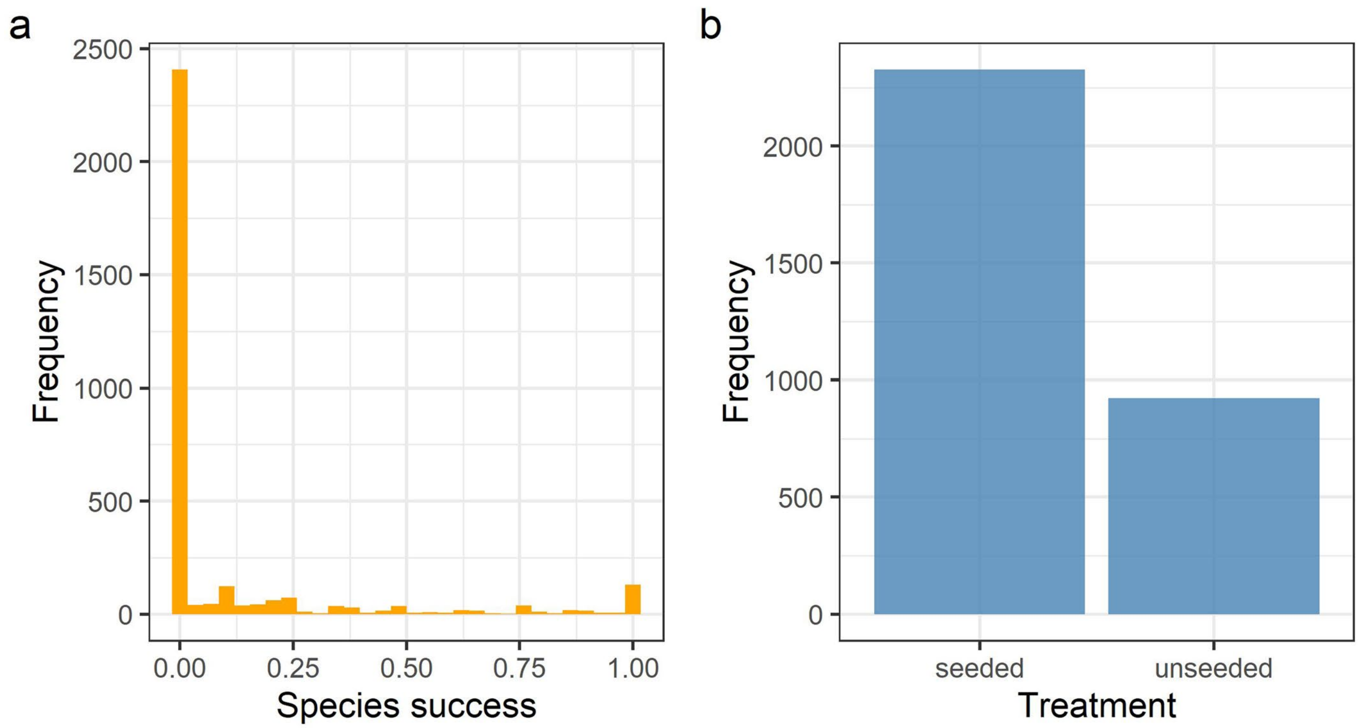
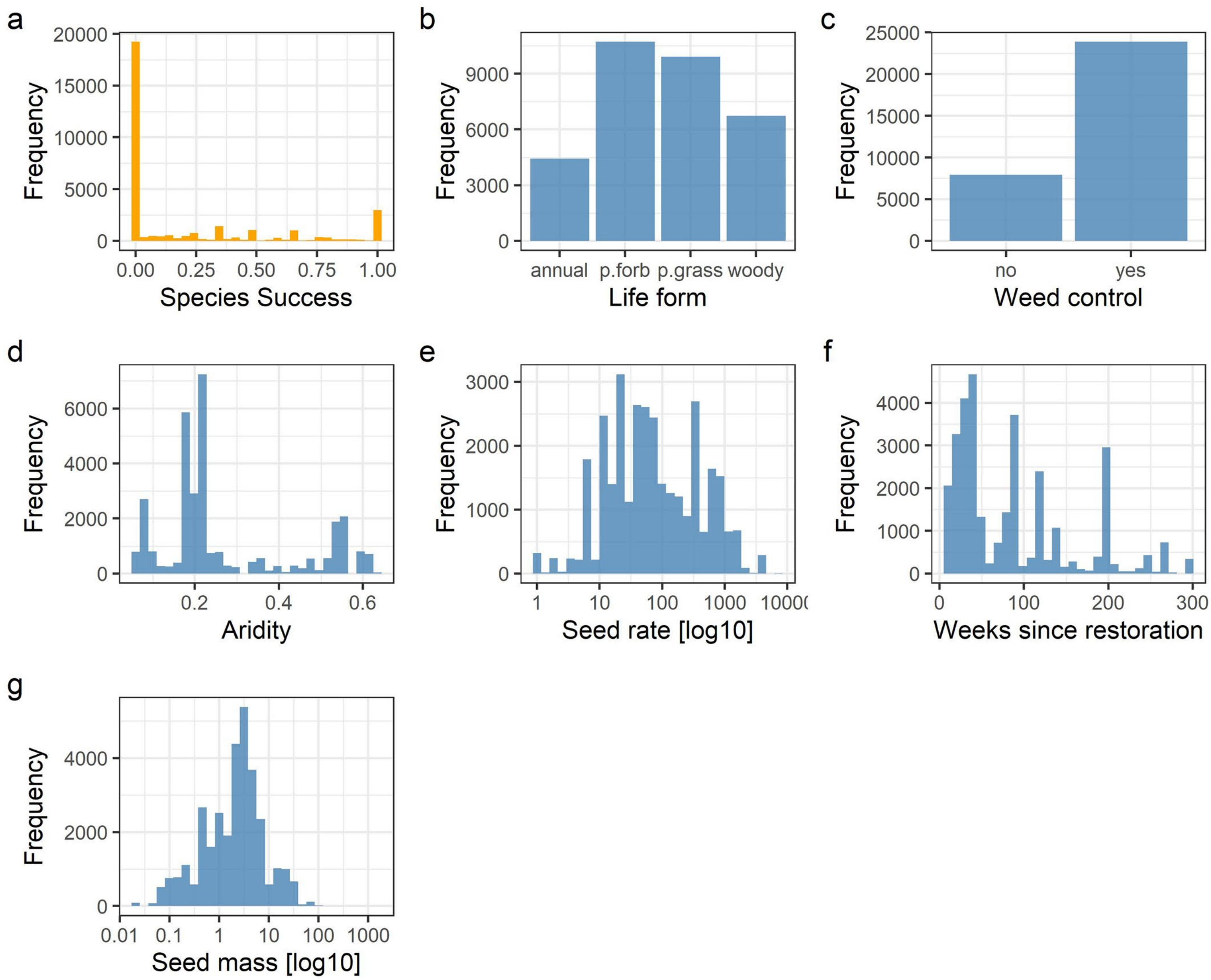


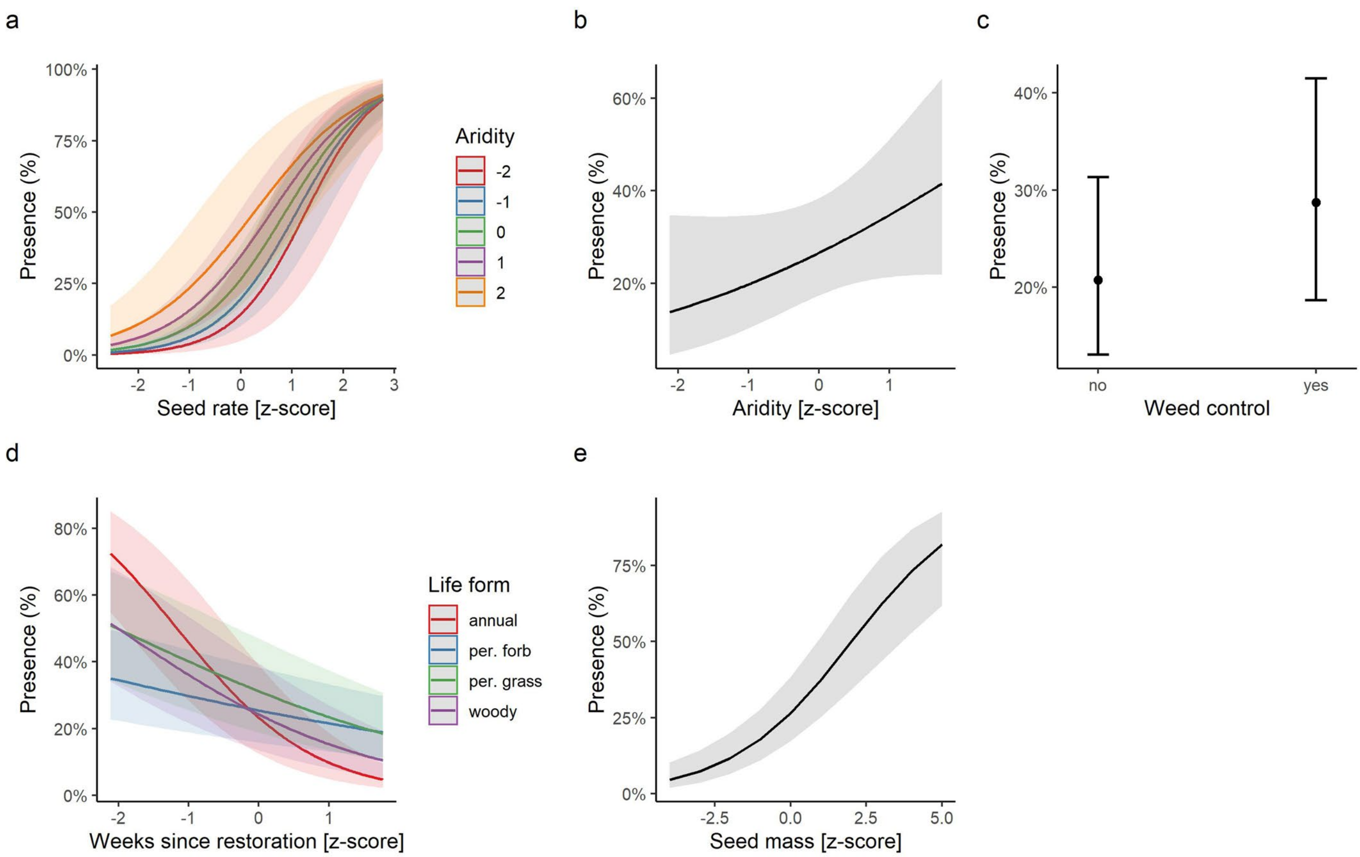
Extended Data Fig. 1 | Distribution of native and exotic richness of seeded species. (**a**) Frequency distribution of species richness across treatments. (**b**) Richness of seeded native species across regions. (**c**) Relationship between richness of seeded species and aridity, and (**d**) Richness of seeded exotic species across regions.



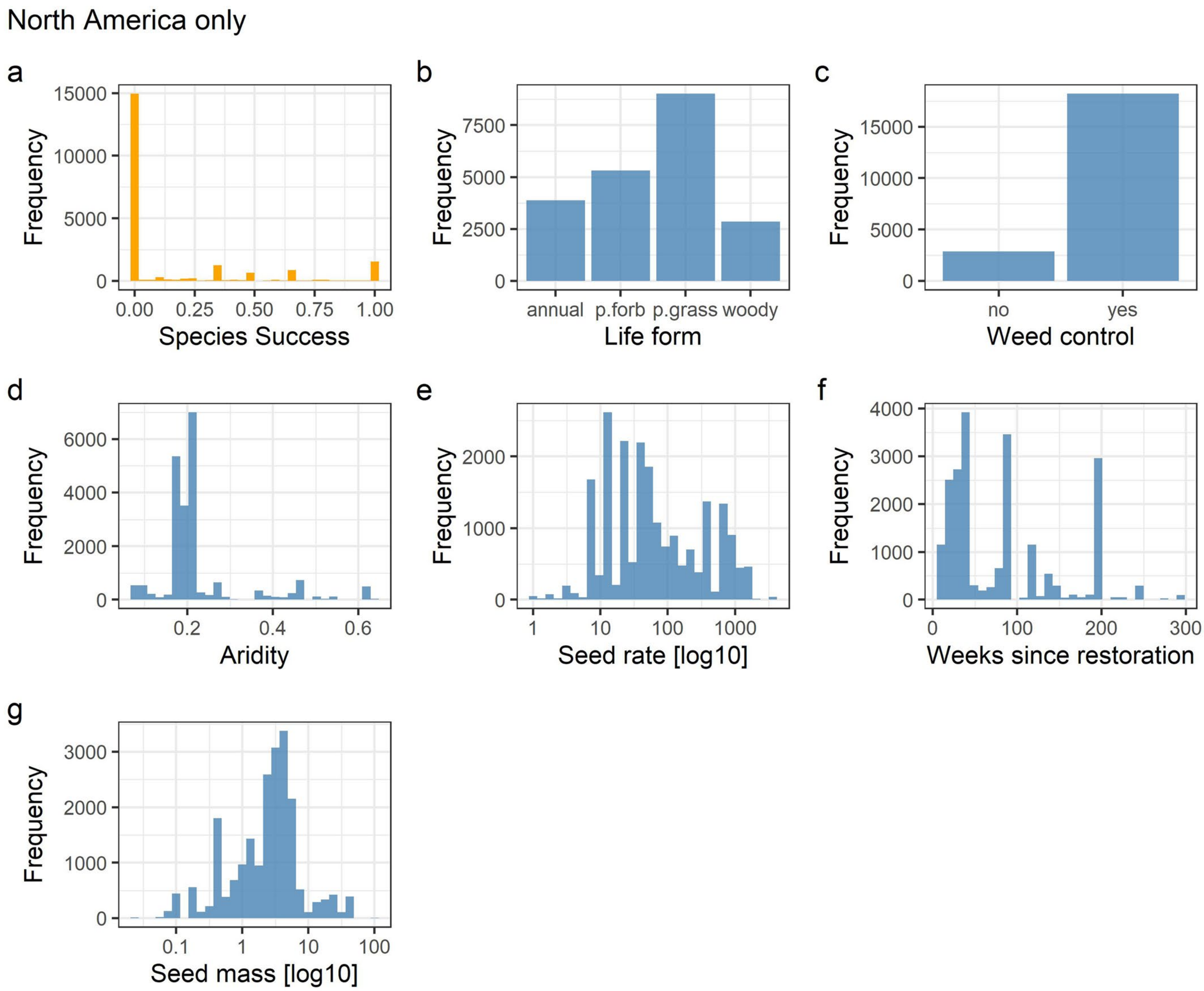
Extended Data Fig. 2 | Frequency distribution of response and predictors for initial recruitment. (**a**) Frequency distribution of species success (response) and (**b**) seeded and unseeded treatments (predictor).



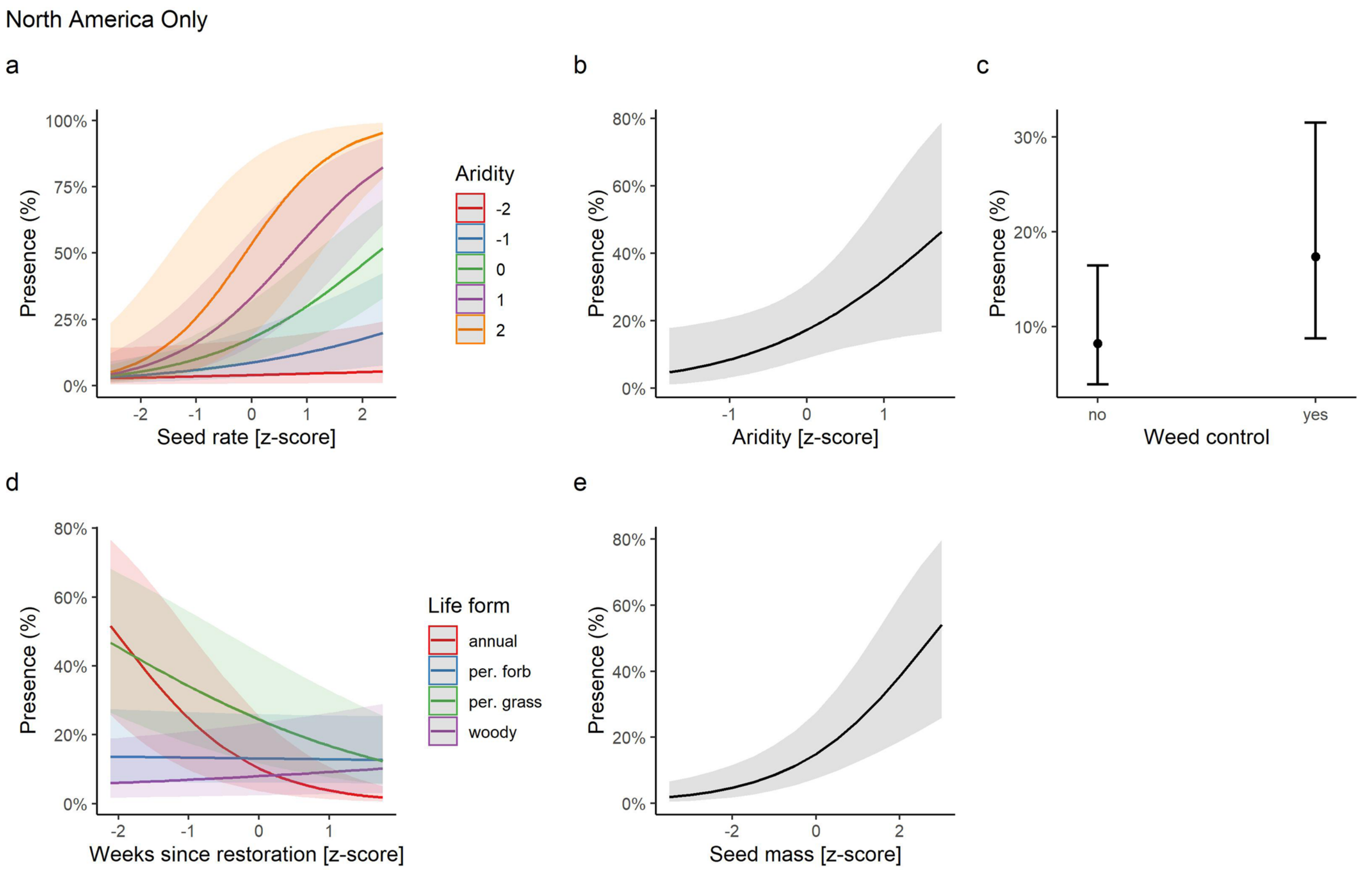
Extended Data Fig. 3 | Frequency distribution of response and predictors for Q3 (trends in vegetation development). (**a**) Frequency distribution of species success (response), and predictors: (**b**) life form, (**c**) weed control), (**d**) aridity, (**e**) seed rate, (**f**) weeks since restoration and (**g**) seed mass (g).



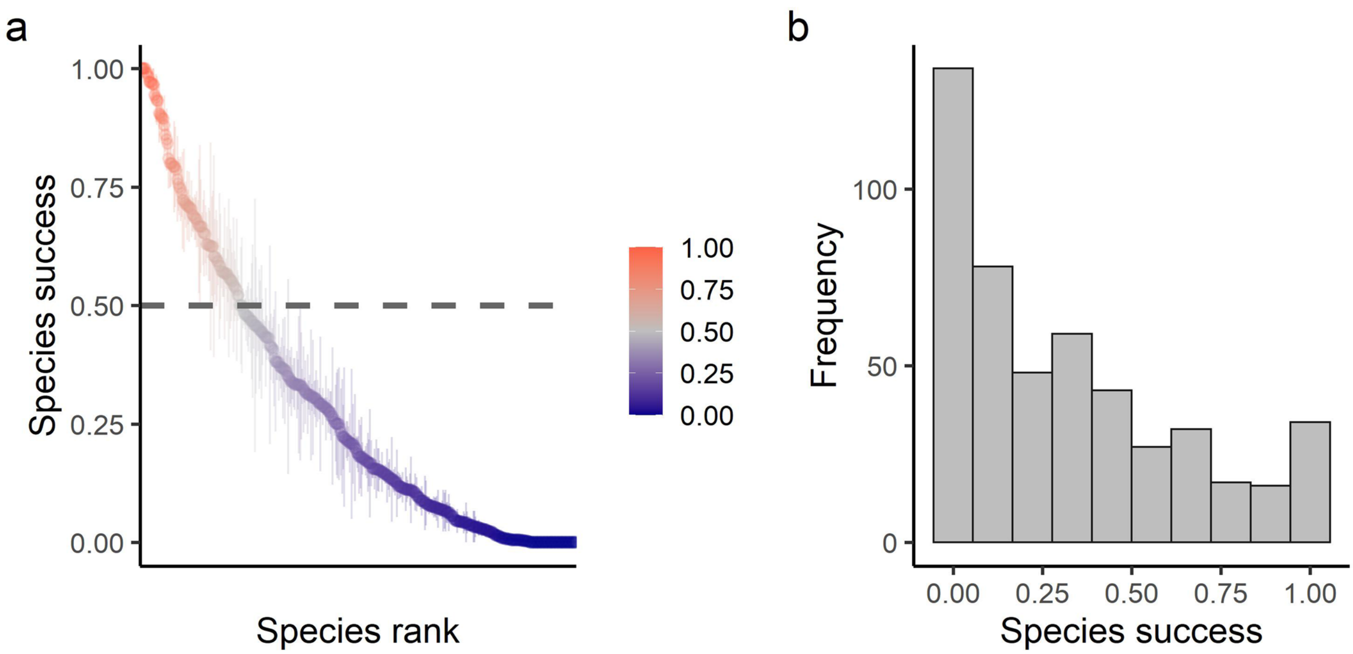
Extended Data Fig. 4 | Predicted species presence (%) across biotic and abiotic drivers. (**a**) seed rate, (**b**) site aridity, (**c**) weed control, (**d**) time since restoration, and (**e**) seed mass. Solid lines (a, b, d, f) and dots (c) indicate population-level predictions (that is marginal means) conditioned on the fixed effects. Confidence bands and error bars represent 95% confidence intervals. Continuous predictors (a, b, d, e) are shown after centering and standardization (z-score transformation).



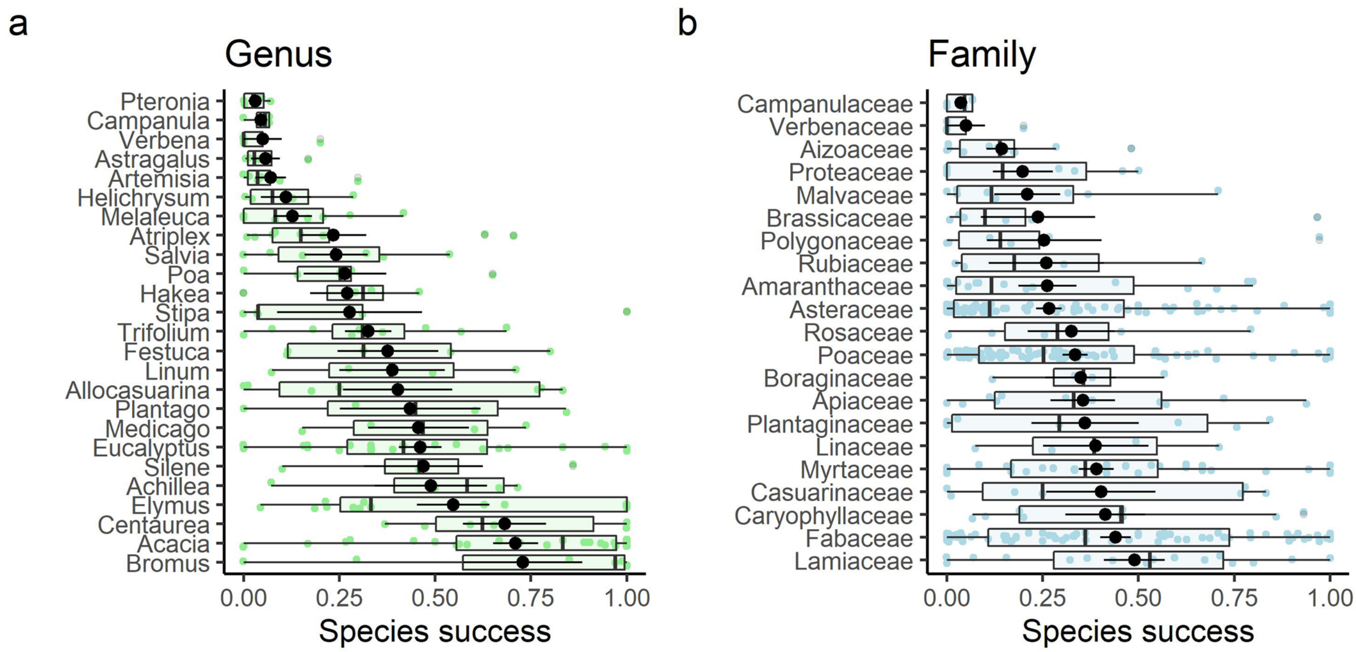
Extended Data Fig. 5 | Frequency distribution of response and predictors for Q3 (North America only, trends in vegetation development). (**a**) Frequency distribution of species success (response), and predictors: (**b**) life form, (**c**) weed control), (**d**) aridity, (**e**) seed rate, (**f**) weeks since restoration and (**g**) seed mass (g). Data was cropped to studies performed in North America.



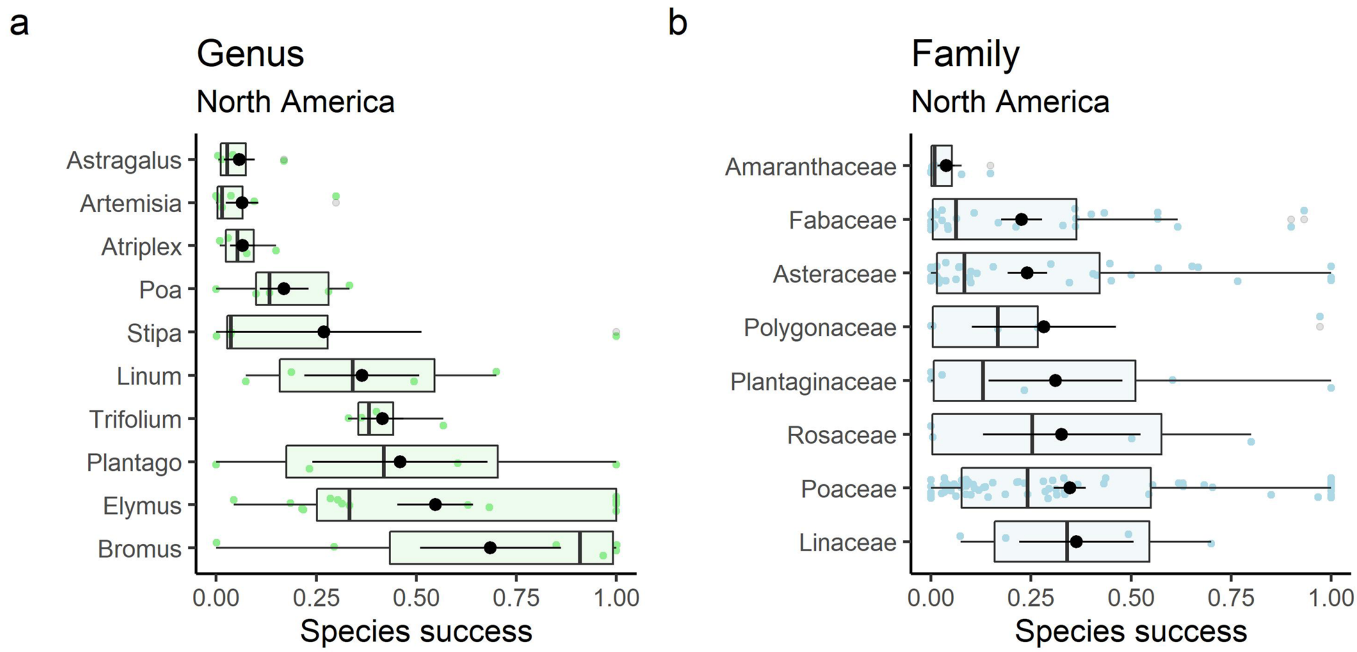
Extended Data Fig. 6 | Predicted species presence (%) across biotic and abiotic drivers (North America only). (**a**) seed rate, (**b**) site aridity, (**c**) weed control, (**d**) time since restoration, and (**e**) seed mass. Solid lines (a, b, d, f) and dots (c) indicate population-level predictions (that is marginal means) conditioned on the fixed effects. Confidence bands and error bars represent 95% confidence intervals. Continuous predictors (a, b, d, e) are shown after centering and standardization (z-score transformation). Data was cropped to studies performed in North America.



Extended Data Fig. 7 | Distribution of species success. Average probability of success (presence) ± standard error across 488 angiosperms seeded species (**a**). Species that occurred in less than 3 treatments were excluded from analysis. Each point represents a single species. The color gradient indicates the average probability of presence ranging from zero (blue) to one (red). The distribution of average probabilities is represented in the histogram on panel (**b**).



Extended Data Fig. 8 | Distribution of genus and family's success. Average probability of success (presence) ± standard error for genus (**a**) and families. Only families and genera with more than 3 species are shown. Each point represents a single species.



Extended Data Fig. 9 | Distribution of genus and family's success (North America). Average probability of success (presence) ± standard error for genus (a) and families. Only families and genera with more than 3 species are shown. Each point represents a single species. Data was cropped to studies performed in North America.

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All studies must disclose on these points even when the disclosure is negative.

Study description	The Global Arid Zone Project (GAZP), established in 2018, brings together an international research collaboration to develop a global database of dryland restoration research. As of this analysis, the project comprised restoration outcomes from 174 dryland sites on six continents, encompassing 594,065 observations of 671 plant species. We used this database to evaluate patterns of restoration outcome and assess biotic and abiotic determinants of restoration success, including seeding rate, site aridity, and species lifeform
Research sample	The target data sets include any restoration project, i.e. a project aimed at assisting recovery of a native ecosystem, located in drylands, seeding a minimum of three species, with at least one native species included in the mix. We specified drylands as arid or semiarid landscapes following the United Nations Food and Agriculture Organization (FAO) description, where arid regions were defined as receiving mean annual precipitation less than 300mm and semiarid regions as receiving mean annual precipitation between 300 and 600mm. We gathered project information on the sites, restoration treatments, and species involved, as well as vegetation responses, reported either as cover or density per area. All data were collected directly from researchers or practitioners and then processed into a set database structure. Data collection began in January 2018 and is still ongoing. For the purposes of this analysis, we used data collected up until August 2019, reflecting a total of 20 months of active collection and processing time.
Sampling strategy	Researchers and projects for inclusion were found using two methods. The first method of data sourcing was to use the extensive networks of each project organizer and contributor. Restoration is a relatively new field, and dryland restoration a small subfield within the larger scientific effort. The second was a literature review. Using the Web of Science, we searched ((ecosystem OR environment*) AND (restor* OR re-creat* OR rehabilitat*) AND (seed)) with a result of 2,734 papers, and after manually-filtering titles and abstracts, 67 of these matched the inclusion requirements above-mentioned. The largest excluders were precipitation constraints and multi-species seeding requirements. The corresponding author of each publication was then contacted and the raw data requested. Additionally, the authors were asked if colleagues in their larger restoration network had potentially appropriate studies and would be willing to contribute. The literature search was intended to be a launch point for a snowball sampling strategy, and was effective in expanding the potential participant base.
Data collection	Data was gathered directly from the primary researchers. It was processed by either the corresponding author (Dr. Shackelford) or her Research Assistant. Processing involved standardizing all data to a uniform format. Species taxonomy and measurement units were standardized across data sets. Plant names were standardized after The Plant List v1.1 database (WFO 2013). All spatial measurements were converted to m or m2, all coordinates were converted to decimal degrees, volumetric measurements were converted to mL and temperature to °C, and all seeding rates were transformed to estimated seeds m-2. Many data sets were provided in weight of seeds per area, and these were transformed using seed weight averages from the Seed Information Database. This allowed all data sets to include the same treatment structure of seeds per area, which could be linked to at least a subset of the response data in plants/area. For each project, we acquired additional data for each site, including coarse topography, historical climate, and land cover class. We also collected species-level trait data, primarily from the TRY database. All database details are included in supplemental information.
Timing and spatial scale	The collected studies range across different temporal and spatial scales, details of which are recorded within the database.
Data exclusions	Once the database was compiled and analysis began, we excluded any data point that contained missing values in the response or predictor variables (<5%). We also excluded one species (total of six records) that was seeded at a rate higher than 10,000 seeds per square meter. Finally, we limited time points. For the initial recruitment model, we used only the first time point of each study, no later than three years post-seeding. For the time series model, we limited times to between eight weeks and six years to ensure adequate representation across the full time gradient. After reviewer comments, we also excluded any site above the 0.65 aridity index threshold for a "dryland".
Reproducibility	The analysis will be reproducible by request. This is a subset of the current database (which continues to grow), and some of the data may not ever be fully released for public use, depending on the preferences of individual contributing authors. So far, no data is more restricted than 'by request only'. However, for the exact portion of the database used here, anyone aiming to reproduce the analysis will need to contact the corresponding author directly.
Randomization	Not applicable.
Blinding	Not applicable.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging