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RESEARCH ARTICLE

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COSST: A tool to facilitate seed provenancing for climate-smart ecosystem restoration

Mateus C. Silva[1] | Peter Moonlight[2] | Rafael S. Oliveira[3] | Lucy Rowland[1] | R. Toby Pennington[1,4]

[1]Department of Geography, Faculty of Environment, Science and Economy, University of Exeter, Exeter, UK

[2]Botany, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

[3]Department of Plant Biology, Institute of Biology, University of Campinas, Campinas, Brazil

[4]Tropical Diversity Section, Royal Botanic Garden Edinburgh, Edinburgh, UK

Correspondence
Mateus C. Silva
Email: mateuscardosobio@gmail.com

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Abstract

1. Selecting the best seed sources is a key step in ecological restoration planning especially under climate change. Seed-provenancing strategies include composite, aiming to reproduce natural gene flow; predictive, focusing on future climate adaptation; and climate-adjusted, a combination of composite and predictive. Yet, implementing different seed-provenancing principles remains a challenge.
2. To fill this methodological gap, we developed the Climate-Oriented *Seed-Sourcing Tool* (COSST), a tool built in R capable of suggesting priority areas for seed sourcing according to composite, predictive, or climate-adjusted strategies, as well as the restoration site and focal species.
3. The tool derives its inputs from species distribution models, which require occurrence and climate data only. COSST accommodates multiple climatic variables, weights the variables according to species-specific sensitivities, and accounts for uncertainties between climate forecasts.
4. We demonstrated the flexibility of COSST using *Caryocar brasiliense* (pequi), a tree native to the Brazilian Cerrado, as a case study. The tool identified optimal areas for collecting *C. brasiliense* seeds and estimated the proportion of seeds to be sourced from various suppliers. We made available an R code for running COSST along with a Shiny application for data visualization.
5. *Synthesis and applications*. Our tool can guide where to source seeds for species lacking range-wide information on genetic structure, which is the case for a substantial proportion of the tropical flora, where ecosystem restoration is of paramount importance.

KEYWORDS
climate-adjusted provenancing, composite provenancing, ecological restoration, native seeds, predictive provenancing, seed sourcing, species distribution models

1 | INTRODUCTION

Ecosystem restoration is central to reducing and reversing biodiversity loss and the erosion of ecosystem services (IPBES, 2018; Leclère et al., 2020). However, positive biodiversity outcomes require restoration projects to be successful over long periods in the face of continued climate change (Prober et al., 2019; Zabin et al., 2022). Extreme weather events can push a restoration site back to a degraded state (Suding et al., 2004), making climate change a key challenge to restoring ecosystems worldwide (Frietsch et al., 2023). Seeds are the main basis for active restoration on land and they carry part of the genetic pool of the population they were sourced from. Practitioners can take advantage of natural genetic variability to select seed genotypes more resilient to future climates and climate extremes (Broadhurst et al., 2008; Hancock & Hughes, 2014; Havens et al., 2015). The origin of seeds is known to affect seed germination rates (Lortie & Hierro, 2022), as well as survival (Gross et al., 2017), growth (Gellie et al., 2016), and the phenology of adult plants (Bucharova et al., 2022; Pizza et al., 2023; Rushing et al., 2021). Therefore, seed-provenancing decision-making has the potential to climate-proof restoration projects (Vitt et al., 2022).

Seed-provenancing guidelines have been debated in the ecological restoration community (Dupré la Tour et al., 2020). Prioritizing seeds from the single geographically closest population (i.e., local provenancing) is a longstanding principle based on the assumption that local genotypes are adapted to the restoration site's local conditions. The local provenancing concept is often subjective, as nativity is a gradient rather than a discrete unit (Dupré la Tour et al., 2020). Therefore, arbitrary buffers around the restoration site representing the 'local population' may constrain seed supply capacity to conform with local provenancing principles (Gibson-Roy et al., 2021) or even lead to overharvesting (Broadhurst et al., 2008). Furthermore, the strict use of local seeds may come at the cost of inbreeding depression due to deleterious allele proliferation and loss of genetic variation (McKay et al., 2005). Finally, local seeds might instead show maladaptation as the climate is changing and may differ from the conditions the genotypes evolved in (Wilczek et al., 2014), jeopardizing long-term restoration success.

Other strategies have been proposed as an alternative to local provenancing (Breed et al., 2018). Composite provenancing addresses the genetic diversity issue by allowing the contribution of several populations to the seed mix (Aitken & Whitlock, 2013; Breed et al., 2018). In this strategy, the contribution of donor sites decreases with the geographical distance to the restoration site, mimicking natural genetic flow (Havens et al., 2015). Predictive provenancing addresses the maladaptation issue by favouring seed collection in populations theoretically adapted to the future climate at the restoration site (Broadhurst et al., 2008; Havens et al., 2015). Yet, the predictive approach has been criticized due to the risk of outbreeding depression (Bucharova et al., 2019). To reduce this risk, *climate-adjusted provenancing* was developed aiming to mix local seeds with non-local seeds from populations that match the predicted climate. Climate-adjusted provenancing is a combination of composite and predictive strategies, maximizing climate adaptiveness and genetic variation while minimizing genetic risks (Prober et al., 2015).

It remains a challenge to implement climate-oriented seed-provenancing strategies, such as climate-adjusted and predictive provenancing. Conventionally, seed transfer zones (STZ) have been used to support provenancing decision-making (Durka et al., 2017; Jørgensen et al., 2016). STZ can be defined as areas designed to limit genetic contamination from seed exchange and progress has been made in accounting for climate change when designing such zones (Fremout et al., 2021; Marinoni et al., 2021). Another approach is mapping contemporary climates that are analogous to the predicted future climate at the restoration site (Shryock et al., 2018). However, both STZ and climate match approaches often weigh climatic variables evenly (e.g., annual rainfall, temperature; but see Shryock et al. (2018)), which are known to affect each species differently (Harrison, 2021; Harrison et al., 2017; St. Clair et al., 2022). Furthermore, climatic forecasts vary considerably between Global Circulation Models (GCMs), which generates uncertainty in designing climate-smart seed mixes. Effective restoration planning requires, therefore, a novel seed-provenancing approach which encompasses species-specific sensitivities to different climatic variables, controls for climatic forecast uncertainties across the space, and is practical to implement.

Here we introduce the Climate-Oriented *S*eed *S*ourcing *T*ool (COSST), a tool built in R designed to operationalize seed-provenancing strategies for ecosystem restoration (https://github.com/silva-mc/COSST). The tool is based on Species Distribution Models (SDMs) and provides seed-provenancing guidance in the absence of genetic and experimental data. COSST identifies priority areas (ranging from 0 to 1) for sourcing seeds across the species range to restore a site specified by the user. When collection sites of commercial species are known, COSST can estimate the percentage of seeds to be purchased from different vendors. The tool allows the user to generate predictions based on three seed-provenancing strategies alternative to local provenancing: composite (not climate-oriented), predictive (fully climate-oriented), or climate-adjusted (balance between the previous ones). COSST weights climatic variables by their relative importance derived from SDMs and controls for the uncertainty in climate projections in the case of climate-adjusted provenancing. First, we describe the mathematical basis of the tool. Then, we demonstrate its applicability in the Brazilian Cerrado, a tropical global biodiversity hotspot. Specifically, we applied the tool to two actual restoration sites (~650 km apart), for single and multiple restoration-priority species ($N=3$), and under the three focal provenancing strategies.

2 | MATERIALS AND METHODS

2.1 | The Climate-Oriented Seed-Sourcing Tool (COSST)

The COSST framework (Figure 1) generates a raster layer where the cell values (i.e., COSST priority index) correspond to the priority of the pixel as a seed source given the species of interest and target restoration site. The restoration site is defined as the approximate centroid of the location to be restored (coordinates). Using gridded climatic data (raster), COSST produces three raster layers, one for each seed-provenancing strategy (composite, climate-adjusted, and predictive, see introduction for definitions). When seed-sourcing site coordinates are known, the user can obtain the fraction of seeds to be purchased from each site by dividing the COSST index of each site by the total sum.

2.1.1 | Input data

The first input to COSST is SDMs. Presence-only SDM algorithms, such as MaxEnt, require only species occurrence and bioclimatic data. Testing for multicollinearity and retaining only independent bioclimatic variables is essential to avoid overfitting SDMs. COSST uses two SDM outputs: the species range map (*R*) and the relative importance of the bioclimatic variables (*v*) to predict *R*. *R* is the binary projection of the SDM, representing the range of the species inferred from its climatic requirements. *R* sets the COSST spatial extent by restricting it to the species' range, but it is not an essential input (hence, its absence in Figure 1). In the case of MaxEnt, *v* corresponds to the permutation importance of the bioclimatic variables. COSST also requires the same baseline bioclimatic data (*B*) used to run the SDMs (e.g., 1981–2010) and the same data for a future timeframe (*F*, e.g., 2011–2040). The last input to COSST is the restoration site coordinates (*s*).

2.1.2 | Composite provenancing strategy

COSST implements composite provenancing by calculating the Euclidean distance (*D*) between each potential seed source pixel (i.e., species range) and the restoration site. *D* is normalized and subtracted from 1, returning the proximity of each seed source pixel to the restoration site (Equation 1).

$$\text{Composite} = 1 - \text{scale}(D) \tag{1}$$

The normalization function rescales the data to vary between 0 and 1 (Equation 2).

$$\text{scale}(x) = \frac{x - x_{\min}}{x_{\max} - x_{\min}} \tag{2}$$

2.1.3 | Predictive provenancing strategy

COSST implements predictive provenancing by calculating the similarity between the future climate at the restoration site and the baseline climate across the species range (*R*), hereafter the future climate match (*C*). The bioclimatic variables are the same ones used for fitting the SDM. We recommend that COSST is run with an average of GCM forecasts. We first extract the future bioclimatic variables at the restoration site $\left(F_i^s\right)$ and then subtract F_i^s (vector) from B_i (raster layer from a stack). The product is normalized and inversed by subtracting it from 1 (Equation 3) to generate the climate match of variable *i* (C_i), corresponding to the similarity between the pixel's baseline climate and the restoration site's future climate (Equation 3).

$$C_i = 1 - \text{scale}\left(\left|B_i - F_i^s\right|\right) \tag{3}$$

where *i* represents one of the *n* bioclimatic variables. C_i values are multiplied by the bioclimatic variable permutation importance derived from the SDM (v_i) to weigh each by their importance. Note that v_i must be expressed as a fraction and not a percentage. Predictive provenancing optimization is achieved by summing and normalizing the bioclimatic layers (*n* being the number of variables; Equation 4).

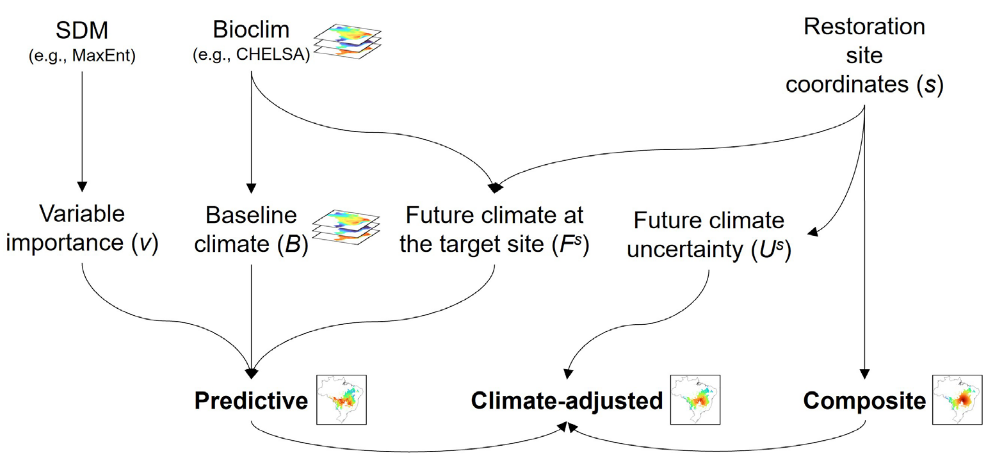

FIGURE 1 Climate-Oriented Seed-Sourcing Tool (COSST) data flow. Inputs consist of the species distribution model (SDM) outputs, bioclimatic layers (Bioclim), and the coordinates of the target restoration site (*s*). The tool combines the relative importance of the bioclimatic variables (*v*), the baseline climate (*B*) across the species range (derived from the SDM), and future climate projection in the restoration site (F^s) to create a seed-sourcing priority index for the predictive provenancing. The coordinates of the restoration site feed into the composite provenancing optimization. Finally, the climate-adjusted layer results from the combination of predictive and composite layers alongside the future uncertainty at the restoration site (U^s).

$$\text{Predictive} = \sum_{i=1}^{n} C_i \times v_i \quad (4)$$

2.1.4 | Climate-adjusted provenancing strategy

COSST implements climate-adjusted provenancing by summing composite versus predictive provenancing indexes. We include a climate uncertainty parameter (U^s) defined as the standard deviation of the future climate at the restoration site across the GCMs. U^s is used to weight C, so the impact of future climate matches for climate-adjusted provenancing decisions is lower in sites where the future climate is uncertain. The tool calculates the normalized standard deviation of each bioclimatic variable across GCMs (sdF_i). A sdF_i equal to 1 corresponds to a pixel with the greatest GCM divergence for variable i across R. sdF_i is multiplied by the importance of the bioclimatic variable i (v_i). We sum and normalize all bioclimatic variables (1 to n; Equation 5). Finally, COSST determines the uncertainty of climate forecasts at the restoration site (U^s) by extracting U at the site coordinate s (Equation 6).

$$U = \sum_{i=1}^{n} \text{scale}(sdF_i) \times v_i \quad (5)$$

$$U^s = U \cap s \quad (6)$$

Climate-adjusted provenancing index is given by Equation 7.

$$\text{Climate-adjusted} = \text{scale}\left(\left(\text{Predictive} \times U^s\right) + \text{Composite}\right) \quad (7)$$

2.2 | Case study

2.2.1 | The Brazilian Cerrado

We applied COSST to the Brazilian Cerrado, a region that covers one-quarter of Brazil's territory. Tropical savannas and grasslands are the dominant biome in the Cerrado region, representing 78% of the vegetation cover before large-scale human occupation (Rodrigues et al., 2022). About 12,000 flowering plant species are native to the Cerrado and 40% of this flora is endemic (B.F.G. Brazilian Flora Group, 2015). However, half of the Cerrado native vegetation has been lost to cattle ranching and intensive agriculture (MapBiomas, 2023). The combination of high endemism levels and rapid land-use change has made the Brazilian Cerrado a global 'hotspot' for biodiversity conservation (Myers et al., 2000) and ecological restoration (Strassburg et al., 2020). Brazil's ambition is to restore 2.1 Mha of Cerrado vegetation by 2030 (MMA, 2017). Native seed suppliers, cooperatives led by Indigenous peoples and local communities that harvest, process, and sell seeds of native species (Schmidt et al., 2019), play a major role in Brazil's ecosystem restoration strategy (Urzedo et al., 2020). Therefore, providing practical guidelines on seed mix design, especially seed-provenancing, will be key to achieving national restoration pledges.

2.2.2 | Applying COSST to realistic scenarios

We showed two applications of the tool: seed source prioritization—aiming to map seed-sourcing priority areas to restore a particular site, and seed mix design—aiming to estimate seed demand from multiple suppliers. In both applications, we explored the outcomes of different seed-provenancing strategies (composite, climate-adjusted, and predictive) for two restoration sites using one (single species) and three species (multi-species). The two restoration sites are 653 km apart. The first is a mining site in Niquelândia (State of Goiás; 14°21′0.3168″ S 48°24′0.0468″ W, 1084 m a.s.l.). Mining activities in the region started approximately in 1994 and the soil remains exposed (MapBiomas, 2023). The second is an abandoned Eucalyptus plantation in Montezuma (State of Minas Gerais; 15°20′10.8852″ S 42°24′34.6104″ W, 1105 m a.s.l.). *Eucalyptus* sp. trees were planted approximately in 1997 and the plantation was abandoned in 2012 (MapBiomas, 2023).

We focused on the *Caryocar brasiliense* Cambess. (pequi) for single-species applications due to their ecological and socioeconomic value. *C. brasiliense* is a tree widespread in the Cerrado savannas and its fruit pulp and nuts are consumed across Brazil, providing income to local communities. In addition to *C. brasiliense*, we included *Hymenaea stigonocarpa* Mart. ex Hayne (jatobá-do-cerrado) and *Qualea grandiflora* Mart (pau-terra-grande) in the multi-species applications. These two species are widespread across Cerrado savannas (Bridgewater et al., 2004) and commonly traded by major Cerrado seed suppliers: Restauradores da RDS Nascentes Geraizeiras (RDS), Rede de Sementes do Cerrado (RSC), Rede de Sementes do Xingu (RSX), and VerdeNovo (VN; see Silva et al., 2022). Both *H. stigonocarpa* and *Q. grandiflora* have uses, including timber, medicinal, and ornamental value (Ribeiro et al., 2023). The precise polygon delimiting the seed collection areas of each species was not available, so we considered the seed-sourcing sites as the centroid of the municipalities where the seed suppliers operate and assumed that all species are collected across all sites (Silva et al., 2022). Although this was an approximation to illustrate the tool, users can provide the coordinate of the seed-sourcing area centroid to increase COSST accuracy.

2.2.3 | Data processing and presentation

We used the MaxEnt algorithm to fit SDMs (Elith et al., 2011; Phillips et al., 2017; Phillips & Dudík, 2008). Refer to Silva et al. (2024) and Appendix S1 for the analytical pipeline and model specifications. We presented the seed-source prioritization application by showing the COSST index, referred to as 'seed sourcing priority areas'. For the multi-species analysis, we binarized the COSST index per species using an arbitrary threshold of 0.75 (representing the third quartile), summing up the binary layers, and excluding pixels equal to zero. The final map shows areas that are high priority for seed sourcing across multiple species. As an additional analysis, we ran a Pearson correlation to test the association between the COSST index calculated under predictive and composite provenancing strategies. We presented the seed mix design application by extracting the COSST index at the seed-sourcing sites (i.e., approximate coordinate) and converting it into percentages by dividing it by the total. We also summed the extracted COSST index across all the sourcing sites of a given supplier to estimate the theoretical contribution of each vendor to the seed mix. Contribution is defined as the percentage of seeds originating from each supplier in the seed mix. It is worth noting that summing the COSST index may place greater emphasis on suppliers with multiple sourcing sites and using an average instead of a sum could be an alternative. All analyses were made using the R environment (v.4.2.3). The R code is available at https://github.com/silva-mc/COSST and requires Java to run.

3 | RESULTS

3.1 | Mapping seed-sourcing priority areas

COSST was able to generate seed-sourcing priority maps tailored to the seed provenancing and restoration site chosen by the user (Figure 2). Under predictive provenancing, the spatial distribution of COSST indexes around each restoration site differed considerably. For example, for site 1 potential seed-sourcing sites to the north of the restoration site had lower suitability (green shades) because their baseline climate does not match the restoration site's future climates. In contrast, for site 2, all nearby pixels (with savanna cover) showed high-priority values. Still considering *C. brasiliense*, there was a positive correlation between the COSST index calculated under composite and predictive provenancing, but the correlation coefficient was higher at site 2 ($r = 0.61$, $p < 0.001$), relative to site 1 ($r = 0.41$, $p < 0.001$; Figure S1). The COSST prioritization applied to multiple species (*H. stigonocarpa*, *Q. grandiflora*) generated similar results to the prioritization based on *C. brasiliense* (Figure 3; Figures S2 and S3).

3.2 | Designing seed mixes with multiple suppliers

COSST was capable of mapping seed-sourcing priorities across seed suppliers, following different seed-provenancing strategies, and at different restoration sites. Considering a single species (*C. brasiliense*), COSST suggested RSC be the main seed supplier for site 1

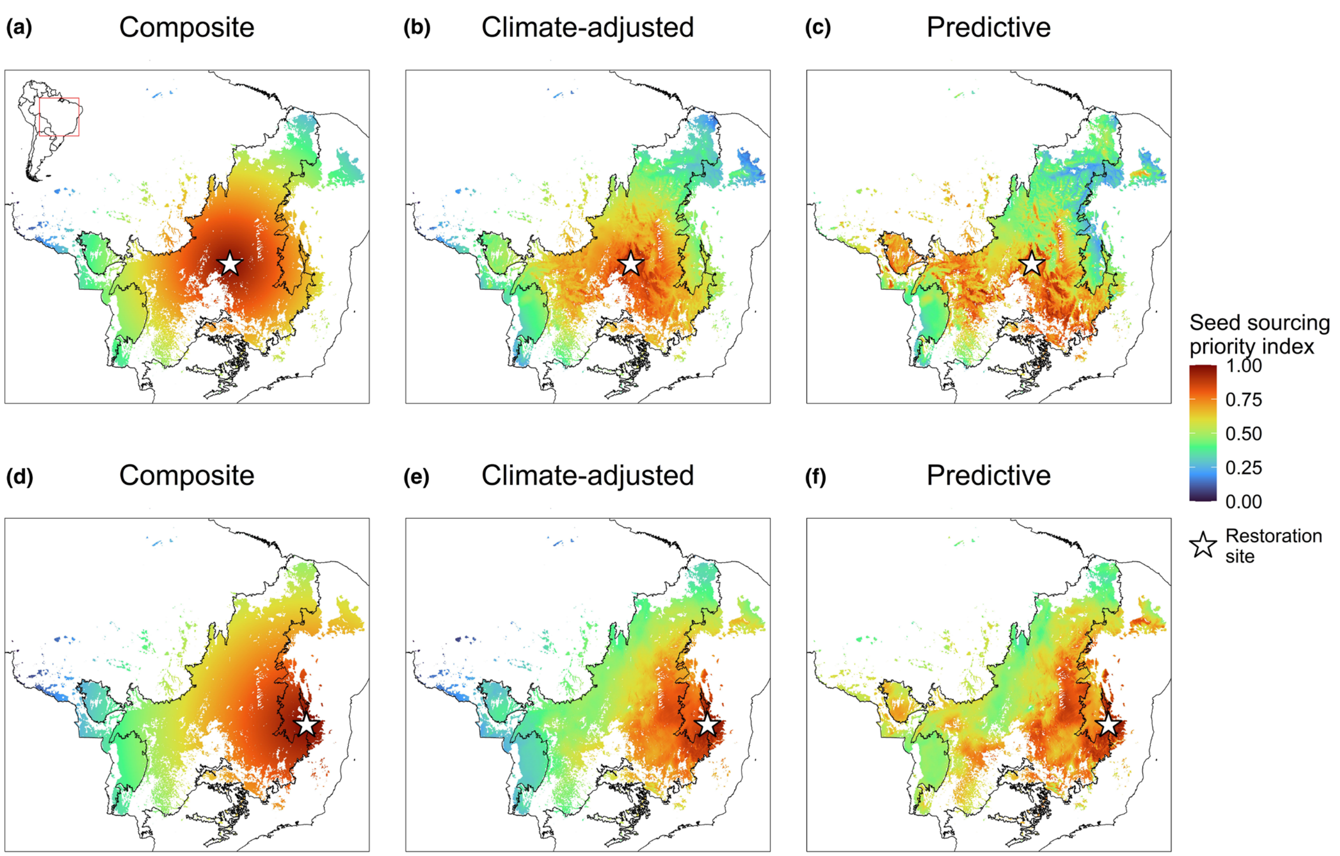

FIGURE 2 Priority areas for sourcing seeds of *Caryocar brasiliense* (pequi) generated by COSST (Seed-source prioritization for single species). Predictions produced for (a–c) a mining site in Central Cerrado and (d–f) an abandoned *Eucalyptus* plantation in Eastern Cerrado and based on the (a, d) composite, (b, e) climate-adjusted, and (c, f) predictive seed-provenancing strategy. The coloured area represents the *C. brasiliense* range excluding pixels with less than 10% of savanna and grassland cover in 2021. Warmer colours indicate high-priority areas and cooler colours low-priority areas. The red square in the top left corner of panel a shows the study area within Brazil's borders. The star marks the location of the restoration site. The outer polygon delimits Brazil's boundaries and the inner polygon Cerrado's boundaries.

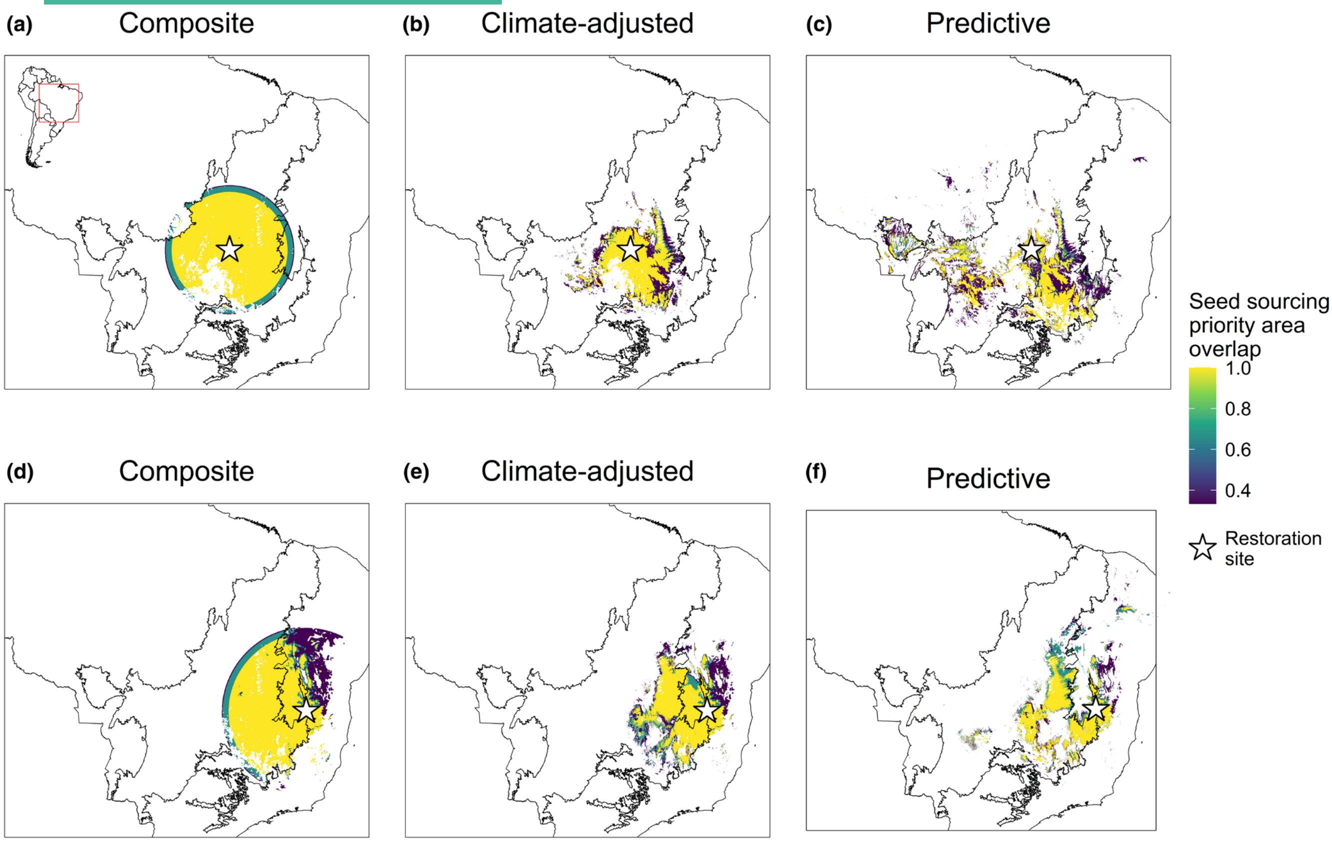

FIGURE 3 Priority areas for sourcing seeds of multiple species generated by COSST (Seed-source prioritization for multiple species). The studied species were the *Caryocar brasiliense* (pequi), *Hymenaea stigonocarpa*, and *Qualea grandiflora*. Predictions produced for (a–c) a mining site in Central Cerrado and (d–f) an abandoned *Eucalyptus* plantation in Eastern Cerrado and based on the (a, d) composite, (b, e) climate-adjusted, and (c, f) predictive seed-provenancing strategy. The coloured area represents the overlap between single-species seed-sourcing priority maps binarized using a 0.75 cutoff, excluding pixels with less than 10% of savanna and grassland cover in 2021. Brighter colours indicate areas that are considered high priority for multiple species. The red square in the top left corner of panel a shows the study area within Brazil's borders. The star marks the location of the restoration site. The outer polygon delimits Brazil's boundaries and the inner polygon Cerrado's boundaries.

(total contribution of 31%–33%) and RDS for site 2 (34.1%–36.5%) regardless of the provenancing strategy chosen (composite, climate-adjusted, or predictive; Figure 4). The greatest difference related to the provenancing optimization was in the contribution of RDS to source seeds at site 1 under composite (22.3%) versus predictive strategy (24.5%). Considering the sum of each site and between the three seed-provenancing strategies, the contribution of individual sourcing sites to the seed mix varied from ca. 4.1%–8.4% for site 1 and from ca. 3.4%–7.4% for site 2. However, it should be noted that 13 out of 18 sites sourced by RSX and one out of six sites sourced by RSC are located outside the distribution range of *C. brasiliense* (open points in Figure 4). Considering multiple species, RSC remained the principal vendor at site 1 and RDS at site 2 across all seed-provenancing strategies (Figure 5).

4 | DISCUSSION

We present the COSST a new resource to support seed-provenancing decision-making for ecosystem restoration. When applied to the Brazilian Cerrado, the tool showed high sensitivity to the restoration location since the priority index and seed contribution per supplier were consistently higher in the restoration site surroundings. Provenancing and species choices provide a secondary refinement to the tool predictions. Below we discuss the advances, assumptions, and challenges to implement COSST in restoration projects.

Compared with previous tools, COSST's novelty lies in adjusting the prioritization index to the chosen provenancing strategy and focal species. The Diversity for Restoration (D4R) tool implements climate-adjusted provenancing through a dynamic STZ approach where 50% of the seed mix comes from the current seed zone and 50% from the projected future seed zones (Fremout et al., 2022). Similarly, the Climate Distance Mapper also uses a seed zone framework to implement predictive principles by estimating the match between present and future climates (Shryock et al., 2018). Our tool, on the other hand, allows the user to choose between a spectrum of strategies ranging from composite (geographically optimized) to climate-adjusted (intermediate) and predictive (climatically optimized). It is also possible to precisely adjust the weighting

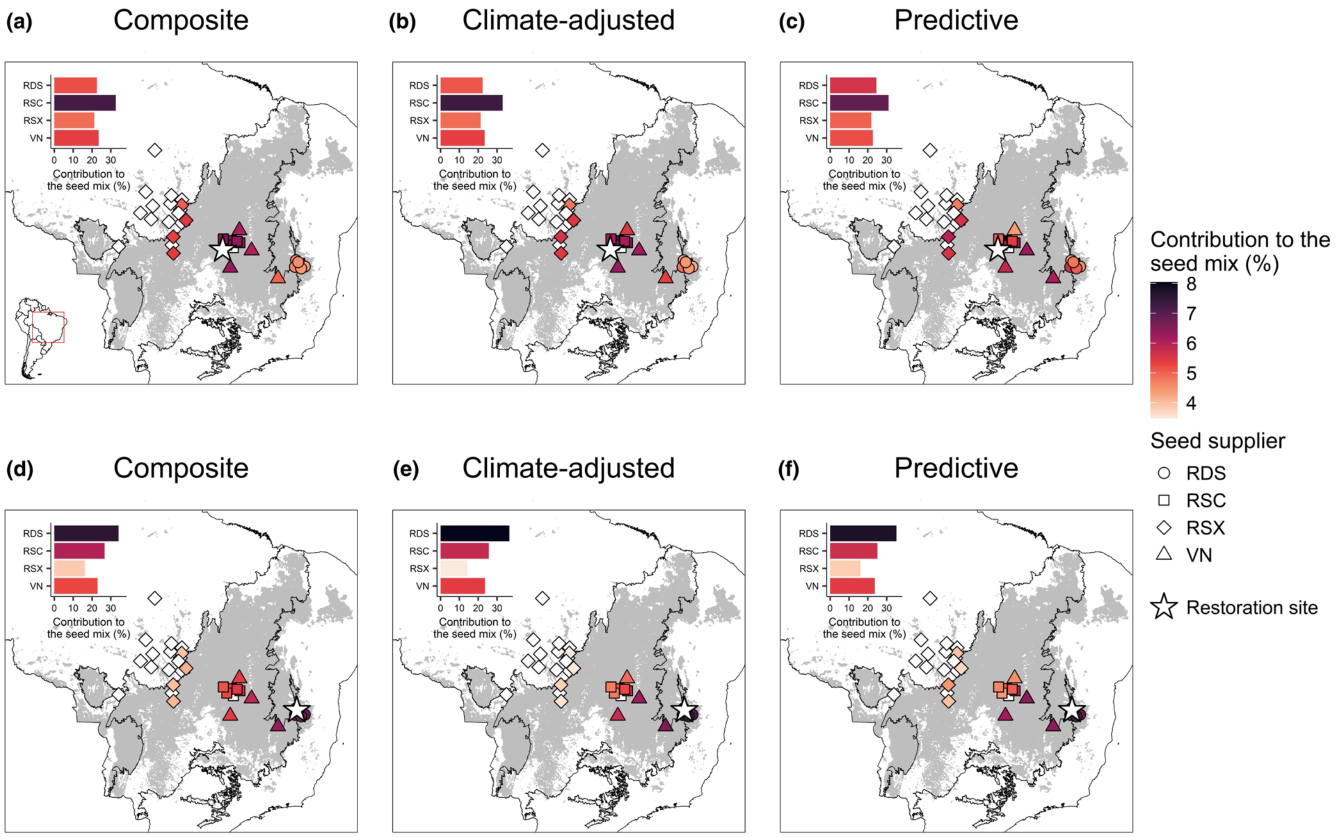

FIGURE 4 Seed contribution per supplier for *Caryocar brasiliense* (pequi) generated by COSST (Seed mix design for single species). Predictions produced for (a–c) a mining site in Central Cerrado and (d–f) an abandoned *Eucalyptus* plantation in Eastern Cerrado and based on the (a, d) composite, (b, e) climate-adjusted, and (c, f) predictive seed-provenancing strategy. The area in grey represents the *C. brasiliense* range excluding pixels with less than 10% of savanna and grassland cover in 2021. The points represent *C. brasiliense* seed-sourcing sites by four major seed suppliers in the Cerrado. The point colour is proportional to the contribution (%) of each sourcing site to the final seed mix. Darker-coloured points represent high-contribution sourcing sites and white points represent sourcing sites outside the species range or with <10% of savanna and grassland cover. The red square in the bottom left corner of panel a shows the study area within Brazil's borders. The star marks the location of the restoration site. The outer polygon delimits Brazil's boundaries and the inner polygon Cerrado's boundaries. The insert graphs (top left) show the summed contribution of each seed supplier to the final seed mix. RDS, Restauradores da RDS Nascentes Geraizeiras (circles); RSC, Rede de Sementes do Cerrado (squares); RSX, Rede de Sementes do Xingu (lozenges); VN, VerdeNovo (triangles).

of geographical versus climatic optimization in COSST calculations (see Appendix S2). Furthermore, STZ are useful for handling several species at once but may fall short if there is no congruent population genetic structure among species, which is the case for Amazonian trees (Coronado et al., 2019), or if the whole distribution of a narrow-range species falls within a single seed zone. COSST avoids this issue by focusing on species-specific climatic distances constrained by the species range rather than generic polygons, being more ecologically meaningful when handling one species at a time. In fact, the ability of our tool to tailor its calculations per species using SDM-derived weights also differentiates it from Restore and Renew (Rossetto et al., 2019), another provenancing tool implementing the same provenancing strategies as COSST. Additionally, our tool also penalizes sites where the future climate is uncertain under climate-adjusted provenancing, favouring the 'local-is-best' logic instead. Finally, COSST complements existing species selection tools (e.g., Coutinho et al., 2023; Laughlin et al., 2018) by providing guidance on the best seed sources after the species have been chosen given the restoration targets.

The main assumption of COSST is the prevalence of intra-specific adaptation to climate, especially when the user selects climate-adjusted or predictive strategies. Evidence of climate adaptation exists for the Cerrado flora, but only for a handful of species (Appendix S3; Figure S4). The climate component of the tool may lose power if the genotypes of a species are not in equilibrium with their baseline climate (Wilczek et al., 2014) or if they are adapted to soil conditions rather than climate. However, we argue that our tool remains applicable even when local adaptation assumptions are not met. Genetic diversity tends to increase with the geographical distance between the populations (Pfeilsticker et al., 2021). In the case of *C. brasiliense*, COSST suggests some level of seed contribution from suppliers farther apart regardless of the seed-provenancing strategy chosen. If the practitioner follows the tool suggestion, a small fraction of seeds from distant populations should amplify

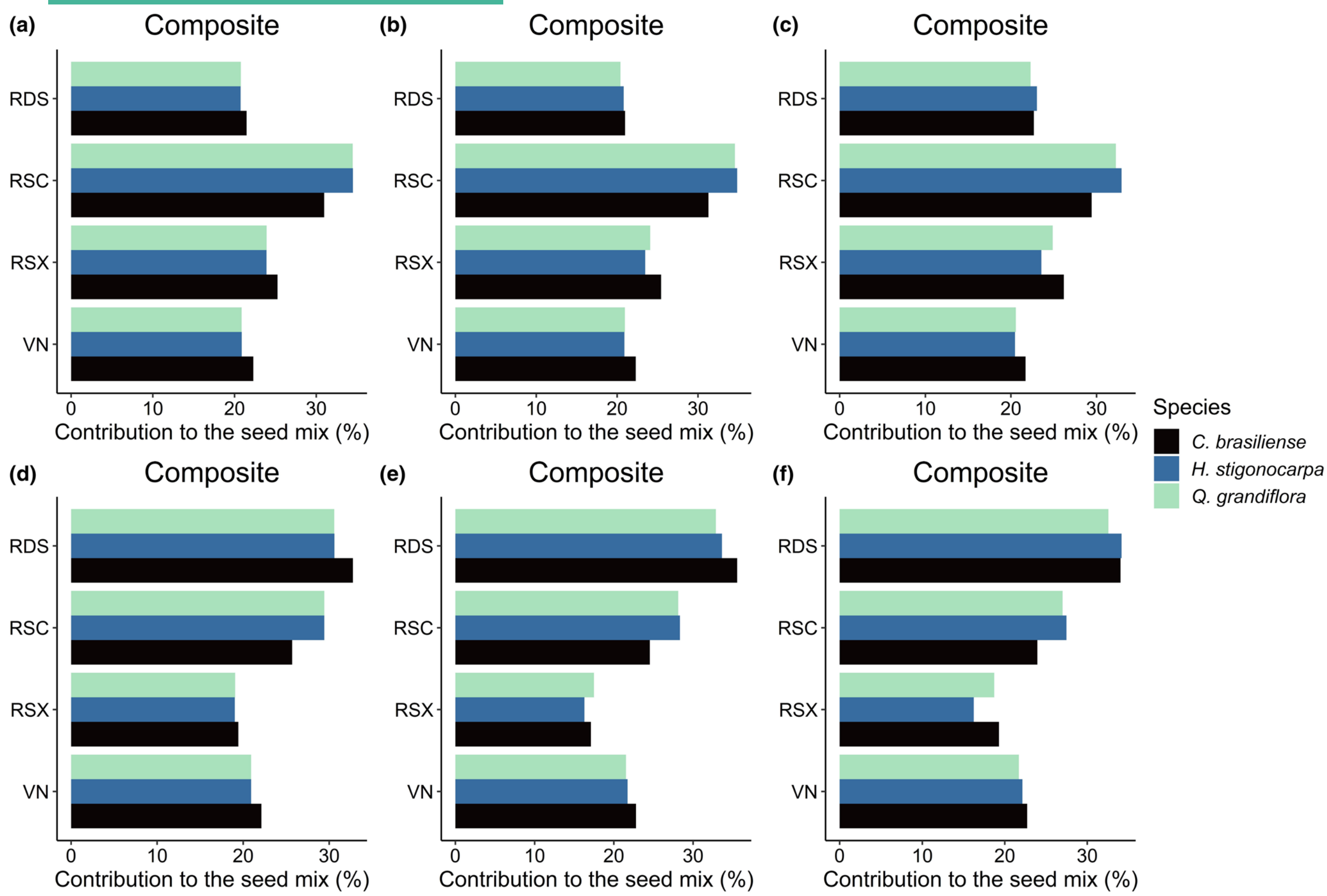

FIGURE 5 Seed contribution per supplier for multiple species generated by COSST (Seed mix design for multiple species). Predictions produced for (a–c) a mining site in Central Cerrado and (d–f) an abandoned *Eucalyptus* plantation in Eastern Cerrado and based on the (a, d) composite, (b, e) climate-adjusted, and (c, f) predictive seed-provenancing strategy. The bar shows the summed contribution (%) of each seed supplier to the final seed mix for each species. The set of species was composed of *Caryocar brasiliense* (pequi), *Hymenaea stigonocarpa*, and *Qualea grandiflora*. RDS, Restauradores da RDS Nascentes Geraizeiras; RSC, Rede de Sementes do Cerrado; RSX, Rede de Sementes do Xingu; VN, VerdeNovo.

genetic variation, increase adaptability, and reduce the risk of inbreeding depression (Kremer et al., 2012; McKay et al., 2005). At the same time, there was a predominance of local seeds in the *C. brasiliense* simulated seed mixes (RSC in site 1 and RDS in site 2), which reduces the risk of outbreeding depression due to the dilution of adaptive genes (genetic swamping) or the disruption of interacting gene networks and ploidy levels (hybrid breakdown) (Frankham et al., 2011; Hufford & Mazer, 2003). Therefore, COSST augments genetic diversity regardless of the climate match optimization, the aspect of biological diversity most relevant for evolutionary rescue under climate change (Aitken & Whitlock, 2013).

Implementing the tool will depend on overcoming two challenges starting with improving seed traceability. Several countries use wild populations for seed production (Atkinson et al., 2021; Bosshard et al., 2021; Giacomini et al., 2023), but the locations of these populations are often unavailable. Some suppliers are moving towards making these data accessible, for example, the Seeds of Success programme (Barga et al., 2020; Haidet & Olwell, 2015) and the Native Seed Vendors map (https://appliedeco.org/nativeseednetwork/find-seed/) in North America. A georeferenced map of where seeds are being collected from is the first step for applying COSST at a large scale. Aligned to this map, vendors will need to tag and separate seed batches per locality (Pedrini & Dixon, 2020), which is a logistical challenge for large seed suppliers, such as RSX, since seeds are often combined into a single mix per species and seed storage facility (Urzedo et al., 2020). Finally, strengthening seed storage technology and infrastructure is the second step to scaling up the tool. COSST encourages some level of seed transport over long distances, making it critical to develop techniques to ensure the viability of the seeds from harvesting to sowing phases (De Vitis et al., 2020; Shaw et al., 2020).

Accounting for seed production limitations and transport costs could increase the applicability of the tool even further. Sites will differ in the volume of seeds that can be collected there due to differences in the size of the vegetation remnants, species abundance, and number of seed collectors (Pedrini et al., 2020). Moreover, seeds can be produced ex situ (e.g., native seed farms) (Gibson-Roy, 2023) or stored over time (De Vitis et al., 2020), further increasing the seed production potential of a site. At present, COSST assumes that all sourcing sites have an equal seed production capacity. If seed production capacity is made available, it is possible to convert the COSST index into the volume/mass of seeds per sourcing site using the maximum seed production capacity as a cap. Another important consideration concerns the additional costs to the restoration project by seed transport from multiple vendors (Schmidt et al., 2019). Composite, climate-adjusted, and predictive strategies assume practitioners will purchase some degree of seeds from vendors far from the restoration site contrary to local provenancing. Sourcing seeds from multiple rather than a single site is more expensive and less practical in the short term but it can pay off in the long term (Jalonen et al., 2018). A restoration cost model revealed that augmenting genetic diversity by sourcing seeds from several populations increased seed collection costs by 33% but reduced maintenance costs by 18% (e.g. replanting) (Nef et al., 2021). Since maintenance represented more than half of total restoration costs, genetically diverse seed mixes reduced restoration costs by 11% over time. Future work can include estimated seed transportation costs in COSST, alongside costs avoided by ensuring the genetic quality of the seed mixes.

5 | CONCLUSION

COSST provides a novel and generalizable tool to apply seed-provenancing principles in restoration planning. The tool can be applied to any plant species, provided there are sufficient occurrence records available to fit SDMs. The tool is likely most relevant in the tropics, where a vast number of species with different range sizes and climatic sensitivities require tailored seed-provenancing guidelines. Here, we focused on wild population seed collection, but COSST can also inform priority areas to source seeds for ex situ seed or seedling production. The tool can support not only practitioners in seed-sourcing decision-making but also suppliers in identifying priority areas for establishing new seed-sourcing sites. By connecting theory and application, we hope our tool can help practitioners maximize ecosystem restoration success under a changing climate.

AUTHOR CONTRIBUTIONS

Mateus C. Silva, Lucy Rowland, and R. Toby Pennington conceived the ideas and designed the methodology; Mateus C. Silva collated and analysed the data and led the writing of the manuscript. Peter Moonlight and Rafael S. Oliveira contributed critically to the drafts. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors confirm no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

No original data were used in the article and the original data are available on Silva et al. (2022). The latest version of the code can be found at https://github.com/silva-mc/COSST, while the original version can be accessed via https://doi.org/10.5281/zenodo.14265511 (Silva, 2024).

ORCID

Mateus C. Silva https://orcid.org/0000-0002-4281-3400
Lucy Rowland https://orcid.org/0000-0002-0774-3216

REFERENCES

Aitken, S. N., & Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics*, *44*(1), 367–388. https://doi.org/10.1146/annurev-ecolsys-110512-135747

Atkinson, R. J., Thomas, E., Roscioli, F., Cornelius, J. P., Zamora-Cristales, R., Franco Chuaire, M., Alcázar, C., Mesén, F., Lopez, H., Ipinza, R., Donoso, P. J., Gallo, L., Nieto, V., Ugarte, J., Sáenz-Romero, C., Fremout, T., Jalonen, R., Gaisberger, H., Vinceti, B., & Kettle, C. (2021). Seeding resilient restoration: An indicator system for the analysis of tree seed systems. *Diversity*, *13*(8), 367. https://doi.org/10.3390/d13080367

B.F.G. Brazilian Flora Group. (2015). Growing knowledge: An overview of seed plant diversity in Brazil. *Rodriguésia*, *66*(4), 1085–1113. https://doi.org/10.1590/2175-7860201566411

Barga, S. C., Olwell, P., Edwards, F., Prescott, L., & Leger, E. A. (2020). Seeds of success: A conservation and restoration investment in the future of U.S. lands. *Conservation Science and Practice*, *2*(7), 1–12. https://doi.org/10.1111/csp2.209

Bosshard, E., Jalonen, R., Kanchanarak, T., Yuskianti, V., Tolentino, E., Warrier, R. R., Krishnan, S., Dzulkifli, D., Thomas, E., Atkinson, R., & Kettle, C. J. (2021). Are tree seed systems for forest landscape restoration fit for purpose? An analysis of four Asian countries. *Diversity*, *13*(11), 575. https://doi.org/10.3390/d13110575

Breed, M. F., Harrison, P. A., Bischoff, A., Durruty, P., Gellie, N. J. C., Gonzales, E. K., Havens, K., Karmann, M., Kilkenny, F. F., Krauss, S. L., Lowe, A. J., Marques, P., Nevill, P. G., Vitt, P. L., & Bucharova, A. (2018). Priority actions to improve provenance decision-making. *BioScience*, *68*(7), 510–516. https://doi.org/10.1093/biosci/biy050

Bridgewater, S., Ratter, J. A., & Ribeiro, J. F. (2004). Biogeographic patterns, diversity and dominance in the cerrado biome of Brazil. *Biodiversity and Conservation*, *13*(12), 2295–2317. https://doi.org/10.1023/B:BIOC.0000047903.37608.4c

Broadhurst, L. M., Lowe, A., Coates, D. J., Cunningham, S. A., McDonald, M., Vesk, P. A., & Yates, C. (2008). Seed supply for broadscale restoration: Maximizing evolutionary potential. *Evolutionary Applications*, *1*(4), 587–597. https://doi.org/10.1111/j.1752-4571.2008.00045.x

Bucharova, A., Bossdorf, O., Hölzel, N., Kollmann, J., Prasse, R., & Durka, W. (2019). Mix and match: Regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. *Conservation Genetics*, *20*(1), 7–17. https://doi.org/10.1007/s10592-018-1067-6

Bucharova, A., Lampei, C., Conrady, M., May, E., Matheja, J., Meyer, M., & Ott, D. (2022). Plant provenance affects pollinator network: Implications for ecological restoration. *Journal of Applied Ecology*, *59*(2), 373–383. https://doi.org/10.1111/1365-2664.13866

Coronado, E. N. H., Dexter, K. G., Hart, M. L., Phillips, O. L., & Pennington, R. T. (2019). Comparative phylogeography of five widespread tree species: Insights into the history of western Amazonia. *Ecology and Evolution*, *9*(12), 7333–7345. https://doi.org/10.1002/ece3.5306

Coutinho, A. G., Carlucci, M. B., & Cianciaruso, M. V. (2023). A framework to apply trait-based ecological restoration at large scales. *Journal of Applied Ecology*, *60*(8), 1562–1571. https://doi.org/10.1111/1365-2664.14439

De Vitis, M., Hay, F. R., Dickie, J. B., Trivedi, C., Choi, J., & Fiegener, R. (2020). Seed storage: Maintaining seed viability and vigor for restoration use. *Restoration Ecology*, *28*(S3), S249–S255. https://doi.org/10.1111/rec.13174

Dupré la Tour, A., Labatut, J., & Spiegelberger, T. (2020). Unraveling the concept of local seeds in restoration ecology. *Restoration Ecology*, *28*(6), 1327–1334. https://doi.org/10.1111/rec.13262

Durka, W., Michalski, S. G., Berendzen, K. W., Bossdorf, O., Bucharova, A., Hermann, J., Hölzel, N., & Kollmann, J. (2017). Genetic differentiation within multiple common grassland plants supports seed transfer zones for ecological restoration. *Journal of Applied Ecology*, *54*(1), 116–126. https://doi.org/10.1111/1365-2664.12636

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Frankham, R., Ballou, J. D., Eldridge, M. D. B., Lacy, R. C., Ralls, K., Dudash, M. R., & Fenster, C. B. (2011). Predicting the probability of outbreeding depression. *Conservation Biology*, *25*(3), 465–475. https://doi.org/10.1111/j.1523-1739.2011.01662.x

Fremout, T., Thomas, E., Bocanegra-González, K. T., Aguirre-Morales, C. A., Morillo-Paz, A. T., Atkinson, R., Kettle, C., Roy González, M., Alcázar-Caicedo, C., González, M. A., Gil-Tobón, C., Gutiérrez, J. P., Moscoso-Higuita, L. G., López-Lavalle, L. A. B., de Carvalho, D., & Muys, B. (2021). Dynamic seed zones to guide climate-smart seed sourcing for tropical dry forest restoration in Colombia. *Forest Ecology and Management*, *490*, 119127. https://doi.org/10.1016/j.foreco.2021.119127

Fremout, T., Thomas, E., Taedoumg, H., Briers, S., Gutiérrez-Miranda, C. E., Alcázar-Caicedo, C., Lindau, A., Kpoumie, H. M., Vinceti, B., Kettle, C., Ekué, M., Atkinson, R., Jalonen, R., Gaisberger, H., Elliott, S., Brechbühler, E., Ceccarelli, V., Krishnan, S., Vacik, H., … Muys, B. (2022). Diversity for Restoration (D4R): Guiding the selection of tree species and seed sources for climate-resilient restoration of tropical forest landscapes. *Journal of Applied Ecology*, *59*(3), 664–679. https://doi.org/10.1111/1365-2664.14079

Frietsch, M., Loos, J., Löhr, K., Sieber, S., & Fischer, J. (2023). Future-proofing ecosystem restoration through enhancing adaptive capacity. *Communications Biology*, *6*(1), 377. https://doi.org/10.1038/s42003-023-04736-y

Gellie, N. J. C., Breed, M. F., Thurgate, N., Kennedy, S. A., & Lowe, A. J. (2016). Local maladaptation in a foundation tree species: Implications for restoration. *Biological Conservation*, *203*, 226–232. https://doi.org/10.1016/j.biocon.2016.08.036

Giacomini, F. L., Prempeh, J. A., Jalonen, R., Vinceti, B., Ekue, M., Bosshard, E., Burslem, D. F. R. P., & Kettle, C. J. (2023). Seeding African forest and landscape restoration: Evaluating native tree seed Systems in four African countries. *Diversity*, *15*(9), 981. https://doi.org/10.3390/d15090981

Gibson-Roy, P. (2023). Limitations and successes for grassy community restoration: An Australian perspective. *Global Ecology and Conservation*, *47*, e02644. https://doi.org/10.1016/j.gecco.2023.e02644

Gibson-Roy, P., Hancock, N., Broadhurst, L., & Driver, M. (2021). Australian native seed sector practice and behavior could limit ecological restoration success: Further insights from the Australian native seed report. *Restoration Ecology*, *29*(7), 1–12. https://doi.org/10.1111/rec.13429

Gross, C. L., Fatemi, M., & Simpson, I. H. (2017). Seed provenance for changing climates: Early growth traits of nonlocal seed are better adapted to future climatic scenarios, but not to current field conditions. *Restoration Ecology*, *25*(4), 577–586. https://doi.org/10.1111/rec.12474

Haidet, M., & Olwell, P. (2015). Seeds of success: A national seed banking program working to achieve long-term conservation goals. *Natural Areas Journal*, *35*(1), 165–173. https://doi.org/10.3375/043.035.0118

Hancock, N., & Hughes, L. (2014). Turning up the heat on the provenance debate: Testing the "local is best" paradigm under heatwave conditions. *Austral Ecology*, *39*(5), 600–611. https://doi.org/10.1111/aec.12122

Harrison, P. A. (2021). Climate change and the suitability of local and non-local species for ecosystem restoration. *Ecological Management & Restoration*, *22*(S2), 75–91. https://doi.org/10.1111/emr.12520

Harrison, P. A., Vaillancourt, R. E., Harris, R. M. B., & Potts, B. M. (2017). Integrating climate change and habitat fragmentation to identify candidate seed sources for ecological restoration. *Restoration Ecology*, *25*(4), 524–531. https://doi.org/10.1111/rec.12488

Havens, K., Vitt, P., Still, S., Kramer, A. T., Fant, J. B., & Schatz, K. (2015). Seed sourcing for restoration in an era of climate change. *Natural Areas Journal*, *35*(1), 122–133. https://doi.org/10.3375/043.035.0116

Hufford, K. M., & Mazer, S. J. (2003). Plant ecotypes: Genetic differentiation in the age of ecological restoration. *Trends in Ecology & Evolution*, *18*(3), 147–155. https://doi.org/10.1016/S0169-5347(03)00002-8

IPBES. (2018). *The IPBES assessment report on land degradation and restoration*. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. https://doi.org/10.5281/zenodo.3237392

Jalonen, R., Valette, M., Boshier, D., Duminil, J., & Thomas, E. (2018). Forest and landscape restoration severely constrained by a lack of attention to the quantity and quality of tree seed: Insights from a global survey. *Conservation Letters*, *11*(4), 1–9. https://doi.org/10.1111/conl.12424

Jørgensen, M. H., Elameen, A., Hofman, N., Klemsdal, S., Malaval, S., & Fjellheim, S. (2016). What's the meaning of local? Using molecular markers to define seed transfer zones for ecological restoration in Norway. *Evolutionary Applications*, *9*(5), 673–684. https://doi.org/10.1111/eva.12378

Kremer, A., Ronce, O., Robledo-Arnuncio, J. J., Guillaume, F., Bohrer, G., Nathan, R., Bridle, J. R., Gomulkiewicz, R., Klein, E. K., Ritland, K., Kuparinen, A., Gerber, S., & Schueler, S. (2012). Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters*, *15*(4), 378–392. https://doi.org/10.1111/j.1461-0248.2012.01746.x

Laughlin, D. C., Chalmandrier, L., Joshi, C., Renton, M., Dwyer, J. M., & Funk, J. L. (2018). Generating species assemblages for restoration and experimentation: A new method that can simultaneously converge on average trait values and maximize functional diversity. *Methods in Ecology and Evolution*, *9*(7), 1764–1771. https://doi.org/10.1111/2041-210X.13023

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H. M., Chaudhary, A., De Palma, A., DeClerck, F. A. J., Di Marco, M., Doelman, J. C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J. P., Hill, S. L. L., Humpenöder, F., Jennings, N., Krisztin, T., … Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, *585*(7826), 551–556. https://doi.org/10.1038/s41586-020-2705-y

Lortie, C. J., & Hierro, J. L. (2022). A synthesis of local adaptation to climate through reciprocal common gardens. *Journal of Ecology*, *110*(5), 1015–1021. https://doi.org/10.1111/1365-2745.13664

MapBiomas. (2023). Collection 8 of the annual land cover and land use maps of Brazil (1985–2022). *MapBiomas Data*. https://doi.org/10.58053/MapBiomas/VJIJCL

Marinoni, L., Parra Quijano, M., Zabala, J. M., Pensiero, J. F., & Iriondo, J. M. (2021). Spatiotemporal seed transfer zones as an efficient restoration strategy in response to climate change. *Ecosphere*, *12*(5), 3462. https://doi.org/10.1002/ecs2.3462

McKay, J. K., Christian, C. E., Harrison, S., & Rice, K. J. (2005). "How local is local?" A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology*, *13*(3), 432–440. https://doi.org/10.1111/j.1526-100X.2005.00058.x

MMA. (2017). *Planaveg: Plano Nacional de Recuperação da Vegetação Nativa*. MMA. https://www.gov.br/mma/pt-br/assuntos/servicosambientais/ecossistemas-1/conservacao-1/politica-nacional-de-recuperacao-da-vegetacao-nativa/planaveg_plano_nacional_recuperacao_vegetacao_nativa.pdf

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Nef, D. P., Gotor, E., Wiederkehr Guerra, G., Zumwald, M., & Kettle, C. J. (2021). Initial investment in diversity is the efficient thing to do for resilient forest landscape restoration. *Frontiers in Forests and Global Change*, *3*, 1–10. https://doi.org/10.3389/ffgc.2020.615682

Pedrini, S., & Dixon, K. W. (2020). International principles and standards for native seeds in ecological restoration. *Restoration Ecology*, *28*(S3), S286–S303. https://doi.org/10.1111/rec.13155

Pedrini, S., Gibson-Roy, P., Trivedi, C., Gálvez-Ramírez, C., Hardwick, K., Shaw, N., Frischie, S., Laverack, G., & Dixon, K. (2020). Collection and production of native seeds for ecological restoration. *Restoration Ecology*, *28*(S3), S228–S238. https://doi.org/10.1111/rec.13190

Pfeilsticker, T. R., Buzatti, R. S. O., Muniz, A. C., Bueno, M. L., Lemos-Filho, J. P., & Lovato, M. B. (2021). Genetic and functional leaf trait diversity throughout the distribution of two Cerrado tree species: Testing the centre-periphery hypothesis. *Journal of Biogeography*, *48*(9), 2258–2274. https://doi.org/10.1111/jbi.14148

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, *40*(7), 887–893. https://doi.org/10.1111/ecog.03049

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, *31*(2), 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Pizza, R. B., Foster, J., & Brudvig, L. A. (2023). Where should they come from? Where should they go? Several measures of seed source locality fail to predict plant establishment in early prairie restorations. *Ecological Solutions and Evidence*, *4*(2), 1–13. https://doi.org/10.1002/2688-8319.12223

Prober, S. M., Byrne, M., McLean, E. H., Steane, D. A., Potts, B. M., Vaillancourt, R. E., & Stock, W. D. (2015). Climate-adjusted provenancing: A strategy for climate-resilient ecological restoration. *Frontiers in Ecology and Evolution*, *3*, 1–5. https://doi.org/10.3389/fevo.2015.00065

Prober, S. M., Doerr, V. A. J., Broadhurst, L. M., Williams, K. J., & Dickson, F. (2019). Shifting the conservation paradigm: A synthesis of options for renovating nature under climate change. *Ecological Monographs*, *89*(1), e01333. https://doi.org/10.1002/ecm.1333

Ribeiro, J. F., Kuhlmann, M., Ogata, R. S., de Oliveira, M. C., Vieira, D. L. M., & Sampaio, A. B. (2023). *Guia de plantas do recomposição cerrado para da vegetação nativa*. Embrapa.

Rodrigues, A. A., Macedo, M. N., Silvério, D. V., Maracahipes, L., Coe, M. T., Brando, P. M., Shimbo, J. Z., Rajão, R., Soares-Filho, B., & Bustamante, M. M. C. (2022). Cerrado deforestation threatens regional climate and water availability for agriculture and ecosystems. *Global Change Biology*, *28*(22), 6807–6822. https://doi.org/10.1111/gcb.16386

Rossetto, M., Bragg, J., Kilian, A., McPherson, H., van der Merwe, M., & Wilson, P. D. (2019). Restore and renew: A genomics-era framework for species provenance delimitation. *Restoration Ecology*, *27*(3), 538–548. https://doi.org/10.1111/rec.12898

Rushing, N. S., Flint, S. A., & Shaw, R. G. (2021). Latitude of seed source impacts flowering phenology and fitness in translocated plant populations. *Restoration Ecology*, *29*(8), 1–12. https://doi.org/10.1111/rec.13464

Schmidt, I. B., de Urzedo, D. I., Piña-Rodrigues, F. C. M., Vieira, D. L. M., de Rezende, G. M., Sampaio, A. B., & Junqueira, R. G. P. (2019). Community-based native seed production for restoration in Brazil – The role of science and policy. *Plant Biology*, *21*(3), 389–397. https://doi.org/10.1111/plb.12842

Shaw, N., Barak, R. S., Campbell, R. E., Kirmer, A., Pedrini, S., Dixon, K., & Frischie, S. (2020). Seed use in the field: Delivering seeds for restoration success. *Restoration Ecology*, *28*(S3), S276–S285. https://doi.org/10.1111/rec.13210

Shryock, D. F., DeFalco, L. A., & Esque, T. C. (2018). Spatial decision-support tools to guide restoration and seed-sourcing in the desert southwest. *Ecosphere*, *9*(10), e02453. https://doi.org/10.1002/ecs2.2453

Silva, M. (2024, December). Climate-Oriented Seed Sourcing Tool (COSST). *Zenodo*. https://doi.org/10.5281/zenodo.14265511

Silva, M. C., Moonlight, P., Oliveira, R. S., Pennington, R. T., & Rowland, L. (2022). Toward diverse seed sourcing to upscale ecological restoration in the Brazilian Cerrado. *Frontiers in Ecology and Evolution*, *10*, 1–10. https://doi.org/10.3389/fevo.2022.1045591

Silva, M. C., Rowland, L., Oliveira, R. S., Pennington, R. T., & Moonlight, P. (2024). Elevation modulates the impacts of climate change on the Brazilian Cerrado flora. *Diversity and Distributions*, *30*(5), 1–15. https://doi.org/10.1111/ddi.13832

St. Clair, J. B., Richardson, B. A., Stevenson-Molnar, N., Howe, G. T., Bower, A. D., Erickson, V. J., Ward, B., Bachelet, D., Kilkenny, F. F., & Wang, T. (2022). Seedlot selection tool and climate-smart restoration tool: Web-based tools for sourcing seed adapted to future climates. *Ecosphere*, *13*(5), 1–18. https://doi.org/10.1002/ecs2.4089

Strassburg, B. B. N. N., Iribarrem, A., Beyer, H. L., Cordeiro, C. L., Crouzeilles, R., Jakovac, C. C., Braga Junqueira, A., Lacerda, E., Latawiec, A. E., Balmford, A., Brooks, T. M., Butchart, S. H. M., Chazdon, R. L., Erb, K. H., Brancalion, P., Buchanan, G., Cooper, D., Díaz, S., Donald, P. F., … Visconti, P. (2020). Global priority areas for ecosystem restoration. *Nature*, *586*(7831), 724–729. https://doi.org/10.1038/s41586-020-2784-9

Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, *19*(1), 46–53. https://doi.org/10.1016/j.tree.2003.10.005

Urzedo, D., Piña-Rodrigues, F., Feltran-Barbieri, R., Junqueira, R., & Fisher, R. (2020). Seed networks for upscaling forest landscape restoration: Is it possible to expand native plant sources in Brazil? *Forests*, *11*(3), 259. https://doi.org/10.3390/f11030259

Vitt, P., Finch, J., Barak, R. S., Braum, A., Frischie, S., & Redlinski, I. (2022). Seed sourcing strategies for ecological restoration under climate change: A review of the current literature. *Frontiers in Conservation Science*, *3*, 1–16. https://doi.org/10.3389/fcosc.2022.938110

Wilczek, A. M., Cooper, M. D., Korves, T. M., & Schmitt, J. (2014). Lagging adaptation to warming climate in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(22), 7906–7913. https://doi.org/10.1073/pnas.1406314111

Zabin, C. J., Jurgens, L. J., Bible, J. M., Patten, M. V., Chang, A. L., Grosholz, E. D., & Boyer, K. E. (2022). Increasing the resilience of ecological restoration to extreme climatic events. *Frontiers in Ecology and the Environment*, *20*(5), 310–318. https://doi.org/10.1002/fee.2471

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Input data and settings of the Species Distribution Models.

Appendix S2. Composite-predictive continuum.

Appendix S3. Evidence of local adaptation in the Brazilian Cerrado.

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