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RESEARCH ARTICLE

Cost-effective ecological restoration

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Ecological restoration is a multibillion dollar industry critical for improving degraded habitat. However, most restoration is conducted without clearly defined success measures or analysis of costs. Outcomes are influenced by environmental conditions that vary across space and time, yet such variation is rarely considered in restoration planning. Here, we present a cost-effectiveness analysis of terrestrial restoration methods to determine how practitioners may restore the highest native plant cover per dollar spent. We recorded costs of 120 distinct methods and described success in terms of native versus non-native plant germination, growth, cover, and density. We assessed effectiveness using a basic, commonly used metric (% native plant cover) and developed an index of cost-effectiveness (% native cover per dollar spent on restoration). We then evaluated success of multiple methods, given environmental variation across topography and multiple years, and found that the most successful method for restoring high native plant cover is often different from the method that results in the largest area restored per dollar expended, given fixed mitigation budgets. Based on our results, we developed decision-making trees to guide practitioners through established phases of restoration—*site preparation*, *seeding and planting*, and *maintenance*. We also highlight where additional research could inform restoration practice, such as improved seasonal weather forecasts optimizing allocation of funds in time or valuation practices that include costs of specific outcomes in the collection of in lieu fees.

Key words: California grassland, coastal sage scrub, community assembly, ecological economics, in lieu mitigation fee, invasive species, mitigation funds, restoration economy

Conceptual Implications

- There can be large differences in the cost-effectiveness of restoration, highlighting the need for defined metrics of success.
- Metrics of success must be selected prior to developing decision-making trees, because different metrics point to different courses of action.
- The most cost-effective methods (those that result in the highest native cover per dollar spent) are not necessarily the methods that result in the highest cover regardless of cost.
- The target or "reference" community that is the goal of the restoration has a big impact on cost-effectiveness.
- Environmental variation also has a big impact on cost-effectiveness.

Introduction

Annually, billions of dollars are spent recovering degraded habitat (Woodworth 2006; Malakoff 2012). An increasing number of publications and entire journals (such as this publication) evaluate restoration methods, often in the context of ecological theory (Hobbs & Norton 1996; Suding et al. 2004; Verdu et al. 2012). Despite substantial investments and study, restoration practitioners lack critical information necessary to determine what methods will successfully and quickly restore a habitat at the lowest cost (Robbins & Daniels 2012). The literature points to key decision-making challenges, including poorly identified success metrics, limited cost information, and challenges in understanding environmental variation.

Although projects restoring vegetation are often undertaken to mitigate for development on pristine habitat elsewhere (Young 2000), success metrics—where they are specified—vary greatly depending on the group performing or mandating restoration (Ruiz-Jaen & Aide 2005*a*). Selecting a target "reference" community to restore (SER 2004) may be difficult because heavily degraded areas have little native cover to use as a reference (Clewell & Rieger 1997), and different vegetation types co-occur across climate zones (Archer et al. 1995). Despite mitigation projects being driven by law, specific benchmarks are often short-term ecological metrics, such as native plant cover values, that may not project

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long-term trajectories (Zedler & Callaway 1999; Suding 2011). Other methods for evaluating success include the change in native cover or the proportion of native to non-native species (Maron et al. 2013). One goal for the field is to evaluate more complex success metrics, such as ecosystem services (Benayas et al. 2009; Wortley et al. 2013). Although measurement of ecosystem services is an ideal that we may strive to achieve to measure restoration success, required data do not exist for most ecosystems, and measurements and analyses required are time consuming (Daily et al. 2009).

The second challenge facing restoration is that, with few exceptions (Birch et al. 2010; Busch et al. 2010; Gerla et al. 2012), costs of different restoration methods are not usually reported in the literature (Robbins & Daniels 2012). Academic authors are not always familiar with restoration costs when restoration is performed at larger scales, and practitioners who are familiar with costs may not compare techniques in experimental settings (Holl & Howarth 2000; Brudvig 2011). A recent review found that only 2.5% of published restoration studies reported both ecological and economic data (Wortley et al. 2013). The result is that restoration practitioners lack reliable information to evaluate restoration cost-effectiveness and experimentalists have not contributed to the effort. Comprehensive analyses and tools that can support decision-making in diverse settings are needed to optimize conservation resources within the multibillion dollar annual restoration industry (Acuna et al. 2013). One approach is to compare the cost-effectiveness of restoration techniques by analyzing cost per number of surviving individuals, per growth of seedlings, or per probability of meeting specific thresholds of success (Ahtikoski et al. 2010; Grose 2013). Here, we determine cost-effectiveness by dividing the resulting native cover post-restoration by costs per hectare. Such calculations of cost-effectiveness of restoration actions are critical to ensure that limited funds are spent in the best manner and to avoid wasting money on ineffective actions (Birch et al. 2010; Wilson et al. 2011; Auerbach et al. 2014).

Lastly, environmental variation influences results of restoration, yet such variability is rarely considered by practitioners, policymakers, or funding agencies in evaluating cost or in measuring method effectiveness (Bakker et al. 2003; Matthews et al. 2009; Brudvig 2011). For example, slope and aspect are known to influence plant community composition (Kirkpatrick & Hutchinson 1980; Kutiel & Lavee 1999; Bennie et al. 2006), yet few studies incorporate such environmental characteristics in their assessment of restoration methods, and even fewer consider details like precipitation amount and timing (Jones 2000; Lana et al. 2006). Precipitation is the single largest driver of plant cover in many ecosystems (Huxman et al. 2004), yet inter-annual variation in cover associated with rainfall is often missing from evaluations of restoration success and is difficult to consider in the planning process.

Here, we present the first comprehensive analysis of the cost-effectiveness of different plant restoration methods, presenting results from an extensive experimental manipulation in southern California. We do not attempt to comprehensively solve all three challenges facing practitioners, but employ an approach for evaluating costs, basic and stage-specific success metrics, along with environmental variation that informs decision-making. Our particular case study represents a site initially dominated by invasive species, with the goal of determining how best to increase native cover and of optimizing what native cover could be achieved over a large area with fixed monetary investment. We varied methods across (1) *site preparation*, which consisted of removing non-natives to reduce biotic filters preventing native plant establishment; (2) *seeding and planting*, which involved removing dispersal filters by adding natives found in the "reference" community species pool; and (3) *maintenance*, or continued removal of non-natives to reduce the likelihood of competitive exclusion (Fig. 1). We tracked exact expenditures and evaluated slope and aspect effects on restoration success across a 25-ha experimental area. We evaluated several of the most basic and commonly used metrics of restoration success across multiple treatments, including germination of native and non-native species, along with end-of-season native plant cover. In our system, native plant cover prior to restoration was close to zero, so measuring native cover after restoration was similar to reporting the change in native cover. We developed decision-making trees for practitioners using results of our cost-effectiveness analyses. Our analyses provide a foundation to support new decision-making tools for practitioners and policymakers, while also tackling basic questions in science, and linking academic ecology with a profession of practice.

Methods

The West Loma Ecological Restoration Experiment is a watershed located in the Santa Ana Mountains in southern California, United States (33.7647°N 117.7382°W, Fig. 1). Plant cover prior to restoration consisted almost entirely of non-native annual grasses (e.g. *Bromus diandrus*, *Brachypodium distachyon*, and *Avena fatua*) and non-native forbs (all *Brassica nigra*), with only 3% native species. The purpose of this restoration, primarily funded by the landowner, was (1) to utilize goals and methods that would inform planned mitigation projects under similar conditions; and (2) to maximize cost-effectiveness and basic success criteria used in the region, given the challenges of limited access, tens of acres needing restoration, highly variable terrain, and very limited use of irrigation.

The dichotomy of vegetation in this Mediterranean system (coastal sage scrub, a shrub-dominated system, and California grassland, commonly referred to as "Prairie" due to the abundance of forbs), which presents many functional plant types, along with several globally problematic invasive species, is relevant to challenges in restoration across the globe. Mean annual precipitation is 324 mm, but there is high inter-annual variation. Total seasonal rainfall during three planting years was 595, 224, and 161 mm, and the amount of precipitation in the rain event that triggered germination during the 3 years was 19, 28, and 24 mm (Santiago Dam Station, Coop ID # 047987, 33°47′N, 117°43′W, elev. 26 m). To the best of our knowledge, the entire site experienced the same level of historical disturbance, including cattle grazing from approximately 1850 until 2002, and two

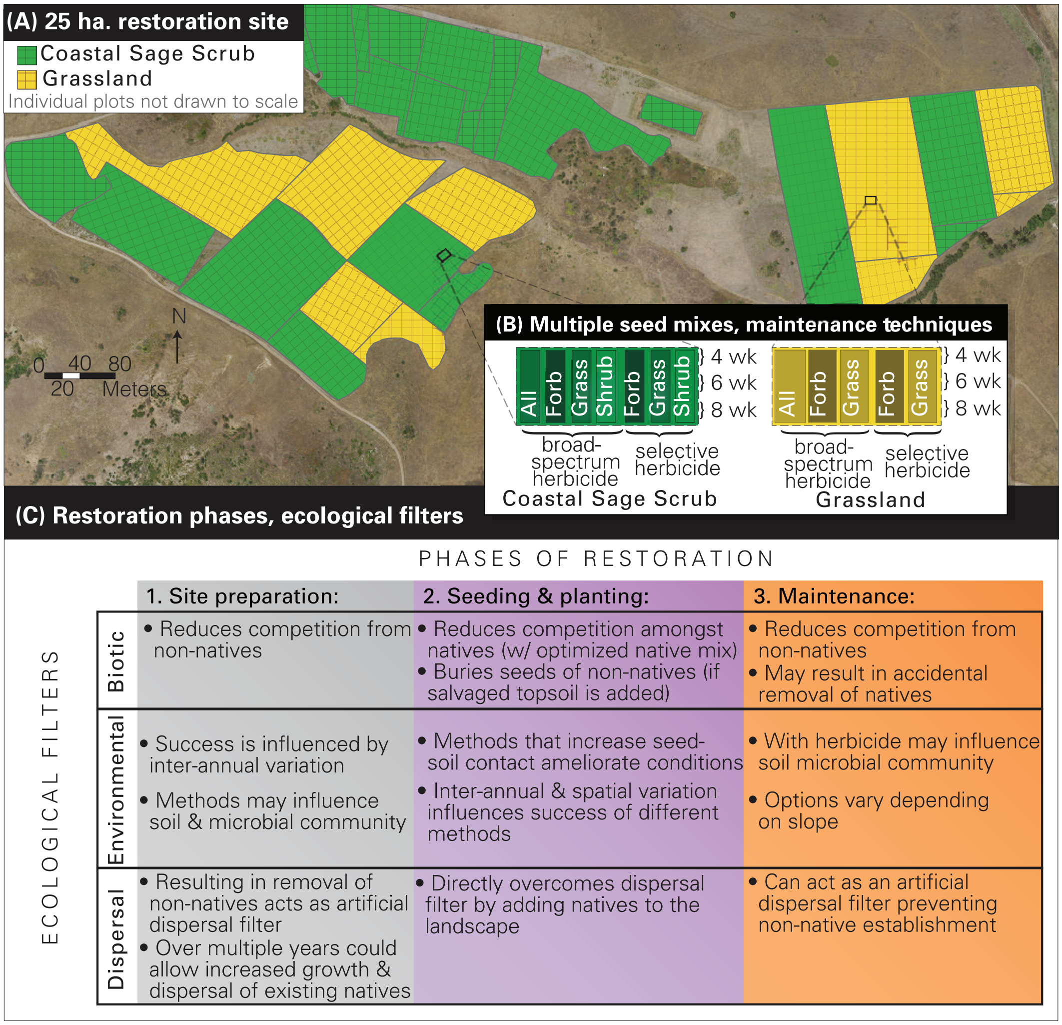

Figure 1. The West Loma Restoration Experiment. (A) Aerial image of the 25-ha restoration project, with areas color coded by the native community seeded or planted, (B) diagram illustrating some of the different native seed mixes and maintenance techniques tested, and (C) table illustrating how the three main phases of restoration (illustrated with different colors) relate to the concept of ecological filters that determine community assembly.

fires in the last 50 years (1967 and 2007). Historical remnant vegetation included coastal sage scrub and California grassland. Slopes varied from 5 to 70%, restricting large equipment use to locations less than 30% (Fig. S1).

In this case study, *site preparation* began in 2009 with a tractor mower and attached reel flail, weed eaters, or goats, depending on slope (Figs. S1 & S2). With the exception of the goat grazed area, subsequent weed control consisted of glyphosphate (1.2–2.4 L/ha) applications, applied with a boom sprayer on moderate slopes and hand sprayers on steep slopes. *Seeding and planting* followed between 1 and 3 years of *site preparation* (to test for the cost-effectiveness of different time investments in *site preparation*), and replicate plots were arranged in blocks of coastal sage scrub and grassland deliberately placed in different slope positions (upper or lower) and aspect (north vs. south). Seeding of plots occurred 2 weeks after a final application of herbicide coincident with the first winter-season rains. Seeded plots received a mix of species from one functional group (grass, forb, or shrub) or a mix of all functional groups combined (“all” mix), with endomycorrhizal inoculate (Fig. 1). Pure live seed (PLS) pounds per acre (kg per hectare) differed slightly from year to year to achieve balanced representation among species of a given functional group (Table S1). Seeding approaches included a Truax® FLEXII Grass Drill (Truax Co., Inc., New Hope, MN, U.S.A.), hand broadcasting followed by tamping with a McLeod, and imprint seeding (custom built cylinder with toothed notches forming an approximately 225 cm^2 triangular divot). Some seeded areas were supplemented with container plants (either 3.8×12.7 cm cones, 3.2×6.4 cm grass cones, or $5.1 \times 5.1 \times 8.1$ cm pots; Table S2) to determine whether the added cost of containers was worth the added native cover. Salvaged topsoil (approximately 20 cm) from intact coastal sage scrub bulldozed in late December 2010 was applied to a 0.76-ha area (Fig. S2), smoothed approximately 10 cm thick, creating seven 6-m wide strips of 80–90 m in length. Some *maintenance* occurred at all sites because past studies have found much lower native cover in areas without weed control (Kimball et al. 2014). *Maintenance* return interval varied (4, 6, and 8 weeks) to assess effort and intensity on moderate slope areas. For these treatments, weed control occurred by early season hand pulling and late season concentrated glyphosate (17%) distributed with a weed wiper sponge applicator (The Red Weeder®, Smucker Manufacturing, Inc., Harrisburg, OR, U.S.A.). In addition, broadleaf (Element 4 [triclopyr], 2.4 L/ha) and grass-specific (Fusilade II [Fluazifop], 1.8 L/ha) herbicide treatments applied as a mist with a backpack sprayer were compared to glyphosate applied with a weed wiper by applying Element and Fusilade solutions to only grass and only shrub and forb-seeded areas, respectively. These particular methods are applicable to our case study, but the evaluation of cost-effectiveness could be applied globally.

We recorded daily labor rates by activity, equipment use, and treatment during restoration (Table S2). Because of area-dependent relationships of some variables, we scaled specific treatments to 1–3 ha in order to provide realistic contrasts applicable to implementation. Large equipment costs are included either as a rental expense or as a depreciation cost based on useful life. We utilized professional, trained labor pools to determine costs (Irvine Ranch Conservancy staff, or local landscaping, erosion control, or agricultural companies). Costs do not include overhead, planning, time spent traveling to the restoration/field site, or labor and materials for marking experimental treatments, such as flagging and staking, as each of these areas vary by restoration entity, location, and science goals. Mowing rates included in analyses are based on events timed to maximize efficiency, which is at the beginning of the growing season. Mowing rates, particularly with handheld weed eaters, slow substantially after fresh growth of annual vegetation. Costs do include preparation time for seeding or planting, such as mixing seed and calibrating drill seeders, subdividing the seed mix into bags for even distribution of broadcast seeding, and loading and dispersing container plants.

Seed rates were determined per species based on general establishment success from previous seeding experience by the Irvine Ranch Conservancy and local practitioners. Because seed lots differ in collection year, method cleaned, or storage conditions, seed rates were based on the weight of PLS, adjusting bulk seed weight from a given lot to match PLS rates. Based on comparisons of multiple lots over a few years, we found that percent PLS (which includes germination and purity) tended to average 25% for shrubs and 50% for grasses and forbs. The cost of seed was calculated by multiplying the weight of PLS per unit area (acres or hectares) by the bulk price by weight. This cost per unit area was multiplied by 4 for shrubs and by 2 for grasses and forbs to obtain a realistic price based on bulk weight of seed lots that is also consistent across seeding events in the study (Tables S1).

Site preparation phase success was indicated by low germination of non-native species and high native germination, because each season of non-native germination and growth followed by non-native removal ("grow and kill" cycle) is intended to deplete the non-native seed bank and allow natives to overcome establishment filters imposed in part by competition (Moyes et al. 2005; Potthoff et al. 2005). The abundance of seedlings was determined within five 25 × 25 cm quadrats placed every 10 m along several 50 m transects within treatments across all years. This quadrat size was selected as appropriate for the size and frequency of seedlings in our system, consistent with other monitoring methods (Keeley & Fotheringham 2005). Control transects were sampled outside of treatments. Overall success following completion of all three phases of restoration was measured as % native cover across all areas in late spring of 2013 using a point-intercept method. Although we recognize that including other metrics of success would be ideal, this basic metric of success was collected because it is correlated with a decrease in non-native cover, and was the required metric for parts of this restoration project as well as for the majority of mitigation projects in this region (Suding 2011; Wortley et al. 2013). Most contrasts had extremely large sample sizes (27 treatment blocks were sampled for coastal sage scrub and 37 for grassland).

Statistical Analysis and Data Treatment

Site Preparation. We used a general linear model (GLM; Proc Genmod in SAS with logit link) to test whether density of non-native species (sampled approximately 14 days after the first rain event of the season) depended on aspect, year of sampling (to test for interannual variation), or the interaction between the two. This model is analogous to a two-way analysis of variance (ANOVA) except that residuals were assumed to be binomially distributed (typical for count data) rather than normally distributed. Proc Genmod was also used to test whether density of non-native species (sampled in areas not planted with natives) depended on *site preparation* treatment within each year. Years were tested separately because not all treatments were applied in all years. Tukey post hoc comparisons were done to determine differences among treatments. We also used this method to determine whether the density of native species that germinated following seeding depended on the *site preparation* treatment.

Seeding and Planting. We used Proc Genmod in SAS to determine whether germination of native coastal sage scrub plants in February 2011 varied depending on hand-seeding technique (with or without tamping). We used ANOVA (Proc GLM in SAS) to determine whether ln-transformed density of the perennial bunchgrass, *Stipa pulchra*, depended on seeding method (drill vs. broadcast seeding). This comparison was performed in the plots seeded in year 2, and seeding method, maintenance schedule, seed mix, and all interactions were all included as independent variables in the analysis.

Maintenance. We used mixed model ANOVAs (Proc Mixed in SAS) to test whether the cover of native plants depended on herbicide type (selective vs. broad spectrum), maintenance schedule (4, 6, or 8 weeks), or the interaction between the two. Block was included as a random factor. Each functional group within each community was tested separately. The "all combined" seed mix was not included because only broad-spectrum herbicide was used on that mix.

Separate analyses were performed on the cover of each functional group in the broad-spectrum herbicide plots to determine whether cover of that particular functional group depended on seed mix (shrub, forb, grass, and all combined in the coastal sage scrub plots and grass, forb, and all combined in the grassland plots), maintenance schedule, or the interaction between the two. In all cases, Tukey post hoc tests were used to determine differences among maintenance schedules and/or seed mixes. Mixed model ANOVA was also used to determine whether the native plant cover in the all seed mixes varied depending on community (coastal sage scrub vs. grassland).

Cost-Effectiveness. We used multiple regression to calculate standardized regression coefficients for *site preparation*, *seeding and planting*, and *maintenance* phases of restoration to determine the relative contribution of money spent at each phase on the percent cover of native plants in 2013. This analysis was performed using all areas for which we had data on average percent cover in 2013 ($N = 87$, Table S2, results in Table S3A). To control for the effect of time (plant growth) on cover in 2013, we also ran the analysis with only data from areas planted in the second year ($N = 74$, Table S3B).

We performed linear regressions (Proc REG in SAS) to investigate the relationship between costs per hectare and measures of effectiveness (either percent cover of native plants or density of native plants per m^2). To investigate the cost-effectiveness of site preparation methods, we performed two separate regressions, one with ln-transformed non-native density and the other with native density as the dependent variables and costs as independent variables. We used data only from south-facing slopes to control for the effect of slope aspect. We also used linear regression to determine whether cover of native plants, as measured by point-intercept methods in 2013, varied depending on the costs of different methods of seeding and planting. For this analysis, we included only "all seed mixes" on south-facing slopes with 8-week maintenance schedules. To determine whether native plant cover varied depending on the costs of different maintenance methods and the slope aspect (north- vs. south-facing slopes), we performed analysis of covariance (ANCOVA) using Proc GLM in SAS with cover as the dependent variable and aspect and cost as independent variables.

We calculated an index of cost-effectiveness as percent cover native plants in 2013/total cost per hectare of all phases of restoration through 2013 in \$1,000 (Table S2). Residuals from linear models with the index as the dependent variable were not initially normally distributed, so the ratio of native cover/cost was arcsine square root transformed to meet the assumptions of ANOVA, and the transformed index value was used in all analyses. We used one-way ANOVA (Proc GLM in SAS) to determine whether the transformed index of cost-effectiveness varied depending on aspect (north- vs. south-facing slope, $N = 87$). To determine whether cost-effectiveness depended on slope steepness (moderate vs. steep slopes), we performed a separate ANOVA only on treatments applied on south-facing slopes ($N = 48$) because there were no steep, north-facing slopes. ANOVAs tested for cost-effectiveness of herbicide by analyzing all seed mixes for which both broad-spectrum and selective herbicides were used ($N = 62$). To determine the influence of seed mix (forb vs. shrub vs. grass vs. all combined) on cost-effectiveness, we performed ANOVA only on plots treated with broad-spectrum herbicide ($N = 54$), because the combined seed mix was not treated with selective herbicide. ANOVA was also used to determine whether the cost-effectiveness index in the all seed mixes varied depending on community (coastal sage scrub vs. grassland). Some areas restored to coastal sage scrub, but not grassland, were on steep slopes, so we also performed the ANOVA with only moderate-sloped areas.

Results

Site Preparation

Success of *site preparation* was determined by contrasting abundances of native and non-native seedlings by treatment and time because of this case study's focus on reducing non-native species from the seed bank. Costs ranged from \$0/ha (no site prep) to \$5,389/ha, depending on the number of years "grow and kill" cycles were applied and on specific *site preparation* technique (Table S4). It appeared that non-native germination could be suppressed by investment in more expensive techniques (Fig. S3), yet in dry conditions during fall and winter germination, plots with very low investment also resulted in a reduction of the biotic filter (low non-native germination). Interestingly, variation among years was much greater than within years, highlighting the importance of interannual variation. This also made an assessment of the most cost-efficient *site preparation* technique difficult (results comparing *site preparation* techniques are in Table S5). The hypothesized decision-making tree presented herein derived from the likely application of this idea by practitioners of seasonal forecasts to schedule *seeding and planting* in wet years to maximize success of native recruitment (Fig. 4A).

Seeding and Planting

The *seeding and planting* phase tested several commonly used techniques to directly overcome filters limiting native community assembly. Hand seeding followed by raking and tamping on steep slopes was the most expensive seeding method at \$4,942/ha, and resulted in significantly more native seedlings than hand seeding without raking and tamping (Table S6A). The least expensive seeding method was drill seeding with a tractor (\$754/ha), which is not an option on slopes that are too steep to effectively pull drill seeders, but which was significantly more effective than hand seeding of grasses (Table S6B). An increase in spending on *seeding and planting* increased the cover of native plants (Fig. 2). Seeding coastal sage scrub species resulted in a higher cover of native plants than grassland species (mixed model ANOVA $F_{[1,189]} = 66.98$, $p < 0.0001$, Fig. 3, Table S7). Within the coastal sage scrub community, *seeding and planting* of shrubs, grasses, and forbs separately

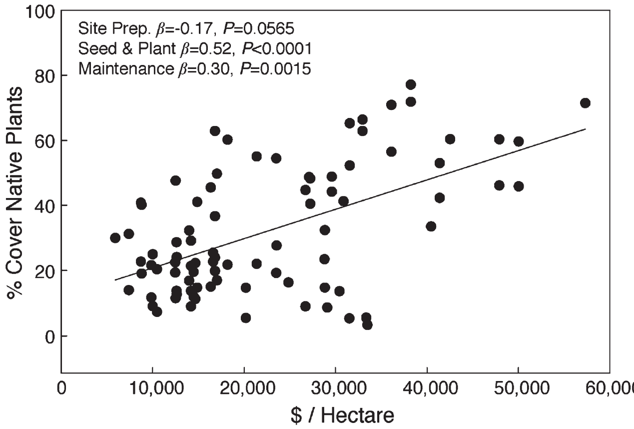

Figure 2. Total restoration costs and the cover of native plants. Each dot represents a unique treatment combination. For each treatment combination, the average % cover collected using point-intercept methods in spring 2013 is plotted against the total cost. Sample sizes for each treatment combination are given in Table S2. The line is from a multiple regression on areas planted in the second year of the study (fall 2011), where $R^2 = 0.43$, $p < 0.0001$. Inset indicates standardized regression coefficients for each phase of restoration.

resulted in greater cover of each functional group than planting them all together, indicating relatively greater competition among than between functional groups of establishing natives (biotic filter, Table S6, Fig. 1). Within the grassland community, cover of each functional group did not vary depending on seed mix (Table S6). For areas planted in the same year, funds spent on *seeding and planting* resulted in higher native cover on north-facing slopes than on south-facing slopes (Fig. 3).

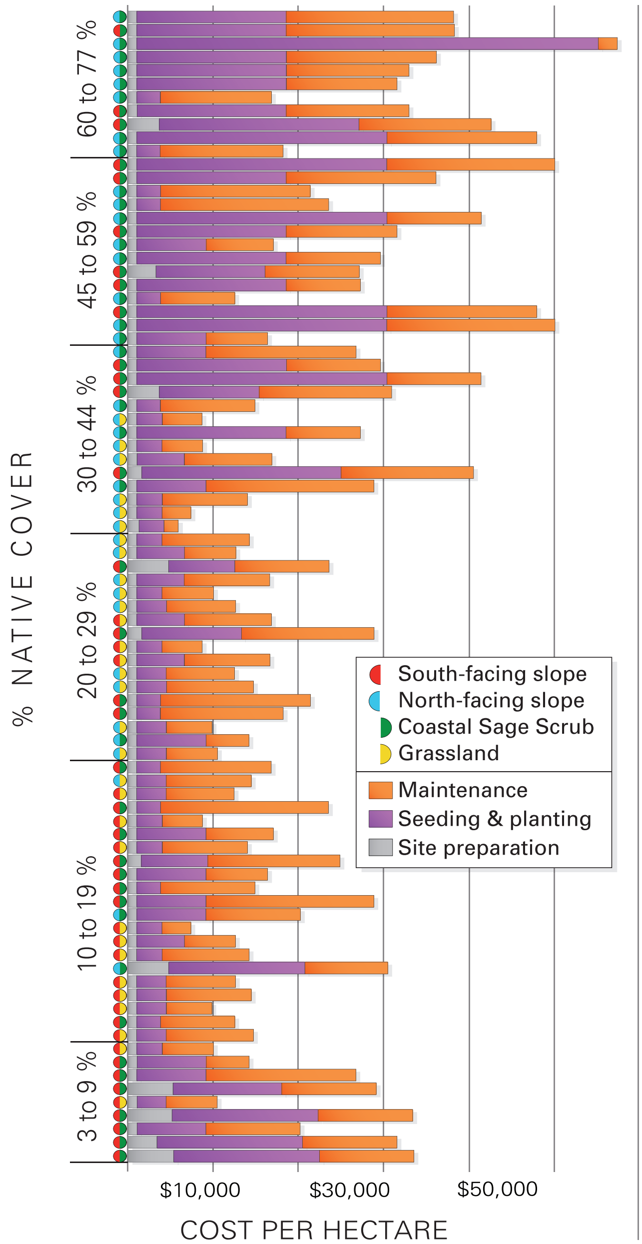

Figure 3. Cost-effectiveness of restoration treatments. The cost per hectare of different restoration treatments at different phases (illustrated with different colors) and their resulting native % cover in spring 2013. Circles on the left indicate whether the area was on a north-facing or a south-facing slope (left half of circle) and whether the area was restored to coastal sage scrub or grassland (right half of circle).

Maintenance

Options for reducing non-natives and increasing natives during the *maintenance* phase ranged from $1,857 to $11,440/ha/year (Table S9). Selective herbicides were not an option in mixed functional group plantings where they would kill native plants, which restricted the success and increased the cost of weeding in mixed group plantings (Table S10). Greater spending on *maintenance* generally increased the percent cover of native plants (Fig. 2, Fig. S4), as did more frequent *maintenance* for all coastal sage scrub seed mixes and for mixes containing grasses in the grassland community (Table S8). North- versus south-facing slopes varied in the impact of *maintenance* on native cover, such that the same maintenance performed on north-facing slopes resulted in significantly greater native cover than on south-facing slopes (Fig. 3, Fig. S4).

Overall Cost-Effectiveness

As expected, the costs of all restoration phases were generally related to native plant cover in our system ($R^2 = 0.43$, Fig. 2). Multiple regression analysis indicated that money spent on the *seeding and planting* phase most strongly influenced success (standardized regression coefficient, $\beta = 0.52$, Figs. 2 & 3, Table S3, Part IA), although money spent on *maintenance* also positively influenced native cover ($\beta = 0.30$, Figs. 2 & 3, Fig. S4). When evaluated across the entire time series, funds spent on *site preparation* had a negative relationship with native cover ($\beta = -0.17$, Figs. 2 & 3, Table S3, Part IB). This is partially due to how areas planted in the first year had more time to grow prior to sampling in 2013. It also reflects the reality of the higher expenses incurred across multiple years of *site preparation* compared with fractional gains in cover from a reduction in non-native performance. When constrained to areas planted in the same year, there was a tendency toward a negative relationship of funds spent on *site preparation* and native cover ($p = 0.057$, Table S3), indicating that greater monetary investment in this phase was not related to good native establishment.

Restoration cost-effectiveness (index calculated as percent native cover/cost per hectare) varied dramatically (index values ranged from 0.27 to 5.07) for each treatment across all restoration phases. Although the transportation and use of salvaged topsoil from habitat being developed resulted in a high cover of native plants (Fig. 4B), this method was by far the most expensive. Despite how effective this method was at overcoming dispersal filters by adding native plant seeds and soil microbiota, along with biotic filters by burying seeds of non-natives, the effectiveness index was in the lower 50% of all values across treatments due to the expense (1.25, Table S2). The two methods with the highest cost-effectiveness index values were drill seeding of grassland grasses (4.68) and imprint seeding of coastal sage scrub forbs (3.80, Table S2) on moderate, north-facing slopes, which ameliorated environmental restrictions on establishment. The most cost-effective methods (resulting in highest native plant cover per dollar spent) were not necessarily methods that resulted in highest native plant cover regardless of costs. The method combination that resulted in highest native cover was imprint seeding of coastal sage scrub shrubs and planting of container shrubs, followed by a 4-week *maintenance* schedule on a north-facing slope, which had a cost-effectiveness index of 2.02 (Fig. 4B, Table S2).

Restoration on north-facing slopes was 2.0 times more cost-effective on average and consistently resulted in greater native cover than on south-facing slopes (Fig. 3, Tables S2 & S3). Restoration on the moderate south-facing slope was more cost-effective than on the steep south-facing slope (Table S3). Restoration to grassland was significantly more cost-effective than restoration to coastal sage scrub (2013 data, Table S3), due to how difficult establishment is for shrubs on steep slopes (Fig. 3). Across moderate slopes only, both habitats were equally cost-effective (Table S3).

Discussion

In this study, we used an experimental approach to evaluate how practitioners might invest limited funds on different methods and stages of ecological restoration to achieve success in a terrestrial ecosystem that is driven by substantial interannual variation in precipitation. Contrasting the costs and successes of more than 120 well-established and widely used restoration treatment combinations provides the following important conclusions: (1) there can be order-of-magnitude differences in success of cost-equivalent restoration, and (2) environmental filters that influence community assembly in complex topographies and temporally variable environments can have a large effect on cost-effectiveness, and (3) the selected restoration target or "reference" community influences cost-effectiveness, which when combined with fixed funds for investment affects the spatial magnitude of potential habitat area restored. Thus, by careful consideration of methods, sequencing of stages in the context of weather, landscape position, and reference community, the amount of land that can be successfully restored to a desired threshold of native plant cover can be increased by an order of magnitude. Flexible business practices, such as scheduling *seeding and planting* in mesic environments or investing in additional *maintenance* in wet conditions, all dramatically influenced restoration success and effectiveness.

Different *seeding and planting* methods can succeed in reaching equivalent high percentage of native cover with very different costs. For example, (1) using an imprinter to seed shrub-only mixes followed by a 4-week *maintenance* schedule of spot treatment with broad-spectrum herbicide, and (2) applying salvaged topsoil followed by an 8-week schedule with the same herbicide, both resulted in greater than 70% native cover. Yet the second method costs $19,000 more per hectare than the first. Although details of the exact methods are specific to our system, the implication—evaluating costs allows for informed decisions regarding best practices—may be applied broadly. Such differences in cost-effectiveness are driven in part by success metric. If we had chosen species diversity as our metric, the addition of salvaged topsoil would have resulted in both highest absolute % cover of native plants in a treated area and also the most cost-effective practice to employ.

It is unclear whether the ecological benefit of restoration is maximized by a higher percent native cover at a single site, or greater total area restored with somewhat lower percent native cover. On average, restoring lands to 40% native cover instead of 50% would free up funds to treat 80% more area, something that may be desired given the known effects of spatial scale on controlling species diversity and population dynamics (Schoener 1976; Pimm et al. 1995). Such a trade-off in fund allocation dramatically influences the spatial scale of habitat recovery for potentially mobile species relying upon this vegetation. If the greatest overall cover of plants per dollar were the measure of success (our "index of effectiveness"), our analysis points to a third, very different course of action than the two listed in the above section: imprint seeding of coastal sage scrub forbs or drill seeding of grass maintained with Element® every 4–8 weeks (Table S2). Such site- and system-specific details are included to demonstrate how an index of effectiveness may be used to guide the restoration economy, and how different success metrics influence the analyses. The desired community for restoration also has a substantial influence on assessments of cost-effectiveness: restoring an area to grassland was more cost-effective than restoring to coastal sage scrub, but resulted in native cover per area that was approximately 10% less (Table S3). The conservation implications of such fixed differences in cover as a function of habitat type are poorly understood outside the context of specific species-recovery plans. However, this is an important consideration for impacting the allocation of funds in systems where the predisturbance communities are unknown and variation in reference community is acceptable.

Environmental variation strongly influenced restoration success and cost-effectiveness (Table S5, Part E). Although the importance of environmental filters at the community level is

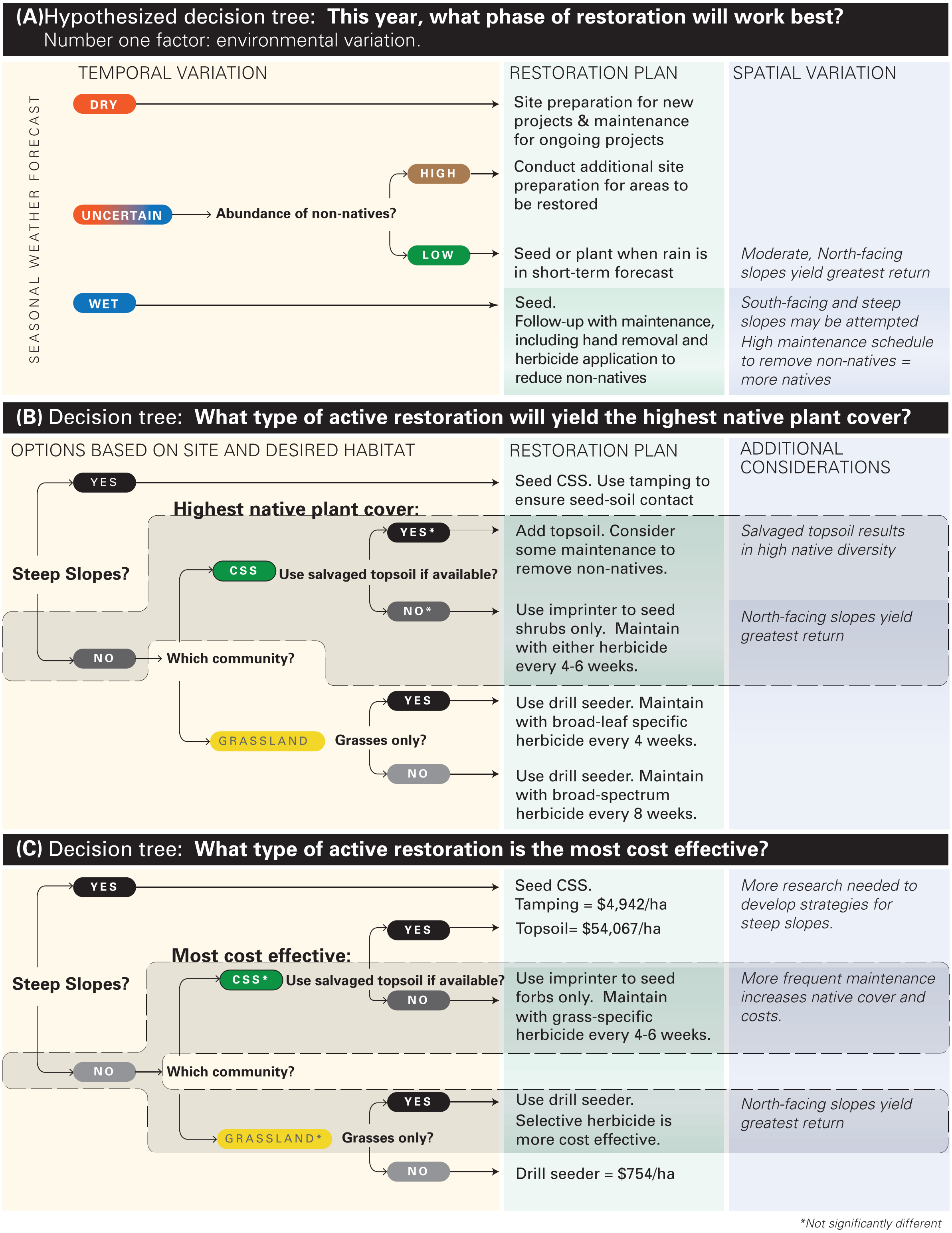

Figure 4. Decision-making tools for practitioners. Examples of decision-making tools that can be adapted to different geographies to help restoration practitioners factor cost into their decision-making in a more purposeful way. (A) Tool based on our results suggesting that the decision of whether to seed or conduct additional *site preparation* depends on the seasonal weather forecast, (B) the best course(s) of action (outlined in gray) when success is determined by high native plant cover, and (C) when success is determined by cost-effectiveness. Color coding of different plant communities and phases of restoration follows that established in Figures 1 and 3.

understood in natural systems, such filtering is less frequently examined in artificially assembled communities (Cleland et al. 2013; Hulvey & Aigner 2014). Year of measurement influenced non-native abundance in our control transects, consistent with previous findings that such interannual variation affects seed germination and community composition (Snyder & Tartowski 2006; Kimball et al. 2012) and that establishment is generally greater in wet years (Bakker et al. 2003). The strongly significant effect of year planted on the density of native and non-native germination and the negative relationship between funds spent on *site preparation* and resulting native % cover suggest that *site preparation* should only be continued beyond a first year if a wet season is not predicted. The effect of *seeding and planting* natives in a high resource year seem to be greater than further reduction of non-natives. Such decisions regarding whether to seed natives or to conduct additional years of *site preparation* depend strongly on seasonal weather forecasts (Bakker et al. 2003; Cox & Allen 2011). Emerging climatological models have the potential for more accurate predictions of upcoming wet years (Hao et al. 2013), which would ideally allow for several-month lead-time decisions on whether to continue *site preparation* or immediately seed and plant natives.

As expected given their greater exposure, higher temperatures, and drier soils in the northern hemisphere (Kutiel & Lavee 1999), restoration on south-facing slopes was significantly less successful than on north-facing slopes (Table S3). Similarly, probably due to erosion and restrictions on soil volume and moisture availability, restoration on steeper slopes was less successful (Bochet et al. 2009). Overlaying spatially varying metrics of success would be important to planning effective landscape-scale restoration. For example, policymakers could require a lower % cover of natives on south-facing than on north-facing slopes in mitigation projects, or use measurements of erosion as a success metric on steep slopes. Regardless of how success is measured, our results indicate that decision-makers and project managers could improve landscape-scale cost-effectiveness by considering spatial variation in environmental factors to the greatest extent possible. Even as they are improving by orders of magnitude, seasonal weather forecasts will of course always operate with a level of uncertainty, but slope aspect and steepness are known and predictable.

Showing that restored system benefits exceed expended costs is important to justify land use policies, and is a future research priority (Clewell & Rieger 1997; Aronson et al. 2010; Acuna et al. 2013). Economic valuation of ecosystem services is one approach to quantifying benefits (Costanza et al. 1997; Bullock et al. 2011). Services of restored habitat might include retention of soil and water, the movement, cycling, and sequestration of elements, and the trophic complexity of the area (Clewell & Rieger 1997; Costanza et al. 1997; Suding 2011), but few projects currently measure ecosystem services in their postrestoration monitoring (Ruiz-Jaen & Aide 2005*b*). Another approach is to value the restored system according to society's willingness to pay for the natural habitat (Bonnieux & LeGoffe 1997) or by habitat equivalency analysis, a compensation method for damaged habitats (Shaw & Wlodarz 2013). One alternate possibility for determining value is by the "in lieu" or "take" fee charged to develop equivalent intact habitat. In Orange County, CA, the fee to develop coastal sage scrub without mitigation is currently $160,618/ha, whereas the fee to develop grassland is $0/ha (Nature Reserve of Orange County). This study shows significant variation in the cost to restore an acre of habitat ($8,719/ha–$18,223/ha, not including overhead, for all areas with the highest cost-effectiveness values, Table S2). This comparison highlights the resources that may be applied to support restoration. However, more robust scientific valuations of coastal sage scrub and grassland are necessary before cost–benefit analyses can be used to justify development policies.

The analysis presented here is the first to demonstrate how knowledge of costs for restoration, combined with clearly defined success metrics and an understanding of environmental variation, can inform decision-making associated with different business practices in the restoration economy. We identified general areas where research can help maximize investment in conservation (such as more complex success metrics, data on costs at scale, and evaluations of environmental variation), using our model system to highlight the potential best course of action for practitioners under different measures for success (high native cover or highest cover of natives per dollar spent on a specific area). The science of ecology, combined with cost-effectiveness analyses to produce decision-making tools, can ensure that large restoration expenditures are as successful as possible in restoring biodiversity and ecosystem services. As ecology transitions from an academic endeavor to a profession that benefits an economy, it is important to challenge our basic science with applied problems, developing best operational schemes and guiding the investment of money associated with the management of biological diversity. Taken together, this analysis suggests that coordination among scientists, policymakers, and practitioners is terribly important to determine best mandated success requirements for individual restoration projects and optimal project scheduling to effectively utilize funds across heterogeneous years of resource input. New measures of success that rely on quantifying ecosystem services need to be folded into cost-effectiveness decision tools to support the sustainability of the industry.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Map demonstrating slope of the study area (color scale). The year in which *seeding and planting* occurred is indicated in black, with overlaid hatching.
Figure S2. Map showing site preparation technique and the year in which *seeding and planting* occurred. Color coding matches the colors of treatments in Table S2, showing the site preparation methods.
Figure S3. Costs of different methods of *site preparation* and resulting metrics of success. Success metrics include low density of non-natives (A) and high density of natives (B). The triangle in A indicates our hypothesis regarding the influence of environmental variation, with the gray area indicating the range of non-native germination we expect to be possible, given different amounts of monetary investment and with variable precipitation. Specifically, we expect that dry years result in low non-native germination even without money spent on *site preparation* (while wet years would result in high non-native germination without any funds spent on *site preparation*), but high monetary investment guarantees low non-native germination regardless of precipitation. There was no significant relationship between ln-transformed non-native germination and dollars spent ($R^2 = 0.1140$, $p = 0.1359$). The relationship between cost and native germination was even less ($R^2 = -0.0487$, $p = 0.4427$). Numbers indicate the year in which data were collected (1 = 2010, 2 = 2011, 3 = 2012), highlighting the importance of interannual variation in precipitation. Total seasonal rainfall during 3 years was 595, 224, and 161 mm, and the amount of precipitation in the rain event that triggered germination during the 3 years was 19, 28, and 24 mm. (C) Mean non-native germination (±1 SE) in 2012 is illustrated to demonstrate that, in any given year, *site preparation* treatment does have a significant effect on the germination of non-natives. Letters indicate results of a Tukey post hoc test, where shared letters indicate no significant difference among treatments.
Figure S4. Costs of different *maintenance* methods and the resulting cover of native plants. The same treatments were replicated on north- versus south-facing slope, which highlights the role of environmental variation. ANCOVA results: cost, $F_{[1,83]} = 49.67$, $p < 0.0001$; aspect, $F_{[1,83]} = 23.84$, $p < 0.0001$.
Table S1. Seeding costs.
Table S2. Complete table of all areas, with all costs broken down into categories. Color coding in the first column matches the color of areas on map in Figure S2. Note that, for some treatment combinations, native % cover data were not collected in 2013 and the index of cost-effectiveness could not be calculated.
Table S3. Results from statistical tests on the cost-effectiveness of restoration.
Table S4. Costs of site preparation per area of the restoration project, including the cost of each technique and measures of effectiveness.
Table S5. Results from analyses comparing site preparation techniques.
Table S6. Results from statistical tests comparing different *seeding and planting* techniques.
Table S7. Results of statistical tests comparing *seeding and planting* with different seed mixes.
Table S8. Effects of environmental variation on *seeding and planting*.
Table S9. Maintenance costs for different community types.
Table S10. Results from analysis of maintenance methods.

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