RESEARCH ARTICLE

Best served deep: The seedbank from salvaged topsoil underscores the role of the dispersal filter in restoration practice

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Funding information
The Western Australia Department of Parks and Wildlife

Co-ordinating Editor: Borja Jiménez-Alfaro

Abstract

Questions: Globally, ecological restoration is required to restore degraded landscapes and to contribute to biodiversity conservation. Ecological theory suggests that manipulating dispersal, abiotic and biotic filters limiting plant re-establishment will improve restoration outcomes. Here, we manipulated spread depth of soil containing a salvaged soil seedbank (dispersal filter), soil compaction (abiotic filter) and herbivore grazing (biotic filter) in a topsoil transfer experiment to test their effects on restoration success.

Location: *Banksia* woodland of the Swan Coastal Plain, Western Australia.

Methods: Topsoil (upper ~7 cm) with its seedbank was removed from a donor site (20 ha) of recently cleared native vegetation and transferred to six recipient restoration sites (16 ha). Deep (10 cm thick) and shallow (5 cm thick) layers of topsoil were applied in a fully factorial experiment, with and without soil ripping and fencing, respectively. We analysed emergence, survival and functional types (alien/native, life form, fire response) of all vascular plant species for two consecutive years after topsoil transfer.

Results: The most successful restoration treatment was deep topsoil with a mean density of 14.3 m^{-2} native perennial germinants in year one and 7.3 m^{-2} in year two. Application of deep topsoil increased native seedling emergence by 34% and decreased weed density by 21% compared with shallow topsoil. Overall seedling survival across the two-year period was unaffected by filter treatments (range 0.6%–5%). After two years, the resulting plant community was 6%–38% weed species and of native perennial species, 12%–48% were capable of resprouting.

Conclusions: Manipulation of the dispersal filter alone, that is deep topsoil application, can lead to near-equivalent native species number emerging on restoration sites as compared to pre-cleared woodland. However, more research is required to test additional restoration tools to improve survival of biodiverse plant communities. For example, targeted herbicide application coupled with soil ripping to improve weed management and native seedling establishment.

1 | INTRODUCTION

In the face of ongoing clearing of native vegetation, it is evident that conservation alone is not an adequate strategy to impede biodiversity loss (Simmonds *et al.*, 2019; Breed *et al.*, 2020). Thus, ecological restoration is a critical element of biodiversity conservation strategies, and the application of ecological theory can inform restoration of biological diversity and function to degraded sites (Zirbel & Brudvig, 2020). A key contribution of ecology has been to assess the role of ecological filters in plant community assembly and how they can be manipulated to restore native ecosystems (Temperton & Hobbs, 2004; Hulvey & Aigner, 2014). Filters are ecological factors that can limit establishment in the local plant community by sequentially including species from the available species pool that are compatible with each filter (Funk *et al.*, 2008). Relevant ecological filters include dispersal limitation, abiotic and biotic filters (Keddy, 1992). In restoration, rebuilding an ecosystem usually requires modification of multiple filters to encourage native species recruitment, while suppressing undesirable, typically non-native species that tend to grow on degraded sites (Fattorini & Halle, 2004). Understanding how these filters interact in restoration settings is essential in guiding the recovery of native ecosystems (Wainwright *et al.*, 2018; Helm *et al.*, 2019).

Dispersal filters affect arrival of propagules at a restoration site and include both limited natural dispersal and efficacy of artificial dispersal (Standish *et al.*, 2007; Birnbaum *et al.*, 2017). Strong dispersal limitation tends to lead to poor recruitment and intervention relies on planting or supplemental seeding of native species (Zobel *et al.*, 2000; Zamin *et al.*, 2018; Jiménez-Alfaro *et al.*, 2020). To overcome dispersal limitation seeds can be broadcast, sown, added or transferred via salvaged topsoil. The seeds stored in topsoils are increasingly valued for restoration due to their cost-efficiency (Koch M. & Richard, 2007; Ferreira & Vieira, 2017; Schmidt *et al.*, 2020). This option is especially important for restoration of plant communities which store seeds for a large proportion of species in the soil seedbank and when topsoil becomes available due to ongoing vegetation clearing and land development (Rokich *et al.*, 2000; Holmes, 2001; Hall *et al.*, 2010). Additionally, the topsoil will normally contain native microbiota that facilitate the re-assembling of the native ecosystem (Birnbaum *et al.*, 2017). Thus, dispersal filters can impact arrival of not just plants but other organisms beneficial for successful restoration as well.

Abiotic filters include physical, chemical and climatological factors such as soil compaction, fertility, topography and microclimate, among others, which could limit seed germination and survival of plant species (Bassett *et al.*, 2005; Gilardelli *et al.*, 2015). For example, soil compaction due to use of heavy machinery may limit both seed radicle and seedling root penetration to deeper soil layers and reduce seedling establishment (Kew *et al.*, 2007). Biotic filters include species interactions among trophic levels such as herbivory (Cleland *et al.*, 2013; Halassy *et al.*, 2016) or within trophic levels via competition (i.e. weeds; Weston & Duke, 2003). Control of herbivores (e.g., using exclosures) may reduce trampling, spread of weed propagules and grazing pressure on seedlings in their early stages of emergence and establishment (Duncan & Holdaway, 1989; Schultz *et al.*, 2011; Watts *et al.*, 2019). Filters may act singly or in combination to influence community assembly, for example, land-use legacies, such as compacted soil (abiotic filter) and weed-dominated soil seedbank (biotic filter), can limit native plant establishment by increasing the competitive effect of dominant non-native species (Kulmatiski *et al.*, 2006). Indeed, filters will differentially affect species. In addition to the provenance status (native or weed), we predict that filters will impact distribution of key plant functional types relating to life history (perennial or annual), provenance status (native or weed) and disturbance response (seeder or resprouter).

In this study, we investigated the role of key ecological filters in determining restoration success using topsoil transferred from a remnant woodland. To do so, we partnered with government and industry to implement the transfer of salvaged topsoil from *Banksia* woodland onto a degraded old-field in a peri-urban setting in southwestern Australia. Filters were manipulated in a fully factorial experiment and included spread depth of transferred topsoil (dispersal limitation), ripping of topsoil and subsoil to reduce compaction (abiotic), and exclosures to reduce grazing and trampling pressure (biotic), to quantify their effects on seedling emergence and survival one and two years after restoration. In particular, we hypothesised that: (a) overcoming the dispersal filter by increasing the depth of topsoil spread would increase the species richness and density of native plants (more propagules), and decrease the density of weeds that emerged from the underlying degraded soil (fewer propagules); (b) overcoming the abiotic filter by ripping restoration site soils would aid native seedling survival and establishment by alleviating soil compaction, aiding water infiltration and encouraging root growth; and (c) overcoming the biotic filter by excluding herbivores (fence) would increase native species seedling establishment and survival. We further hypothesised that the three filter treatments should have an additive effect on native seedling emergence and establishment, with the additive effect of filter treatments producing a plant assemblage reflecting most closely that of the reference ecosystem: low weed infestation and high abundance of perennial resprouters.

2 | METHODS

2.1 | Study setting

This study was conducted in *Banksia* woodland of the Swan Coastal Plain in southwestern Australia (Figure 1a, Appendix S1). Intact
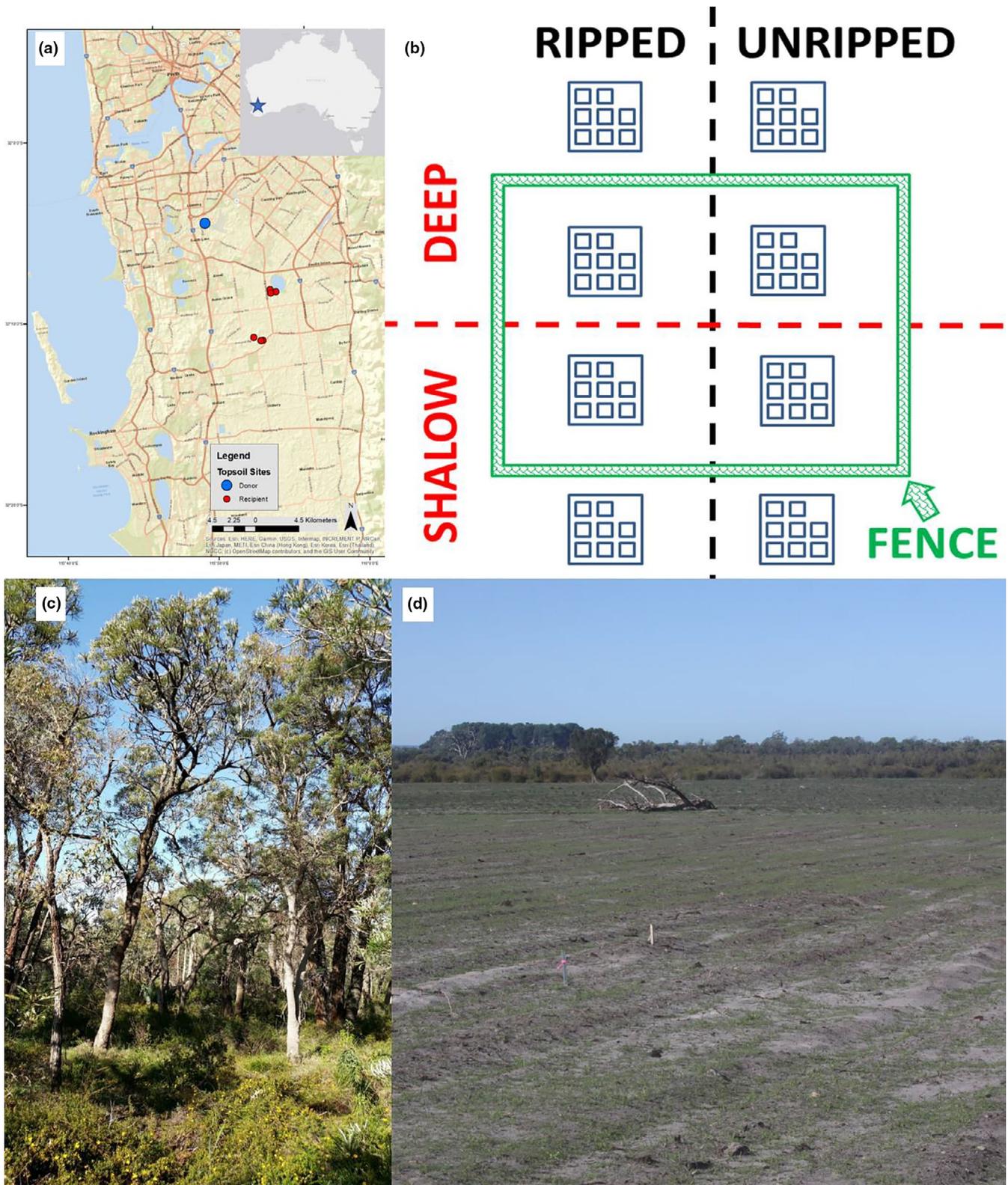
FIGURE 1 Topsoil study sites (a), experimental design (b), image of intact *Banksia* woodland prior to clearing (c) and restoration site after topsoil transfer (d). (b): Within each of the six restoration sites, we established eight clusters (13 m × 13 m), each of which was assigned to one of the unique treatment combinations (6 sites × 8 clusters per site = 48 total plots [increased to 72 in 2013]). Each cluster contained eight to twelve survey plots (2 m × 2 m). For more detailed map see Appendix S2

Banksia woodland is comprised of one or more tree *Banksia* species (typically 5–9 m tall *B. attenuata* and *B. menziesii*), an emergent ~8–20 m tall tree layer co-dominated by *Eucalyptus* and/or *Allocasuarina* species, and a species-rich understorey dominated by shrub, sedge and rush species. Total richness recorded at the topsoil donor site prior to clearing was 90 native species (unpubl. data) with

an average of 50 species per 100 m², which represents a small subset of the ~600 native plant species recorded for *Banksia* woodland of the Swan Coastal Plain overall (Stevens *et al.*, 2016) and is typical of high beta-diversity recorded in the southwestern Australian floristic bioregion (Gibson *et al.*, 1994).

Banksia woodland community dynamics are largely determined by responses to fire, herbivory, climate, and more recently, weed invasion (Department of the Environment, 2016). The climate of the region is Mediterranean-type with cool wet winters and long dry summers (Cowling *et al.*, 1996). Since the 1970s, the climate has been warming and drying (Andrys *et al.*, 2017) and this change, coupled with impacts of land-use change and weed invasion, is likely to impact further the future distribution of *Banksia* woodlands (Yates *et al.*, 2010; Standish *et al.*, 2012). For the study years 2012 and 2013, rainfall at the closest climate station was 747 mm and 877 mm respectively (mean rainfall 2002–2020 793 mm; Bureau of Meteorology, 2020). Due to clearing for urban expansion, *Banksia* woodlands have been listed as a Threatened Ecological Community (Department of the Environment, 2016). Our experiment was established as part of a biodiversity offset programme that aimed to restore *Banksia* woodland onto degraded land to "offset" the clearing of remnant *Banksia* woodland elsewhere (Waryszak *et al.*, 2017).

2.2 | Experimental design, implementation and data collection

In March 2012, 20 ha of *Banksia* woodland was cleared at Jandakot, Western Australia (32.096010° S, 115.865178° E, Figure 1a). Topsoil was stripped to a depth of ~7 cm using a front-end loader and immediately transferred by truck to six restoration sites approximately 20 km to the south of the donor site with the aim to maximise viability of the transferred seed store (e.g., Rokich *et al.*, 2000). Full restoration site details are provided by Brundrett *et al.* (2020).

At each recipient (degraded) site topsoil was stripped to ~5 cm to remove extant weeds and to reduce the potential impact of soil-stored weed seeds on subsequent restoration. Three site-scale treatments were applied (Figure 1b):

1. Topsoil depth (dispersal filter): To provide two levels of propagule availability, half of each restoration site was capped with a 5 cm deep layer of transferred topsoil (shallow), and the other half with a 10 cm deep layer (deep) using heavy machinery (grader), thus doubling the number of seeds available in the deep treatment.
2. Topsoil ripping (abiotic filter): To ameliorate the potential effect of soil compaction on seedling root growth, a vehicle-towed winged tine was used to rip restoration site soil to 300 mm. The ripped layer included the newly transferred topsoil and underlying degraded site subsoil. Rip line spacing was set at 0.5 m. Ripping was applied to half of both shallow and deep topsoil depth treatment areas at each of the six restoration sites in mid-June (winter) 2012.

3. Fencing (biotic filter): half of each study site was fenced during the winter of 2012 to protect germinants from herbivores, primarily rabbits (*Oryctolagus cuniculus*) and western grey kangaroos (*Macropus fuliginosus*). Fencing extended 90 cm above-ground and 30 cm below-ground. Four unfenced clusters per site were used as controls to examine the additive effects of herbivore exclosures and the other two treatments.

Donor topsoil was transferred to restoration study sites in mid–April (autumn) 2012. Within each restoration site we established eight clusters of 13 m × 13 m. Each cluster comprised eight 2 m × 2 m plots in the first growing season after topsoil transfer and twelve in the second season (six sites × 8 clusters = 48 in 2012 increased to 72 in 2013). The decision to increase the number of survey plots within each cluster was dictated by high seedling mortality recorded after the first summer dry season.

The experiment was fully established by July 2012. We expected most seedlings to emerge in July–September 2012, in response to winter–spring rainfall and temperature cues (Bell *et al.*, 1993), and a small pulse of seedlings to emerge in the second year of the experiment (i.e. spring 2013). The summer dry season is a bottleneck to seedling establishment in Mediterranean-climate systems (Vesk & Dorrough, 2006), so we anticipated mortality of native recruits to occur in summer 2012/13 and 2013/14 and for this to be reflected in survival data collected in the autumn of 2013 and 2014. Therefore, native plant species seedlings were identified and counted for replicate 2 m × 2 m plots in spring 2012, ~three months after the experiment was established, to determine recruitment, and spring 2013, 15 months after establishment, to measure the second pulse of seedling emergence. Seedlings that were difficult to ID were grown in the related glasshouse project (Fowler *et al.*, 2015), thereby facilitating difficult identification. The densities of annual and perennial weed species were recorded in four replicated 0.25 m × 0.25 m micro-plots located in the centre of each subcardinal quadrant (NE, NW, SW, SE within each 2 m × 2 m plot.

To understand how manipulation of the abiotic filter affected the physical environment of germinants and seedlings, we measured soil moisture (depths: 100 mm, 200 mm, 300 mm, 400 mm, 600 mm, 1,000 mm) and compaction to a depth of 1 m at random locations ($n = 12$ and $n = 30$, respectively). To measure soil moisture, we used PR2/6 multi-depth soil moisture probe (Delta-T Devices Ltd, Cambridge, UK, measured monthly between September 2012 – September 2015). To measure soil resistance, we used a cone penetrometer (Penetrologger with 1 cm² and a 60° top angle cone [Eijkelkamp, Giesbeek, The Netherlands], that logged data at 1 mm increments, logged singly in September 2013). Soil moisture and compaction means and 95% confidence intervals were calculated and are presented comparing ripped and unripped sites (control); statistical analysis of moisture and compaction relative to plots was not possible owing to the sampling occurring outside plots and requiring destructive sampling (penetrometer).

FIGURE 2 Mean richness and diversity (Shannon-Wiener index) of native perennial seedlings emerging under three site-scale filter manipulation treatments for the two spring seasons following topsoil transfer (±95% CI, 4 m^{-2}): spring 2012 and spring 2013. Treatments were: abiotic, ripped and unripped; biotic, fenced and open; dispersal, deep and shallow topsoil ($n = 192$ in spring 2012, $n = 288$ in spring 2013)
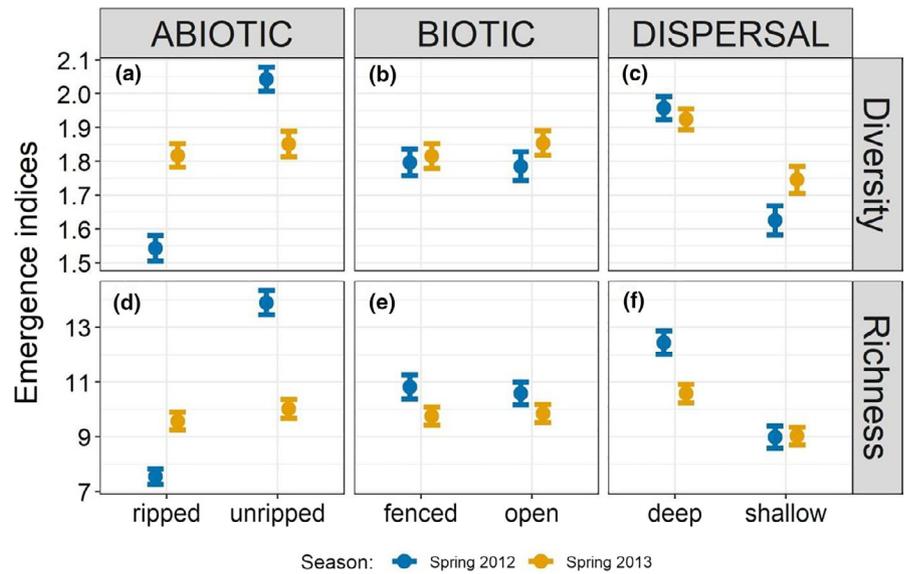
2.3 | Data analysis

We analysed counts of emerged native perennials, native annuals and weed species in spring 2012 and spring 2013 (separate model for each pulse of recruitment, Appendix S2). Data are available from Mendeley Data Repository (Waryszak *et al.*, 2020). Hierarchical generalised linear mixed-effect modelling was used to analyse these data to accommodate the combination of fixed and random effects. All filter treatments were treated as fixed effects while sites ($n = 6$) and clusters ($n = 8$) were included as random effects. Data were non-normally distributed, as expected for count data (O'Hara & Kotze, 2010), and modelled with a Poisson distribution. Scatterplots and histograms of model residuals were assessed visually to ensure homogeneity of variance. Treatment effects on seedling richness and Shannon–Wiener diversity were also tested using a separate generalised mixed-effect model. Non-metric multidimensional scaling ordination (NMDS) was used to examine compositional differences in emergent seedling communities. Relative abundances of three dichotomous plant functional groups of seedlings emerging from the transferred topsoils were compared visually (means ± 95% CI), i.e. species provenance (weed or native), disturbance response (resprouter or seeder) and life history (annual or perennial).

To quantify the effect of treatments on seedling survival, data were analysed by assessing effects of individual summer dry periods (i.e. spring 2012 to autumn 2013, spring 2013 to autumn 2014) and across both summers (spring 2012 to autumn 2014). Individual seedlings were treated as unique observations with their survival being a binary outcome. Therefore, a binomial error distribution was applied within a hierarchical generalised linear mixed-effects framework to analyse survival of seedlings in relation to applied treatments and their two-way interactions during each of the three named time intervals. The species identity, six study sites and eight study clusters on each site were included as random terms in the model. The assumptions of random effects to be normally distributed with a variance of one and mean of zero were met (assessed graphically).

To assess effect of treatments on soil moisture and resistance, mean values of soil resistance and their 95% confidence intervals (95% CI) were computed for depths of 100 mm, 200 mm, 300 mm, 400 mm, 600 mm and 1,000 mm. Effects were assessed visually; a lack of 95% confidence interval overlap among depths was interpreted as evidence of statistically significant difference.

All computations and figures were performed using R software (Team, 2017) including "ggplot2" (Wickham, 2016), "dplyr" (Wickham *et al.*, 2019) and the "lme4" R package (Bates *et al.*, 2014). Satterthwaite approximation of degrees of freedom was used to calculate *p*-values (Schaalje *et al.*, 2002). Package "vegan" was used to perform NMDS (Oksanen *et al.*, 2013). Mean densities were computed on untransformed data, standardised to 1 m^{-2}. Standard errors (*SE*) were used when reporting mean densities and percent survival in the main text.

3 | RESULTS

Overall, a total of 160 native species were detected (128 perennials, 32 annuals) across two emergence seasons (Appendix S2). Maximum richness of native perennial seedlings emerging from the transferred topsoil in spring 2012 and 2013 were 30 and 29 (4 m^{-2}), respectively. Topsoil spread with no ripping treatment (abiotic filter) recorded significantly higher richness of native perennials in spring 2012 compared to ripped sites ($t = 4.70$, $p < 0.001$, Figure 2a, Appendix S2). No interactive effect of treatments on richness nor on diversity was detected (Appendix S2). Similarly, no clear separation was observed in NMDS (Appendix S2) among compositions between different topsoil treatments.

Annuals dominated plant density in the restoration study sites in the growing season (55%–72%, spring 2012) and decreased after the dry summer (4%–15%, autumn 2014, Table
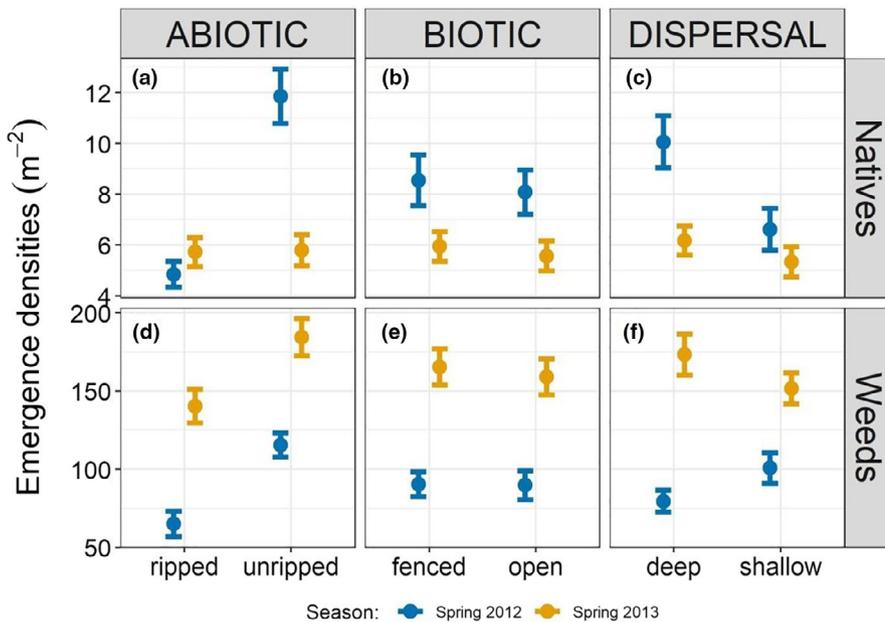
FIGURE 3 Mean densities of native perennials and weeds (m^{-2} ± 95% CI) emerging under three site-scale filter manipulation treatments in two spring seasons following topsoil transfer; spring 2012 and spring 2013. Filter manipulation treatments were: abiotic, ripped and unripped; biotic, fenced and open; dispersal, deep and shallow (n = 192 in spring 2012, n = 288 in spring 2013)

S1). As most of the annuals were weeds, proportion of natives increased from 16%–25% in spring 2012 to 49%–95% in autumn 2014. Resprouters represented 24%–31% of seedlings emerging in spring 2012 and were the most frequent surviving types, overall 45%–73% and within native perennials 12%–48% in autumn 2014 (Appendix S2).

The most frequently occurring native perennial species in the first emerging season were seeders, including *Gompholobium tomentosum* (94%), *Leucopogon conostephioides* and *Bossiaea eriocarpa* (Appendix S2). Resprouter species were less frequent but included *Gastrolobium capitatum (67%), Laxmannia sessiliflora* and *Hibbertia hypericoides*. Annual native species included the very frequent

TABLE 1 Effects of topsoil treatments on emergence (spring 2012) and survival odds for native perennial seedlings over the first growing season after topsoil transfer, from spring 2012 (spr12) to autumn 2013 (aut13)

Topsoil treatment	Term	Estimate	SE	t	P	Emergence time
(Intercept)	(intercept)	**4.1**	0.2	24.4	**<0.001**	spr12
Topsoil ripping	Ripped [rip]	**−1.0**	0.2	−5.8	**<0.001**	spr12
Fence installation	Open [fence]	−0.2	0.2	−1	0.3	spr12
Topsoil depth	Shallow [transdepth]	**−0.7**	0.2	−3.8	**<0.001**	spr12
Rip:fence	Ripped:open	0.11	0.25	0.45	0.65	spr12
Fence:depth	Open:shallow	0.26	0.25	1.1	0.29	spr12
Rip:depth	Ripped:shallow	0.14	0.24	0.58	0.56	spr12

Model: glmer(sum4m2 ~ rip+fence + Transdepth + rip*fence + fence*Transdepth + rip*Transdepth + (1|site/cluster), family = Poisson(link="log"), data = native.perennials.year.one)

Topsoil treatment	Term	Estimate	SE	t	P	Survival time
(Intercept)	Intercept	**−3.7**	0.5	−7.7	<0.001	spr12 to aut13
Topsoil ripping	Ripped	**1.2**	0.5	2.3	**0.02**	spr12 to aut13
Fence installation	Open	0.7	0.6	1.2	0.23	spr12 to aut13
Topsoil depth	Shallow	0.4	0.5	0.7	0.47	spr12 to aut13
Rip:fence	Ripped:open	−1.1	0.7	−1.6	0.11	spr12 to aut13
Fence:depth	Open:shallow	−0.8	0.7	−1.2	0.23	spr12 to aut13
Rip:depth	Ripped:shallow	−0.4	0.7	−0.6	0.58	spr12 to aut13

Model: glmer(Survival ~ rip + fence + Depth + rip*fence + fence*Depth + rip*Depth + (1|site/cluster) + (1|speciescode), data = spr12.to.aut13, family = "binomial")

Note: SE denotes standard errors. Significant effects are in bold when P < 0.05.

FIGURE 4 Mean densities (m^{-2}) of native perennials (±95% CI) for two seasons: autumn of 2013 and 2014, one and two years after topsoil transfer. The effects of treatments manipulating three ecological filters: abiotic: topsoil rip (ripped and unripped); biotic: topsoil exclosures (fenced and open); and dispersal manipulation topsoil spreading depth (deep and shallow) are presented in full combinations
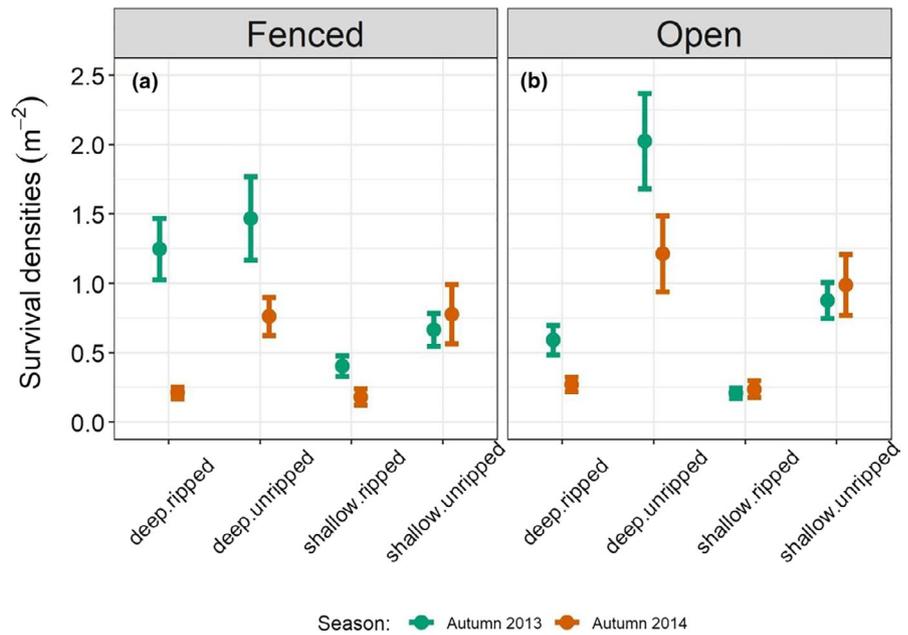
Trachymene pilosa (87%), *Podotheca gnaphalioides* and *Austrostipa compressa*. Annual weeds were even more abundant, and included *Hypochaeris glabra* (94%), *Arctotheca calendula*, *Ursinia anthemoides*, *Avena barbata*, *Briza maxima*, and *Vulpia myuros* (up to 23 m^{-2}). Seedlings of the perennial weedy grass *Ehrharta calycina*, were also common (18%).

3.1 | Emergence

Deep topsoil had a significantly higher density of germinants (10.4 ± 0.6 m^{-2}) compared with shallow topsoil (6.9 ± 0.5 m^{-2}) in the first year ($t = -3.8$, $p < 0.001$, Figure 3c, Table 1). Similarly, in the second year, mean density of emerging perennials was lower on shallow (5.3 ± 0.3 m^{-2}) compared to deep topsoil (6.1 ± 0.2 m^{-2}, $t = -2.4$, $p < 0.02$, Appendix S2). Deep topsoil was also associated with significantly reduced weed emergence densities (79.5 ± 3.5 m^{-2}) in the first year compared to shallow topsoil (100.8 ± 5 m^{-2}, $t = -2.94$, $p < 0.003$, Figure 3f, Appendix S2) but had no effect on weed density in the second year (Figure 3d–f).

Ripped soils had significantly fewer native perennial germinants in the first year (4.8 ± 0.3 m^{-2}) compared to unripped controls (11.8 ± 0.5 m^{-2}, $t = -5.8$, $p < 0.001$, Figure 3a). In the second year, there was no effect of ripping on native emergence densities ($t = -0.5$, $p = 0.60$, Figure 3a, Appendix S2). Ripping decreased weed emergence (65 ± 4.1 m^{-2}) and emergence of annual natives (6 ± 0.5 m^{-2}) in the first year (autumn 2013) compared to unripped topsoil (115 ± 3.9 m^{-2}, $t = -6.78$, $p < 0.001$, Figure 3d and 17 ± 1 m^{-2}, $t = -6.9$, $p < 0.001$, Appendix S2).

Fenced (exclosures) sites showed no significant difference in densities of native perennial germinants (8.5 ± 0.5 m^{-2}) when compared to unfenced sites (8.1 ± 0.4 m^{-2}) in spring 2012 ($t = -1$, $p = 0.3$,

Figure 3b, Table 1). No between-treatments interactive effect on emergence densities was detected.

There was a relatively strong site effect with highest native perennial emergence densities being 47% higher (site ForNW, $t = 8.4$, $p < 0.001$) compared to the least populated site (site AnkM, Appendix S2). Although there was a strong site effect, emerging plant communities were similar in composition across all sites (Appendix S2). Emergence densities of native perennial seedlings were strongly correlated with seedling richness in both emergence seasons: spring 2012 ($r = 0.7$, $t = 27$, $p < 0.001$) and in spring 2013 ($r = 0.7$, $t = 24$, $p < 0.001$).

3.2 | Survival

The highest density of surviving seedlings to autumn 2014 was observed on deep and unripped plots (1.21 ± 0.3 m^{-2}, Figure 4b, Appendix S2). Survival in the first year was only affected by ripping, with no significant effects of fencing, topsoil depth, or their interactions. Ripped plots recorded higher survival in autumn 2013, 12.5% ±1.1 compared to 7.8% ±0.7 in unripped plots ($t = 2.3$, $p = 0.02$, Table 1). The fencing treatment showed no significant effect on survival of first recruits to autumn 2014 ($t = 0.7$, $p = 0.46$, Appendix S2).

Mean survival of perennial native seedlings over the first growing season (spring 2012 to autumn 2013) ranged from 5.6%–19.8% (reduced to 0.6%–5% over the two-year period, from spring 2012 to autumn 2014) and for emergents in the second growing season (spring 2013 to autumn 2014) survival ranged from 0.1% to 5.1% (Appendix S2). The native perennials that emerged and survived in the highest numbers were *Cartonema philydroides*, *Gompholobium tomentosum*, *Hibbertia subvaginata*, *Laxmannia ramosa* and *Scholtzia involucrata*.

3.3 | Soil moisture and resistance

Mean soil moisture was relatively lower under ripping treatment to a depth of 300 mm compared to unripped (3.1% vs 4.6%) and higher at deeper depths (8.5% vs 7.9% at 1,000 mm, Figure 5a). Soil resistance increased gradually down the soil profile and peaked at 600 mm (Figure 5b). The maximum soil resistance of 7.1 MPa ± 0.01 (*SE*) was detected under ripping treatment (at the depth of 600 mm). A significant loosening effect of furrowing was observed at the depth of 100 mm with 1.1 MPa recorded in ripped in contrast to 1.5 MPa ± 0.03 (*SE*) in unripped soil.

4 | DISCUSSION

4.1 | Salvaged topsoil seedbank is most valuable when least disturbed

Our results show that direct topsoil transfer from cleared native *Banksia* woodland to a degraded old-field is a promising restoration tool (manipulation of dispersal filter) through the initial germination of numerous seedlings from many native plant species. Two other filter treatments (abiotic and biotic) had no additive effect on seedling emergence. The highest density and diversity of native seedling emergence occurred for deep topsoil treatment when left unripped. If topsoil was spread at a greater depth, a significant increase in seedling densities was recorded over the two emergence seasons, suggesting that "maximum depth, minimum disturbance" is the most valuable restoration technique when using transferred topsoil. Strong emergence of native perennials occurred in two discrete (spring) pulses of recruitment following topsoil transfer with emergence in year one being significantly higher than emergence in year two. However, on average, we found that estimated field densities of native perennials that emerged from transferred deep and unripped topsoil in year one (14.3 m^{-2}) were well below the emergence densities detected in other topsoil studies. For example, a glasshouse bulk germination study on pre-transfer topsoil found that the density of native perennials could be as high as 1,692–4,239 germinants m^{-2} in the top 5 cm of the soil profile (Fowler *et al.*, 2015). Yet, densities were reduced compared to the pre-transfer samples (to 648 m^{-2} in the top 10 cm, Fowler *et al.*, 2015). It is likely that in situ results differed from those of ex situ trials as conditions in the field cannot be controlled to the same extent as can be done in the glasshouse (for example, thin topsoil spread and optimum moisture were provided in the glasshouse, but were not feasible in a large, field-based context).

4.2 | Salvaged topsoil seedbank transferred compositionally similar assemblies initially and promoted species with resprouting strategies

Vegetation surveys analysed in this study showed no difference between species composition in relation to treatments. Nine native species were common across most plots (>50% of plots) and these masked any differences between plots owing to the presence of other less common species. Composition of seedlings emerging from the transferred topsoil was heavily skewed towards understorey species with as little as 0.1% of propagules belonging to tree species. Large trees like *Eucalyptus* spp., which store their seeds in the canopy (i.e. are serotinous), were poorly represented in the topsoil soil seedbank and required return to these sites primarily by planting and direct seeding (Brundrett *et al.*, 2020). Similarly, post-fire resprouter species (species that recover after fire by resprouting from starch-storing stem, rhizome, tuber or roots e.g., *Hibbertia hypericoides*), which dominated plant communities at the topsoil donor site (Brundrett *et al.*, 2020), emerged on average 2.5-fold
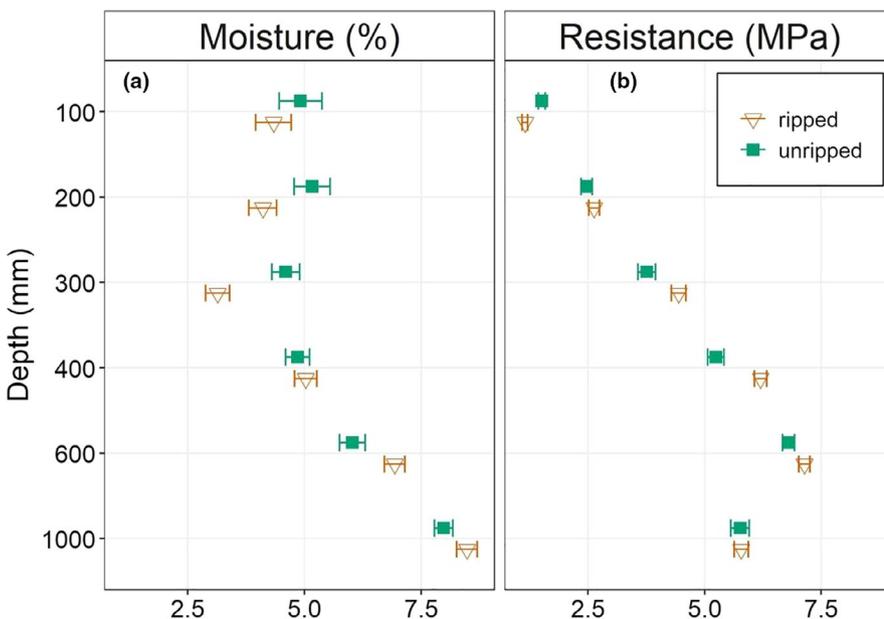
FIGURE 5 Mean soil moisture (%) and resistance (MPa, ±95% CI) at six depths: 100 mm, 200 mm, 300 mm, 400 mm, 600 mm and 1,000 mm. Soil moisture (*n* = 12) and resistance (*n* = 30) were measured at the combination of topsoil ripping treatments (ripped and unripped, see also Appendix S2)

less frequently from the transferred topsoil than seeder species. However, species with a resprouting strategy demonstrated higher survival against summer water shortage and high soil compaction as they comprised 45%–73% of established native perennials by autumn 2014 compared with seeder species. As the majority of seeders on sites that died back were also weeds, this study underscores the importance of topsoil transfer in overcoming dispersal limitation in restoration practices. As many native species do not disperse seeds far from their parent this limits their colonisation of degraded areas but topsoil transfer spreads their seeds widely and enables them to emerge and establish even under competition from weeds (Johnson *et al.*, 2018; Stanbury *et al.*, 2018). Parts of the study sites that received no topsoil remained highly weed-infested and showed no native plant regeneration without intervention (PW, pers. obs., November 2012). Moreover, an added advantage of transferred topsoil is that the complex biological interactions within topsoil, for example between native propagules, seedlings and soil microbiota, are retained and transferred to the recipient site, prospectively further enhancing establishment success (Bulot *et al.*, 2014; Birnbaum *et al.*, 2017; Gorzelak *et al.*, 2020). Topsoil microbiota could interact with ecological filters present on restoration sites, for example, by forming mutualistic associations and increasing uptake of essential nutrients by emerging plants (Burkle & Belote, 2015; Cross *et al.*, 2019).

4.3 | Higher emergence and survival on deep topsoil (dispersal filter)

Manipulation of the dispersal filter by applying a thick layer of topsoil onto the restoration site had a positive effect on native perennial species emergence in both years. Higher emergence densities of native perennials were recorded on deep topsoil (~10 cm) compared with the shallow topsoil (~5 cm). This is in contrast to other research where shallow topsoil spread is recommended due to low emergence capabilities of propagules from species of Mediterranean-climate systems (Bond *et al.*, 1999; Traba *et al.*, 2004). Small-sized seeds are typically found in the soil seedbanks of the Mediterranean-type ecosystems in Australia (Rokich *et al.*, 2000) and the majority of the seedlings emerging from the topsoil used in this study were small-seeded species. During the topsoil stripping and transfers the seedbank contained within the topsoil will undergo a process of mixing and homogenisation, i.e. viable seeds are likely dispersed throughout the transferred soil (Fowler *et al.*, 2015). While size may limit the regeneration of deeply buried propagules, it is likely that in our study the disadvantage of deep burial was counteracted by the greater number of seeds contained in the greater thickness of soil. It is also likely that the soil-stored seeds had a lower exposure to transfer-related deterioration (e.g., friction) when topsoil was spread at the greater thickness and resulted in a better quality seeding mix overcoming the dispersal limitation filter (Long *et al.*, 2015; Farrell & Fehmi, 2018).

Shallow vs. deeper topsoil placement represents an important issue from a land management point of view because quality topsoil is a cost-effective but scarce resource (Traba *et al.*, 2004; Koch, 2007). Conversely, while a thinner spread of topsoil may maximise the area that can be rehabilitated, the thinner topsoil layer may also result in overall lower native perennial species densities as shown in this study. Additionally, an increase in the depth of transferred soil is likely to have a suppressing effect on local weed species (Rivera *et al.*, 2014), which had abundant propagules in existing soils at these sites. As shown in this study weed species tended to be more sparsely distributed across the sites with thick topsoil applications. Higher weed densities were observed along rip lines in many parts of these sites (MB, pers. obs.), presumably due to mixing of soil (with abundant weed seeds) from the pre-restoration surface into the transferred topsoil layer. The highest final densities of native perennials were recorded on sites that had deep topsoil but were unripped, suggesting that overall low survival rate was offset by high emergence densities in spring. A relatively low survival may relate to a negative effect of severe summer drought and underscores the importance of directing the restoration efforts towards establishing as many seedlings as possible under Mediterranean conditions so some will survive the inevitable summer water deficit (Lloret *et al.*, 2005).

4.4 | Unalleviated compaction leads to low seedling densities on ripped topsoil (abiotic filter)

Topsoil ripping was intended to alleviate soil compaction due to vehicle movement over freshly spread topsoil. Here, the ripping treatment applied to the transferred topsoil (to a depth of 300 mm) did the opposite of what we intended. With exception of the top (200 mm) and bottom (1,000 mm) depths, soil resistance recorded under ripping treatment was higher compared to that of unripped soil. While lower soil resistance in the top 200 mm was likely related to lower soil moisture, the higher soil resistance below 300 mm depth was associated with higher moisture there.

Mean densities of emerging native perennials were significantly lower on ripped sites compared to unripped controls. Sparsely emerging native seedlings on ripped sites showed significantly higher chance to survive over the first summer drought but this effect was not detected over the two-year period. Survival of native perennials was much lower in the second year than in the first. This is likely due to a number of reasons including competition from the very high weed infestation in 2013 (15–38-fold higher density in 2013 than in 2012) and summer water stress due to seedling roots failing to access deeper soil moisture because of high compaction below the rip depth (300 mm). Access to deep soil moisture is critical to seedling survival over the summer dry season. A severe contrast between an upper loose and lower compact soil layer may lead to failure of the roots to enter the deeper soil layer, causing proliferation of roots in the upper part of the profile and loss of access to deeper soil moisture (Bengough *et al.*, 2011) which is rapidly depleted over the dry season.

4.5 | No short-term effect of fencing on seedlings' emergence or survival (biotic filter)

Manipulation of the biotic filter via the installation of fencing did not affect the emergence or survival of native seedlings either in the first year after topsoil transfer or the second. Fenced exclosures are a common tool used to prevent grazing of emerging seedlings and thus enhance native species richness (Eldridge *et al.*, 2018). However, in this study, there was no difference in seedling emergence between fenced and unfenced areas. The effect of grazers on young seedlings is likely to be variable throughout the year with annuals likely eaten during the wet season (Landsberg *et al.*, 2002). Hence, the pressure on perennials is probably most intense in the critical summer dry season when annuals have disappeared (Nield *et al.*, 2015). However, grazing was not a large problem within the timeframe of this study (PW, pers. obs., 2012), and this may be due to the small population size of seedlings but also the low activity and dietary preferences of grazers such as kangaroos and rabbits in the semi-urban landscape of this study area. The outcome of fencing in relation to seedling emergence densities and survival is likely to be dependent on the year as well as site location, with different levels of human and wildlife traffic.

4.6 | Distribution of plant functional types on transferred topsoil

Weed densities (69% annual species) increased over time with densities in the second year 51% higher than in the first year after topsoil transfer. The lowest weed densities were associated with ripping. Soil ripping significantly reduced densities of emerging weeds in the first and second years after topsoil transfer. Overall, the relative abundance of weeds at the restoration sites in the first growing season (75%–84%, Appendix S2) was more than double the percentage of weeds (36%) detected in pre-transfer glasshouse studies (Fowler *et al.*, 2015) and underscores the importance of effective weed management of locally dispersed weeds. Scalping of the recipient site prior to the application of topsoil may not have been sufficient to reduce the weedy soil seedbank. Many weedy annuals are wind-dispersed, and abundant in the peri-urban landscape, so weed seeds may have blown into experimental plots after their establishment. Weeds that emerged in spring 2012 produced abundant seeds that produced seedlings in spring 2013, showing that well-planned weed management is required for successful restoration programmes using transferred topsoil (Funk *et al.*, 2020), for example timely herbicide application to control weeds before the emerge of native species (Standish *et al.*, 2007).

5 | CONCLUSIONS

In our study, overcoming the dispersal filter through transfer of salvaged topsoil produced the best restoration outcomes. Increasing the availability of readily germinable seed by applying a deep layer (10 cm) of soil was more effective than employing a shallow layer (5 cm). Deep topsoil transfer also had a greater suppressive effect on weed densities on the degraded restoration site. The positive effect of deep topsoil on native perennial densities was consistent across the first two pulses of seedling emergence and translated to highest densities for this treatment. However, survival over the two-year period was low, ranging from 0.6% to 5% regardless of the topsoil treatment. This implies a very important role of summer water stress in seedling mortality as a key driver of restoration success, possibly exacerbated by the biotic filter of weed competition. It is likely that extreme summer water stress prevented detection of differences in survival between some treatments as the final densities and richness were dramatically reduced. The overall native plant species number after two years decreased almost four-fold (from 160 to 44). The strongly negative effect of soil ripping treatment on emergence densities contrasts with the negative effects of compaction at depth (likely detrimental to root growth), which together suggests that heavy ripping equipment should be used to alleviate compaction to the greatest possible depth (at least 800 mm) prior to the application of topsoil and shortly after the emergence of local annual weeds. The biotic filter of fencing plots to exclude gazers showed no effect on the establishment of seedlings. However, our study was over a short time period and given a longer time frame there may be deleterious effects of grazers.

Some authors have suggested that topsoil seedbanks are depauperate and weedy (Hopfensperger, 2007; Bossuyt & Honnay, 2008; Vandvik *et al.*, 2016). However, our evidence is that the topsoil from a high-quality source did suppress weed recruitment and was a reservoir of seeds of native species resulting in recruitment of a diverse native plant assemblage. Our findings are consistent with the conclusions of Vandvik *et al.* (2016) after analysis of a global dataset that seedbanks can produce a community at least as similar to that from which they are sourced. Seedbanks from environments that are subject to highly variable weather conditions and/or where recruitment is primarily after episodic disturbances, such as fire, are more likely to be useful in restoration in contrast to seedbanks from areas where recruitment is relatively predictable on an annual basis, as the seed content is the result of many years of seed accumulation. This study confirms that topsoil salvaged from cleared woodland can be used to establish seedlings of many native species. Longer-term monitoring of survival and performance would be helpful to understand assembly trajectories of plant functional diversity and for assessing the ultimate success of topsoil transfer as a tool for restoration. Furthermore, an extension of this study would be to examine other abiotic and biotic filters, such as climate conditions, pre-transfer soil compaction at the recipient site, and weed management to reduce competitive exclusion by weeds, which could result in improved restoration outcomes.

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REFERENCES
Andrys, J., Kala, J. & Lyons, T.J. (2017) Regional climate projections of mean and extreme climate for the southwest of Western Australia (1970–1999 compared to 2030–2059). *Climate Dynamics*, 48, 1723–1747.

Bassett, I.E., Simcock, R.C. & Mitchell, N.D. (2005) Consequences of soil compaction for seedling establishment: Implications for natural regeneration and restoration. *Austral Ecology*, 30, 827–833. https://doi.org/10.1111/j.1442-9993.2005.01525.x

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). *Fitting linear mixed-effects models using lme4*. arXiv Prepr. arXiv1406.5823.

Bell, D., Plummer, J. & Taylor, S. (1993) Seed germination ecology in southwestern Western Australia. *The Botanical Review*, 59, 24–73. https://doi.org/10.1007/bf02856612

Bengough, A.G., McKenzie, B.M., Hallett, P.D. & Valentine, T.A. (2011) Root elongation, water stress, and mechanical impedance: A review of limiting stresses and beneficial root tip traits. *Journal of Experimental Botany*, 62, 59–68. https://doi.org/10.1093/jxb/erq350

Birnbaum, C., Bradshaw, L.E., Ruthrof, K.X. & Fontaine, J.B. (2017) Topsoil stockpiling in restoration: Impact of storage time on plant growth and symbiotic soil biota. *Journal of Experimental Botany*, 35, 237–245. https://doi.org/10.3368/er.35.3.237

Bond, W.J., Honig, M. & Maze, K.E. (1999) Seed size and seedling emergence: an allometric relationship and some ecological implications. *Oecologia*, 120, 132–136. https://doi.org/10.1007/s004420050841

Bossuyt, B. & Honnay, O. (2008) Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science*, 19, 875–884.

Breed, M.F., Cross, A.T., Wallace, K., Bradby, K., Flies, E., Goodwin, N. *et al* (2020) Ecosystem restoration: A public health intervention. *EcoHealth*, 1–3. https://doi.org/10.1007/s10393-020-01480-1

Brundrett, M., Wisolith, A., Collins, M., Longman, V. & Clarke, K. (2020) *Several complementary methods of plant establishment are required for effective restoration of banksia woodland*. bioRxiv 2020.07.09.195131. doi: https://doi.org/10.1101/2020.07.09.195131

Bulot, A., Provost, E. & Dutoit, T. (2014) A comparison of different soil transfer strategies for restoring a Mediterranean steppe after a pipeline leak (La Crau plain, South-Eastern France). *Ecological Engineering*, 71, 690–702 https://doi.org/10.1016/j.ecoleng.2014.07.060

Bureau of Meteorology (2020) *Climate Data Online [WWW Document]*. http://www.bom.gov.au/climate/data/ (accessed 2.2.20).

Burkle, L.A. & Belote, R.T. (2015) Soil mutualists modify priority effects on plant productivity, diversity, and composition. *Applied Vegetation Science*, 18, 332–342. https://doi.org/10.1111/avsc.12149

Cleland, E.E., Larios, L. & Suding, K.N. (2013) Strengthening invasion filters to reassemble native plant communities: soil resources and phenological overlap. *Restoration Ecology*, 21, 390–398. https://doi.org/10.1111/j.1526-100X.2012.00896.x

Cowling, R.M., Rundel, P.W., Lamont, B.B., Kalin Arroyo, M. & Arianoutsou, M. (1996) Plant diversity in Mediterranean-climate regions. *Trends in Ecology & Evolution*, 11, 362–366. https://doi.org/10.1016/0169-5347(96)10044-6

Cross, A.T., Ivanov, D., Stevens, J.C., Sadler, R., Zhong, H., Lambers, H. & *et al* (2019) Nitrogen limitation and calcifuge plant strategies constrain the establishment of native vegetation on magnetite mine tailings. *Plant and Soil*, 1–21.

Department of the Environment (2016) *Banksia Woodlands of the Swan Coastal Plain: a nationally-protected ecological community [WWW Document]*. http://www.environment.gov.au/biodiversity/threatened/publications/banksia-woodlands-swan-coastal-plain-guide (accessed 7.20.18).

Duncan, K. & Holdaway, R. (1989) Footprint pressures and locomotion of moas and ungulates and their effects on the New Zealand indigenous biota through trampling. *New Zealand Journal of Ecology*, 12, 97–101.

Eldridge, D.J., Delgado-Baquerizo, M., Travers, S.K., Val, J., Oliver, I., Dorrough, J.W. & *et al* (2018) Livestock activity increases exotic plant richness, but wildlife increases native richness, with stronger effects under low productivity. *Journal of Applied Ecology*, 55, 766–776. https://doi.org/10.1111/1365-2664.12995

Farrell, H.L. & Fehmi, J.S. (2018) Seeding alters plant community trajectory: Impacts of seeding, grazing and trampling on semi-arid re-vegetation. *Applied Vegetation Science*, 21, 240–249. https://doi.org/10.1111/avsc.12340

Fattorini, M. & Halle, S. (2004) The dynamic environmental filters model: how do filtering effects change in assembling communities after disturbance? In: Temperton, V.M., Hobbs, R.J., Nuttle, T. and Halle, S. (Eds.) *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice*. Washington, D.C.: Island Press, pp. 96–114.

Ferreira, M.C. & Vieira, D.L.M. (2017) Topsoil for restoration: Resprouting of root fragments and germination of pioneers trigger tropical dry forest regeneration. *Ecological Engineering*, 103, 1–12. https://doi.org/10.1016/j.ecoleng.2017.03.006

Fowler, W.M., Fontaine, J.B., Enright, N.J. & Veber, W.P. (2015) Evaluating restoration potential of transferred topsoil. *Applied Vegetation Science*, 18, 379–390.

Funk, J.L., Cleland, E.E., Suding, K.N. & Zavaleta, E.S. (2008) Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution*, 23, 695–703.

Funk, J.L., Parker, I.M., Matzek, V., Flory, S.L., Aschehoug, E.T., D'Antonio, C.M. *et al* (2020) Keys to enhancing the value of invasion ecology research for management. *Biological Invasions*, 22, 2431–2445. https://doi.org/10.1007/s10530-020-02267-9

Gibson, N., Keighery, B.J., Keighery, G.J., Burbidge, A.H. & Lyons, M.N. (1994) *A Floristic survey of the southern Swan Coastal Plain, Unpublished report for the Australian Heritage Commission, prepared by Department of Conservation and Land Managment and the Conservation Council of Western Australia (Inc.)*. Department of Conservation and Land Managment.

Gilardelli, F., Sgorbati, S., Armiraglio, S., Citterio, S. & Gentili, R. (2015) Ecological filtering and plant traits variation across quarry geomorphological surfaces: Implication for restoration. *Environmental Management*, 55, 1147–1159. https://doi.org/10.1007/s00267-015-0450-z

Gorzelak, M., McAmmond, B.M., van Hamme, J.D., Birnbaum, C., Thomsen, C. & Hart, M. (2020) Soil microbial communities in long-term soil storage for sand mine reclamation. *Ecological Restoration*, 38, 13–23. https://doi.org/10.3368/er.38.1.13

Halassy, M., Singh, A.N., Szabó, R., Szili-Kovács, T., Szitár, K. & Török, K. (2016) The application of a filter-based assembly model to develop best practices for Pannonian sand grassland restoration. *Journal of Applied Ecology*, 53, 765–773. https://doi.org/10.1111/1365-2664.12618

Hall, S.L., Barton, C.D. & Baskin, C.C. (2010) Topsoil seed bank of an oak–hickory forest in eastern Kentucky as a restoration tool on surface mines. *Restoration Ecology*, 18, 834–842. https://doi.org/10.1111/j.1526-100X.2008.00509.x

Helm, J., Dutoit, T., Saatkamp, A., Bucher, S.F., Leiterer, M. & Römermann, C. (2019) Recovery of Mediterranean steppe vegetation after cultivation: Legacy effects on plant composition, soil properties and functional traits. *Applied Vegetation Science*, 22, 71–84. https://doi.org/10.1111/avsc.12415

Holmes, P.M. (2001) Shrubland restoration following woody alien invasion and mining: effects of topsoil depth, seed source, and fertilizer addition. *Restoration Ecology*, 9, 71–84. https://doi.org/10.1046/j.1526-100x.2001.009001071.x

Hopfensperger, K.N. (2007) A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos*, 116, 1438–1448. https://doi.org/10.1111/j.2007.0030-1299.15818.x

Hulvey, K.B. & Aigner, P.A. (2014) Using filter-based community assembly models to improve restoration outcomes. *Journal of Applied Ecology*, 51, 997–1005. https://doi.org/10.1111/1365-2664.12275

Jiménez-Alfaro, B., Frischie, S., Stolz, J. & Gálvez-Ramírez, C. (2020) Native plants for greening Mediterranean agroecosystems. *Nature Plants*, 6, 209–214. https://doi.org/10.1038/s41477-020-0617-3

Johnson, A.L., Borowy, D. & Swan, C.M. (2018) Land use history and seed dispersal drive divergent plant community assembly patterns in urban vacant lots. *Journal of Applied Ecology*, 55, 451–460. https://doi.org/10.1111/1365-2664.12958

Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157–164.

Kew, G.A., Mengler, F.C. & Gilkes, R.J. (2007) Regolith strength, water retention, and implications for ripping and plant root growth in bauxite mine restoration. *Restoration Ecology*, 15, S54–S64. https://doi.org/10.1111/j.1526-100X.2007.00293.x

Koch, J.M. (2007) Restoring a Jarrah Forest understorey vegetation after bauxite mining in Western Australia. *Restoration Ecology*, 15, S26–S39. https://doi.org/10.1111/j.1526-100X.2007.00290.x

Koch, M.J. & Richard, J.H. (2007) Synthesis: is Alcoa successfully restoring a Jarrah forest ecosystem after bauxite mining in Western Australia? *Restoration Ecology*, 15, S137–S144. https://doi.org/10.1111/j.1526-100X.2007.00301.x

Kulmatiski, A., Beard, K.H. & Stark, J.M. (2006) Soil history as a primary control on plant invasion in abandoned agricultural fields. *Journal of Applied Ecology*, 43, 868–876. https://doi.org/10.1111/j.1365-2664.2006.01192.x

Landsberg, J., James, C.D., Maconochie, J., Nicholls, A.O., Stol, J. & Tynan, R. (2002) Scale-related effects of grazing on native plant communities in an arid rangeland region of South Australia. *Journal of Applied Ecology*, 39, 427–444.

Lloret, F., Peñuelas, J. & Estiarte, M. (2005) Effects of vegetation canopy and climate on seedling establishment in Mediterranean shrubland. *Journal of Vegetation Science*, 16, 67–76. https://doi.org/10.1111/j.1654-1103.2005.tb02339.x

Long, R.L., Gorecki, M.J., Renton, M., Scott, J.K., Colville, L., Goggin, D.E. et al (2015) The ecophysiology of seed persistence: A mechanistic view of the journey to germination or demise. *Biological Reviews*, 90, 31–59. https://doi.org/10.1111/brv.12095

Nield, A., Monaco, S., Birnbaum, C. & Enright, N. (2015) Regeneration failure threatens persistence of Persoonia elliptica (Proteaceae) in Western Australian jarrah forests. *Plant Ecology*, 216, 189–198. https://doi.org/10.1007/s11258-014-0427-7

O'Hara, R.B. & Kotze, D.J. (2010) Do not log-transform count data. *Methods in Ecology and Evolution*, 1, 118–122. https://doi.org/10.1111/j.2041-210X.2010.00021.x

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B. et al (2013). *Vegan: community ecology package*. R-package version 2.0-10.

Rivera, D., Mejías, V., Jáuregui, B.M., Costa-Tenorio, M., López-Archilla, A.I. & Peco, B. (2014) Spreading topsoil encourages ecological restoration on embankments: soil fertility, microbial activity and vegetation cover. *PLoS One*, 9, e101413. https://doi.org/10.1371/journal.pone.0101413

Rokich, D.P., Dixon, K.W., Sivasithamparam, K. & Meney, K.A. (2000) Topsoil handling and storage effects on woodland restoration in Western Australia. *Restoration Ecology*, 8, 196–208. https://doi.org/10.1046/j.1526-100x.2000.80027.x

Schaalje, G.B., McBride, J.B. & Fellingham, G.W. (2002) Adequacy of approximations to distributions of test statistics in complex mixed linear models. *Journal of Agricultural, Biological, and Environmental Statistics*, 7, 512–524.

Schmidt, K.T., Maltz, M., Ta, P., Khalili, B., Weihe, C., Phillips, M. et al (2020) Identifying mechanisms for successful ecological restoration with salvaged topsoil in coastal sage scrub communities. *Diversity*, 12, 150. https://doi.org/10.3390/d12040150

Schultz, N.L., Morgan, J.W. & Lunt, I.D. (2011) Effects of grazing exclusion on plant species richness and phytomass accumulation vary across a regional productivity gradient. *Journal of Vegetation Science*, 22, 130–142. https://doi.org/10.1111/j.1654-1103.2010.01235.x

Simmonds, J.S., Sonter, L.J., Watson, J.E.M., Bennun, L., Costa, H.M., Dutson, G. et al (2019) Moving from biodiversity offsets to a target-based approach for ecological compensation. *Conservation Letters*, 13, e12695. https://doi.org/10.1111/conl.12695

Stanbury, K.E., Stevens, J.C. & Ritchie, A.L. (2018) Legacy issues in post-pine restoration environments: weeds compromise seedling growth and function more than edaphic factors. *Land Degradation & Development*, 29, 1694–1704 https://doi.org/10.1002/ldr.2945

Standish, R.J., Cramer, V.A., Wild, S.L. & Hobbs, R.J. (2007) Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in Western Australia. *Journal of Applied Ecology*, 44, 435–445. https://doi.org/10.1111/j.1365-2664.2006.01262.x

Standish, R.J., Fontaine, J.B., Harris, R.J., Stock, W.D. & Hobbs, R.J. (2012) Interactive effects of altered rainfall and simulated nitrogen deposition on seedling establishment in a global biodiversity hotspot. *Oikos*, 121, 2014–2025.

Stevens, J.C., Rokich, D.P., Newton, V.J., Barrett, R.L. & Dixon, K.W. (2016) *Banksia woodlands: a restoration guide for the Swan Coastal Plain*. Crawley, Western Australia: UWA Publishing.

Team, R.C. (2017) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing; 2014.

Temperton, V.M. & Hobbs, R.J. (2004) The search for ecological assembly rules and Its relevance to restoration ecology. In: Temperton, V.M., Hobbs, R.J., Nuttle, T. and Stefan, H. (Eds.) *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice*. Island Press, pp. 35–54.

Traba, J., Azcárate, F.M. & Peco, B. (2004) From what depth do seeds emerge? A soil seed bank experiment with Mediterranean grassland species. *Seed Science Research*, 14, 297–303 https://doi.org/10.1079/SSR2004179

Vandvik, V., Klanderud, K., Meineri, E., Måren, I.E. & Töpper, J. (2016) Seed banks are biodiversity reservoirs: species–area relationships above versus below ground. *Oikos*, 125, 218–228.

Vesk, P.A. & Dorrough, J.W. (2006) Getting trees on farms the easy way? Lessons from a model of eucalypt regeneration on pastures. *Australian Journal of Botany*, 54, 509–519. https://doi.org/10.1071/BT05188

Wainwright, C.E., Staples, T.L., Charles, L.S., Flanagan, T.C., Lai, H.R., Loy, X. *et al* (2018) Links between community ecology theory and ecological restoration are on the rise. *Journal of Applied Ecology*, 55, 570–581. https://doi.org/10.1111/1365-2664.12975

Waryszak, P. (2017) *Evaluating emergence, survival, and assembly of Banksia woodland communities to achieve restoration objectives following topsoil transfer.* PhD thesis. Murdoch University, Perth, Australia.

Waryszak, P., Fontaine, J., Ladd, P., Enright, N., Standish, R. & Brundrett, M. (2020) *"Dataset: seedlings emergence and survival following topsoil transfer, Western Australia.* Mendeley Data. https://doi.org/10.17632/g447pxnj6c.1

Watts, S.H., Griffith, A. & Mackinlay, L. (2019) Grazing exclusion and vegetation change in an upland grassland with patches of tall herbs. *Applied Vegetation Science*, 22, 383–393. https://doi.org/10.1111/avsc.12438

Weston, L.A. & Duke, S.O. (2003) Weed and crop allelopathy. *Critical Reviews in Plant Sciences*, 22, 367–389. https://doi.org/10.1080/713610861

Wickham, H. (2016) *ggplot2: Elegant graphics for data analysis.* New York: Springer-Verlag.

Wickham, H., François, R., Henry, L. & Müller, K. (2019) *dplyr: A Grammar of Data Manipulation.*

Yates, C.J., McNeill, A., Elith, J. & Midgley, G.F. (2010) Assessing the impacts of climate change and land transformation on Banksia in the South West Australian Floristic Region. *Diversity and Distributions*, 16, 187–201.

Zamin, T.J., Jolly, A., Sinclair, S., Morgan, J.W. & Moore, J.L. (2018) Enhancing plant diversity in a novel grassland using seed addition. *Journal of Applied Ecology*, 55, 215–224. https://doi.org/10.1111/1365-2664.12963

Zirbel, C.R. & Brudvig, L.A. (2020) Trait–environment interactions affect plant establishment success during restoration. *Ecology*, 101, e02971. https://doi.org/10.1002/ecy.2971

Zobel, M., Otsus, M., Liira, J., Moora, M. & Möls, T. (2000) Is small-scale species richness limited by seed availability or microsite availability? *Ecology*, 81, 3274–3282. https://doi.org/10.1890/0012-9658(2000)081[3274:ISSSRL]2.0.CO;2

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Detailed description of vegetation, climate and geology of study sites

Appendix S2. Detailed output of statistical models and mapping of experimental design