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META-ANALYSIS

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Global meta-analysis of soil-disturbing vertebrates reveals strong effects on ecosystem patterns and processes

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Abstract

Aim: Organisms that disturb the soil while foraging or creating shelter (ecosystem engineers) can have profound effects on ecosystems. Soil ejecta from these disturbances can enhance surface nutrients and the resulting depressions accrue organic matter and develop into biological hotspots. Here, we describe a global meta-analysis of studies that assessed the impacts of vertebrate soil disturbance on both biotic and abiotic components of ecosystems.

Location: Global land surface.

Time period: 1941–2016.

Major taxa studied: Vertebrates.

Methods: After conducting a systematic literature search, we quantitatively synthesized the findings of 149 published studies that compared disturbed and undisturbed surfaces. Our meta-analysis included 64 engineer species, primarily comprised of rodents and a subset of other mammals.

Results: We found that vertebrate soil disturbance significantly enhanced soil nitrogen (by 77%) and phosphorus (35%), and the productivity (32%) and recruitment (32%) of vascular plants. Disturbances had a greater cover of bare soil (126%) than undisturbed controls, and higher abundances of secondary vertebrates (1,233%), that use pre-constructed burrows as shelter and foraging grounds. Soil disturbance significantly reduced water run-off (63%) and the abundance of biocrusts (82%). Soil disturbance effects generally intensified with increasing aridity, and the magnitude of soil disturbance effects was not moderated by the area of the disturbance. Disturbances older than 12 months were more distinct from the surrounding matrix than fresh disturbances. The phylogeny of engineers was unrelated to their ecosystem effects, indicating that the same functionality could readily evolve in different taxa.

Main conclusions: In general, disturbances become localized patches of elevated functioning, providing strong evidence that vertebrate engineers, especially those in drylands, are an important source of environmental heterogeneity.

KEYWORDS
biopedturbation, bioturbation, ecosystem engineering, faunalpedturbation, fertile islands, heterogeneity, meta-analysis, soil disturbance, zoogeomorphology

1 | INTRODUCTION

Positive (facilitatory) interactions among organisms are equally as important as negative (competitive) interactions in structuring ecosystems (see e.g. Bruno, Stachowicz, & Bertness, 2003; Machicote, Branch, & Villarreal, 2004). Terrestrial vertebrates, for example, can modify plant species composition by dispersing seeds or alter the dominant plant growth form through grazing (Chew, 1974; Kerley & Whitford, 2000). Positive interactions can also result from non-trophic mechanisms such as ecosystem engineering, whereby an organism induces a change in the physical environment that alters the availability of resources to other organisms or to themselves (Jones, Lawton, & Shachak, 1994). For example, Indian crested porcupines (*Hystrix indica*) create surface pits in order to consume bulbs of the desert tulip (*Tulipa systola*) in the Negev Desert. Although the porcupines consume 60–90% of the bulbs, the conditions for the remaining bulbs are enhanced by the additional water and nutrient-rich sediment captured by the pits (Gutterman, 1987). Soil disturbances such as these are the most well-documented form of ecosystem engineering in terrestrial vertebrates (Coggan, Hayward, & Gibb, 2018) and will be the focus of the present study.

It is useful to conceptualize soil disturbance as two distinct physical processes resulting in (a) the excavation of a pit, scrape, resting form or burrow and (b) the deposition of a mound of soil (ejecta mound) adjacent to the disturbance (Figure 1). The depression created by soil removal acts as an accreting surface, which gradually infills with eroding sediment, litter, water, seeds and other organic materials. Vacated burrows often become habitat for secondary animals, such as burrowing owls (*Athene cunicularia hypugaea*), Florida mice (*Podomys floridanus*) and various lizard and beetle species, which use the burrows as shelter and foraging grounds (Casas-Crivillé & Valera, 2005; Davidson, Lightfoot, & McIntyre, 2008; Lantz, Conway, & Anderson, 2007). The ejecta mound acts as an eroding surface and the constituent material is redistributed across the landscape by fluvial and aeolian erosion until the original surface eventually re-emerges. In some cases, ejecta mounds may be stabilized by vegetation and biocrust, and become persistent topographical features (Eldridge, 2004).

In the act of removing soil, vertebrate engineers remove groundstorey plants and expose the subsoil, often reducing soil aggregation and altering surface microclimate (Platt, Kolb, Kunhardt, Milo, & New, 2016). Soil removal reduces run-off, and has often been reported to increase soil moisture and infiltration, by creating a macropore, removing hydrophobic soil crusts or compacted layers and clearing plants, which extract a portion of soil water (Valentine, Bretz, Ruthrof, Fisher, & Hardy, 2017). Soil ejecta, however, covers an existing soil surface, smothering groundstorey plants. Soil ejecta often has a markedly different chemical signature to the original topsoil in terms of pH, cations, and carbon and nitrogen pools (Eldridge & Koen, 2008; Kerley, Whitford, & Kay, 2004). As soil nutrient pools recover in the depression and the ejecta is redistributed, plants and soil organisms begin to recolonize the disturbed surfaces.

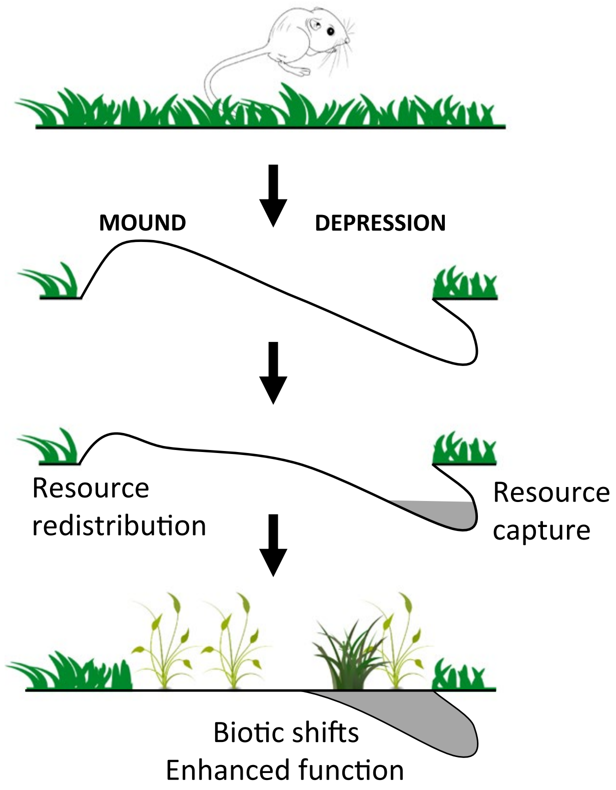

FIGURE 1 Conceptual diagram of soil disturbance, showing the two types of structures produced (an ejecta mound and a depression) and how they change over time. The depression infills with eroding sediment, water and organic matter. The ejecta mound is redistributed across the landscape by erosion. Both types of structures can lead to compositional shifts in biota

We analysed published data on the effects of vertebrate engineers on plants, soils and associated biota to derive a global synthesis. There have been several important qualitative reviews of vertebrate engineers, with foci on biotic interactions (Coggan et al., 2018), soil function (Platt et al., 2016) and specific systems such as drylands (Whitford & Kay, 1999). However, quantitative syntheses thus far have been restricted to properties relating to diversity and biomass (Romero, Gonçalves-Souza, Vieira, & Koricheva, 2015; Root-Bernstein & Ebensperger, 2013). There has yet to be a quantitative synthesis at the global scale that examines both the biotic and abiotic effects of vertebrate engineers. Such a synthesis is timely if we are to advance our understanding of the ecological dimensions of vertebrate engineers, how they influence a wide range of patterns and processes across a range of ecosystems, how these impacts vary under different climate conditions, and thus the likely impacts of their loss from ecosystems or their reintroduction into degraded ecosystems.

Ecosystem theory suggests that the impact of vertebrate engineers should increase with declining ecosystem productivity (Wright and Jones 2004). This would occur because the capture of even small amounts of resources such as water and organic matter within surface disturbances in resource-poor environments would result in the creation of patches that are distinctly resource-rich compared with the surrounding matrix. We might also expect that larger disturbances would have more pronounced impacts on ecosystem properties because they could influence processes that occur at broader spatial scales (Wiens, 1989). Vegetation is also known to recover more slowly on larger soil disturbances (Rogers & Hartnett, 2001). Consequently our synthesis aimed to address three important questions relating to how vertebrate engineers affect ecosystems by disturbing soil: (a) what are the global ecosystem effects of soil disturbance by vertebrates?; (b) are any impacts of disturbance greater in more arid ecosystems?; and (c) does the impact of disturbance vary with the size or age of the disturbance? We also examined whether phylogeny was important in explaining variation in these effects among species.

2 | METHODS

2.1 | Literature search

Records were collected by systematically searching online databases and then screened in accordance with Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (see Supporting Information Appendix S1). A list of data sources can be found in the Appendix. Soil disturbance is known by many terms, depending on the field of science, the disturbing agents and the biome in which the disturbance is being investigated (Cavin & Butler, 2015). Ecosystem engineering and several variants of biopedturbation (e.g. faunalpedturbation) are used by ecologists, while zoogeomorphology and ichnology are more commonly used by geoscientists. We captured research from both fields by searching Google Scholar and the Institute for Scientific Information (ISI) Web of Knowledge for the following keyword strings: biopedturbation, biopedoturbation, faunalpedoturbation, faunalturbation, 'foraging pits' and zoogeomorphology. Records were also retrieved from the complete reference lists of seven key review papers (see Supporting Information Appendix S1). The relevant literature on wild boar (*Sus scrofa*) was so extensive that a study by Barrios-Garcia and Ballari (2008), despite its singular focus on wild boar, was chosen as a key paper to ensure that all pertinent studies were captured by our search. Studies published at any date up to and including November 2016 were included.

Retrieved records were screened to identify primary peer-reviewed publications that compared an ecosystem effect of soil disturbance by a vertebrate against a paired undisturbed control. Only one included study was manipulative (Prugh & Brashares, 2012), and the majority of comparisons were conducted at the patch scale (disturbance versus undisturbed adjacent control). We restricted our study to terrestrial ecosystems and excluded human-created disturbances. We chose not to include soil temperature and cations as properties because their roles in ecosystem processes are not well characterized. Only clay content was included as a measure of soil texture due to strong correlations with silt and sand content. We excluded aquatic disturbing agents unless they directly impacted a terrestrial property. The full criteria are shown in Supporting Information Appendix S1. From the studies that satisfied our criteria, we extracted the raw means and variances of the measured ecosystem properties. Data presented in figures were extracted using the Figure Calibration plugin in ImageJ (Schneider, Rasband, Eliceiri, Schindelin, & Arganda-Carreras, 2012).

2.2 | Moderating variables

We collected data on three moderators: aridity, disturbance area and disturbance age. We extracted values of the aridity index (precipitation/potential evapotranspiration) for each location from the Consultative Group for International Agricultural Research Consortium for Spatial Information (CGIAR-CSI) Global-Aridity Database (http://www.cgiar-csi.org; Zomer, Trabucco, Bossio, & Verchot, 2008). We took the additive inverse of the aridity index (i.e. aridity = −1 × aridity index), so that higher values corresponded to greater dryness. The disturbance area and body mass of each vertebrate species were extracted from various sources (see Supporting Information Appendix S2). Disturbance area was calculated as the total horizontal area of disturbed soil, including underground tunnels and ejecta mounds. Aridity and disturbance area were log(x) transformed to improve normality and z-transformed (standardized) in order to improve the interpretation of regression coefficients by putting them all on a common scale (Schielzeth, 2010).

Exact disturbance age was rarely reported, as this can usually only be determined in artificial disturbances, but we were able to extract a binary variable from most studies comprising fresh disturbances (< 1 year old) and old disturbances (≥ 1 year old). 'Active' or 'occupied' soil disturbances were treated as fresh disturbances, although we acknowledge that this approach is coarse and does not capture the complexities of disturbance history. Fresh disturbances were assigned a value of −1 and old disturbances a value of 1, such that the mean was approximately 0 and standard deviation approximately 1, and therefore the variable could be reliably compared with other standardized moderators (see Gelman, 2008). Note that this coding does not allow for the calculation of separate slopes for fresh and old disturbances. Rather, the single slope estimate indicates the relative effects (slope is positive when the effect is greater in old disturbances).

2.3 | Data analysis

To examine the mean effects of soil disturbance, we calculated the log response ratio, lnRR, for each data pair (Hedges, Gurevitch, & Curtis, 1999). The log response ratio was calculated as $\ln(x_D) - \ln(x_U)$, where x_D is the mean value for the disturbed site and x_U the value for the undisturbed site. Thus, negative values of lnRR represent situations where soil disturbance reduces a particular property and vice versa. We used a single imputation to manage zeros in the data set, which comprised 0.7% of all effect sizes (Lajeunesse, 2013; Nakagawa, 2015). That is, when $x_D = 0$, we set lnRR to the lowest value of lnRR in the data set and then solved for x_D. The same process was used to replace zeros in undisturbed means, but in this case, we set lnRR to the highest value. For zeros in standard deviation (*SD*), we performed a linear regression of $\ln(x) \sim \ln(SD)$ and used the regression coefficients to back-calculate *SD* values (Nakagawa, 2015).

Our final data set included 24 ecosystem properties. Properties with fewer than 10 effect sizes and that could not be grouped into other properties were removed (e.g. biocrust richness). The final data set comprised 1,609 effect sizes from 149 studies, published from 1941 to 2016 (see Appendix).

The intercept model (i.e. meta-analysis) and meta-regression were performed in R (R Core Team, 2017) using the *metafor* package version 1.9–8 (Viechtbauer, 2010). The intercept model is the model that derives the centre and spread of all effect sizes, while the meta-regression incorporates moderators (fixed effects) to account for variation in the effect sizes. The estimate derived from the intercept model is largely uninformative because we expect many of the ecosystem effects of soil disturbance to have different signs and effectively cancel out. However, the intercept model is useful in partitioning variance among random factors, which in this case are phylogeny, species, study and residual variance. Phylogeny was implemented as a correlation matrix derived from an ultrametric phylogenetic tree, which was based on data provided by the Open Tree Taxonomy (Hinchliff, Smith, Allman, Burleigh, & Chaudhary, 2015). The transformation between phylogenetic tree and correlation matrix, using the 'vcv' function in the R package *ape* (Paradis, Claude, & Strimmer, 2004), assumed the Brownian model of evolution. The intercept model enabled us to partition the variance among random factors. I^2 (heterogeneity) is the variation among effect sizes that is not accounted for by the sampling error variance (Higgins & Thompson, 2002). The meta-regression included four moderators – disturbance age, disturbance area, property and the interaction of property and aridity – in addition to the four random effects. As a measure of variance in each model, we created a covariance matrix to account for effect sizes with shared controls (Noble, Lagisz, & O'dea, & Nakagawa, 2017). True intercepts and standard errors were calculated for each level of ecosystem property so that results reflected group means rather than contrasts to a reference group. We considered a result significant when the 95% confidence interval (CI) did not cross zero. We calculated the variance accounted by moderators as marginal R^2 (sensu Nakagawa & Schielzeth, 2013).

Only two vertebrate species were measured in their non-native range, the European rabbit (*Oryctolagus cuniculus*) and the wild boar. These species were also measured in their native ranges, allowing us to explore differences in soil disturbance effects among native and non-native ranges. Ecosystem engineers in non-native ranges are known in some cases to promote further invasions of exotic species, so one difference might be a greater effect on biotic composition in the non-native range (Crooks, 2002). We therefore conducted a separate meta-regression with range status as a fixed effect and study as a random effect using only data from these two species (N = 235). These data were insufficient to include interactions with different ecosystem properties in the model.

2.4 | Publication bias

Funnel plots were produced by plotting the precision (or inverse standard error) of log response ratios against the meta-analytic residuals (sensu Nakagawa & Santos, 2012), which were extracted using Markov chain Monte Carlo techniques in the R package *MCMCglmm* version 2.24 (Hadfield, 2010; Hadfield & Nakagawa, 2010). We also performed a trim-and-fill test (Duval & Tweedie, 2000) using the R_0 estimator and a modified version of Egger regression (sensu Sterne & Egger, 2005) to assess publication bias.

3 | RESULTS

3.1 | Variety and extent of soil disturbances by vertebrates

Our final data set included 64 vertebrate animal species; 60 of which were mammals and 40 of which were rodents (see Supporting Information Appendix S2). Birds and reptiles were markedly underrepresented. Vertebrate engineers caused five types of soil disturbance: burrows (73.4% of animals), foraging digs (17.2%), resting digs (3.1%), areas of trampled soil (1.6%) and wallows (1.6%). Two animals in the data set, the greater bilby (*Macrotis lagotis*) and the burrowing bettong (*Bettongia lesueur*), had documented effects of both foraging digs and much larger burrows. The distribution of animal mass was highly skewed towards smaller animals, with 75% of species weighing less than 5 kg, although the study did include several large ungulates (see Supporting Information Appendix S2). Wild boar, which disturb soil while excavating plant tubers and fossorial animals, constituted 20% of the extracted estimates (15% of studies), the most of any included species. Larger animals tended to produce small foraging digs and resting forms rather than burrows, which were generally more spatially expansive.

The vast majority of studies (95.3%) were conducted in the midlatitudes, with the remaining studies (4.7%) being conducted in the tropics (Figure 2). The USA was an area of particularly high research output (46% of studies). Apart from tundra (N_{tundra} = 4), all major community types were well represented (N_{forest} = 261, $N_{woodland}$ = 212, $N_{shrubland}$ = 458, $N_{grassland}$ = 674).

3.2 | Effects of soil disturbance on ecosystem properties

Our meta-analysis showed that soil disturbance did not consistently enhance or reduce the studied ecosystem properties [lnRR: 0.039 (95% CI: −0.053 – 0.130); Table 1]. Rather, the effects of soil disturbance varied among properties (Figure 3, Table 2). Disturbance significantly enhanced plant recruitment and productivity, both by 32%, and soil nitrogen and phosphorus, by 77 and 35%, respectively. Disturbed areas also had more bare soil (126%), and more secondary vertebrates (e.g. various birds and lizards) using the space as habitat (1,233%). The abundances of vascular plants and biocrusts were reduced by 23 and 82%, respectively, and run-off was reduced by 63%. Although not significant, disturbance generally increased soil respiration, clay content, invertebrate activity and soil moisture, while reducing soil compaction and stability.

The marginal R^2 from the meta-regression model was 27.52. The effects of soil disturbance did not vary significantly with disturbance

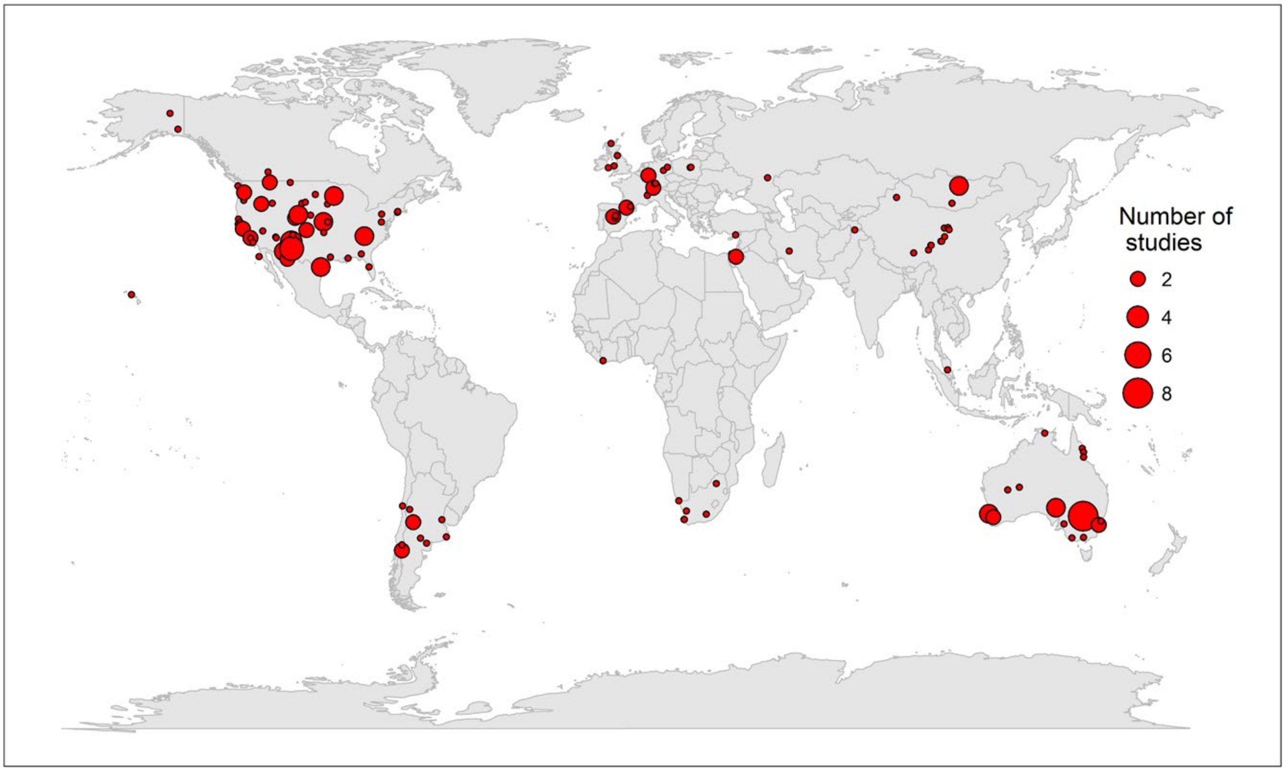

FIGURE 2 World map showing the locations of all included studies of soil-disturbing vertebrates

TABLE 1 Summary of global meta-analysis of soil-disturbing vertebrates (*n* = number of effect sizes, *k* = number of soil-disturbing species, CI = confidence interval)

n	*k*	Estimate	*SE*	$I^2_{[total]}$	$I^2_{[phylogeny]}$	$I^2_{[species]}$	$I^2_{[study]}$	$I^2_{[residual]}$	Lower CI (5%)	Upper CI (95%)
1,609	64	0.039	0.047	.997	.000	.024	.255	.718	−0.053	0.130

area [lnRR: −0.056 (95% CI: −0.151 – 0.039)]. However, disturbances ≥ 1 year old were more distinct from undisturbed controls (typically the surrounding matrix) than fresh disturbances. Modelling the interaction of ecosystem property and aridity revealed that, for most properties, disturbances became increasingly distinct from the surrounding matrix as aridity increased (Figure 3). Most notably, disturbance effects on soil nitrogen and phosphorus, soil respiration, and plant productivity and density were greater in more arid systems. By contrast, the effects of soil disturbance on biocrust abundance, root biomass and the abundance of secondary vertebrates were greater in more humid systems.

We found very high heterogeneity in the intercept model (I^2 = .997), which indicates a high degree of unexplained variation (Table 1). Soil-disturbing activities were largely unrelated to the phylogenetic relatedness of animal species ($I^2_{[phylogeny]}$ < .001) but were similar within a species ($I^2_{[species]}$ = .024). The model also showed moderate between-study variance ($I^2_{[study]}$ = .255) and high variance at the effect size level ($I^2_{[residual]}$ = .718).

For European rabbits and wild boar, there were negligible differences in soil disturbance effects among native and non-native ranges (Supporting Information Appendix S3).

3.3 | Publication bias

Visual inspection revealed no obvious asymmetry in the funnel plot (Figure 4). Trim-and-fill tests supported this assertion, estimating no missing studies. Egger regression further indicated no significant publication bias in the data (z = 1.751, p = .080).

4 | DISCUSSION

Much has been written on the non-trophic, engineering effects of soil-disturbing animals on properties as broad as soil chemistry, habitat amelioration and plant community dynamics (Hastings, Byers, Crooks, Cuddington, & Jones, 2007; Lavelle, Decaëns, Aubert, Barot, & Blouin, 2006; Wright, Jones, & Flecker, 2002). Despite this large body of work, there has been no quantitative global synthesis of animal effects on ecosystems across the full range of ecosystem properties. Here, we used an extensive global data set of peer-reviewed literature to assess the non-trophic effects of soil-disturbing vertebrates. Compared with undisturbed soil, we found that soil disturbance reduced plant abundance, biocrust abundance and

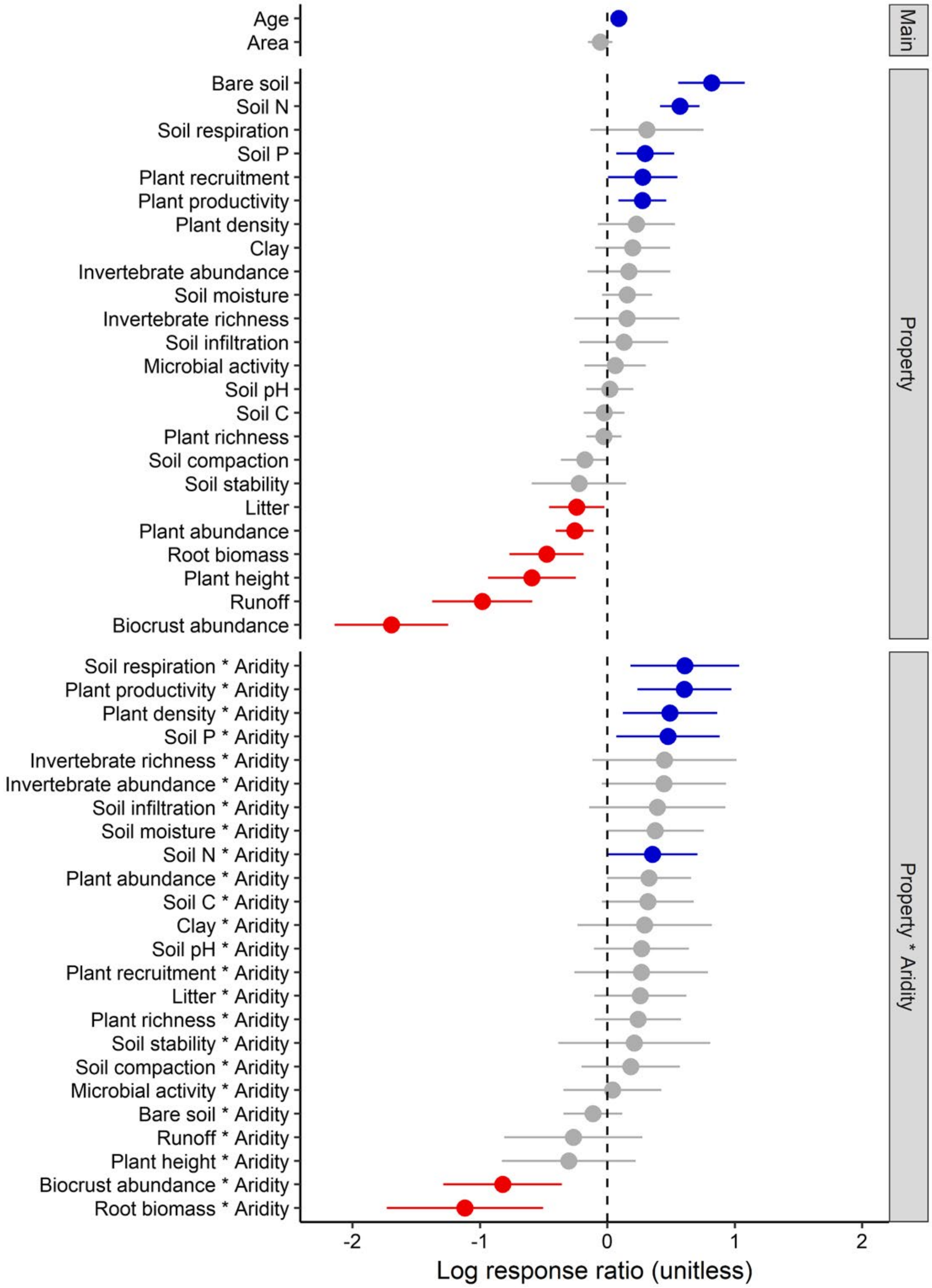

FIGURE 3 The effects of disturbance age and area ('main effects') on vertebrate soil disturbance, and the effects of vertebrate soil disturbance on ecosystem properties and the interaction of properties and aridity. Significant results are shown in red (negative) and blue (positive), and error bars represent 95% confidence intervals. One property, the abundance of secondary vertebrates, was excluded from the figure for graphical reasons (but see Table 2)

run-off, and enhanced soil nitrogen, soil phosphorus, plant productivity, plant recruitment, the abundance of secondary vertebrates and the cover of bare soil. Most of these effects intensified with increasing aridity. Disturbances that had recovered for at least 1 year were more distinct from the surrounding matrix than fresh disturbances. There was no evidence that the phylogeny of engineers is an important determinant of their ecosystem effects. Our study provides strong empirical evidence that surface disturbance by vertebrate engineers has substantial effects on a range of ecosystem properties.

TABLE 2 Summary of meta-regression model (R^2 = 27.52; *n* = number of effect sizes; *k* = number of soil-disturbing species)

Moderator	Levels	*n*	*k*	Estimate	*SE*	Lower CI (5%)	Upper CI (95%)
Disturbance age		1,609	64	0.091	0.03	0.032	0.149
Disturbance area		1609	64	−0.056	0.049	−0.151	0.039
Property	Bare soil	33	15	0.817	0.133	0.557	1.077
	Biocrust abundance	15	6	−1.695	0.228	−2.141	−1.249
	Clay	24	9	0.198	0.15	−0.096	0.492
	Invertebrate abundance	47	7	0.169	0.166	−0.157	0.494
	Invertebrate richness	14	6	0.153	0.21	−0.259	0.565
	Litter	65	15	−0.241	0.111	−0.457	−0.024
	Microbial activity	46	10	0.062	0.123	−0.18	0.303
	Plant abundance	228	28	−0.256	0.076	−0.405	−0.107
	Plant density	46	9	0.228	0.154	−0.075	0.53
	Plant height	23	6	−0.593	0.176	−0.938	−0.247
	Plant productivity	96	24	0.275	0.096	0.086	0.463
	Plant recruitment	61	12	0.278	0.139	0.006	0.55
	Plant richness	220	31	−0.027	0.071	−0.165	0.111
	Root biomass	29	10	−0.477	0.149	−0.769	−0.185
	Run-off	21	6	−0.983	0.2	−1.375	−0.59
	Soil compaction	69	17	−0.177	0.095	−0.364	0.01
	Soil C	125	23	−0.026	0.082	−0.186	0.134
	Soil infiltration	39	8	0.131	0.178	−0.217	0.479
	Soil N	158	28	0.569	0.079	0.413	0.724
	Soil P	58	16	0.298	0.116	0.07	0.526
	Soil pH	67	18	0.02	0.094	−0.165	0.205
	Soil respiration	12	6	0.31	0.226	−0.133	0.752
	Soil stability	17	5	−0.222	0.189	−0.593	0.148
	Soil moisture	67	15	0.156	0.1	−0.04	0.351
	Vertebrate abundance	29	3	2.591	0.752	1.117	4.065
Property * aridity	Bare soil	33	15	−0.113	0.118	−0.344	0.118
	Biocrust abundance	15	6	−0.822	0.237	−1.287	−0.356
	Clay	24	9	0.293	0.269	−0.234	0.819
	Invertebrate abundance	47	7	0.443	0.249	−0.044	0.931
	Invertebrate richness	14	6	0.447	0.289	−0.118	1.013
	Litter	65	15	0.259	0.185	−0.103	0.62
	Microbial activity	46	10	0.04	0.196	−0.343	0.424
	Plant abundance	228	28	0.327	0.168	−0.003	0.657
	Plant density	46	9	0.491	0.189	0.121	0.862
	Plant height	23	6	−0.303	0.268	−0.828	0.222
	Plant productivity	96	24	0.605	0.188	0.236	0.973
	Plant recruitment	61	12	0.266	0.267	−0.258	0.79
	Plant richness	220	31	0.24	0.172	−0.097	0.578
	Root biomass	29	10	−1.118	0.313	−1.732	−0.505
	Run-off	21	6	−0.268	0.277	−0.81	0.274
	Soil compaction	69	17	0.183	0.197	−0.203	0.569
	Soil C	125	23	0.319	0.184	−0.042	0.679

(Continues)

TABLE 2 (*Continued*)

Moderator	Levels	*n*	*k*	Estimate	*SE*	Lower CI (5%)	Upper CI (95%)
	Soil infiltration	39	8	0.392	0.273	−0.143	0.926
	Soil N	158	28	0.354	0.18	0.001	0.707
	Soil P	58	16	0.476	0.207	0.071	0.88
	Soil pH	67	18	0.268	0.19	−0.105	0.64
	Soil respiration	12	6	0.608	0.217	0.182	1.034
	Soil stability	17	5	0.21	0.304	−0.385	0.806
	Soil moisture	67	15	0.376	0.195	−0.006	0.758
	Vertebrate abundance	29	3	−6.59	2.841	−12.157	−1.023

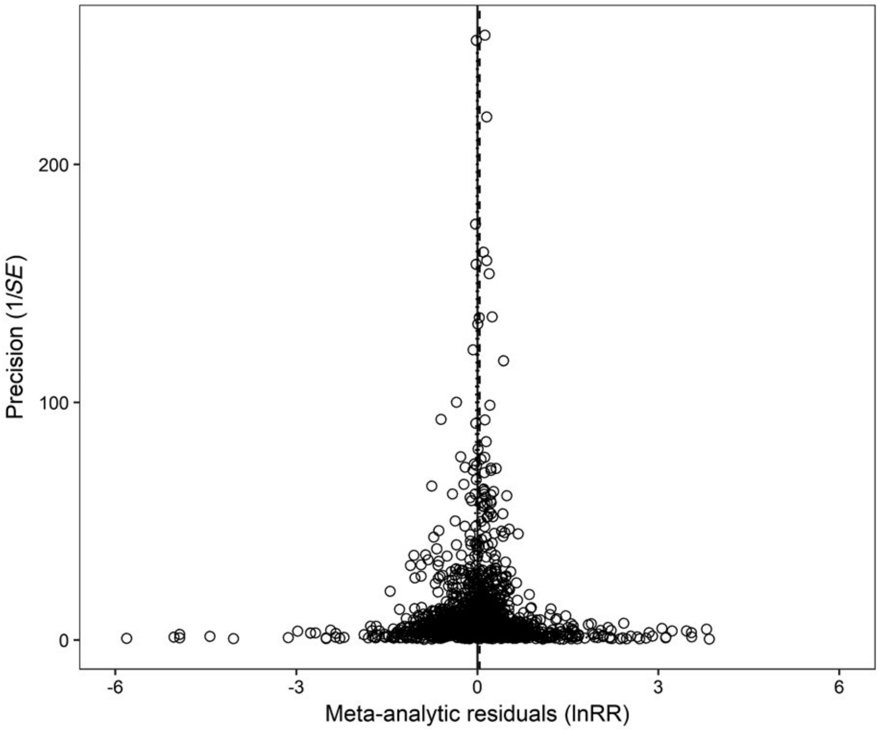

FIGURE 4 Funnel plot showing precision (inverse standard error) against meta-analytic residuals from the meta-regression model of the effects of vertebrate soil disturbance. The dashed line represents the meta-analytic mean. lnRR = log response ratio

In general, the findings from our meta-analysis are consistent with our predictions. It is clear that burrows are important habitat for secondary vertebrates, with 12 times greater abundances than undisturbed surfaces. In some cases, secondary burrow inhabitants can further modify the disturbance, initiating a "burrowing cascade" (Kinlaw & Grasmueck, 2012). Unsurprisingly, run-off was reduced by disturbance, which is known to enhance soil porosity and break up hydrophobic soil crusts (Platt et al., 2016). Elevated levels of soil nitrogen and phosphorus in disturbances are probably due to trapped organic matter (James, Eldridge, & Hill, 2009), and in some cases, nutrient-rich soils being translocated from deeper soil layers during excavation (Platt et al., 2016). Non-engineering effects, such as excretions and food residue left by the animal, could have also played a role in this nutrient effect (Platt et al., 2016). Our analysis revealed that soil disturbances promote plant recruitment and productivity, reinforcing the notion that disturbances are favourable sites for plant germination and growth, largely due to the elevated nutrient levels (Alkon, 1999; James et al., 2009). The finding that disturbances reduced plant height is probably confounded by burrowing animals actively consuming or clearing vegetation around the burrow (Arias, Quintana, & Cagnoni, 2005; Eldridge & Myers, 2001; Whicker & Detling, 1988).

Given that disturbance generally promotes plant recruitment, the finding that soil disturbance reduces plant abundance might seem counter-intuitive. However, most (73%) of the plant abundance measurements were recorded within 1 year of the disturbance being created. These data are thus likely to represent a temporary phase between plants being cleared or smothered during excavation and new plants recolonizing. Rates of plant recolonization on soil disturbances are not well known, but in a humid grassland system, Rogers, Hartnett, and Elder (2001) found that plant richness and biomass recovered to pre-disturbance levels after 2 years. Increases in bare soil cover are also, in large part, representative of the initial phase of post-disturbance recovery, with 76% of measurements recorded within 1 year of disturbance. Although biocrust effects are similarly biased, disturbances might also reduce biocrust abundance in the long term by promoting vascular plant recruitment and productivity. Vascular plants tend to suppress biocrusts through shading and litter fall (Zhang, Aradottir, Serpe, & Boeken, 2016).

Soil disturbance initiates substantial shifts in biotic community composition so that accreting and eroding surfaces often support a community that is distinct from the surrounding matrix (Aplet, Anderson, & Stone, 1991; Gómez-Garcia, Borghi, & Giannoni, 1995; Jones, Halpern, & Niederer, 2008). Shifts may occur stochastically or because disturbances favour organisms with particular resource requirements or traits relating to colonization and disturbance tolerance (Eldridge & James, 2009). Past studies have generally observed a shift towards more annual plant dominated communities (Eldridge & Simpson, 2002; Kyle, Kulmatiski, & Beard, 2008; Moroka, Beck, & Pieper, 1982). While disturbances often support distinct species assemblages, overall richness may not change. Our finding that soil disturbance did not have a significant effect on plant or invertebrate richness either indicates that richness tends to be maintained through compositional shifts or that richness effects are highly variable among different systems. The latter explanation is supported by Root-Bernstein and Ebensperger (2013), who report that soil disturbance tends to have strong negative or positive effects on richness, depending on factors such as study scale and fertility. Although undetectable by our patch-scale analysis, reported shifts in biotic composition indicate that soil disturbance plays a critical role in maintaining a mosaic of patches at the landscape scale (Eldridge & James, 2009; Korn & Korn, 1989; Yoshihara, Ohkuro, Bayarbaatar, & Takeuchi, 2009). For example, McMillan, Pfeiffer, and Kaufman (2011) found that 16% of their recorded plant species only occurred in bison wallows, implying that soil disturbances can be a refuge for species that cannot persist elsewhere. Parallels can be drawn to other forms of disturbance, such as fire or treefalls, which also promote species richness by enhancing environmental heterogeneity (Jonsson & Esseen, 1990; Safford & Harrison, 2004; Stein, Gerstner, & Kreft, 2014).

A recurring issue in the biopedturbation literature is the lack of temporal replication (Coggan et al., 2018). While some effects of soil disturbance are instantaneous (e.g. enhanced surface roughness), others occur after several months or years. These effects are also variable in time. For example, Gutterman, Golan, and Garsani (1990) report that plant richness and biomass followed a unimodal relationship with time such that they were maximized when a porcupine (*Hystrix indica*) digging was 50–60% infilled. Using a coarse binary index, we were able to detect a general effect of disturbance age, indicating that many effects of disturbance may intensify with age. Although we were unable to model the interaction of age and ecosystem property due to statistical limitations, we expect this effect is driven by soil nutrients, which gradually accrue over time, and properties associated with plants, which recolonize over months or years depending on certain traits (Rogers & Hartnett, 2001). Further studies are needed to improve our understanding of the progression of ecosystem effects throughout the life of a soil disturbance.

It is thought that disturbances are particularly important in drylands, creating fertile 'islands' of locally elevated nutrients, which can be the only niches able to support biotic activity in the otherwise resource-poor matrix (Garner & Steinberger, 1989; James & Eldridge, 2007; Ochoa-Hueso, Eldridge, Delgado-Baquerizo, Soliveres, & Bowker, 2018). This assertion was borne out in our results, which showed that the effects of soil disturbance on most properties intensified with increasing aridity. The role of soil-disturbing vertebrates as a source of heterogeneity is thus more important in low productivity systems. We found significant positive interactions between aridity, and plant productivity and density, and soil P and N. Our work also suggests, therefore, that the effects of soil-disturbing animals on these properties will increase as global drylands experience shifts to lower rainfall and higher temperatures (Huang, Yu, Guan, Wang, & Guo, 2016). For example, disturbances might partially mediate reductions in plant productivity with increases in aridity. Similarly, soil P, which is largely under abiotic control and derived mainly from parent material (Lambers, Brundrett, Raven, & Hopper, 2011), is likely to increase with the increased soil disturbance and erosion that typically accompanies increased aridity.

Our study failed to find an important effect of phylogeny, indicating that effects are not phylogenetically controlled and therefore, that the same functionality could readily evolve in different taxa. However, given that 94% of the ecosystem engineers in our study were mammals (67% of which were rodents), additional studies on the effects of soil disturbance by amphibians, reptiles and birds are necessary to confirm there are no phylogenetic effects. We did find that engineers from the same species tended to have similar disturbance effects, which could be driven by similarities in disturbance morphologies and rates of production (Eldridge, Koen, Killgore, Huang, & Whitford, 2012). With respect to boar and rabbit disturbances, the finding that effects were consistent across native and non-native ranges indicates that ecosystems respond similarly to the same type of disturbance.

There is considerable misunderstanding of the ecological importance of ecosystem engineers globally. Some engineering fauna, such as plateau pikas (*Ochotona* spp.) and zokors (*Eospalax* spp.), are actively exterminated due to the perception that they compete with livestock for forage and that they degrade ecosystems through their soil disturbance (Fan et al., 1999; Zhang, Zhang, & Liu, 2003). This perception is thought to have originated from a spurious correlation between the densities of these rodents and grassland degradation (Smith, Zahler, & Hinds, 2006). It is now well established that overgrazing was the main cause of the degradation, and the degraded state provided favourable conditions for pikas and zokors (Zhang et al., 2003). There is mounting evidence that plateau pikas facilitate nutrient cycling and grass productivity through burrowing, although these effects are dependent on population density (Pang & Guo, 2017; Yu, Pang, Wang, Jin, & Shu, 2017). Given their important role in ecosystems, we would expect the loss of ecosystem engineers such as pikas to have substantial consequences for ecosystem functioning (Fleming, Anderson, Prendergast, Bretz, & Valentine, 2014). Reintroducing locally extinct engineers or introducing novel engineers may prove to be a viable strategy to manage degraded landscapes (Manning, Eldridge, & Jones, 2015).

4.1 | Concluding remarks

There still remains much to be learned about the effects of soil disturbance on ecosystems such as the roles of birds and reptiles, and whether the reintroduction of locally extinct engineers could help to restore ecosystem functions to states that were typical prior to anthropogenic change. While not all the effects would be considered facilitatory (e.g. biocrust abundance is reduced by disturbance), our study highlights the fact that vertebrate engineers play an important role in ecosystems, creating a mosaic of nutrient-rich, highly productive patches. Given that engineers disturb 0.34–30% of the soil surface annually in areas where they are prevalent (Bragg, Donaldson, & Ryan, 2005; Hobbs & Mooney, 1985), and a single engineering organism can displace up to 4.8 tonnes of soil per year (Garkaklis, Bradley, & Wooller, 2004), vertebrate disturbances are a major source of heterogeneity at fine spatial scales. Like other disturbances such as fire, the environmental heterogeneity created by soil disturbance is a substantial driver of biodiversity at the landscape scale (Davidson & Lightfoot, 2008).

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DATA ACCESSIBILITY

All data and code supporting the results have been deposited in the Open Science Framework, 10.17605/OSF.IO/CA7QK .

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BIOSKETCHES

Max Mallen-Cooper is a functional ecologist who explores how various phenomena, including soil disturbance and climate change, affect functioning in a range of diverse ecosystems. Recently, Max has begun to use biological soil crusts as a model system to examine the functional consequences of climate change and land use change.

Shinichi Nakagawa and **David Eldridge** are leading experts in the fields of meta-analysis and soil disturbance, respectively.

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APPENDIX: DATA SOURCES

Included study	Study code
Agnew, W., et al. (1986). Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. Journal of Range Management 39:135–139.	Ag
Andersen, D. C. and Macmahon, J. A. (1985). Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, *Thomomys talpoides*. The American Midland Naturalist 114:62–69.	An
Arias, S. M., et al. (2005). Vizcacha's influence on vegetation and soil in a wetland of Argentina. Rangeland Ecology and Management 58:51–57.	Ar
Ashton, D. and Bassett, O. (1997). The effects of foraging by the superb lyrebird (*Menura novae-hollandiae*) in *Eucalyptus regnans* forests at Beenak, Victoria. Australian Journal of Ecology 22:383–394.	As
Ayarbe, J. P. and Kieft, T. L. (2000). Mammal mounds stimulate microbial activity in a semiarid shrubland. Ecology 81:1150–1154.	Ay
Bancroft, W. J., et al. (2005a). Burrow building in seabird colonies: a soil-forming process in island ecosystems. Pedobiologia 49:149–165.	Ba
Bancroft, W. J., et al. (2005b). Burrowing seabirds drive decreased diversity and structural complexity, and increased productivity in insular-vegetation communities. Australian Journal of Botany 53:231–241.	Bh
Bancroft, W. J., et al. (2008). Vertebrate fauna associates of the Wedge-tailed Shearwater, *Puffinus pacificus*, colonies of Rottnest Island: influence of an ecosystem engineer. Papers and Proceedings of the Royal Society of Tasmania 142:21–30.	Bt
Baron, J. (1982). Effects of feral hogs (*Sus scrofa*) on the vegetation of Horn Island, Mississippi. The American Midland Naturalist 107:202–205.	Bn
Barrios-Garcia, M. N. and Simberloff, D. (2013). Linking the pattern to the mechanism: How an introduced mammal facilitates plant invasions. Austral Ecology 38:884–890.	Bg
Barrios-Garcia, M. N., et al. (2014). Disparate responses of above-and belowground properties to soil disturbance by an invasive mammal. Ecosphere 5:1–13.	Bs
Barth, C., et al. (2014). Soil change induced by prairie dogs across three ecological sites. Soil Science Society of America Journal 78:2054–2060.	Bx
Bartz, S., et al. (2007). Response of plant and rodent communities to removal of prairie dogs (*Cynomys gunnisoni*) in Arizona. Journal of Arid Environments 68:422–437.	Bz
Boeken, B., et al. (1995). Patchiness and disturbance: plant community responses to porcupine diggings in the central Negev. Ecography 18:410–421.	Bo
Boeken, B., et al. (1998). Annual plant community responses to density of small-scale soil disturbances in the Negev Desert of Israel. Oecologia 114:106–117.	Be

Included study	Study code
Borchard, P. and Eldridge, D. J. (2011). The geomorphic signature of bare-nosed wombats (*Vombatus ursinus*) and cattle (*Bos taurus*) in an agricultural riparian ecosystem. Geomorphology 130:365–373.	Bf
Borchard, P., et al. (2009). Do bare-nosed wombat (*Vombatus ursinus*) mounds influence terrestrial macroinvertebrate assemblages in agricultural riparian zones? Australian Journal of Zoology 57:329–336.	Bd
Bragg, C. J., et al. (2005). Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes. Journal of Arid Environments 61:261–275.	Bj
Bratton, S. P. (1974). The effect of the European wild boar (*Sus scrofa*) on the high-elevation vernal flora in Great Smoky Mountains National Park. Bulletin of the Torrey Botanical Club 101:198–206.	Br
Bravo, L. G., et al. (2009). European rabbits as ecosystem engineers: warrens increase lizard density and diversity. Biodiversity and Conservation 18:869–885.	Bv
Brock, R. E. and Kelt, D. A. (2004). Keystone effects of the endangered Stephens' kangaroo rat (*Dipodomys stephensi*). Biological Conservation 116:131–139.	Bk
Bryce, R., et al. (2013). Metapopulation dynamics of a burrowing herbivore drive spatio-temporal dynamics of riparian plant communities. Ecosystems 16:1165–1177.	By
Bueno, C. G., et al. (2013). Occurrence and intensity of wild boar disturbances, effects on the physical and chemical soil properties of alpine grasslands. Plant and Soil 373:243–256.	Bu
Burbidge, A. A., et al. (2007). Relict *Bettongia lesueur* warrens in Western Australian deserts. Australian Zoologist 34:97–103.	Bi
Bykov, A., et al. (2008). Accumulation of moisture and soil erosion in the territory of social vole (*Microtus socialis*) settlements in the northern Caspian Lowland. Eurasian Soil Science 41:902–906.	Bl
Canals, R. M. and Sebastià, M. T. (2000). Soil nutrient fluxes and vegetation changes on molehills. Journal of Vegetation Science 11:23–30.	Ca
Chapman, T. F. (2013). Relic bilby (*Macrotis lagotis*) refuge burrows: assessment of potential contribution to a rangeland restoration program. The Rangeland Journal 35:167–180.	Ch
Clark, K. L., et al. (2016). Burrowing herbivores alter soil carbon and nitrogen dynamics in a semi-arid ecosystem, Argentina. Soil Biology and Biochemistry 103:253–261.	Cl
Coggan, N. V., et al. (2016). Termite activity and decomposition are influenced by digging mammal reintroductions along an aridity gradient. Journal of Arid Environments 133:85–93.	Co
Contreras, L. C. and Gutiérrez, J. R. (1991). Effects of the subterranean herbivorous rodent *Spalacopus cyanus* on herbaceous vegetation in arid coastal Chile. Oecologia 87:106–109.	Cg

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APPENDIX: (CONTINUED)

Included study	Study code
Coppock, D., et al. (1983). Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1–9.	Ck
Cuevas, M. F., et al. (2012). Effects of wild boar disturbance on vegetation and soil properties in the Monte Desert, Argentina. Mammalian Biology-Zeitschrift für Säugetierkunde 77:299–306.	Cu
Curtin, C., et al. (2000). On the role of small mammals in mediating climatically driven vegetation change. Ecology Letters 3:309–317.	Cn
Cushman, J., et al. (2004). Variable effects of feral pig disturbances on native and exotic plants in a California grassland. Ecological Applications 14:1746–1756.	Cs
Davidson, A. D. and Lightfoot, D. C. (2006). Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. Ecography 29:755–765.	Dv
Davidson, A. D. and Lightfoot, D. C. (2007). Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. Ecography 30:515–525.	Da
Davidson, A. D. and Lightfoot, D. C. (2008). Burrowing rodents increase landscape heterogeneity in a desert grassland. Journal of Arid Environments 72:1133–1145.	Dl
Desmet, P. and Cowling, R. (1999). Patch creation by fossorial rodents: a key process in the revegetation of phytotoxic arid soils. Journal of Arid Environments 43:35–45.	Dt
Dunham, A. E. (2011). Soil disturbance by vertebrates alters seed predation, movement and germination in an African rain forest. Journal of Tropical Ecology 27:581–589.	Dh
Dunkell, D. O., et al. (2011). Runoff, sediment transport, and effects of feral pig (*Sus scrofa*) exclusion in a forested Hawaiian watershed. Pacific Science 65:175–194.	Dk
Duval, B. and Whitford, W. G. (2009). Camel spider (Solifugae) use of prairie dog colonies. Western North American Naturalist 69:272–276.	Dw
Duval, B. D. and Whitford, W. G. (2012). Reintroduced prairie dog colonies change arthropod communities and enhance burrowing owl foraging resources. Immediate Science Ecology 1:12–23.	Du
El-Bana, M. I. (2009). Effects of the abandonment of the burrowing mounds of fat sand rat (*Psammomys obesus* Cretzschamar 1828) on vegetation and soil surface attributes along the coastal dunes of North Sinai, Egypt. Journal of Arid Environments 73:821–827.	Ed
Eldridge, D. J. and Koen, T. B. (2008). Formation of nutrient-poor soil patches in a semi-arid woodland by the European rabbit (*Oryctolagus cuniculus* L.). Austral Ecology 33:88–98.	Ek
Eldridge, D. J. and Mensinga, A. (2007). Foraging pits of the short-beaked echidna (*Tachyglossus aculeatus*) as small-scale patches in a semi-arid Australian box woodland. Soil Biology and Biochemistry 39:1055–1065.	Em
Eldridge, D. J. and Myers, C. A. (2001). The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland. Journal of Arid Environments 47:325–337.	El
Eldridge, D. J. and Rath, D. (2002). Hip holes: kangaroo (*Macropus* spp.) resting sites modify the physical and chemical environment of woodland soils. Austral Ecology 27:527–536.	Er
Eldridge, D. J. and Simpson, R. (2002). Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. Basic and Applied Ecology 3:19–29.	Es
Eldridge, D. J. and Whitford, W. G. (2009). Badger (*Taxidea taxus*) disturbances increase soil heterogeneity in a degraded shrub-steppe ecosystem. Journal of Arid Environments 73:66–73.	Ew
Eldridge, D. J. (2009). Badger (*Taxidea taxus*) mounds affect soil hydrological properties in a degraded shrub-steppe. The American Midland Naturalist 161:350–358.	Ee
Eldridge, D. J. (2011). The resource coupling role of animal foraging pits in semi-arid woodlands. Ecohydrology 4:623–630.	Eg
Eldridge, D. J., et al. (2006). Short-term vegetation and soil responses to mechanical destruction of rabbit (*Oryctolagus cuniculus* L.) warrens in an Australian box woodland. Restoration Ecology 14:50–59.	Ec
Eldridge, D. J., et al. (2010). Interactive effects of three ecosystem engineers on infiltration in a semi-arid Mediterranean grassland. Ecosystems 13:499–510.	Eb
Eldridge, D. J., et al. (2012). Animal foraging as a mechanism for sediment movement and soil nutrient development: evidence from the semi-arid Australian woodlands and the Chihuahuan Desert. Geomorphology 157:131–141.	Ef
Eviner, V. T. and Chapin, F. S. (2005). Selective gopher disturbance influences plant species effects on nitrogen cycling. Oikos 109:154–166.	Ev
Fields, M. J., et al. (1999). Burrowing activities of kangaroo rats and patterns in plant species dominance at a shortgrass steppe-desert grassland ecotone. Journal of Vegetation Science, 10, 123–130.	Fi
Fox, J. F. (1985). Plant diversity in relation to plant production and disturbance by voles in Alaskan tundra communities. Arctic and Alpine Research 17:199–204.	Fo

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APPENDIX: (CONTINUED)

Included study	Study code
Gálvez-Bravo, L., et al. (2011). European rabbit (*Oryctolagus cuniculus*) engineering effects promote plant heterogeneity in Mediterranean dehesa pastures. Journal of Arid Environments 75:779–786.	Bc
Garkaklis, M. J., et al. (1998). The effects of woylie (*Bettongia penicillata*) foraging on soil water repellency and water infiltration in heavy textured soils in southwestern Australia. Australian Journal of Ecology 23:492–496.	Ga
Garkaklis, M. J., et al. (2003). The relationship between animal foraging and nutrient patchiness in south-west Australian woodland soils. Soil Research 41:665–673.	Gk
Gómez-Garcia, D., et al. (1995). Vegetation differences caused by pine vole mound building in subalpine plant communities in the Spanish Pyrenees. Vegetatio 117:61–67.	Go
Grant, W., et al. (1980). Effects of pocket gopher mounds on plant production in shortgrass prairie ecosystems. The Southwestern Naturalist 25:215–224.	Gr
Groot Bruinderink, G. and Hazebroek, E. (1996). Wild boar (*Sus scrofa* L.) rooting and forest regeneration on podzolic soils in the Netherlands. Forest Ecology and Management 88:71–80.	Gb
Guo, Q. (1996). Effects of bannertail kangaroo rat mounds on small-scale plant community structure. Oecologia 106:247–256.	Gu
Gurney, C. M., et al. (2015). Restoration of native plants is reduced by rodent-caused soil disturbance and seed removal. Rangeland Ecology and Management 68(4): 359–366.	Gy
Gutterman, Y. (1997a). Ibex diggings in the Negev Desert highlands of Israel as microhabitats for annual plants. Soil salinity, location and digging depth affecting variety and density of plant species. Journal of Arid Environments 37:665–681.	Gt
Gutterman, Y. (1997b). The influences of depressions made by ibex on the annual vegetation along cliffs of the Zin Valley in the Negev Desert highlands, Israel. Israel Journal of Plant Sciences 45:333–338.	Gn
Hagenah, N. and Bennett, N. C. (2013). Mole rats act as ecosystem engineers within a biodiversity hotspot, the Cape Fynbos. Journal of Zoology 289:19–26.	Hb
Hakonson, T. (1999). The effects of pocket gopher burrowing on water balance and erosion from landfill covers. Journal of Environmental Quality 28:659–665.	Hk
Hancock, G., et al. (2015). Does introduced fauna influence soil erosion? A field and modelling assessment. Science of the Total Environment 518:189–200.	Ha
Hartley, L. M., et al. (2009). Introduced plague lessens the effects of an herbivorous rodent on grassland vegetation. Journal of Applied Ecology 46:861–869.	Hr
Heske, E. J., et al. (1993). Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. Oecologia 95:520–524.	He
Hobbs, R. J. and Mooney, H. A. (1991). Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. Ecology 72:59–68.	Ho
Ickes, K., et al. (2001). Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. Journal of Tropical Ecology 17:191–206.	Ic
Inouye, R., et al. (1987). Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota. Oecologia 72:178–184.	In
Isselin-Nondedeu, F., et al. (2006). Contributions of vegetation cover and cattle hoof prints towards seed runoff control on ski pistes. Ecological Engineering 27:193–201.	Is
James, A. I., et al. (2010). Foraging pits, litter and plant germination in an arid shrubland. Journal of Arid Environments 74:516–520.	Ja
Jones, C. C., et al. (2008). Plant succession on gopher mounds in western Cascade meadows: consequences for species diversity and heterogeneity. The American Midland Naturalist 159:275–286.	Jo
Kaczor, S. A. and Hartnett, D. C. (1990). Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida sandhill community. The American Midland Naturalist 123:100–111.	Ka
Korn, H. and Korn, U. (1989). The effect of gerbils (*Tatera brantsii*) on primary production and plant species composition in a southern African savanna. Oecologia 79:271–278.	Kk
Kotanen, P. M. (1995). Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian coastal prairie. Ecography 18:190–199.	Kn
Kretzer, J. E. and Cully, J. F. (2001a). Prairie dog effects on harvester ant species diversity and density. Journal of Range Management 54:11–14.	Kr
Kurek, P., et al. (2014). Burrowing by badgers (*Meles meles*) and foxes (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest. Ecological Research 29:1–11.	Ku
Kuznetsova, T. A., et al. (2013). Desert gerbils affect bacterial composition of soil. Microbial Ecology 66:940–949.	Kz

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APPENDIX: (CONTINUED)

Included study	Study code
Kyle, G. P., et al. (2008). Influence of pocket gopher mounds on nonnative plant establishment in a shrubsteppe ecosystem. Western North American Naturalist 68:374–381.	Ky
Lara, N., et al. (2007). Effect of herbivory and disturbances by tuco-tucos (*Ctenomys mendocinus*) on a plant community in the southern Puna Desert. Arctic, Antarctic, and Alpine Research 39:110–116.	La
Laundré, J. W. (1998). Effect of ground squirrel burrows on plant productivity in a cool desert environment. Journal of Range Management: 638–643.	Lu
Li, X. G., et al. (2009). Dynamics of soil properties and organic carbon pool in topsoil of zokor-made mounds at an alpine site of the Qinghai–Tibetan Plateau. Biology and Fertility of Soils 45:865–872.	Li
Litaor, M. I., et al. (1996). The influence of pocket gophers on the status of nutrients in alpine soils. Geoderma 70:37–48.	Lt
Liu, Y., et al. (2013). Effects of plateau pika (*Ochotona curzoniae*) on net ecosystem carbon exchange of grassland in the Three Rivers Headwaters region, Qinghai-Tibet, China. Plant and Soil 366:491–504.	Lb
Mahan, C. G. and Yahner, R. H. (2000). Effects of forest fragmentation on behaviour patterns in the eastern chipmunk (*Tamias striatus*). Canadian Journal of Zoology 77:1991–1997.	My
Malizia, A. I., et al. (2000). Influence of the subterranean herbivorous rodent *Ctenomys talarum* on vegetation and soil. Zeitschrift für Säugetierkunde 65:172–182.	Ml
Martínez-Estévez, L., et al. (2013). Prairie dog decline reduces the supply of ecosystem services and leads to desertification of semiarid grasslands. PLoS ONE 8: e75229.	Ma
Martinsen, G. D., et al. (1990). Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community. Oecologia 83:132–138.	Me
McMillan, B. R., et al. (2011). Vegetation responses to an animal-generated disturbance (bison wallows) in tallgrass prairie. The American Midland Naturalist 165:60–73.	Mc
Milton, S., et al. (1997). Effects of small-scale animal disturbances on plant assemblages of set-aside land in Central Germany. Journal of Vegetation Science 8:45–54.	Mn
Mitchell, J., et al. (2007). Ecological impacts of feral pig diggings in north Queensland rainforests. Wildlife Research 34:603–608.	Mt
Mohr, D., et al. (2005). Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. Soil Biology and Biochemistry (4): 693–700.	Mh
Moody, A. and Jones, J. A. (2000). Soil response to canopy position and feral pig disturbance beneath *Quercus agrifolia* on Santa Cruz Island, California. Applied Soil Ecology 14:269–281.	Mj

Included study	Study code
Moroka, N., et al. (1982). Impact of burrowing activity of the bannertail kangaroo rat on southern New Mexico desert rangelands. Journal of Range Management 35:707–710.	Mo
Naderi, G., et al. (2011). Effect of vegetation and soil conditions on burrow structure and site selection of rare desert rodent – Iranian Jerboa (*Allactaga firouzi*). Polish Journal of Ecology 59:403–411.	Nd
Nugent, D. T., et al. (2014). Interactions between the superb lyrebird (*Menura novaehollandiae*) and fire in south-eastern Australia. Wildlife Research 41:203–211.	Nu
O'meilia, M., et al. (1982). Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management 35:580–585.	Om
Platt, W. J. (1975). The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs 45:285–305.	Pl
Prugh, L. R. and Brashares, J. S. (2012). Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. Journal of Animal Ecology 81:667–678.	Pb
Questad, E. J. and Foster, B. L. (2007). Vole disturbances and plant diversity in a grassland metacommunity. Oecologia 153:341–351.	Qf
Rebollo, S., et al. (2002). Vole mound effects and disturbance rate in a Mediterranean plant community under different grazing and irrigation regimes. Plant Ecology 169:227–243.	Rb
Reichman, O. and Jarvis, J. (1989). The influence of three sympatric species of fossorial mole-rats (Bathyergidae) on vegetation. Journal of Mammalogy 70:763–771.	Re
Reichman, O. and S. C. Smith (1985). Impact of pocket gopher burrows on overlying vegetation. Journal of Mammalogy 66:720–725.	Rc
Reichman, O. (1988). Comparison of the effects of crowding and pocket gopher disturbance on mortality, growth and seed production of *Berteroa incana*. The American Midland Naturalist 120:58–69.	Ra
Reichman, O., et al. (1993). Distinct animal-generated edge effects in a tallgrass prairie community. Ecology 74:1281–1285.	Rn
Rezsutek, M. and Cameron, G. N. (2000). Vegetative edge effects and pocket gopher tunnels. Journal of Mammalogy 81:1062–1070.	Rz
Risch, A. C., et al. (2010). Grubbing by wild boars (*Sus scrofa* L.) and its impact on hardwood forest soil carbon dioxide emissions in Switzerland. Oecologia 164:773–784.	Ri
Rogers, W. E., et al. (2001). Effects of plains pocket gopher (*Geomys bursarius*) disturbances on tallgrass-prairie plant community structure. The American Midland Naturalist 145:344–357.	Ro

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APPENDIX: (CONTINUED)

Included study	Study code
Sanguinetti, J. and Kitzberger, T. (2010). Factors controlling seed predation by rodents and non-native *Sus scrofa* in Araucaria araucana forests: potential effects on seedling establishment. Biological Invasions 12:689–706.	Sa
Schiffman, P. M. (1994). Promotion of exotic weed establishment by endangered giant kangaroo rats (*Dipodomys ingens*) in a California grassland. Biodiversity and Conservation 3:524–537.	Sc
Schooley, R., et al. (2000). Influence of small-scale disturbances by kangaroo rats on Chihuahuan Desert ants. Oecologia 125:142–149.	Sy
Seastedt, T., et al. (1986). Microarthropods and nematodes in kangaroo rat burrows. The Southwestern Naturalist 31:114–116.	Se
Seifan, M., et al. (2010). Contribution of molehill disturbances to grassland community composition along a productivity gradient. Acta Oecologica 36:569–577.	Sf
Sherrod, S. K. and Seastedt, T. R. (2001). Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. Biogeochemistry 55:195–218.	Sh
Siemann, E., et al. (2009). Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. Forest Ecology and Management 258:546–553.	Si
Simkin, S. M., et al. (2001). Plant response following soil disturbance in a longleaf pine ecosystem. Journal of the Torrey Botanical Society 128:208–218.	Sb
Singer, F. J., et al. (1984). Effects of wild pig rooting in a deciduous forest. The Journal of Wildlife Management 48:464–473.	Sr
Spencer, S. R., et al. (1985). Influence of pocket gopher mounds on a Texas coastal prairie. Oecologia 66:111–115.	Sn
Stapp, P. (2007). Rodent communities in active and inactive colonies of black-tailed prairie dogs in shortgrass steppe. Journal of Mammalogy 88:241–249.	Sp
Summerhayes, V. S. (1941). The effect of voles (*Microtus agrestis*) on vegetation. Journal of Ecology 29:14–48.	Su
Swihart, R. K. and Picone, P. M. (1991). Effects of woodchuck activity on woody plants near burrows. Journal of Mammalogy 72:607–611.	St
Swihart, R. K. (1991). Influence of *Marmota monax* on vegetation in hayfields. Journal of Mammalogy 72:791–795.	Sw
Tardiff, S. E. and Stanford, J. A. (1998). Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology 79:2219–2228.	Ta
Taylor, D., et al. (2011). The impact of feral pigs (*Sus scrofa*) on an Australian lowland tropical rainforest. Wildlife Research 38:437–445.	Ty
Theimer, T. C. and Gehring, C. A. (1999). Effects of a litter-disturbing bird species on tree seedling germination and survival in an Australian tropical rain forest. Journal of Tropical Ecology 15:737–749.	Th
Travers, S. K., et al. (2012). Animal foraging pit soil enhances the performance of a native grass under stressful conditions. Plant and Soil 352:341–351.	Tr
Umbanhowar Jr, C. E. (1992). Abundance, vegetation, and environment of four patch types in a northern mixed prairie. Canadian Journal of Botany 70:277–284.	Um
Valentine, L. E., et al. (2016). Scratching beneath the surface: Bandicoot bioturbation contributes to ecosystem processes. Austral Ecology.	Va
Villarreal, D., et al. (2008). Alteration of ecosystem structure by a burrowing herbivore, the plains vizcacha (*Lagostomus maximus*). Journal of Mammalogy 89:700–711.	Vi
Wang, T.-C., et al. (2008). Four-year dynamic of vegetation on mounds created by zokors (*Myospalax baileyi*) in a subalpine meadow of the Qinghai-Tibet Plateau. Journal of Arid Environments 72:84–96.	Wa
Wei, X., et al. (2007). Soil erosion and vegetation succession in alpine Kobresia steppe meadow caused by plateau pika—a case study of Nagqu County, Tibet. Chinese Geographical Science 17:75–81.	Wb
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APPENDIX: (CONTINUED)

Included study	Study code
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APPENDIX: (CONTINUED)

Studies (uncited elsewhere in the manuscript) from which body mass or disturbance area data were retrieved	Study code
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