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Bioturbation by echidna (*Tachyglossus aculeatus*) in a forest habitat, south-western Australia

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ABSTRACT

Bioturbation by digging animals is important for key forest ecosystem processes such as soil turnover, decomposition, nutrient cycling, water infiltration, seedling recruitment, and fungal dispersal. Despite their widespread geographic range, little is known about the role of the short-beaked echidna (*Tachyglossus aculeatus*) in forest ecosystems. We measured the density and size of echidna diggings in the Northern Jarrah Forest, south-western Australia, to quantify the contribution echidna make to soil turnover. We recorded an overall density of 298 echidna diggings per hectare, 21% of which were estimated to be less than 1 month old. The average size of digs was 50 ± 25 mm in depth and 160 ± 61 mm in length. After taking into account seasonal digging rates, we estimated that echidnas turn over 1.23 tonnes of soil ha^{-1} year^{-1} in this forest, representing an important role in ecosystem dynamics. Our work contributes to the growing body of evidence quantifying the role of these digging animals as critical ecosystem engineers. Given that the echidna is the only Australian digging mammal not severely impacted by population decline or range reduction, its functional contribution to health and resilience of forest ecosystems is increasingly important due to the functional loss of most Australian digging mammals.

Keywords: animal digging, biopedturbation, echidna, ecosystem engineering, ecosystem processes, Jarrah forest, soil turnover, *Tachyglossus aculeatus*.

Introduction

Many mammal species dig for food or refuge (Eldridge and James 2009). These bioturbation activities are important for key ecosystem processes, including soil turnover and soil formation (Garkaklis *et al.* 2004; Davies *et al.* 2019), litter decomposition (Decker *et al.* 2019; Eldridge and Koen 2021), nutrient cycling (Garkaklis *et al.* 2003; Valentine *et al.* 2017), water infiltration (Garkaklis *et al.* 1998, 2000), seedling recruitment and vegetation growth (Valentine *et al.* 2018), microbial community development (Eldridge *et al.* 2015, 2017) and fungal dispersal (Dundas *et al.* 2018; Tay *et al.* 2018; Hopkins *et al.* 2021). For example, quenda (*Isoodon fusciventer*), woylie (*Bettongia penicillata*) and echidna (*Tachyglossus aculeatus*) diggings are less hydrophobic and have greater moisture content than undisturbed soil (Garkaklis *et al.* 1998; Eldridge and Mensinga 2007; Valentine *et al.* 2017), and quenda and echidna diggings accumulate more fine litter and a greater diversity and abundance of seeds (Eldridge and Koen 2021). Although each digging is relatively small, the density of diggings can amount to a substantial amount of soil displaced (Garkaklis *et al.* 2004), and animal digging can therefore be significant for broader scale landscape processes (reviewed by Fleming *et al.* 2014; Mallen-Cooper. 2019).

Australia once supported a large diversity of digging mammal species. However, many digging mammals are now extinct or are functionally extinct, having suffered marked range contractions (Fleming *et al.* 2014) due to habitat destruction and predation by introduced predators (Woinarski *et al.* 2015). Australia's record of mammal species extinction over the last 200 years is greater than that of any other part of the world (McKenzie *et al.* 2007), and the loss of digging mammals represents a crucial loss of important ecosystem engineers. Echidnas are one of the only remaining digging animals in Australia that have not been severely impacted by population decline and range contraction over the last 200 years (Fleming *et al.* 2014). Echidnas are considered as 'Least Concern' by the IUCN (International Union for Conservation of Nature Red List of Threatened Species) (Woinarski *et al.* 2014) and are likely to have persisted due to their protective spines and antipredatory behaviour, as well as their generalist foraging behaviour focusing on ants and termites, for which there is minimal competition (Abensperg-Traun 1991; Fleming *et al.* 2014).

Echidnas are estimated to spend 12% of their time digging (Clemente *et al.* 2016), making a substantial contribution to soil turnover. They excavate distinctive circular shallow pits and create shallow bulldozing tracks (collectively hereafter 'digs') while foraging for ants and termites (Eldridge 2011). Their foraging digs capture more water than undug soil, with sorptivity and steady-state infiltration in digs being approximately twice as much as for undug soils (Eldridge and Mensinga 2007). Echidna digs also capture 2–7 times as much litter and debris and three times as many seeds compared with undug areas (Eldridge and Mensinga 2007; Mallen-Cooper *et al.* 2019). Foraging digs can also act as a buffer to high temperatures, with ~2°C cooler temperatures recorded below litter at the base of echidna digs compared with the adjacent soil surface (Eldridge and Mensinga 2007). The increased moisture, nutrients and temperature create a suitable environment for microbial activity (Eldridge *et al.* 2017), with soil respiration being about 30% higher than non-dug soils (Eldridge and Mensinga 2007), and present a suitable site for seed germination and plant growth, with a greater biomass of native grass seedlings growing within echidna foraging digs than on the adjacent undisturbed soil surface (Travers *et al.* 2012).

Given their wide geographic range and the multiple ecological processes affected by echidna digging activities, these monotremes make an important contribution to ecosystem health (Paine 1995; Eldridge and James 2009). Their persistence in the face of introduced predators suggests that their contribution to ecosystem processes is likely to become progressively more important. However, little is known about the role of echidnas in many forest ecosystems. Echidnas are present across the Northern Jarrah Forest in south-western Australia, a significant forest ecosystem of >1 million hectares with enormous environmental, scientific, cultural and economic value (Bartle and Slessar 1989; Dell and Havel 1989; Nichols and Muir 1989; Pearce 1989; Stoneman *et al.* 1989). The aim of our study was to quantify the density of echidna diggings and estimate their contribution to soil turnover in this forest ecosystem.

Materials and methods

The Northern Jarrah Forest (Fig. 1) is located in the Southwest Australian Floristic Region (SWAFR), which is a biodiversity hotspot (Myers *et al.* 2000) with more than 8370 native vascular plant taxa (Gioia and Hopper 2017). The forest canopy is dominated by *Eucalyptus marginata* Donn ex Sm. (jarrah) and *Corymbia calophylla* R. Br. K.D. Hill and L.A.S. Johnson (marri). The forest overlies Archaean granite and metamorphic rocks that are capped by an extensive lateritic duricrust and interrupted by intermittent granite outcrops (Churchward and Dimmock 1989). The soils are highly leached and extremely infertile (Mulcahy 1960).

The region has a Mediterranean-type climate, with a cool, wet winter and most (~80%) rainfall falling between April and October, and a long seasonal summer drought that may last 4–7 months (Gentilli 1989; Bates *et al.* 2008). There is a strong west–east rainfall gradient, ranging from 1100 mm per year on the western edge (Darling Scarp) to ~700 mm per year in the east and north of the region (Gentilli 1989). Average temperatures are 22.6–34.7°C in summer, 16.9–30.9°C in autumn, 13.5–18.6°C in winter and 15.3–27.9°C in spring (BOM 2022, Bickley station 009240).

Density of diggings

Transects were established in late-July to early-September 2014 to determine echidna digging densities. Five forest tracks that branched away from the Albany Highway between the suburbs of Bedfordale and Ashendon (Fig. 1), ~36 km south-east of the capital city of Perth, Western Australia, were chosen to serve as individual sites. We established four 100-m-long straight transects at each site, with a minimum distance of 500 m between each transect to avoid dependent results. To avoid edge effects, transects began ~100 m away from the road. Two observers walked on either side of the transect line and recorded the perpendicular distance between echidna diggings and the transect line out to a maximum distance of 5 m on either side of the transect line. This distance from the line could be searched easily so our chances of detecting digs was close to 100%; the total count from both observers was used to calculate density of diggings.

Rather than the anterior–posterior scratch digging common among most digging marsupials (Warburton *et al.* 2013; Martin *et al.* 2019*a*, 2019*b*), due to the musculoskeletal anatomy of their pectoral girdle, which restricts the motion of their digging action, echidnas use their forelimbs in a lateral sprawling motion, rotating the humerus while the forelimb extends to sweep the soil behind. As a consequence of their anatomy and digging action (Augee *et al.* 2006), echidnas therefore create distinctive relatively wide and circular digs.

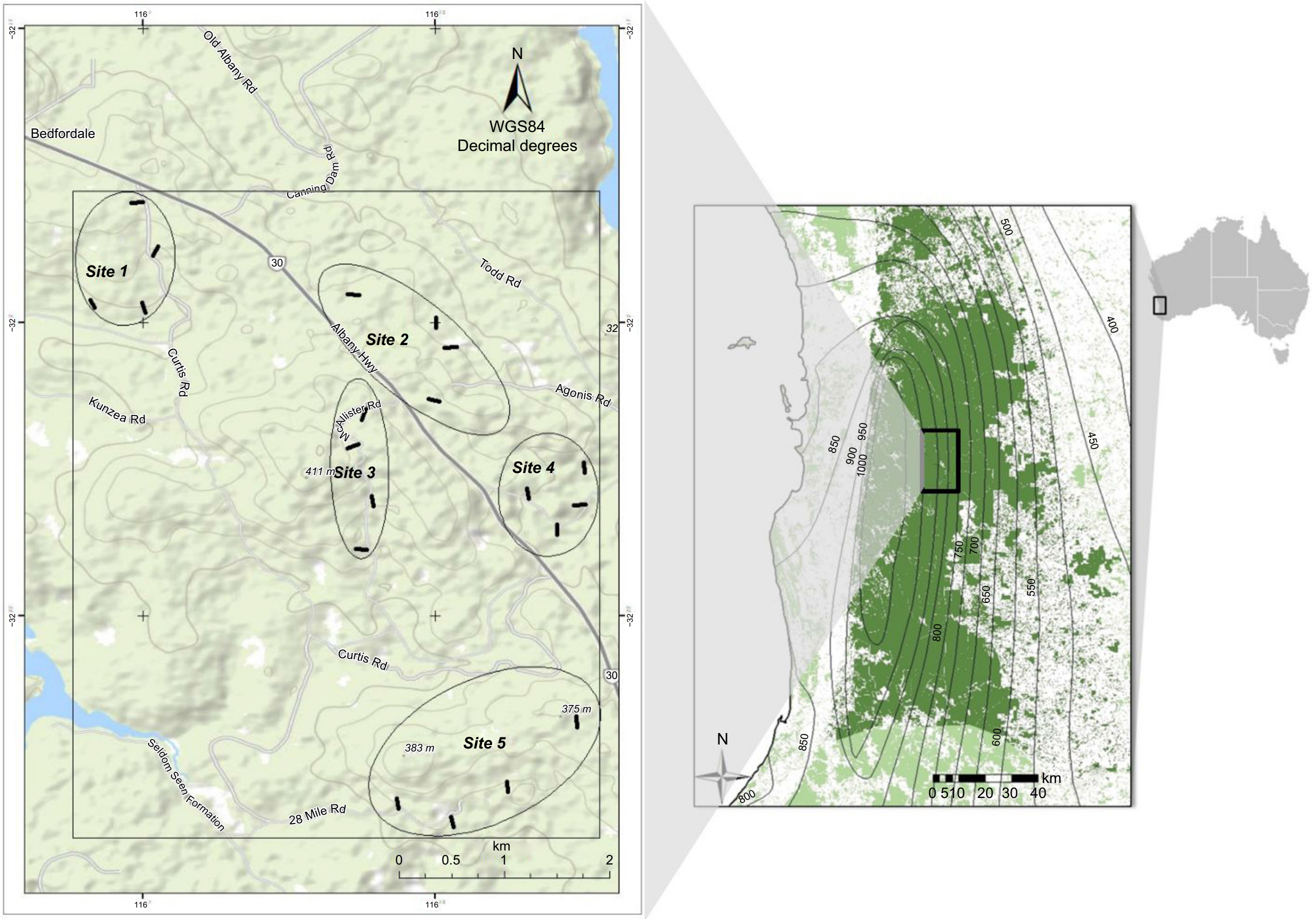

Fig. 1. Study sites used to characterise echidna (*Tachyglossus aculeatus*) digging were located in the Northern Jarrah Forest, south-western Australia. Each site contained four (100 m) line transects (map adapted from Matusick *et al.* 2016).

We recorded the width and depth (mm) of each digging and whether diggings were 'new' (no leaf litter present, sharp edges, and loose soil) or 'old' (containing accumulated leaf litter, soft edges, and compacted soil). As diggings were counted during winter/spring and likely to degrade quickly due to most annual rainfall at this time, we estimate new diggings were less than one month old, supported by timed observations of diggings in the jarrah forest on similar soil types (unpubl. data), and old diggings were estimated to be older than a month, but potentially up to three years old. No estimates of the rate of degradation of echidna diggings in temperate woodlands have been carried out previously, but these observations tally with published data for other landscapes. For example, Eldridge and Kwok (2008) observed that echidna diggings in loamy clays of semiarid woodlands disintegrate rapidly (69% of digs under the canopy and 84% of digs in the open deform and degrade over six months), although echidna digs can still be recognised at three years of age. Furthermore, surveys on the New England Tablelands found recognisable echidna digs persisted for ~6 weeks (Smith *et al.* 1989).

Estimating soil displacement

The width and depth (mm) of 544 diggings recorded along the 20 transects were measured to estimate soil volume displaced. Dig types measured included deeper excavations created during foraging (minimum depth of 50 mm: Fig. 2*a*) and shallower nose pokes (narrow digs with clear evidence of a nose hole and commonly <30 mm depth: Fig. 2*b*). We removed three outlying dig measurements which appeared to be transcription or measurement errors.

To determine the most representative volume measurement, we collected accurate dig volume measurements for 99 new diggings (one outlier measurement was excluded as it was likely to be a transcription error). The measured diggings were randomly selected across the five sites and represented a range of sizes. The volume of each dig was determined by lining the digging with a piece of cling film plastic wrap and then filling to the surrounding soil level with fine, weed-free river sand using a volumetric cylinder (after James and Eldridge 2007) (Fig. 3). These values were compared with volume measurements derived from linear measurements of the same diggings using a

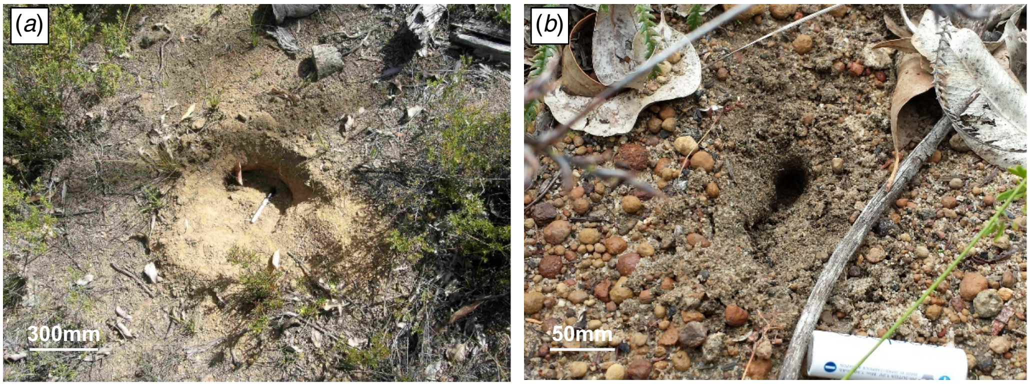

Fig. 2. (*a*) Deeper dig created by foraging echidna (*Tachyglossus aculeatus*), and (*b*) a shallower nose poke created by an echidna. Photos was taken at one of the study sites in the Northern Jarrah Forest, south-western Australia (photo credit: S. Dundas).

Fig. 3. The method for determining the volume of soil displaced by each echidna (*Tachyglossus aculeatus*) dig using a known volume of clean, washed river sand to fill the dig and determine the actual volume of soil displaced. Photo was taken at one of the study sites in the Northern Jarrah Forest, south-western Australia (photo credit: S. Dundas).

Pearson's correlation to determine the most representative volume formula for estimating total dig volume (from strongest to weakest relationship – standard cone: $r_{97} = 0.880$; hemisphere: $r_{97} = 0.875$; elliptical cone: $r_{97} = 0.873$; averaged standard cone and hemisphere: $r_{97} = 0.872$; all $P < 0.001$). We therefore estimated total soil volume (V; mm^3) displaced by echidnas using volume estimates for a standard cone from all measurements. To measure bulk density of soil, standardised soil core samples were collected at each of the five sites (three samples per transect; 12 per site). Samples were weighed after being dried at 52°C for ~40 h. Bulk density was then averaged for each site (Table 1) and these values were used to convert from dig volume to the mass of soil displaced.

The estimation of soil displaced annually by echidnas (tonnes soil; t) was calculated using the new digs only (i.e. diggings created within a 1-month period) averaged across all 20 transects. To account for seasonal changes in echidna foraging activity (Clemente *et al.* 2016), we used published estimates of activity to scale digging activity and derive an annual estimate of soil moved by echidnas. Based on the data presented in Smith *et al.* (1989, fig. 2), we estimated a ratio of soil diggings per season (averaged across months) in relation to winter diggings, as our samples were collected primarily in July/August, which is when echidnas are least active due to low temperatures and reduced food availability (Smith *et al.* 1989; Clemente *et al.* 2016). Seasonal digging rates were estimated to be 2.91 times higher in summer (December–February), 1.07 times higher in autumn (March–May) and 4.40 times higher in spring (September–October).

All five sites were composed of two soil types: Kandosols and Tenosols. To determine whether the texture of the surface soil [<10% or 10–20% clay content based on mapped soil types: Australian Soil Resource Information System (ASRIS) (CSIRO 2018)] influenced the number of diggings along the surveyed transects, we performed a two sample *t*-test assuming unequal variances. To determine if the bulk density of soil for each transect (mean bulk density of three samples taken at each transect) influenced the number of diggings on the transect, we used a generalised additive model with site included as a random factor, using the package *mgcv* (Wood 2011) in R (R Core Team 2022).

Values are presented as means ± 1 s.d. throughout.

Results

Density of echidna digs

The average density of old and new diggings across all sites was 272 ± 100 diggings ha^{-1} (Table 1, Fig. 4). A total of

Table 1. Density (digs per ha^{-1}) of echidna (*Tachyglossus aculeatus*) diggings across the five sites (four 100 m transects per site) in the Northern Jarrah Forest, south-western Australia.

Site	Estimated bulk density	New diggings (no. digs ha^{-1})	Old diggings (no. digs ha^{-1})	All diggings (no. digs ha^{-1})
1	1.74 ± 0.48	130	238	368
2	1.42 ± 0.37	85	178	263
3	1.26 ± 0.45	30	333	363
4	0.89 ± 0.25	8	83	90
5	1.48 ± 0.41	30	248	278
All sites average		56 ± 45	215 ± 83	272 ± 100

New diggings refer to diggings with no leaf litter present in the dig, sharp edges, and loose soil estimated to be <1 month old. Old diggings, identified by accumulation of leaf litter in the dig, soft edges, and compacted soil, were likely to be older than two months.

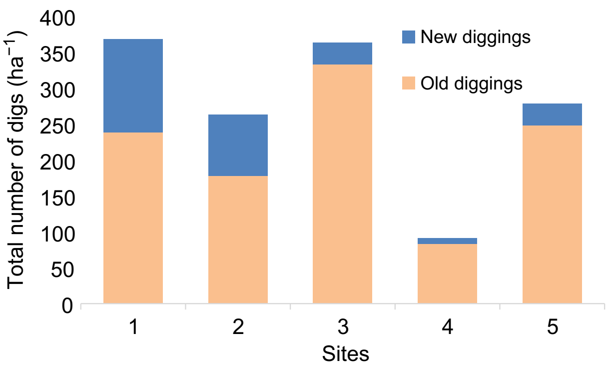

Fig. 4. Total of old and new echidna diggings observed in the Northern Jarrah Forest.

21% of digs measured were classified as new (estimated to be less than one month old); most digs (79%) were therefore classified as old (estimated to be older than two months but less than three years old). The topsoil texture (% clay content) did not influence the number of echidna diggings along transects (t_{16} = 0.64, P = 0.53) nor did bulk soil density (F = 1.17, effective degrees of freedom (edf) = 2.50, P = 0.36).

Estimating soil displacement by echidnas

The average size of echidna digs measured was 50 ± 25 mm in depth and 160 ± 61 mm in length. The total soil volume displaced by echidnas (new digs only) in the Northern Jarrah Forest, measured in winter, was therefore estimated to be 0.0437 tonnes soil ha^{-1} $month^{-1}$. Taking into account seasonal digging rates and extrapolating from the density of new diggings created in a single month, the estimated volume of soil moved by echidnas each year was 1.23 tonnes soil ha^{-1} $year^{-1}$.

Discussion

This study quantifies the substantial contribution to soil turnover made by echidnas in the Northern Jarrah Forest in south-western Australia, turning over an estimated 1.23 tonnes ha^{-1} $year^{-1}$. This is reasonably comparable to the estimates of 1.05 tonnes ha^{-1} $year^{-1}$ for dry sclerophyll forest in Tasmania (Davies *et al.* 2019) (Table 2). By contrast, echidnas turned over only ~0.09 tonnes ha^{-1} $year^{-1}$ at a rural grazing property with dry sclerophyll forest in NSW (Field and Anderson 2003). The differences in reported density of echidna foraging digs is likely to relate to the number of echidnas within these study areas, which will vary according to relative availability of food and shelter resources within each habitat type (Smith *et al.* 1989; Abensperg-Traun and De Boer 1992; Eldridge and Kwok 2008). However, we note that the estimate for a fenced sanctuary (where animals are not able to enter or leave) in Canberra, ACT, is approximately the same range (Munro *et al.* 2019).

The substantial variation in soil displacement by digging mammals across different Australian landscapes (Table 2), could also reflect soil type. The soil texture observed at the study sites (sandy with less than 10% clay or sandy loam with 10–20% clay content) did not influence the density of echidna digs observed at our study sites. However, soils with high clay content become very hard when dry and may be harder for echidnas to dig into, especially after periods of drought.

We measured echidna digs as 50 ± 25 mm in depth, similar to 50–150 mm depth in a study by Eldridge *et al.* (2012). This contrasts with the digs of scratch-digging marsupials that are two- to six-times deeper (e.g. woylies: 100–150 mm in depth: Garkaklis *et al.* 2003; or quenda: average depth 69.6 ± 3.2 mm: Valentine *et al.* 2012). Consequently, echidnas displace substantially less soil than quenda and woylies (Table 2). Diet is the likely explanation for these observed differences between species, with ants and termite runs and nests sought out by echidnas located near the soil surface, compared with the subterranean fungi, tubers and invertebrates foraged on by quenda and woylies (Van Dyck and Strahan 2008; Zosky 2011) being located further down the soil profile.

In the Northern Jarrah Forest, there is generally a period of extended drought during the summer months (~November–March) with soil water stores being

Table 2. Comparison of soil displacement for echidna (*Tachyglossus aculeatus*) and other digging animals (woylie, *Bettongia penicillata*; eastern bettong, *B. gaimardi*; quenda, *Isoodon fusciventer*) across different habitats in Australia.

Species	Habitat type	Surface soil texture (% clay content)[A]	Digging density (no. digs ha^{-1})	Soil displacement (estimated tonnes soil ha^{-1})	Annual soil displacement (estimated tonnes soil ha^{-1} $year^{-1}$)	Reference
Echidna	Dry sclerophyll forest (WA)	Sandy (<10%) and sandy loam to 10–20%)	298	0.17 (winter)	1.23	This study
	Dry sclerophyll forest (Tasmania)	Clay loam (20–30%)			1.05 (all seasons)	Davies et al. (2019).
	Dry sclerophyll forest (NSW)	Clay loam (30–35%)	25		0.09[C] (all seasons)	Field and Anderson (2003)
	Dry sclerophyll forest (ACT) – fenced sanctuary	Sandy loam (10–20%)	[B]		0.16 (winter, spring)	Munro et al. (2019)
	Semiarid woodland (NSW) – intact	Loam to clay loam (30–35%)	[B]	0.73 (all seasons)		Eldridge et al. (2012)
	Semiarid woodland (NSW) – cleared	Loam to clay loam (30–35%)	[B]	1.86 (all seasons)		Eldridge et al. (2012)
	Semiarid rangeland (NSW)	Loam (20–30%)	~125–400		0.46 (summer)	Eldridge and Kwok (2008)
Woylie	Dry sclerophyll forest (WA)	Sandy loam (10–20%)	2550		4.8 (all seasons)	Garkaklis et al. (2004)
Eastern bettong	Dry sclerophyll forest (ACT)	Sandy loam (10–20%)	[B]		0.99 (winter, spring)	Munro et al. (2019)
Quenda	Coastal plain (WA)	Sandy (<10%)	[B]		3.9 (winter)	Valentine et al. (2012)

Season samples were collected are indicated in parentheses.
[A]Based on mapped soil types: Australian Soil Resource Information System (ASRIS) (CSIRO 2018).
[B]Figure for digging density not presented in manuscript.
[C]Published results presented in cubic metres converted to tonnes using average bulk density (1.1 cm^3) recorded for Mulloon Creek (Le Dantec 2016).
WA, Western Australia; ACT, Australian Capital Territory; NSW, New South Wales.

replenished during winter when the region receives most of its annual rainfall (Gentilli 1989). During the annual summer drought, soils with less clay would become particularly water repellent (Harper *et al.* 2000), which is also a possible issue in the sandier soils of the Northern Jarrah Forest. The displacement and mixing of soil caused by foraging echidnas can improve water infiltration and is therefore a key ecological role for maintaining soil, as well as forest, health, especially as climatic conditions become drier and hotter into the future (Diffenbaugh and Field 2013; Cowan *et al.* 2014; Andrys *et al.* 2015).

Limitations of study

We were able to survey only during the winter months when digging rates are likely to be least as temperatures are low and invertebrate activity and therefore food for echidnas tends to be more scarce (Smith *et al.* 1989). Repeated surveys across all seasons would improve our estimates and would be worthwhile given very few studies have assessed annual echidna digging rates. We were able to estimate the age of diggings but a study that involved marking fresh digs would allow for an accurate rate of decay for diggings in this forest.

Conclusions

Bioturbation by digging animals is important for ecosystem processes, affecting soil turnover, decomposition, nutrient cycling, water infiltration, seedling recruitment, and seedling growth. Soil turnover values for echidnas in our study were comparable to those recorded for other digging mammals (Table 2); however, their persistence in natural ecosystems when many other digging mammals have been lost means that the contribution by echidnas to soil turnover and ecosystem processes is likely to be disproportionate to their relative activity. The contribution by echidnas to forest ecosystems could progressively become increasingly important, especially with a drying climate and with the functional extinction of other digging mammal species.

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