Incubation mound-building by megapodes creates novel, high-resource patches in a semi-arid woodland.

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Abstract

1. Desert ecosystems have sparse and heterogeneous resources. Discrete high-resource patches, associated with landscape modulators such as perennial vegetation, act as nutrient sinks in contrast to open, low-resource areas (interpatch matrix). In semi-arid mallee woodlands, malleefowl (*Leipoa ocellata*: Megapodiidae) create large incubation mounds by raking leaf litter and soil from high-resource patches to their mound sites in the interpatch matrix. Despite this conspicuous redistribution of resources, nothing is known about the physical and chemical properties of malleefowl mounds.

2. In this study, we measured groundcover, vegetation structure and composition, and soil chemistry at: malleefowl mounds, high-resource microsites modulated by trees, and in the low-resource interpatch matrix. The high and low-resource microsites were sampled near the mound in the potential Malleefowl disturbance zone, and outside of the

disturbance zone. Mounds were classified into three age categories based on the number of years since they were active.

3. We found that malleefowl mounds were a novel microsite, with soil chemistry more similar to tree-modulated patches and groundcover and vegetation variables more similar to the open, interpatch matrix. Additionally, the novel attributes of the mound persisted beyond 6 years from the last time the mound was active. The effect of malleefowl mound-building activities appeared to extend beyond recently used mounds, with vegetation suppressed in open patches close to the mound.

4. *Synthesis*: Malleefowl redistribute resources from high-resource patches under trees to the open interpatch matrix. Incubation mound-building by animals can be a landscape modulating process via high-resource patch formation and is likely important for ecosystem functioning.

Keywords: Malleefowl, heterogeneity, soil function, ecosystem engineer, megapode, megapodiidae

Introduction

A fundamental feature of desert ecosystems is the spatial organisation of resources into discrete patches (Noy-Meir 1973). This results in high-resource patches, often associated with landscape ‘modulators’ (*sensu* Shachak et al. 2008) such as perennial vegetation, distributed within a matrix of resource-poor interspaces (Ludwig and Tongway 1995). Resource-rich patches are created and maintained through the ‘self-organising’ processes of multiple plant species; which accumulate soil, water, nutrients and leaf litter through positive feedback between local plant density and resource concentration (Aguiar and Sala 1999). For example, nitrogen and organic carbon are concentrated into high-resource patches through water and wind deposition, in addition to the nutrient cycling that occurs *in situ* through the breakdown of leaf litter (Facelli and Pickett 1991). These ‘self-organising’ systems, though often initiated by plants, can also result from the activity of animals, because high-resource patches can enhance invertebrate, vertebrate and soil microbial communities, that aerate soil and increase water infiltration (Daryanto and Eldridge 2012, Nimmo et al. 2013, Ochoa-Hueso et al. 2018).

Fauna can also act as landscape modulators, modifying patch dynamics at larger spatial scales by reorganising resource distribution; a form of 'ecosystem engineering’ (Shachak et al. 2008, Jones et al. 1994). Ecosystem engineering by fauna is facilitative; enhancing local species’ diversity and ecosystem functioning, and is particularly significant in low resource, arid systems (Byers et al. 2006, Eldridge and James 2009, Romero et al. 2015, McCullough Hennessy et al. 2016, Catterall 2018, Decker et al. 2019). The effect of mammals and invertebrates on the chemical and physical properties of soil and, indirectly, on vegetation, have been widely studied (Coggan et al. 2018). Conversely, avian ecosystem engineers have received less attention, despite ground-foraging and mound-building by birds causing impressive movements of leaf litter and soil (Warnken et al. 2004, Webb and Whiting 2006, Jones and Goth 2008, Maisey et al. 2020). For example, superb lyrebirds (*Menura novahollandiae*), turn-over a greater volume of litter and soil than any other vertebrate, influencing litter depth and soil compaction (Maisey et al. 2020). Leaf litter movement by Australian brush-turkeys (*Alectra lathami*), a mound-building megapode, results in lower ground cover, leaf litter, seed and seedling density in the surrounding area (Warnken et al.

2004). In contrast to lyrebirds and brush-turkeys, which both inhabit mesic environments, the malleefowl (*Leipoa ocellata: Megapodiidae*), another mound-building megapode, carries out similar processes in semi-arid and arid environments. While these processes have been studied widely in mesic environments, little is known about how vertebrate-mediated mound building might affect drylands (arid, semi-arid and dry subhumid) soils, where resources are already highly segregated.

Malleefowl rake leaf litter and soil into an incubation mound approximately 4 m in diameter and 1-2 m high (Fig. 1a) containing about 4 tonnes of material, and most commonly positioned in spaces between tree patches (Frith 1959, Weathers and Seymour 1998, Jones and Goth 2008). Litter is collected primarily from the area close to (within 15 m of) the mound, and the heat generated by the decomposing litter, along with solar radiation, is used to incubate the eggs (Frith 1959, Weathers and Seymour 1998, Neilly et al. 2021a). In some regions, malleefowl can re-use the same mound over multiple breeding seasons, until the leaf litter is depleted (Smith et al. 2016), but in others, they generally use different mounds each year (Benshemesh et al. 2020, Neilly et al. 2021a). Active mound densities range from 1.1 to 5.5 mounds per km^2, increasing with rainfall (Frith 1962, Booth 1987). However, inactive mounds persist for many years, and can be four-times more abundant than active mounds (Heather Neilly, unpublished data, 2020).

Malleefowl move substantial quantities of leaf litter and soil, and presumably seed and nutrients, from beneath the dominant landscape modulators, mallee (*Eucalypus* spp.) to the resource poor interspaces, using this litter to construct their mounds. Despite this conspicuous movement of resources, we do not understand how malleefowl mounds relate to the well-defined high and low-resource patches in semi-arid woodlands. In the same system, mammal foraging pits contribute to small-scale patchiness by acting as nutrient sinks and sites for seedling establishment, as well as driving soil microbial communities (Eldridge and Mensinga 2007, Eldridge and James 2009, James et al. 2009, Eldridge et al. 2016). Malleefowl mounds could have a similar effect. Malleefowl population decline could result in the loss of an engineering process, critical to the functioning of mallee woodland systems.

In this study, we aimed to examine malleefowl mound creation as a landscape modulating process. We expected that mounds would be a novel, high-resource microsite, distinct from high-resource patches under trees and the open, interpatch matrix in a mallee woodland. Furthermore, we predicted that tree and open patches close to the malleefowl mound would be affected by malleefowl leaf litter movement and disturbance, resulting in five distinct microsites (the mound, tree and open patches near a mound, tree and open patches far from a mound). Finally, we expected that the effect of malleefowl mound building and disturbance would be greatest in most recently active mounds and diminish with time since activity.

Materials and Methods

Study system

The study was conducted on Calperum Station in the Murray mallee region, near Renmark, South Australia (-33.659°, 140.563°). Calperum was formerly a pastoral property but livestock were removed in 1994. The area is on the boundary between arid and semi-arid, rainfall is highly variable and averages 256 mm. The landscape is characterised by a broad sand sheet (the Woorinen Formation; Lawrence et al. 1988), upon which are superimposed low west-east trending sand dunes dominated by mallee (*Eucalyptus* spp.) woodlands and shrublands communities. The soils are dominated by calcareous earths (Isbell 2021), with abundance carbonate in the profile and therefore high pH levels (Hutton and Dixon 1981). Slopes are generally level of slightly undulating (< 2%).

The dominant overstorey tree species are *Eucalyptus socialis*, *E. oleosa*, *E. dumosa* and *E. gracilis*. Understorey ranges from sparse *Zygophyllum* spp. forbs to extensive areas of spinifex (*Triodia scariosa*) and native shrubs (Senna *artemisiodes ssp*., *Eremophila scoparia* and *Beyeria opaca*). Mallee trees are the dominant biotic patch type in these woodlands and function as resource modulators (Travers and Eldridge 2012). Trees accumulate considerable litter beneath their canopies, providing important habitat for a range of invertebrates (Noble et al. 1996). The accumulation of a dense litter layer around the trees results in frequent fires in mallee landscapes culminating with the build-up of ground fuel, used predominantly by mallee fowl to construct their mounds. The density of mallee trees varies markedly, and projected foliage cover of trees and their understorey litter vary with time since last fire. Typically, cover increases rapidly up to about 30% and stabilises about 30 years after fire (Haslem et al. 2011).

Malleefowl mound selection

Malleefowl mounds have been monitored annually at Calperum since 2012 within three adjacent 4 km x 4 km grids (National Malleefowl Monitoring Grids; National Malleefowl Recovery Team, 2016). All mounds within the grid are visited during the breeding season and recorded as active or inactive. Calperum is at the arid end of the range of malleefowl (Jones and Goth 2008). The average density of active and inactive malleefowl mounds at Calperum is approximately five mounds per km^2 (Heather Neilly, unpublished data, 2018). In August

2018, when malleefowl were preparing their mounds, we selected 12 mounds for study. Four mounds were identified as active within the last three years, and four mounds active between 3-6 years previously. An additional four mounds older than 6 years were selected, randomly, from a larger pool of mounds known to be more than 6 years old. To sub-sample the >6-year mounds, any mound with an average rim height of < 10 cm was excluded from selection. Mounds of this height are classified as ‘long unused’ and ‘very degraded’ and generally have no history of ever being active during the time they have been monitored (National Malleefowl Recovery Team 2016).

Microsites, and plant and soil measurements

At each of the 12 mound locations we selected five microsites (Appendix S1, Figure 1) to test the effects of mounds on biotic and abiotic attributes within the vicinity of the mounds. These microsites were: 1) the mound (Figure 1a), 2) a *Eucalyptus* tree closest and within 15 m of the mound (hereafter ‘Tree near’), 3) an open area between the mound and the nearest tree (‘Open near’), 4) a *Eucalyptus* tree 50 m from the mound (‘Tree far’), and 5) an open area adjacent to the distant tree (‘Open far’). All measurements were taken from within a 5 m by 5 m quadrat centred upon each microsite. The tree and open microsites near the mound represent the zones of potential malleefowl leaf-raking activity, which has been known to extend to 15 m beyond the mound (Priddel and Wheeler 2003). The distant open and tree microsites would be expected to be outside the zone of malleefowl activity.

Within each quadrat we assessed the cover and abundance of all groundstorey plants (to assess plant richness), and the cover of litter, biocrusts (soil lichens and bryophytes) and bare soil. Ten samples of the surface 10 cm of the soil were collected, mixed, and a subsample taken for chemical analyses after air drying and sieving (< 2 mm). Soils were analysed for total organic carbon (using H_2SO_4 added to soil wetted by dichromate solution $Cr_2O_7^{2-}$), available nitrogen (NO_3, using 2M KCl extraction) and available phosphorus (Colwell, 1:100 soil:extract) and pH (1:5 soil:water extract).

Statistical analyses

We used Principal Components Analysis (PCA) to visualise the multivariate composition of microsites in relation to different cover components and soil chemistry. We transformed the data using a Wisconsin double standardization and drew an ordination plot with 95% confidence interval ellipses for each microsite.

Linear mixed modelling was then used to explore potential differences in plant and soil attributes among the five microsites. Microsites were designated as fixed effects and mound location as a random effect. Plant species richness and abundance (counts) of individual species were modelled using Generalised Linear Mixed Models (GLMMs) with a negative binomial distribution, microsite as a fixed effect and mound identity as a random effect. Models were validated by examining deviance residuals. Tukey's HSD test was used to examine pairwise comparisons of significant ($P < 0.05$) effects. Model fit was assessed by calculating the marginal R^2, the proportion of variation explained by the fixed factors, and conditional R^2, the proportion of variance explained by both fixed and random factors (Nakagawa & Schielzeth, 2013). Analyses were performed in R version 3.5.1 (R Core team 2018).

We then used a Relative Interaction Index (RII; Armas et al. 2004) to examine the relative influence of Mound, Open near, and Tree near and Tree far on plant and soil attributes compared with the control site (Open far), the open site furthest from the mound and therefore unaffected by malleefowl activity. The RII for the mound was calculated as RII = $(X_m - X_o)/(X_m + X_o)$, where X is the value of a specific ecological attribute, and X_m and X_o represent the values for Mound and Open far microsites, respectively. A similar procedure was used to calculate the RII for the Open near mound, and both tree locations. The RII is bounded by -1 and 1, with positive values indicating greater levels of a given attribute (plant or soil) in the quadrat within a given microsite and *vice versa*. We calculated the mean and 95% confidence interval (CI) of the RII for each attribute to determine the influence of the particular microsite based on whether the 95% CI crosses the zero line. Confidence intervals were calculated using a bootstrapping approach (Kirby and Gerlanc 2013).

Results

Tree and Open microsites differed significantly in their cover, vegetation, and soil signature, and the Mound microsite displayed characteristics of both Tree and Open (Figure 1b, Table 1, Appendix S2). Mounds were equivalent to Open microsites for bare soil and leaf litter but were more like tree microsites with respect to biocrust cover, soil carbon and soil pH. Soil phosphorus and nitrogen concentrations were greater within mound soils than beneath the trees or in the open. Attributes did not vary between the two tree microsites. Open near microsites had more soil phosphorus than Open far, but all other attributes were not significantly different. Plant cover and richness were greatest in Tree microsites. Only five of the 27 recorded plant species occurred within all microsites (Appendix S3).

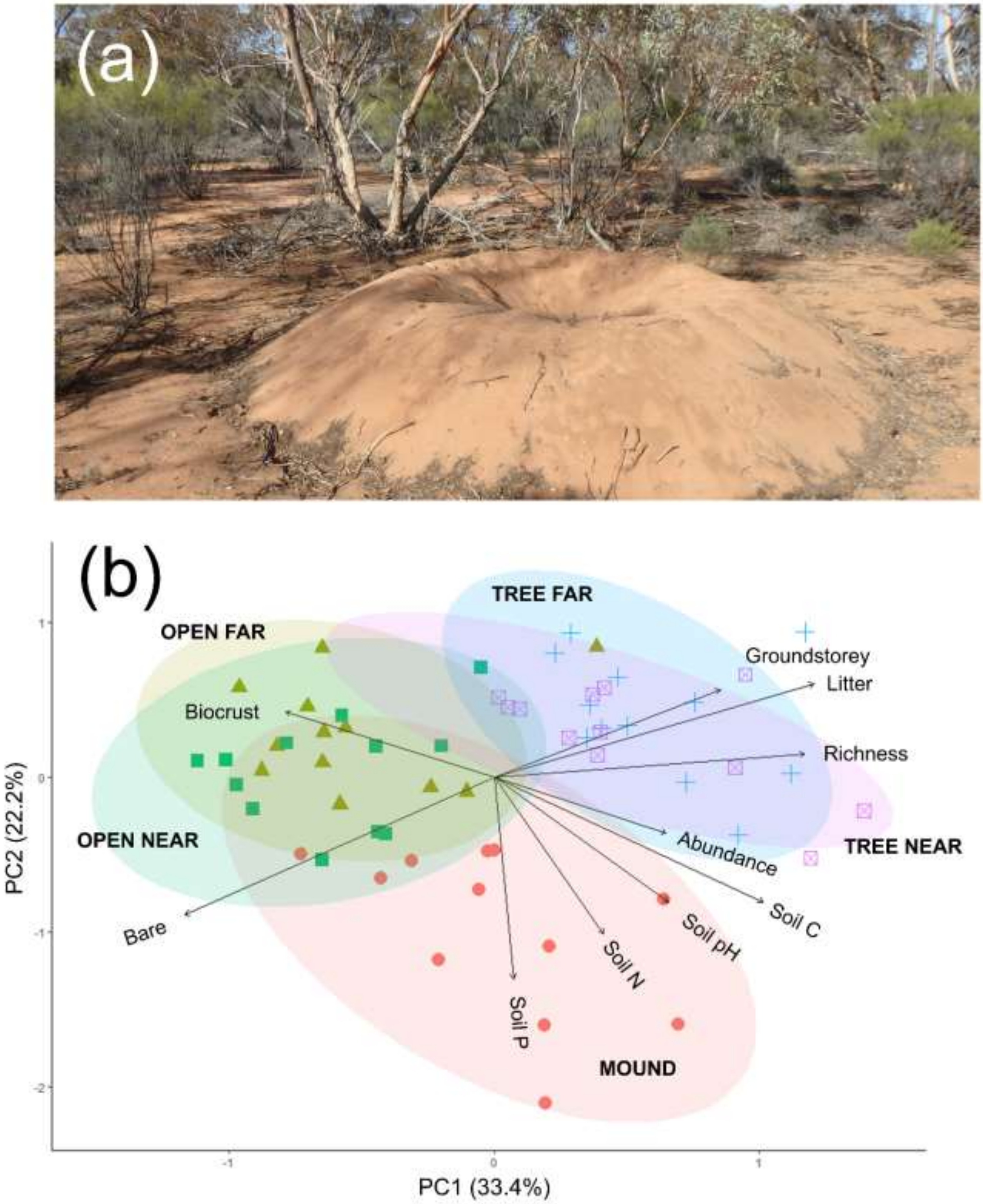

Figure 1: (a) Image of an active malleefowl mound. Note the deep crater within the centre of the mound. (b) Principal Component Analysis ordination plot illustrating the similarity among the four microsites (Mound, Open Near, Tree Near, Tree Far, Open Far). The 95% confidence interval ellipses are based on leaf litter, bare soil, tree canopy, groundstorey vegetation and biocrust cover, plant richness and abundance, and soil attributes (carbon, nitrogen, phosphorus, pH).

Table 1. Means of attributes at five microsites. Lowercase letters indicate significant differences (Tukey's HSD *post hoc*, $p<0.05$) from linear mixed models and generalised linear mixed models (GLMM) where indicated: Response variable ~ Microsite + (1|Mound ID).

Attribute	**Mound**	**Open Near**	**Tree Near**	**Open Far**	**Tree Far**
Bare soil cover (%)	62.9^{a}	52.9^{a}	10.2^{b}	49.2^{a}	4.2^{b}
Leaf litter cover (%)	30.4^{a}	22.9^{a}	84.3^{b}	27.5^{a}	84.6^{b}
Biocrust cover (%)	0.5^{a}	19.2^{b}	1.1^{a}	19.6^{b}	1.7^{a}
Plant abundance [GLMM]	16.8^{a}	7.5^{a}	10.4^{a}	10.2^{a}	11.6^{a}
Plant richness [GLMM]	3.3^{ab}	2.7^{a}	4.9^{b}	3.5^{ab}	4.7^{b}
Groundstorey (plant) cover (%)	12.5^{a}	13.9^{a}	21.3^{ab}	16.8^{ab}	31.6^{b}
Soil carbon (%)	2.36^{a}	0.51^{b}	1.65^{a}	0.42^{b}	1.80^{a}
Soil nitrogen (mg kg^{-1})	8.9^{a}	1.08^{b}	4.01^{b}	1.67^{b}	2.71^{b}
Soil phosphorus (mg kg^{-1})	18.0^{a}	15.08^{b}	11.92^{c}	12.50^{c}	12.25^{c}
pH	7.63^{a}	7.28^{b}	7.58^{a}	7.08^{b}	7.42^{a}

Mounds presented a distinct patch type for some attributes but not others. For example, compared with the Open far (control) microsite, mounds had more soil nitrogen, phosphorus, pH (Figure 2) and carbon (Table 1), but less biocrust cover, and did not differ in the cover of leaf litter (Figure 2). We also found some significant microsite effects among the three different aged mounds (Figure 3). For example, plant richness and cover were lower on the mounds than the Open Far microsite in young (< 3 years) mounds, but this effect dissipated in older mounds (Figures 3 & 4). Similarly, plant abundance was lower on young mounds, but greater in middle-aged mounds. Other attributes showed a consistent effect, with soil pH, phosphorus, nitrogen and carbon consistently greater on the mounds, irrespective of their age, while biocrust was consistently lower on the mounds over time (Figure 4).

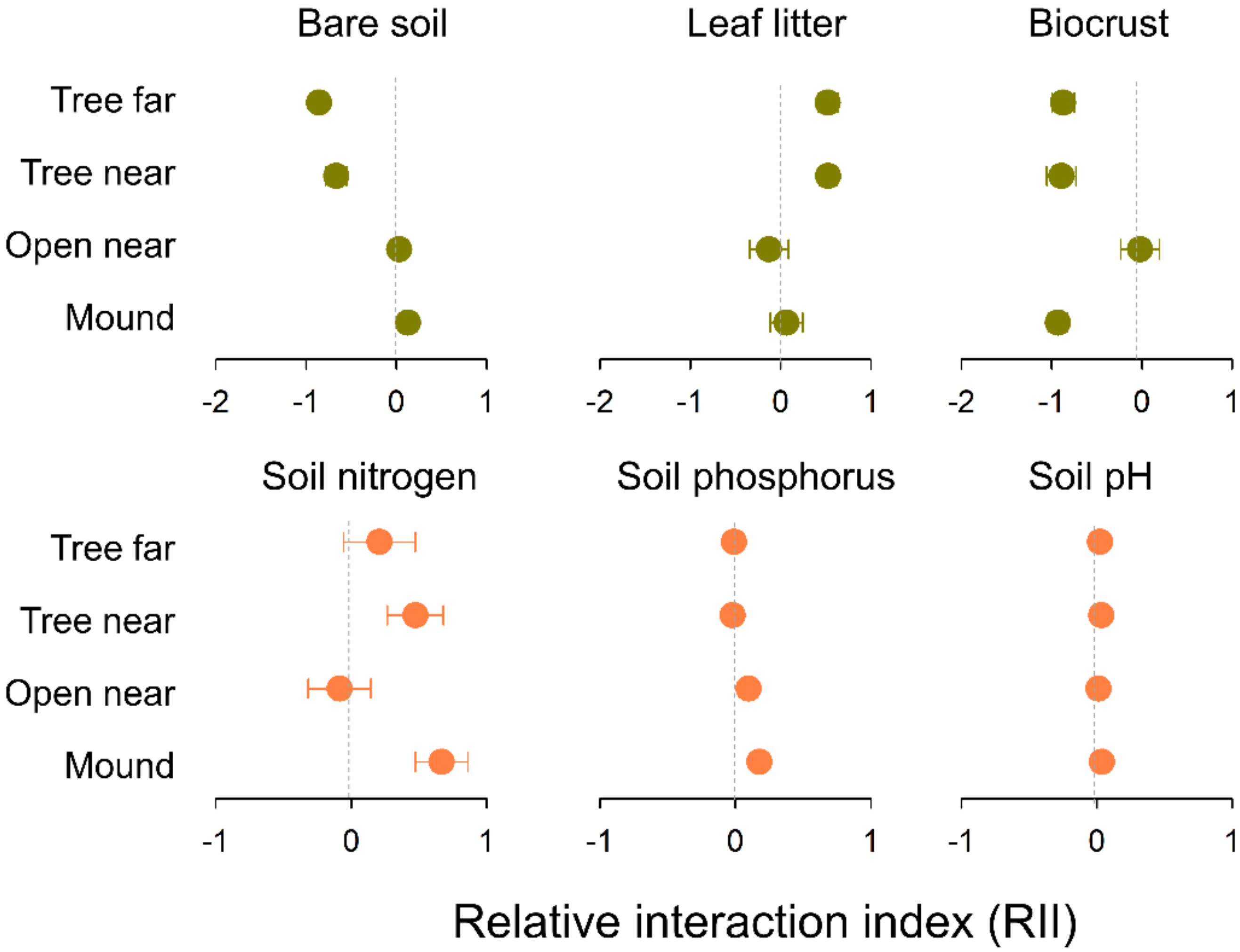

Figure 2. a) Mean (+ 95% CI) RII for the cover of bare soil, leaf litter, and biocrust, and soil nitrogen, phosphorus and pH for the four microsites in relation to the distant open microsite.

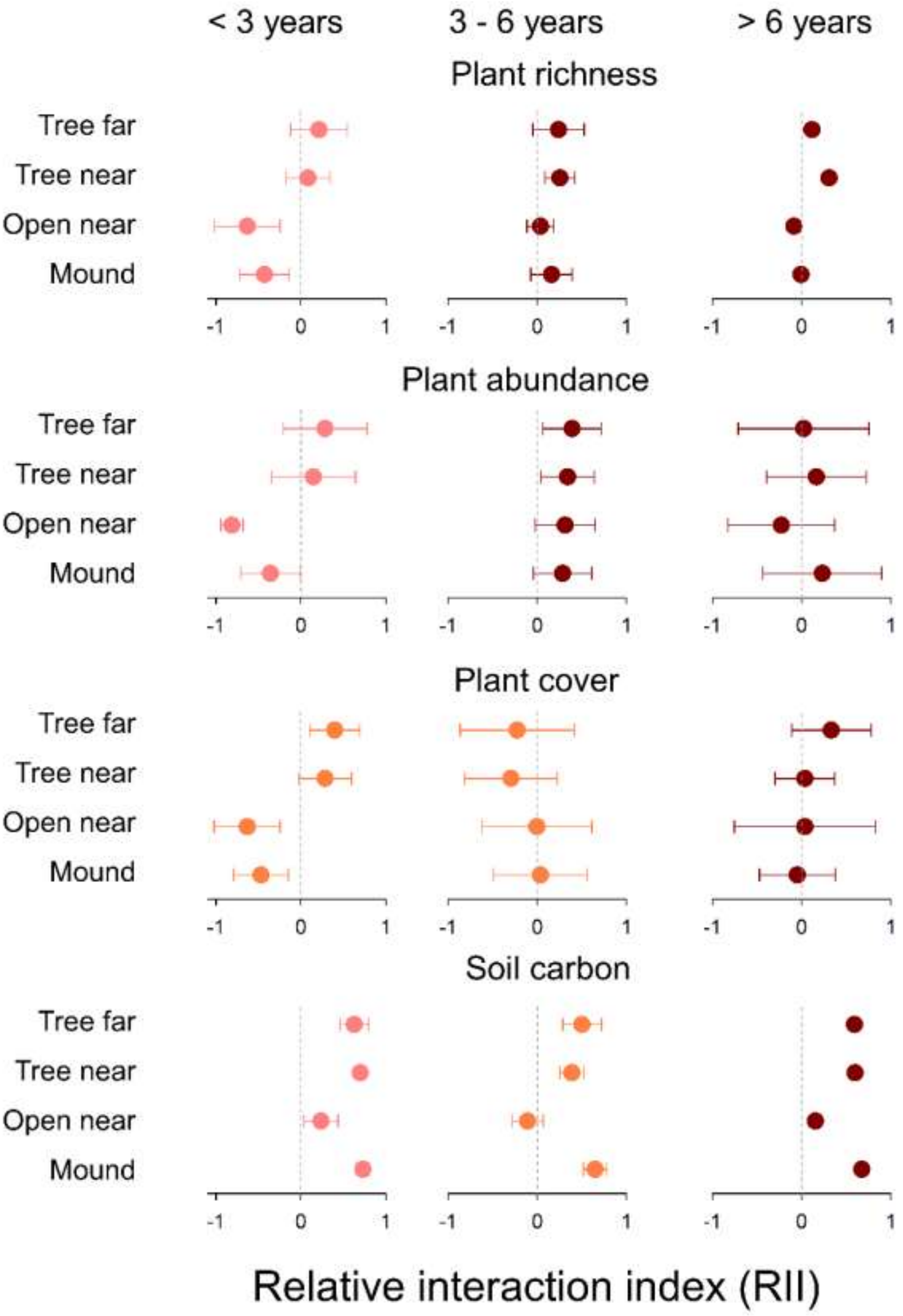

Figure 3. Mean (+ 95% CI) RII for plant richness, abundance and groundstorey vegetation cover, and soil carbon for the four microsites from mounds of different age.

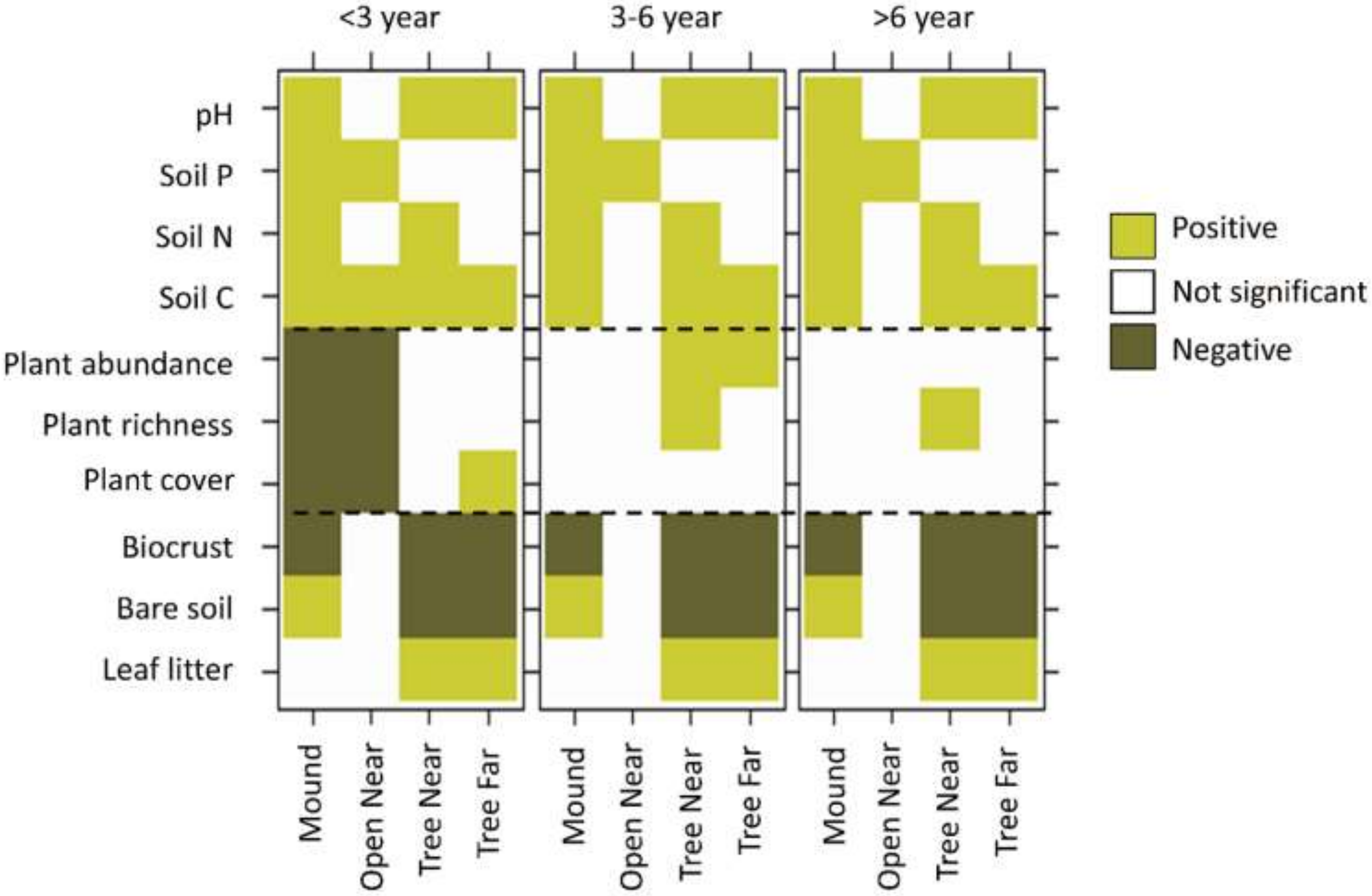

Figure 4. Heatmap illustrating simplified relative interaction index (RII) values: 'positive' indicates mean > 0 and 95% CI did not cross zero, 'negative' indicates mean < 0 and 95% CI did not cross zero, 'Not significant' indicates 95% CI crosses zero. Attribute values are displayed among microsite (Mound, Open Near, Tree Near, Tree Far) and mound age category (<3, 3-6, >6 years).

Discussion

The signature of mounds constructed by the megapode malleefowl included elements of both open and timbered sites. Specifically, mound soils were enriched in P, N, and C, were slightly more alkaline, but their outer surface had a lower cover of litter and biocrusts. Furthermore, differences varied over time and were depended on the specific attribute, with disturbance effects on plants changing over time, but soils remaining relatively unchanged over time. Overall, our results indicate that biogenic structures created by these litter-gathering megapodes represent novel microsites, with ecological conditions differing from those beneath mallee trees, the dominant biotic modulators in these semi-arid wooded systems (Travers and Eldridge 2015).

Resource-rich patches shape the structure and composition of vegetation communities in drylands (Aguiar and Sala 1999, Facelli and Brock 2000, Ochoa-Huesa et al. 2017). Consistent with expectations under the Fertile Island Hypothesis (Garner and Steinberger 1989), we found that plant species richness and vegetation cover were greater under trees than in the open, but that the resource-rich mounds showed none of these vegetation responses. The most parsimonious explanation relates to persistent disturbance around the mound resulting in a clearly defined zone of bare soil surrounding the mound. Disturbance by malleefowl has four major effects. First, it reduces plant cover and abundance, and shifts plant community structure from perennial grasses (e.g., *Austrostipa*) and shrubs (e.g., *Senna* spp.) to fast growing, disturbance-tolerant biennial forbs such as *Chenopodium curvispicatum* and *Maireana pentatropis* (Table S3). Second, disturbance destroys biocrusts, which in mallee woodlands can exceed 80% cover, and are critical drivers or hydrological function (Bowker et al., 2013). Third, litter removal increases bare ground and the cover of fine fuels, which might be sufficient to reduce the connectivity of wildfire (Smith et al. 2016). This indirect effect of mound construction will have a positive feedback effect on subsequent litter production by mallee trees by lengthening the fire return interval (Bradstock 1989). Finally, although the crater in the centre of the mound (Fig. 1a) contains a deep layer of organic material and associated seed (Priddel and Wheeler 1999), it is unknown whether the seed bank differs from that in the open or beneath the trees, or whether mounds are conducive to seed germination and growth.

Although disturbance effects on plants differed over time, the mounds had a unique biogeochemical signature (pH, C, N and P) compared with our control, and this did not change as mounds aged (Figure 4). Differences in soil chemistry beneath trees is due to the capture of C- and N-rich organic matter, and the large mass of organic material beneath their canopies includes frass and detritus from arboreal termites (decomposing material originating from termite activity (Kwok and Eldridge 2015). We detected some slight enhancement of soil pH beneath trees and in the mounds compared with the control Table 1, Figure 4), and this was likely due to greater cation (Ca and Mg) concentrations that are ‘biologically pumped’ from depth by trees and deposited in leaf fall (Noble et al., 1996). Eucalyptus bark is high in Ca ions, and bark shedding can lead to changes in the distribution of these cations beneath the canopy (Weltzin and Coughenour, 1990). Furthermore, Eucalyptus litter decomposes slowly because of the low leaf nutrient and polyphenol levels (Guo and Sims 1999). These properties may also explain the poor growth of vascular plants on the mounds (sensu Sourmare et al. 2015). Finally, we also found that the greatest soil P concentrations in mound soils. Phosphorus is derived from parent material, so that biopedturbation and exposure of subsoil by malleefowl is likely the main source of ecosystem P (Delgado-

Baquerizo et al. 2013), analogous to the effects of rabbit (*Oryctolagus cuniculus*) disturbance on their large underground warrens (Eldridge et al. 2017)

Concluding remarks

Our study indicates that mounds may represent temporal disturbance patches, complicating the longer-term vegetation response to higher resource characteristics of the mound microsite. Our study contributes not only to an understanding of malleefowl as engineers but demonstrates that mound-building megapodes can modulate the distribution of locally derived resources in the creation of a novel microsite. Their repeated use of the same mound could also lead to the inadvertent creation of a second novel microsite; tree patches close the mound that lack the characteristic deep litter. This could explain differences in plant abundance and richness in beneath litter-free canopies (Tree Near) compared with the controls in intermediate-aged mounds. In our study area, however, malleefowl tend to use a different mound every year (Neilly et al. 2021a), and observations of active mounds in previous years suggest that annual litterfall is sufficient to replace the volume used to construct the mound (Heather Neilly, personal observation 2019).

The results of our study have clear implications for the functioning and resilience of mallee woodlands. High-resource patches, including novel (mounds) or altered (litter-depleted trees) patches engineered by megapodes could help to buffer mallee woodlands from disturbance by supplementing the available niches for plants and soils, and therefore, providing a unique biogeochemical environment that support a different suite of microbial communities. These effects could be long-lived, as relict mounds are known to have different chemical signatures many years after abandonment (Noble 1993). Conservation programs that ensure the survival of malleefowl are needed if we are to retain these unique resource accumulating patches that complement existing landscape modulators and help to enhance spatial heterogeneity in wooded eucalypt systems.

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Author Contributions

HN, DJE, PC conceived the ideas and designed methodology; HN collected and analysed data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.560/dryad.xxxx

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