Grazing and aridity have contrasting effects on the functional and taxonomic diversity of ants

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Abstract

Ants are one of the most abundant and ubiquitous organisms on Earth and play critical roles in multiple ecosystem services such as seed dispersal and nutrient cycling. Despite this, the effects of climatic and land use stressors on particular species or groups of ants are poorly known. We conducted a regional field survey across 108 locations in south-eastern Australia, using correlation network analysis and structural equation modelling to identify how ants respond to environmental stressors. We found contrasting relationships amongst ants, and aridity, and vertebrate grazing intensity and history. Increasing aridity was associated with reduced ant richness, whereas increasing grazing intensity was associated with greater ant richness directly, and indirectly, via reductions in litter depth and perennial grass density. However, these taxonomically diverse groups of ant species still shared contrasting responses to increasing aridity and grazing intensity. We found strong associations between grazing, aridity and the abundance of Seed Harvesters, weak indirect relationships with Generalist Foragers, but no relationships for Predators or Sugar Feeders. Taken together, our work identifies contrasting relationships amongst grazing, aridity and ants (ant 'winners' or 'losers') across contrasting ecological contexts. Given that increasing aridity is generally associated with lower grazing intensity, our results suggest that locations with more arid sites will have lower ant richness with fewer Seed Harvesters, whereas more mesic sites with high grazing intensity might increase ant richness, and the abundance of specific ant species. Such knowledge is important if we are to maintain critical ant-mediated functions as Earth becomes drier and grazing intensity increases.

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Introduction

Ants are one of the most abundant and ubiquitous organisms on Earth, occurring in all biomes and continents except Antarctica. Ants provide a range of ecosystem services and

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products that are critical for the maintenance of healthy functional ecosystems and their processes. For example, ants form symbiotic, parasitic, and commensal relationships with other taxa (Glasier, Poore & Eldridge, 2018), which are important for supporting organic matter decomposition, soil formation, soil nutrient and hydrological function (Whitford & Eldridge, 2013), and seed dispersal (Hölldobler & Wilson, 1990). Ants are also known, however, to be highly vulnerable to global change drivers such as grazing and climate (Oliver, Dorrough, Doherty & Andrew, 2016). Compared with vertebrates and plants, however, little is known about the major ecological stressors of the species-level and taxonomic and functional diversity of ants across environmental gradients. This is largely because ant taxonomy is still poorly developed compared with that of vertebrates and plants. Knowing more about the responses of ant communities to global change drivers is essential to better forecast how projected changes in climate will affect ants and the many services they provide in terrestrial systems.

Grazing and aridity are two of the most important global change stressors threatening the well-being of terrestrial organisms. Earth's climate is expected to become drier, and the global land area covered by drylands is predicted to increase, by up to 23%, by the end of the century (Huang, Yu, Guan, Wang & Guo, 2016). Despite this, livestock grazing intensity is increasing in order to supply an increased demand for meat products, putting increased pressure on the structure and functioning of above- and below-ground communities. Increases in aridity are expected to reduce plant production and therefore affect important groups of seed harvesting ants by reducing the abundance and variety of seeds. Conversely, grazing could enhance dominant predatory, at the expense of seed-harvesting ants, altering dispersal mechanisms for many species that rely on ant dispersed mechanisms (myrmechochory; Hughes & Westoby, 1992).

Although we have some understanding of how grazing and aridity will affect broad functional groups of ants (Oliver et al., 2016), we know relatively little about how they might affect individual ant species, or groups of co-occurring species. Ecological network theory suggests that species tend to co-occur in discrete ecological clusters more than expected by chance (Tylianakis & Morris, 2017). These ecological clusters include species with similar ecological preferences and stressors. A knowledge of how ants assemble into ecological networks and clusters provides a novel approach to understanding how specific groups of ants might be affected by increasing aridity and grazing. We would expect changes in grazing, aridity or other environmental stressors that alters vegetation structure and thermal properties (Bestelmeyer, 1997) to have similar effects on ants that cluster into similar ecological groups. For example, a large body of research suggests that the effects of grazing on ants are site specific and vary with ant species (e.g. Barton, Sato, Kay, Florance & Lindenmayer, 2016; Hoffmann, 2010; Read & Andersen, 2000). Similarly, some ants

have been shown to have a lower tolerance to warming (Andrew et al., 2019), which might lead to changes in ecological effects mediated by these ants. Changes in grazing and aridity might affect ant abundance by influencing vegetation cover and biomass, potentially altering ant habitat (Kerley and Whitford, 2000; Barton et al., 2016) and the distribution of nest sites (Soule & Knapp, 1996). Thus, grazing and aridity are likely to favour some groups or clusters of ants (winners, i.e. their abundance increases), whereas other groups or clusters are likely to be disadvantaged (losers, lower abundance). For example, increases in bare soil created by overgrazing will advantage those ants that forage in open areas (winners) but disadvantage those that require dense vegetative cover (losers). Further, increased habitat degradation may affect different clusters of ants by making them less resilient to increasing temperatures (Andrew, Miller, Hall, Hemmings & Oliver, 2019). Understanding the effects of different ecological clusters and their constituent members is important so that we understand how these changes may eventuate given the critical role that ants play in several major ecosystem services.

To address these knowledge gaps, we conducted a field survey across 108 sites in eastern Australia, across gradients in grazing and aridity, and used a combination of ecological network analyses and structural equation modelling. We assessed ant richness and the relative abundance of ant functional groups (e.g. Seed Harvesters, Predators, Generalist Foragers, Sugar Feeders), and identified and assessed ecological clusters of ant taxa that tend to co-occur. Analyses of the response of ants and their different ecological clusters and their networks is a useful approach for identifying those taxa that change with changing aridity and increased grazing. This knowledge is important for making informed decisions about biodiversity conservation such as whether to maintain livestock grazing or fire regimes in conservation reserves, if these management actions are known to affect different groups of ants and therefore the ecological functions that they regulate.

Materials and methods

The study area

Our study was conducted across a large area (0.4 M km^2) of eastern Australia spanning about 900 km from west to east (Appendix S1; Fig. S1). We surveyed a total of 108 sites, 36 from each of three markedly different broad vegetation communities, dominated by either Blackbox (*Eucalyptus largiflorens* F.Muell.), White cypress pine (*Callitris glaucophylla* F.Muell.) or River red gum (*Eucalyptus camaldulensis* Dehnh.). The three communities are used extensively for livestock grazing, with smaller areas for conservation (national parks) and forestry. Across this gradient the climate is Mediterranean and typically semi-arid (Aridity Index = 0.26 to 0.39), with slightly more rainfall during the

six warmer months in the east-central and during the cooler months in the south and south-west. Average rainfall (385 to 460 mm yr^{-1}) and average temperatures (~18 °C) varied little across the sites.

Assessment of grazing intensity

We sampled a range of grazing intensities based on both recent (last 2−3 years) and historic (up to 20+ years) grazing. To assess recent grazing intensity, we identified and counted the dung or pellets of all herbivores (cattle, sheep/goat, kangaroo, rabbits) within five large 25 m^2 quadrats (5 m x 5 m) and herbivores with small numerous pellets (rabbits, kangaroos, sheep) in five small quadrats 0.25 m^2. The large quadrats were spaced every 50 m along a 200 m transect with the smaller quadrats co-located centrally within the large quadrats. Dung and pellet counts are used widely to estimate large herbivore abundance (Johnson & Jarman, 1987). Counts of dung in both small (rabbits, kangaroos, sheep) and large (cattle, kangaroos, sheep) quadrats were converted to mass using a process where we counted, dried and weighed dung to obtain a relationship between dung counts and dry mass for each herbivore (see Eldridge, Delgado-Baquerizo, Travers, Val & Oliver, 2017). We averaged the quadrat data together to obtain a site level measure of grazing for each of the four herbivores. Dung beetles are uncommon across the study area, and thus their effects on dung decomposition would be expected to be small. Because we used the relative mass of dung as a measure of recent grazing intensity, decomposition by biotic agents such as dung beetles, termites or fungi, would be unlikely to have a major effect. To assess historic livestock grazing intensity, we measured the width and depth of all livestock tracks crossing the 200 m transect to derive a total cross-sectional area of livestock tracks for each site (Pringle & Landsberg, 2004).

Soil and vegetation assessment

In the large quadrat we assessed the cover of each plant species and counted the number of perennial grasses > 2 cm basal diameter to calculate the average density of perennial grasses. We also estimated litter cover and measured litter depth, as the average of five points within every small quadrat.

Ant sampling

Ants were sampled at each site using 65 mm-diameter pitfall traps (plastic specimen containers, partly filled with propylene glycol). Five traps were located at each of the five large quadrats to co-locate with grazing intensity, soil and vegetation assessments. The traps were installed in each corner of the 5 m x 5 m quadrat, plus one trap was located centrally within the quadrat. Each pitfall trap was installed flush with the ground surface with a raised cover to prevent loss of material due to rainfall. Traps were left open for five consecutive nights at each site. The contents of the five traps at each large quadrat were bulked into a single container and stored in 80% ethanol for later processing. From the 108 sites a total of 246,946 worker ants were sorted and identified to species and morphospecies (Oliver & Beattie, 1996). However due to the highly skewed nature of raw abundance data for ants, we analysed cumulative presence-absence data for each species across the five large quadrats at each site (integers 0−5). Reference specimens were confirmed by Dr Alan Andersen, Tropical Ecosystems Research Centre, CSIRO, Darwin.

Statistical analyses

Correlation networks

We used correlation network analysis ('co-occurrence networks') to identify ecological clusters of strongly associated ant species. We first calculated all pairwise Spearman's (ρ) rank correlations between all ant taxa (% of total abundance) and focussed exclusively on positive correlations because they provide information on ants with a similar response to changes, similar ecological preferences or similar vulnerabilities such as those brought about by changes in grazing or attributes such as plant and litter cover (Barberán, Fernández-Guerra, Bohannan & Casamayor, 2012). Robust co-occurrence data were considered to be those where a significant spearman correlation ($P < 0.01$) exceeded 0.25 (Barberán et al., 2012). Mathematically, associations where $\rho > 0.25$ are likely to suffer from multi-collinearity, indicating a strong mathematical relationship between two variables. Similarly, biologically we focused only on those ant species that were strongly co-occurring and were more likely to interact similarly within a given environment. We stress, however, that correlation network analyses are only a simplistic representation of complex ecological systems, and it is plausible that networks based on correlations can yield spurious results, so that associations amongst taxa within these networks cannot be directly interpreted as interactions. Notwithstanding this caveat, information derived from our networks is essential for generating novel hypotheses about highly connected and dominant taxa within ecological systems. The network was visualized with the interactive platform Gephi (Bastian, Heymann & Jacomy, 2009) and we used default parameters (network resolution = 1.8 in all cases) to identify modules of the most strongly interacting ant species. We then computed the relative abundance of each module by averaging the standardized relative abundances (z-scores) of the species from each module. This data standardization allowed us to exclude any effect of merging data from different ant functional groups such as predatory and seed harvesters.
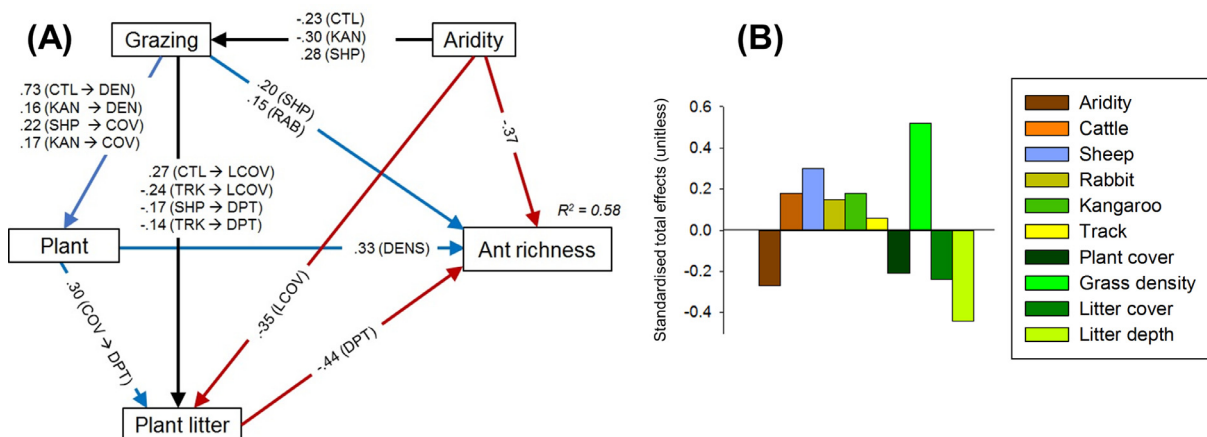
Structural equation modelling

Structural Equation Modelling (SEM) was used to build a system-level understanding of the effects of grazing, plants and litter on the richness, and relative abundance of different clusters of co-occurring ants and ant functional groups. We had three analyses. First, we examined the association amongst grazing, plants and litter, and ant richness, then amongst six of the ten clusters that represented 90% of the total ant richness. Finally, we analysed grazing and litter-plant effects on the relative abundance of four functional groups (Predators, Generalist Foragers, Seed Harvesters, Sugar Feeders). These functional groups are based on information from the Global Ant database (http://globalants.org) and the assignment of different ant taxa is shown in Appendix S3, Table S1. Structural equation modelling allowed us to partition direct and indirect effects of one variable upon another and estimate the strength of any multiple effects. Our SEM analyses were based on an *a priori* model of how we expected ants to respond to differences in grazing, plants and litter (Appendix S2; Fig. S2).

Empirical data were used to test the plausibility of a causal model, based on our *a priori* model, in explaining the direct and indirect relationships amongst variables of interest. We then compared the hypothesised *a priori* pathways with the variance-covariance matrix of our empirical data to calculate an overall goodness-of-fit using the χ^2 statistic. This goodness of fit test estimates the likelihood of the observed data given the *a priori* model structure. Thus, high probability values indicate that models are highly plausible causal structures underlying the observed correlations. Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA)

software. For each of our models, those with low χ^2, high Goodness of Fit Index [GFI] and high Normal Fit Index [NFI]) were interpreted as showing the best fit to our data.

Results

We recorded 320 ant species from the 108 sites over 0.4 M km^2 from eastern Australia. Ant richness declined with increasing aridity and litter depth but increased with increasing grazing intensity and perennial grass density (Fig. 1A). The positive relationship between grazing and ant richness (Fig. 1B) can be partly explained by the fact that increasing grazing is associated with a suppressive effect of litter depth on ant richness and increases in the positive relationship with plant density (Fig. 1A). The correlation network, which aimed to identify groups of co-occurring ant species across our environmental gradients, identified four major groups of ants (hereafter 'clusters'; Fig. 2A) that included 80% of all species: Cluster 1 (57 taxa), Cluster 2 (59 taxa), Cluster 3 (26 taxa) and Cluster 7 (33 taxa), and two minor clusters including a lower number of ant species; Clusters 6 (15) and 10 (7). The remaining clusters (Cluster 4, 5, 8 and 9) had six or fewer taxa (membership of ants by cluster is shown in Appendix S3; Table S2). Clusters grouped ant species that are expected to share similar ecological preferences and vulnerabilities to changing aridity and grazing disturbance, but that belong to different taxonomic and functional groups (Fig. 2B-C). Ant clusters were also largely independent of the four functional groups (Seed harvesters, Generalist foragers, Sugar feeders, Predators), i. e. almost all clusters occurred in all foraging groups, though

Fig. 1. (A) Structural equation models describing the effects of multiple drivers, Aridity (climate), Grazing (sheep, cattle, kangaroos, rabbits, historic livestock grazing), Plants (perennial grass density, Plant cover) and Plant litter (litter cover, litter depth) on ant richness. CTL = cattle, KAN = kangaroo, RAB = rabbit, TRK = historic livestock grazing (tracks), SHP = sheep, LCOV = litter cover, DPT = litter depth, COV = plant cover, DEN = perennial grass density. Numbers adjacent to arrows are path coefficients, which are analogous to partial correlation coefficients and indicative of the effect size of the relationship and may be positive (blue), negative (red) or mixed (black). Only significant ($P < 0.05$) pathways are shown. R^2 represents the total variance in ant richness explained by the model. Model fit: $\chi^2 = 3.9$, df = 10, $P = 0.95$, RMSEA = 0, Bootstrapped $P = 1.0$. (B) Standardised total effects, the sum of direct and indirect effects, derived from the structural equation model (a) above.
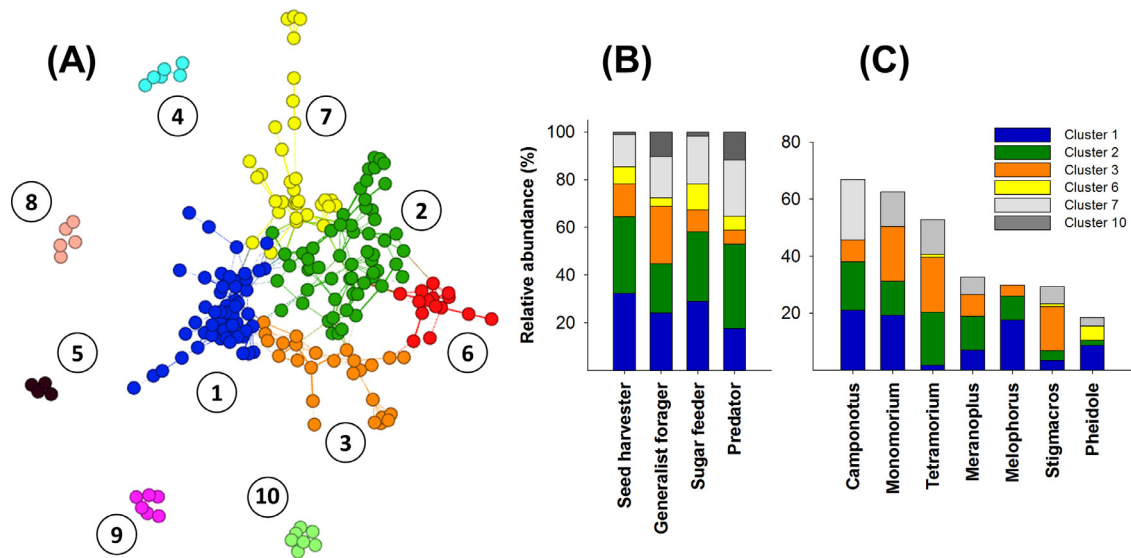
Fig. 2. (A) Correlation network for the 10 clusters (Clusters 1 - 10), (B) relative abundance of six ant clusters (Clusters 1, 2, 3, 6, 7, and 10) within the four ant functional groups, and (C) the relative abundance of the seven most abundant ant genera within each of the ant clusters.

there was a relatively greater abundance of Cluster 10 taxa in the Predator and Generalist forager groups (Fig. 2B). There were also relatively more *Pheidole* spp. in Cluster 6, relatively few *Melophorus* spp. in Cluster 7 and relatively few *Stigmacros* in Cluster 2 (Fig. 2C). Of the 320 ant species, 102 species representing 8% of total ant abundance, were not assigned to a cluster as they were not strongly correlated with other ant species. These 102 species might have very specific environmental preferences not shared with other ant species in our database or be ubiquitous species with broad habitat requirements.

Our SEM analyses provide further evidence for contrasting associations between the richness, community composition (six ecological clusters of ants) and functional groups of ants with increasing aridity and grazing intensity. Overall, increasing aridity was associated with moderate reductions in ant richness (Fig. 1A), but aridity effects differed amongst clusters and functional groups. Increasing aridity was associated with reduced relative abundance of ants in Clusters 1 and 2 (Figs. 3A and B) and Cluster 7 (Fig. S4B) but had no direct effects on the other clusters. Increasing aridity was associated with a lower relative abundance of Seed Harvesters (Fig. 4B) but not with any other functional groups.

Ants in Clusters 1 and 2 also responded similarly to grazing. For example, rabbit grazing was positively associated with the relative abundance of taxa in Clusters 1 and 2 (Figs. 3A and 3B). Sheep grazing was also positively associated with the relative abundance of ants in Cluster 1 (Fig. 3A). Increasing kangaroo grazing was positively associated with increasing abundance of ants in Cluster 1, but the opposite relationship was apparent in Cluster 10 (Fig. 3D). Increasing cattle grazing had a strong negative

association with the relative abundance of Cluster 3 species (Fig. 3C). There was a positive association between sheep grazing and the relative abundance of Cluster 6 (Fig. S4A) ants but no grazing associations for Cluster 7 ants (Fig. S4B). We also found indirect relationships amongst grazing and other clusters. For example, increasing grazing by cattle, sheep and kangaroos was associated with greater relative abundance of Cluster 1, 2 and 3 ants but reduced relative abundance of Cluster 10 ants because of the positive association of grazing with dense grasses or negative association with litter depth (Fig. 3A−C).

We then examined the associations between grazing and environmental variables, and the relative abundance of four ant functional groups, and found marked associations between plant cover, and Generalist Foragers and Seed Harvesters (Fig. 4) but not Predators or Sugar Feeders (not shown), which were largely independent of changing environmental conditions. Further, the relative abundance of Generalist Foragers and Seed Harvesters (Fig. 4) was affected by different drivers. For example, greater plant cover was positively associated with the relative abundance of Seed Harvesters (Fig. 4B) but negatively associated with Generalist Foragers (Fig. 4A). Increasing rabbit grazing was associated with increased relative abundance of Seed Harvesters, whereas sheep grazing reduced their relative abundance, but there were no relationships for Generalist Foragers. Further, increasing sheep and kangaroo grazing enhanced the negative association between plant cover and the relative abundance of Generalist Foragers. The relative abundance of Seed Harvesters was strongly negatively associated with aridity but there were no significant associations between aridity and Generalist Foragers (Fig. 4).
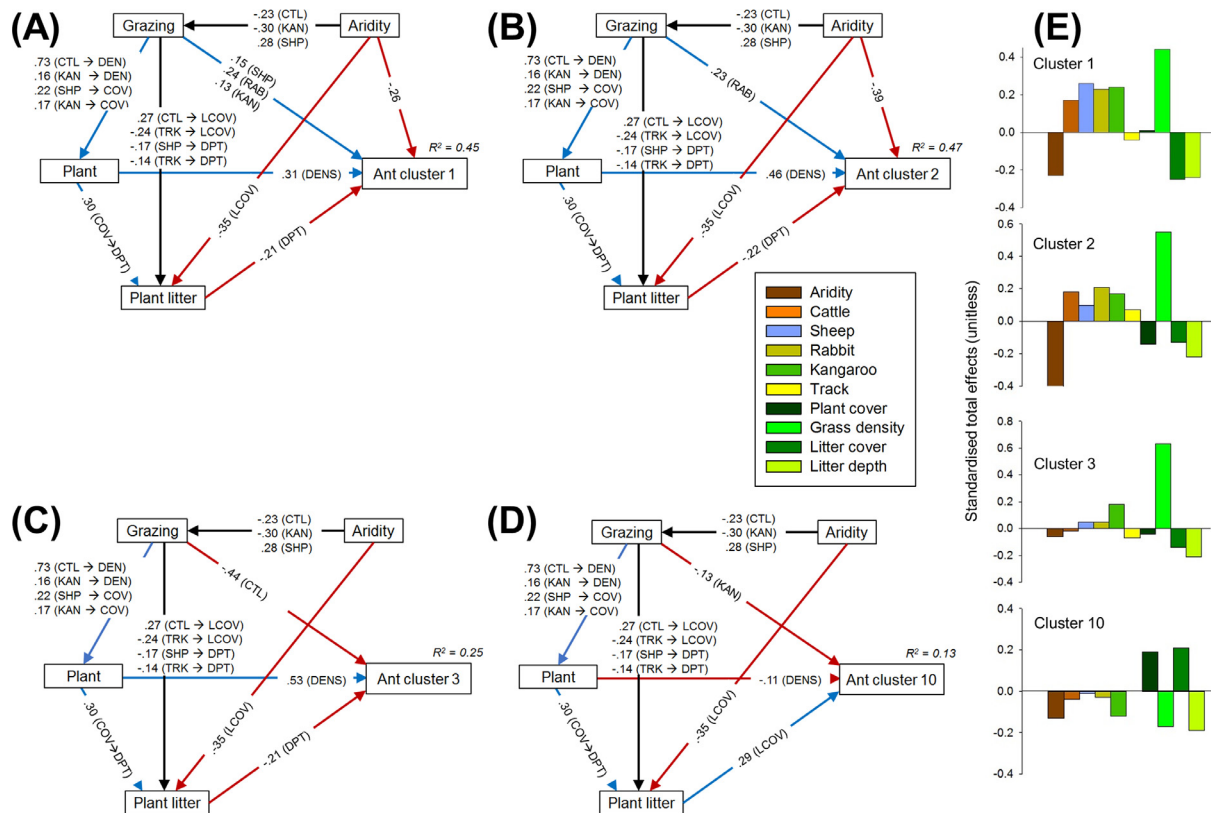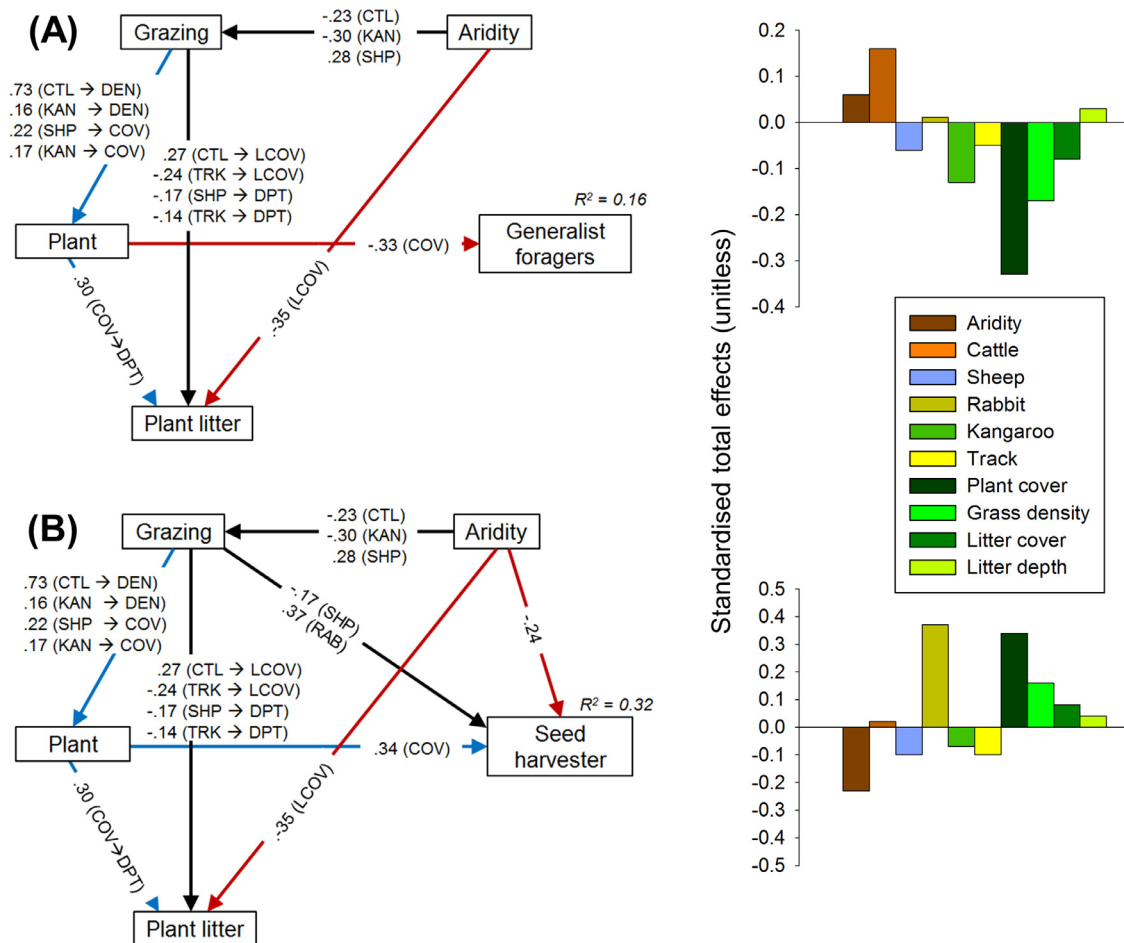
Fig. 3. (a) Structural equation models describing the effects of multiple drivers, Aridity (climate), Grazing (sheep, cattle, kangaroos, rabbits, historic livestock grazing), Plants (perennial grass density, plant cover,) and Plant litter (litter cover, litter depth) on Ant Cluster 1 (A), Cluster 2 (B), Cluster 3 (C) and Cluster 10 (D). CTL = cattle, KAN = kangaroo, RAB = rabbit, TRK = historic livestock grazing (tracks), SHP = sheep, LCOV = litter cover, DPT = litter depth, COV = plant cover, DEN = perennial grass density. Numbers adjacent to arrows are path coefficients, which are analogous to partial correlation coefficients and indicative of the effect size of the relationship and may be positive (blue), negative (red) or mixed (black). Only significant ($P < 0.05$) pathways are shown. R^2 represents the total variance in ant richness explained by the model. Model fit: $\chi^2 = 3.9$, df = 10, $P = 0.95$, RMSEA = 0, Bootstrapped $P = 1.0$. (e). Histograms are standardised total effects, the sum of direct and indirect effects, derived from the structural equation models.

Discussion

We demonstrate that contrasting relationships occur amongst aridity and grazing, and ant richness, clusters of co-occurring ants, and ant functional groups. Our results provide important insights into potential mechanisms that define ants as either winners or losers under different environmental scenarios associated with changes in aridity or different grazing intensities. For example, aridity tended to be associated with lower ant richness, and the abundance of Seed Harvesters, while grazing showed the opposite trend. Similarly, the abundance of some taxa such as *Monomorium magalopos* (Cluster 1) and *Tetramorium* spp. (Cluster 2) were negatively associated with increasing aridity but increased with several measures of grazing intensity, perhaps because they favour bare ground, where soil insolation levels are greater. Grazing further altered ants by modifying several environmental variables, such as perennial grass density and litter depth, with greater intensity of grazing associated with increased ant richness *via* reductions in litter depth, or increases in perennial

grass density (specifically, more smaller grasses, Travers & Berdugo, 2020). Overall, the present study advances our understanding of how and why ants respond to environmental conditions such as changes to soil surface structure (plant density, litter cover), land use pressure (increasing grazing intensity) and environmental conditions. Increasing land use intensification through higher grazing rates will have marked effects on different ant assemblages and functional groups and therefore the critical ecosystem functions and services that they provide.

Increasing aridity was associated with a reduction in ant richness (Fig. 1), and these relationships varied amongst ecological network groups (Fig. 2). For example, the relative abundance of ants in Clusters 1, 2 and 7 declined with increasing aridity, but there were no significant relationships for the other seven clusters. The large ant *Notoncus enormis* (Cluster 7) is known to increase in abundance with increasing tree cover (Nooten et al., 2019), which could explain its negative correlation with increasing aridity, given the declines in tree cover with aridity. Cluster 2 comprised a

Fig. 4. Structural equation models describing the effects of multiple drivers, Climate (aridity), Grazing (sheep, cattle, kangaroos, rabbits, historic livestock grazing), Plants (perennial grass density, plant cover, litter cover, litter depth) on the relative abundance of Generalist foragers (A) and Seed harvesters (B). There were no significant effects of any drivers on Predators or Sugar feeders. CTL = cattle, KAN = kangaroo, RAB = rabbit, TRK = historic livestock grazing (tracks), SHP = sheep, LCOV = litter cover, DPT = litter depth, COV = plant cover, DEN = perennial grass density. Numbers adjacent to arrows are path coefficients, which are analogous to partial correlation coefficients and indicative of the effect size of the relationship and may be positive (blue), negative (red) or mixed (black). Only significant ($P < 0.05$) pathways are shown. R^2 represents the total variance in ant richness explained by the model. Model fit: $\chi^2 = 3.9$, df = 10, $P = 0.95$, RMSEA = 0, Bootstrapped $P = 1.0$. Histograms present the standardised total effects, the sum of direct and indirect effects, derived from the structural equation models immediately to their left. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

large number of seed harvester ants (*Melophorus, Meranoplus, Monomorium, Tetramorium*), which also showed declines with aridity (Fig. 3B), likely reflecting sparser plant cover. In contrast, Generalist foragers, which were dominant in Clusters 1 and 3, would be expected to be advantaged by greater plant cover. A potential explanation for the lack of a relationship between aridity and Cluster 10 ants is that this cluster is dominated by ants that are either subterranean or construct large thermoregulated nests (*Myrmecia*), and therefore are less reliant on conditions at the soil surface.

We also found that some ants showed a response to increased grazing by sheep, and to a lesser extent, rabbits. Part of the mechanism behind these findings appears to be related to the correlations between sheep and cattle grazing and the

density of different perennial grass species (Travers & Berdugo, 2020). A greater density of perennial grasses affects the ability of ants to forage or evade predation from ant-eating vertebrates such as echidnas (*Tachyglossus aculeatus*) or other predatory ants. Denser perennial grasses could be related to the provision of suitable habitat for different founder colonies, ease of constructing nest entrances in more porous soils associated with grasses, or access to a range of underground resources associated with plant roots required by different ants (Hölldobler & Wilson, 1990). The relative abundance of Predatory Rhytidoponerans such as *Rhytidoponera cristata* and *Rhytidoponera maniae* (Cluster 1) increased with greater grass density and grazing pressure, particularly by rabbits. *Rhytidoponera* spp. typically show increasing trends in abundance with disturbance (Hoffman & Andersen, 2003), possibly

because this improves foraging abilities by increasing the cover of bare soil.

The effects of grazing also varied amongst ecological networks and functional groups. Unlike Clusters 1, 2 and 3, the relative abundance of ants in Cluster 7 was uncorrelated with grazing, perennial grass density or litter depth. Ants in Cluster 7 would be considered Generalist Foragers, and some may be arboreal or subterranean, and therefore less reliant on surface conditions for foraging. For example, the opportunist ant *Aphaenogaster barbigula* (Cluster 7) tends aphids on the roots of plants (Saunders, 1967), and their funnel-shaped nest entrances are thought to act as traps for arthropods, releasing them from the need to forage at the soil surface where grazing relationships are strongest (Shattuck, 2008).

Litter cover is widely known to affect ants. Globally, ant body size declines with increasing litter habitat complexity (Farji-Brener, Barrantes & Ruggiero, 2004) and this is related to the efficiency with which ants can negotiate surface litter. A shallower litter layer might increase ant richness by making it easier for a greater range of different-sized ants to forage. The overall effect of grazing was to reduce litter cover and is therefore a likely mechanism explaining how grazing alters ant richness, ecological network groups and functional groups. The relative abundance of species in Cluster 10 increased with greater litter cover as it contained species such as *Polyrachis phryne* and *Myrmecia* spp., which are large-bodied predatory species. Increasing livestock grazing has been shown to reduce both litter cover and depth (Eldridge et al., 2017), thus advantaging some ant taxa such as Seed harvesters (winners) but disadvantaging others such as Generalist foragers (losers). Predatory species such as *Strumigenys perplexa* may benefit from increased litter cover by predating on litter-borne arthropods and larvae. For example, *Myrmecia pyriformis* is a known nocturnal predatory ant that feeds on invertebrates, nectar, grass seeds and leaves, kangaroo scats and homopteran honey dew, by foraging in *Eucalyptus* trees (Haskins & Haskins, 1950; Reid, Narendra, Taylor & Zeil, 2013) which produce abundant litter. Cluster 10 species also showed a positive response to reductions in grass density and therefore increasing bare soil, which favours large-bodied predatory ants by allowing them to hunt over areas of bare open ground more effectively. Positive and negative correlations with litter depth were also apparent for different clusters, with litter depth negatively associated with the relative abundance of ants in Clusters 1, 2 and 3. Deep litter advantages small-bodied ants over large-bodied ants (Radnan, Gibb & Eldridge, 2018) that are able to move freely beneath litter (Gibb & Parr, 2010) and tend to specialise in foraging within litter (Wiescher, Pearce-Duvet & Feener, 2012). Thus, ants in Clusters 1, 2 and 3 may be smaller-bodied ants compared with those in Cluster 10.

We found that grazing was associated with changes in the relative abundance of Generalist Foragers and Seed Harvesters, but not Sugar Feeders or Predators. Our Generalist Forager group comprised mainly small cryptic scavengers and predators that had a negative association with plant cover. Sheep and kangaroo grazing reinforced this negative relationship. Some species in this group, such as *Brachyponera lutea* forage in open areas and recently burnt sites (York, 1994), scavenging from the nests of other ants or termites (myrmecophiles, (Glasier et al., 2018), often co-locating their nests to take advantage of their hosts (Shattuck, 1999; Wheeler, 1936). Others are largely arboreal species (e.g. *Podomyrma* spp.) or tend Hemiptera (e.g. *Calomyrmex albopilosus*; Shattuck, 1999) or caterpillars (e.g. *Frogatella kirbii* Valentine, 1979) so plant composition, rather than plant cover, is likely to be an important driver of this group. In contrast, the relative abundance of seed harvesters increased in response to increasing plant cover, likely reflecting greater seed resources from a greater density and cover of plants (Davison, 1982). Seed harvesters also responded positively to increased grazing by rabbits. Rabbits live in large underground colonies (warrens), which are characterised by large patches of bare soil, often colonised by exotic annual species (Leigh, Wood, Holgate, Slee & Stanger, 1989). Thus, increased rabbit grazing may reflect a greater abundance of small-seeded annual plants or a greater area of bare soil on which to forage.

Concluding remarks

Our study provides some indication, albeit speculative, about how continued grazing (overgrazing) or increasing dryness (aridification) might influence ant communities, though this is based on correlative rather than experimental evidence. Shifts in ant community composition will likely have flow-on effects to important ecosystem services provided by ants. This includes seed dispersal, given that increasing livestock grazing pressure was correlated with the relative abundance of seed harvesting, and therefore seed dispersing, ants. Changes in ant community structure driven by grazing could also alter organic matter decomposition and therefore soil nutrient budgets, as grazing was associated with less litter and thus likely lower organic inputs into the soil. Less litter could mean lower abundance of Cluster 10 ants, such as *Strumigenys perplexa*, a predatory ant that requires deep litter in which to forage (Brown, 1958). The loss of other ants such as *Aphaenogaster barbigula* could also have more far-reaching consequences such as altering hydrological processes. *Aphaenogaster* nest entrances conduct large volumes of water (Eldridge, 1993), so that loss of these ants could potentially alter infiltration-runoff relationships. Land use intensification such as increasing grazing and drier climates will therefore likely have marked effects on ecosystem functions as we move more intensively managed systems.

Declaration of Competing Interest

The authors declare no competing interests.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2020.07.003.

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