Effects of environmental variation and livestock grazing on ant community structure in temperate eucalypt woodlands

Philip S. Barton¹ *, Chloe F. Sato¹, Geoffrey M. Kay¹, Daniel Florance¹, David B. Lindenmayer¹

¹ Fenner School of Environment and Society, The Australian National University, Canberra, Australian Capital Territory, 2601, Australia.

* Corresponding author: philip.barton@anu.edu.au

Running head: Effects of grazing on ant assemblages
ABSTRACT

1. Grazing by livestock is a major ecological disturbance, with potential effects on vegetation, soil, and insect fauna. Ants are a diverse and functionally important insect group with many associations with the ground-layer, yet recent global syntheses question the importance of grazing effects on ant communities relative to vegetation or soil.

2. We examined the effects of vegetation, soil and grazing on the whole ant community, ant functional groups, and abundant species in temperate eucalypt woodlands, southeastern Australia.

3. We found limited influence of grazing on our vegetation and soil measures, except for a positive association between grazing and exotic perennial grass cover. We also found that exotic grass cover had a negative effect on overall ant abundance and richness, but not functional groups or individual species. Soil C:N ratio had a positive effect on the subdominant Camponotini, and leaf litter cover had a positive effect on the abundance of cryptic species. Partial Mantel tests revealed an effect of both environmental and grazing measures on ant assemblage composition, but constrained ordination showed that leaf litter cover, grass biomass, and native and exotic perennial grass cover had stronger correlations with ant community structure than grazing.

4. Our study shows that both environmental variation and grazing play a role in driving ant community structure, but that key environmental variables such as grass biomass and leaf litter cover are particularly important in temperate eucalypt woodlands. Monitoring of ant communities to measure the benefits of changed grazing regimes for biodiversity should consider contemporary grazing pressure as well as the underlying effects of variation in plants and soils.
Keywords: agriculture, biodiversity conservation, environmental stewardship, Formicidae, grazing, insect, invertebrate, modified landscape, monitoring, restoration

INTRODUCTION

Grazing by livestock can be a major disturbance in ecosystems due to its effects on soils and plant communities (Hobbs, 1996; Milchunas & Lauenroth, 1993; Schuman et al., 1999), as well as associated insect fauna (Kruess & Tscharntke, 2002; Seymour & Dean, 1999). As a consequence, the management of grazing is a priority for many land managers with responsibility for the conservation of biodiversity (Lunt et al., 2007; Rook et al., 2004).

Grazing can alter soil and plant attributes over prolonged periods (Hobbs, 1996; Milchunas & Lauenroth, 1993). For soils, this can include both physical and chemical aspects such as compaction from the impact of animal hooves, as well as altered phosphorus and nitrogen levels through plant consumption and redistribution via urine and dung (Beever et al., 2003; Yates et al., 2000). For plants, this can include the introduction and spread of exotic grass species (Driscoll et al., 2014), the selective grazing of different plant species (Dorrough et al., 2007), and changes in the structure, biomass or composition of the ground-layer plant community (Yates et al., 2000). These changes to soils and plant communities have consequences for associated biota, both above and below ground, with many documented cases of changes in animal communities (Foster et al., 2014; Hobbs, 1996; Milchunas et al., 1998).

Ants are a major component of animal biomass and biodiversity in terrestrial ecosystems (Holldobler & Wilson, 1990), and play a critical role in soil health (de Bruyn, 1999) and ecosystem functioning (Evans et al., 2011). The important role of ants in ecosystems, and their often close association with soils (Bottinelli et al., 2015) and plant...
communities (Andersen, 1995) has led to their use as ‘indicators’ of ecosystem health. A major part of this work has been the use of ants as indicators of disturbance (Hoffmann & Andersen, 2003; King et al., 1998; Read & Andersen, 2000), particularly for grazing (Bestelmeyer & Wiens, 1996; Bromham et al., 1999; Hoffmann, 2010; Hoffmann & James, 2011).

There is a substantial literature on ant responses to grazing that has collectively shown location-specific and species-specific responses are common (e.g. Bestelmeyer & Wiens, 2001; Bromham et al., 1999; Hoffmann, 2010; Read & Andersen, 2000; Whitford et al., 1999). Significant effort, therefore, has been invested in the search for general responses of ants to disturbance and their use as bioindicators. This has been aided greatly by the use of ant functional groups, modelled after plant disturbance responses such as disturbance-opportunistic species or disturbance-sensitive species (Andersen, 1995, 1997). Empirical studies and reviews of this approach have supported the use of ant functional groups insofar as providing a useful framework for building predictions about potential ant responses to disturbances, including grazing regimes (Hoffmann, 2010; Hoffmann & Andersen, 2003).

However, important knowledge gaps remain, including the context dependence of ant responses (Hoffmann, 2010), and the relative importance of fine-scale environmental features in influencing ant responses (Yates et al., 2011).

In this study, we examined ant assemblages from sites in a large-scale grazing experiment in a temperate agricultural region of southeastern Australia. Our objective was to examine the relative influence of a suite of grazing, plant, and soil variables on ants with the aim of better understanding which variables drive patterns of ant diversity in this region currently using grazing management to achieve biodiversity restoration. We split our objective into two main questions: (1) how does livestock grazing and environmental variation affect the abundance or species richness of functional groups and common species
of ant? And, (2) how does livestock grazing and environmental variation affect ant
assemblage composition? Previous syntheses of ant responses to grazing have suggested that
disturbance by grazing might be less important for structuring ant communities than natural
variation in vegetation and soil (Hoffmann, 2010; Hoffmann & James, 2011). Put another
way, the presence of livestock might not be as important as the presence of key habitat
attributes in determining the composition of ant communities. We therefore interpreted our
findings in light of this recent synthesis, as well as the generalised responses of ant functional
groups to disturbance and the environment described by Hoffman and Andersen (2003).
Specifically, we predicted that opportunists (e.g. Rhytidoponera spp.) would respond
positively to grazing disturbance (if any response), whereas other functional groups would
show positive associations with features of the environment, such as cryptic species (e.g.
Solenopsis spp.) preferring areas with leaf litter (Hoffmann & Andersen, 2003). We discuss
how our findings might inform biodiversity monitoring in temperate landscapes being
restored via changed livestock grazing regimes.

METHODS

Study area and design
Our study area was located in southeastern Australia, and covers an area approximately 100
km east to west and 150 km north to south (Figure S1). Within this area, 97 sites were
established during 2010-2011 on 29 different farms. All sites were located in Red gum
(Eucalyptus blakelyi) - Yellow box (Eucalyptus melliodora) grassy woodland, which is
characterised by a heterogeneous distribution of eucalypt trees interspersed by open grassland
(Figure S2). This type of grassy woodland was once widespread in southeastern Australia,
but is now a critically endangered ecological community as it has been greatly modified and
reduced in extent due to agricultural practices including grazing (McIntyre et al., 2014).
Farms were grouped into three blocks, each representing a historical grazing practice of either (i) continuous grazing, (ii) long-term holistic grazing (rotational grazing for greater than 10 years), or (iii) short-term holistic grazing (rotational grazing for less than five years). Farms with continuous grazing allow livestock access to sites all year round, whereas farms with holistic grazing typically rotate higher numbers of livestock through sites, but for a limited duration. On each farm, sites were established with one of three different treatments: (i) grazing exclusion; (ii) stewardship; and (iii) ‘business as usual’. Sites with grazing exclusion were not grazed by any livestock. Stewardship sites must not be grazed for the six months of the year during spring and summer periods as part of a contractual obligation to the Environmental Stewardship Program of the Australian government (Lindenmayer et al., 2012). The business-as-usual sites continued grazing in line with the usual practices of the farm (viz. continuous grazing, long-term holistic or short-term holistic grazing). In the long term, these grazing treatments will be used to assess the effectiveness of the Australian Government Environmental Stewardship Program for a range of different biota (Lindenmayer et al., 2012).

**Grazing and environmental variables**

The predominant domestic livestock grazing on farms was by sheep *Ovis aries* and cattle *Bos taurus*. Two measures of livestock grazing pressure were obtained for each site in the previous 12 months as reported by individual landholders. These data were used to generate grazing variables that were used in our analyses: (i) Number of days grazed per year; and (ii) Annual stocking rate. Annual stocking rate was calculated by multiplying the total number of stock grazing on a site by the number of days they were present, and dividing by the area of the site (hectares), and then 365 to give a value per day. Livestock numbers were first standardised to ‘dry sheep equivalent’ to account for differences between sheep and cattle.
Dry sheep equivalent is a standardised measure of feed requirements that allows for comparisons of carrying capacity among different kinds of livestock (McIlwraith, 1997). These two variables were used to represent differences in grazing between the treatments established on each farm.

Field surveys were conducted on each site during January and February 2012 to collect data on ground-layer ecological variables. Sites consisted of a 40 x 200m fixed monitoring area (0.8ha). Nested within each site were two smaller monitoring quadrats (20 x 50m) for measuring vegetation variables. These plots were located at 0-50m and 150-200m along the monitoring site. Within each of these 20 x 50m plots, all tree stems were recorded to 10cm diameter classes (Lindenmayer et al., 2012). A 50m transect was located down the centre of each plot with biometric measurements (Gibbons et al., 2008) taken every metre to assess ground layer native and exotic grass cover, and leaf litter cover. In addition, ground-layer plant biomass was assessed using a rising plate pasture meter to determine average height of ground cover present (Filip’s Manual Folding Plate Meter, Jenquip, New Zealand (Correll et al., 2003).

Soil core samples were collected every 16.5m (n=12) along the centre of the 200m transect of each site. Soil bulk density core samples (10cm diameter x 5cm height steel rings) were taken at 0-5cm soil depth following careful removal of any surface plant and litter biomass present. Following collection, samples 1-4, 5-8, and 9-12 were pooled together to provide three bulked samples per depth per site (see Figure S1). Analysis was performed for each of the three samples per site, and an average was then taken to give a per-site value used in subsequent analyses. Samples were air dried at 35°C for 48 h prior to processing and bulk density was calculated on a sub-sample dried at 105°C for 48 h. Air dried samples were
subsequently crushed, passed through a 2mm sieve, and retained for further chemical
analysis. The > 2mm fraction was separated into organic and non-organic components and
weighed and then discarded. Total carbon and nitrogen was determined with Dumas
combustion analysis (Vario Max, Elementar, Germany) (Matejovic, 1997).

Ant sampling

We sampled ants using pitfall traps that were 250 ml plastic jars dug in flush with the ground
surface, and half-filled with a non-toxic polyethylene glycol solution. Eight traps were placed
in each site, with four traps at the corners of a 5 x 5m square at each end of the site, and
deployed for two weeks in December 2011 to collect ground-active arthropods. Three of the
eight traps were randomly selected and had their ants removed and sorted, with these data
pooled to give one sample per site. All sampling approaches have their limitations, and we
recognise that our sampling approach favoured spatial replication over sampling intensity
within sites, and favoured the more active species of the ant community.

All ant specimens were sorted to subfamily, genus, and species (or morphospecies) by a
specialist at the Australian Museum, Sydney. We placed each ant species into a functional
group using the classification scheme described by Andersen (1995, 1997) (see Table S1).
These were: (i) dominant Dolichoderinae, (ii) subdominant Camponotini, (iii) generalist
Myrmecinae, (iv) opportunists, (v) hot climate specialists, (vi) cryptic species, and (vii) cold
climate specialists.

Statistical analysis

A subset of 78 of the 97 possible sites had the full complement of soil, plant, grazing and ant
data collected, and these sites formed the basis of all subsequent data analysis. It is well
established that livestock grazing can affect soils and plants (Abbott et al., 1979; Yates et al.,
2000), and we recognised that this might lead to confounding of grazing and environmental effects on ants. We therefore used multivariate analysis of variance (MANOVA) to test for the effect of past grazing history on the eight-environmental variables, but found no significant overall effect (Rao F = 1.34, d.f. = 2, P=0.182). This is not to say that past grazing has not had any effect on these variables, but that variation among sites within these broad groupings was not substantially different from variation among sites across all grazing histories. We performed a principle components analysis (PCA) of the eight plant and soil variables and two short-term grazing variables to identify potential co-linearity among variables and broad gradients in environmental variation (Gotelli & Ellison, 2004). We used a correlation matrix of the data as the plant, soil, and grazing variables were quantified using different methods and units.

**Question 1: How does grazing and environmental variation affect the abundance and species richness of functional groups and individual species of ant?** We addressed this first question by using all-subsets generalised linear regression to explore which set of environmental and grazing variables best explained the abundance and species richness of the whole ant assemblage and separate functional groups, as well as the abundance of some individual species. For each model, we used a quasi-Poisson error distribution and a logarithmic link function for ant response variables. Our explanatory variables included the three grazing variables (included grazing history, days grazed per year, stocking rate), three soil variables (soil bulk density, C:N ratio, fraction organic material >2mm) and five vegetation variables (number of tree stems, grass biomass, native grass cover, exotic grass cover, leaf litter cover). We weighted our models using the Schwarz Information Criterion (SIC) (Schwarz, 1978), and present the best two candidate models. All models were run using GenStat 16 software (VSN International, 2013).
Question 2: How does grazing and environmental variation affect ant assemblage composition? To address this second question, we used three different multivariate analyses. First, we used a multi-response permutation procedure (MRPP) to test for a difference in ant assemblage composition among the three grazing history blocks. This test compares the average among-site similarity within each group with the overall similarity among all sites, with greater within-group similarity indicating samples are distinct from the overall set of samples (McCune & Mefford, 2011; Zimmerman et al., 1985). Second, we used partial Mantel tests (McCune & Mefford, 2011; Sokal & Rohlf, 1995) to test the null hypothesis of no correlation between among-site ant assemblage similarity and among-site variation in a second matrix (either environment or grazing) while controlling for a third matrix (either environment or grazing). This test enabled us to examine the independent effects of either the environment or grazing, while controlling for variation in the other. We also tested for a correlation with geographic proximity to see if there was any evidence of spatial autocorrelation in our ant data among sites. For these tests, we used Bray-Curtis distances (Bray & Curtis, 1957) for ant data, and Euclidean distances for our environmental, grazing, and geographic (easting/northing) variables, and determined significance using 9999 permutations of the data. Third, we used Canonical Analysis of Principal Coordinates (CAP) (Anderson & Willis, 2003) to examine how variation in ant assemblage composition was explained by variation in our grazing and environmental variables. This ordination technique uses correlation with continuous variables (our grazing and environmental variables) to constrain axes of variation in ant assemblage composition derived from Principal Coordinates Analysis (metric multi-dimensional scaling) (Anderson & Willis, 2003). We then used a biplot to identify which ant species were strongly correlated with variation among our sites. For all our multivariate analyses, we removed singletons and square-root transformed ant abundance data to reduce the influence of highly abundant species.
RESULTS

Variation in grazing and the environment

Principle components analysis reduced our 10 vegetation, soil, and grazing measures to three new axes that accounted for approximately 63% of total variation in these variables (Table 1). The first axis (PC1) had a high negative loading for grass biomass, and positive loadings for leaf litter, number of tree stems, and C:N ratio, and indicates that most variation among sites can be attributed to co-variation among these variables. The sign of these loadings also indicate that grass biomass decreased when litter, tree stems, and soil C:N ratio increased.

The second axis (PC2) had a high negative loading for large soil organic fragments, and positive loadings for soil bulk density and native grass cover. The sign of the loadings indicated that the soil organic fragments decreased when soil density and native grass cover increased. Notably, the third axis (PC3) had high positive loadings for exotic grass cover and both short-term grazing measures, indicating these variables co-varied with each other (but not with the other plant and soil measures).

Question 1: Ant functional groups and individual species

We collected 87 species of ant (22 061 individuals) from 78 sites (Table S2). The most species-rich genera were the Iridomyrmex (13 species), Monomorium (11 species), Melophorus (10 species), Camponotus (9 species), and Pheidole (9 species), and the most abundant species were Iridomyrmex rufoniger, Pheidole sp B, Monomorium sordidum, and Rhytidoponera metallica. Functionally, the generalist myrmecines were the most diverse functional group (22 species), followed by the dominant dolichoderines (14 species).

All-subsets generalised linear regression revealed exotic perennial grass cover to be the best predictor of the abundance and species richness of the whole ant assemblage (Table 2,
Soil C:N ratio was important for the abundance of the subdominant Camponotini (Fig 2a), the species richness of opportunists, and the abundance of the subdominant Camponotini, dominant Dolichoderinae and cryptic species. Leaf litter cover was an important predictor of the abundance of cryptic species (Fig 2b). Annual stocking rate was found to be the single most important predictor of the abundance of cold climate specialists (Fig 2c). For individual species, the best models were more complex than for functional groups. Although all best models of the individual species had at least one environmental predictor, seven of the eight models also had a grazing predictor, with grazing history the most commonly selected variable. For example, the number of days grazed had a negative effect on *Iridomyrmex rufoniger* (Fig 3a). Native grass cover, in addition to grazing history, had a positive effect on the generalist *Rhytidoponera metallicca* (Fig 3b). The opportunist *Nylanderia* spA was the only individual species that had no grazing variable in the best model and was negatively associated with the number of tree stems (Fig 3c). Additional details of models are given in Tables S3 and S4.

**Question 2: Ant composition**

We found that ant assemblage composition was weakly significantly different among sites grouped by grazing history (MRPP: $T = -1.97$, $A = 0.007$, $P = 0.037$), but that pairwise comparisons between grazing blocks were not significant ($P > 0.05$). Partial Mantel tests indicated a significant correlation between ant assemblage composition and environmental variation when controlling for grazing ($r = 0.161$, $P = 0.002$), and geographic proximity ($r = 0.156$, $P = 0.002$). We also found a significant correlation between ant composition and grazing when controlling for the environment ($r = 0.176$, $P = 0.012$). Notably, no significant correlation was observed for geographic proximity when
controlling for the environmental ($r = -0.045$, $P = 0.206$). This shows there was structuring of the ant community by both the environment and grazing, but not by geographic proximity.

The first two axes of the principal coordinate analysis explained 14.3% and 11.2% of the variation in ant species composition respectively. Constraining these axes by the eight environmental and two grazing variables (Figure 4) revealed that most of the environmental variables were more strongly correlated with variation in the ant community than the grazing variables. In particular, grass biomass and leaf litter cover were strongly correlated with ant assemblage structure along the axis 1, but in opposing directions. Similarly, native and exotic perennial grass cover were strongly correlated, but in opposing directions, with variation in ant composition along axis 2. Several ant species were strongly correlated with the ordination axes, and thus representative of distinct assemblages among our sites (Figure 4). The generalist *Monomorium sordidum* and the Dominant Dolichoderine *Iridomyrmex purpureus* were positively correlated with axis one, and thus characteristic of assemblages found at sites with higher leaf litter. The opportunist *Rhytidoponera metallica*, generalist myrmecine *Monomorium rothsteini*, and dominant dolichoderine *Iridomyrmex rufoniger* had strong positive correlations with axis two, and thus characteristic of assemblages associated with sites with higher native grass cover. Notably, the cold climate specialist *Heteroponera imbellis* was the only species strongly negatively correlated with both axes 1 and 2, and was characteristic of assemblages associated with higher exotic perennial grass cover.

**DISCUSSION**

In this study, we examined the influence of livestock grazing and environmental variation on ant assemblages from sites in a temperate agricultural region in southeastern Australia. Our results provide equivocal support for the global prediction that soil and vegetation have a greater effect on ant community composition than grazing (Hoffmann, 2010; Hoffmann &
This is because we found that grazing history, stocking rate, and days grazed per year were also important for ant abundance, species richness and compositional variation among sites, and suggests a more nuanced role for these different aspects of grazing pressure. Below we discuss our findings in light of the combined effects of the environment and grazing, and the implications of our findings for using reduced grazing to restore ant communities.

**Environmental variation is a key driver of ant community structure**

We found that at least one environmental variable occurred in all of the best models we constructed, except for abundance of cold climate specialists. This includes the whole ant assemblage, different functional groups and individual species, and demonstrates the overall importance of plant and soil attributes on ant community structure. It is notable that exotic grass cover was an important driver of the abundance and richness of the whole ant assemblage (potentially influenced by outliers, Fig 1a), but was not important for functional groups of individual species. This higher level response of the ant community, but not functional groups of individual species, suggests that exotic grass cover could be a general predictor of simpler ant communities with lower diversity. Our constrained ordination showed that grass biomass and leaf litter cover were strongly correlated (but in opposite directions) with the strongest gradient in ant compositional variation (axis 1, Fig. 4). This variation is typical of the structure of grassy eucalypt woodlands, where eucalypt trees are interspersed with patches of grassland (Yates & Hobbs, 1997). The heterogeneous structure of grassy woodlands therefore appears to be an important driver of overall assemblage composition as well as key functional groups. For example, the abundance of cryptic species was best explained by leaf litter (Fig. 2b), which is their preferred habitat (Bestelmeyer & Wiens, 1996; Hoffmann & Andersen, 2003). Leaf litter cover also was positively correlated
with the number of tree stems, and soil C:N ratio. The abundance of the subdominant
Camponotini was positively associated with C:N ratio, indicating they preferred more
wooded areas. In contrast, *Nylanderia* spA (an opportunist) was negatively associated with
the number of tree stems, indicating they prefer more open areas, and this was supported by
our ordination showing a correlation between sites characterised by *Nylanderia* and higher
grassy biomass and native grass cover.

A second important environmental gradient was obvious in our constrained ordination,
and was represented by a change from high exotic perennial grass to high native perennial
grass cover. Sites with high native grass cover were characterised by the occurrence of the
opportunist *Rhytidoponera metallica*, whereas sites with exotic grass cover were
characterised by the presence of the cold climate specialist *Heteroponera imbellis*. Notably,
we also found that exotic grass cover was the best predictor of the abundance and richness of
the overall ant community. However, this variable also was correlated with the two short-
term grazing measures, and highlights the difficulty in separating these confounded and co-
linear measures.

**Effects of grazing**

In addition to environmental effects, we also found compelling evidence of both long-term
(grazing history) effects and short-term (days grazed, stocking rate) effects of grazing on ant
assemblages. Grazing history, stocking rate, or days grazed were frequently identified as
important predictors of the abundance or species richness of ant functional groups we
examined (but not the whole community). It has been suggested that coarse response metrics
such as abundance or richness are often not suitable for detecting the responses of ants to
grazing as they can mask the responses of individual species within the assemblage
(Hoffmann, 2010). However, we also found a significant (albeit weak) difference in ant
assemblage composition between the three grazing history blocks. Past grazing practices therefore appear to be an important driver of differences in ant assemblages. Variation in grazing pressure was also correlated with variation in ant assemblage composition, even after controlling for environmental variation, indicating it has a separate effect in addition to the environment.

We found that eight of the nine individual ant species we analysed had at least one grazing variable in the best model constructed for them. This is more than the general prediction that approximately one quarter to one third of common ant species will display a response to grazing (Hoffmann & James, 2011), although it was to possible to examine all species. Further, the species for which grazing was important were from a mix of functional groups, and not just opportunists as might be expected. For example, we found that *Iridomyrmex rufoniger*, a dominant dolichoderine, had a negative association with the number of days grazed. This contrasts with Lindsay et al. (2009), who found a positive effect of grazing on dominant dolichoderines (i.e. *Iridomyrmex* spp.) in grassy woodland remnants, although their result may have been driven by a different species of *Iridomyrmex*. These apparently idiosyncratic yet common responses to grazing may be due to the different measures of grazing used in our study compared with others (e.g. fixed treatments vs. continuous measures), or other interacting disturbances that may not be accounted for, such as fire history (Foster et al., 2014). A key conclusion from our study is that both historical and contemporary grazing practices appear to be important for shaping ant communities, but that these different measures of grazing may each be important in distinct ways. The builds on other studies of grazing impacts on ants (e.g. Bestelmeyer & Wiens, 1996; Hoffmann & James, 2011) by demonstrating that a single measure of grazing may be insufficient to characterise its influence on insect biodiversity.
Implications for biodiversity restoration

We have shown that grazing, vegetation and soils were important drivers of ant community structure. However, it remains unclear the degree to which historical grazing practices may have altered the environment in our study area, and we found limited evidence of differences in key environmental variables across the three broad grazing history blocks in our study design. However, our principle components analysis did identify co-linearity between exotic perennial grass cover and short-term grazing measures, suggesting some important confounding among key grazing and environmental variables. It is well established that grazing changes soil and plant community attributes (Milchunas & Lauenroth, 1993; Yates et al., 2000), and the impact of grazing on temperate eucalypt woodlands has previously been demonstrated (Bromham et al., 1999; Eldridge et al., 2011; Prober & Wiehl, 2011). In contrast, little is known about the historical diversity patterns of ants in temperate woodlands of southeastern Australia, and it is difficult to conceptualise appropriate restoration goals for ant communities. What is clear, is that restoration actions that target reductions in livestock grazing should lead to improved tree regeneration (Fischer et al., 2009), subsequent increases in tree densities and leaf litter cover, and improved native ground cover and soil organic content (Prober & Wiehl, 2011; Yates et al., 2000). This will benefit some ant functional groups over others, such as cryptic species associated with litter and soil processes, and generalist myrmecines and subordinate camponotini linked to many other ecological processes (Bestelmeyer & Wiens, 1996; Folgarait, 1998; Hoffmann & Andersen, 2003).

Monitoring of ant communities to understand the benefits of changed grazing regimes to restore biodiversity should consider the historical context of gazing, contemporary grazing pressure, as well as the many underlying effects of plants and soils. A key challenge for ant biodiversity restoration in grazing-dominated landscapes will be disentangling grazing from
environmental effects, and aligning this knowledge with restoration goals that focus on returning both ant biodiversity and their ecological functions.

ACKNOWLEDGEMENTS

We thank Derek Smith at the Australian Museum for sorting and identifying ants from our samples. Andrew Higgins at the Australian National University performed the soil chemistry analysis. DBL was funded by an Australian Research Council Laureate Fellowship. Ian Packer from the former Lachlan Catchment Management Authority provided invaluable advice in experimental design and sampling techniques.

SUPPORTING INFORMATION

Figure S1. Location map of our study sites, and a schematic showing arrangement of sampling points for soil, vegetation and ants within each site.

Figure S2. Example of a site from our study area showing the open woodland structure that is typical of the box-gum grassy woodland ecological community. Livestock grazing by sheep or cattle occurred across the sites.

Table S1. Description of ant functional groups.

Table S2. List of ant species arranged by subfamily and functional group, and their count from our pitfall trap samples. Ant specimens were counted and identified to species by a specialist taxonomist, and retained at the Australian Museum, Sydney.

Table S3. Summary of regression models of ant functional groups.

Table S4. Summary of regression models of individual ant species.

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Table 1. Summary of principal component analysis of eight environmental and two grazing variables. Variables with strong axis loadings are shown in bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean ground-layer biomass (kg/ha)</td>
<td>-0.454</td>
<td>0.087</td>
<td>-0.148</td>
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<tr>
<td>Leaf litter cover (%)</td>
<td>0.518</td>
<td>-0.051</td>
<td>-0.018</td>
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<tr>
<td>Number of tree stems (per ha)</td>
<td>0.451</td>
<td>0.102</td>
<td>0.063</td>
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<tr>
<td>Soil C:N ratio</td>
<td>0.482</td>
<td>0.022</td>
<td>-0.164</td>
</tr>
<tr>
<td>Soil organic fragments (% &gt; 2mm)</td>
<td>0.048</td>
<td>-0.675</td>
<td>0.099</td>
</tr>
<tr>
<td>Soil bulk density (g/cm³)</td>
<td>0.131</td>
<td>0.533</td>
<td>0.027</td>
</tr>
<tr>
<td>Native perennial grass cover (%)</td>
<td>-0.196</td>
<td>0.397</td>
<td>0.181</td>
</tr>
<tr>
<td>Exotic perennial grass cover (%)</td>
<td>-0.151</td>
<td>-0.262</td>
<td>0.407</td>
</tr>
<tr>
<td>Annual stocking rate (livestock/ha/yr)</td>
<td>0.054</td>
<td>0.093</td>
<td>0.613</td>
</tr>
<tr>
<td>Days grazed per year</td>
<td>0.080</td>
<td>0.066</td>
<td>0.601</td>
</tr>
<tr>
<td>Percentage variation explained</td>
<td>30.740</td>
<td>17.160</td>
<td>14.700</td>
</tr>
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Table 2. Summary of generalised linear models with top two models of environmental and grazing variables describing the abundance and species richness of the whole ant assemblage, ant functional groups, and individual ant species.

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<thead>
<tr>
<th></th>
<th>SIC</th>
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^GH=Grazing history, GB=Grass biomass, LL=Leaf litter cover, TS=Tree stem count, SCN=Soil C:N ratio, SO=Soil organic fragments > 2mm, SD=Soil bulk density, NPG=Native perennial grass cover, EPG=Exotic perennial grass cover, ASR=Annual stocking rate, DGY=Days grazed per year
Figure 1. Fitted models showing the relationship between percentage exotic perennial grass cover and (a) the abundance and (b) species richness of the ant assemblage. Predicted values are plotted on the original scale.
Figure 2. Fitted models showing the relationship between soil nitrogen, leaf litter and stocking rate variables, and the abundance of (a) subordinate Camponotini, (b) cryptic species, and (c) cold climate specialists, respectively. Predicted values are plotted on the original scale.
Figure 3. Fitted models showing the relationship between grazing and environmental variables and the abundance of (a) *Iridomyrmex rufoniger*, (b) *Rhytidoponera metallica*, and (c) *Nylanderia* spA. Predicted values are plotted on the original scale.
Figure 4. Canonical Analysis of Principal Coordinates ordination showing variation in ant species composition among sites (crosses) and strength and direction of correlations of constraining environmental and grazing variables (dark arrows). Individual ant species (black dots) strongly correlated with the axes in each quadrant of the ordination are also shown to indicate their relative influence on species composition among sites.