RESEARCH ARTICLE

Livestock grazing and forest structure regulate the assembly of ecological clusters within plant networks in eastern Australia

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Abstract

Questions: How do changes in grazing intensity by different herbivores and differences in forest structure affect the assembly of ecological clusters within plant ecological networks in dryland plant communities?

Location: Eastern Australia across an area of 0.4 million km^2.

Methods: We used correlation network analysis and structural equation modelling to examine how changes in grazing intensity, by different herbivores, and differences in forest structure (tree canopy cover, basal area and density) and soil fertility influenced the assembly of ecological clusters of plant communities (i.e. relative abundance of ecological clusters formed by co-occurring plant species within an ecological network) in three forested communities from eastern Australia.

Results: Livestock grazing and forest structure regulated the relative abundance of ecological clusters within plant networks, but their effects on these plant assemblies were highly dependent on the ecological cluster and forest community type, with no single winner or loser across forest types, conditions or grazing intensities. Thus, the relative abundance of some ecological clusters increased under grazing while others declined, a response that was maintained across different forest structures. The relative importance of grazing, forest structure and soil fertility varied across forest community type. The two eucalypt communities exhibited mixed effects of grazing and forest structure (*Eucalyptus largiflorens*) or forest structure only (*Eucalyptus camaldulensis*). In the third (*Callitris glaucophylla*) community, grazing played a larger role in controlling the plant community assembly. Soil fertility (soil C and P) effects were of a similar magnitude to grazing and forest structure, but the effects differed among clusters.

Conclusions: Livestock grazing and forest structure regulated the relative abundance of ecological clusters within networks of plant communities in forests in eastern Australia. Our study uses a novel approach of ecological clusters to show that differences in grazing and forest structure will always disadvantage some plant ecological clusters. Furthermore, changes in one cluster will ultimately affect other clusters. Any changes in management therefore will have varied effects on different ecological plant clusters.

1 | INTRODUCTION

Land-use intensification has had multiple effects on ecosystem properties and processes globally (Godfray et al., 2010). Overgrazing by European livestock has been shown to have substantial negative impacts on ecosystem structure, community composition and functions in areas with a short evolutionary history of grazing by domestic livestock (Eldridge & Soliveres, 2015; Milchunas & Lauenroth, 1993) and these effects are predicted to be greatest in drylands (Gaur & Squires, 2017). Grazing alters plant community composition, favouring exotic species over natives (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2017), and changes the composition of different functional groups (Landsberg, James, Morton, Müller, & Stol, 2003; Travers, Eldridge, Dorrough, Val, & Oliver, 2018). Moreover, changes in forest structure also affect the structure of the understorey herbaceous layer and have been used extensively to increase plant cover and therefore pastoral productivity by removing competition from the woody overstorey (Walker, Robertson, Penridge, & Sharpe, 1986). Both grazing and forest structure have the potential to alter the relative abundance of specific plant community assemblies, but the relative importance and the direct and indirect effects of these two major land management practices on the relative abundance of clusters of plant communities have rarely been considered.

For many years, ecologists have portrayed changes in biotic communities by describing the composition of the constituent taxa, with an emphasis on species-level descriptions. More recently, networks have been used to represent entire communities and their potential complex interconnections (Delmas et al., 2017; Tylianakis, Didham, Bascompte, & Wardle, 2008). Networks provide information on how communities are ordered (e.g. the number of nodes), the size of the network and the connectivity between different species (Delmas et al., 2017). Species within a given network tend to co-occur in discrete clusters (Tylianakis & Morris, 2017) and are likely to show similar responses to different environmental conditions (Delgado-Baquerizo et al., 2018).

Changes in land management practices such as grazing or tree removal are likely to occur at the community level, affecting entire groups of co-occurring plant species. For example, grazing by sheep and European rabbits (*Oryctolagus cuniculus*) has been shown to reduce the establishment of long-lived shrubs such as *Acacia* spp. (Auld, 1990) and other woody plants (e.g. *Callitris glaucophylla*), but have few persistent effects on forbs (Leigh, Wood, Holgate, Slee, & Stanger, 1989) or biennial grasses (Grice & Barchia, 1992). Consequently, the analysis of different ecological networks provides a unique opportunity to identify plant clusters that are advantaged or disadvantaged by land management actions such as grazing or forest tree removal. Such knowledge could be useful to allow us to identify groups of species vulnerable to grazing and to achieve a better understanding of how land-use intensification alters plant community assemblies and, potentially, ecosystem functioning. For example, grazing might lead to increases in ecological clusters of species that support specific ecological processes (e.g. N fixation) or reduce soil C sequestration (Nolan, Sinclair, Eldridge, & Ramp, 2017).

We identified the major ecological clusters within three correlation networks based on plant abundance (% cover) from three forest community types and evaluated how differences in grazing intensity, forest/woodland structure and soil fertility regulated the relative abundance of ecological clusters of co-occurring plant species. We predicted that grazing intensity, forest structure and soil fertility would be key drivers of plant community assembly, but that the importance of these global change drivers would vary with plant cluster and forest community type. If our hypothesis is upheld, the relative abundance of discrete clusters of different plant species should respond differently to changes in grazing, forest structure or soil fertility, allowing us to identify potential winner and loser species associated with these land management practices.

2 | METHODS

2.1 | Study area

The study was conducted at 451 sites across about 0.4 million km² of eastern Australia spanning ~900 km of latitude from east-central New South Wales (NSW) to southern and south-western NSW. The sites were located in woodlands and forests dominated by *Eucalyptus largiflorens* F.Muell. (henceforth Blackbox community), *Callitris glaucophylla* Joy Thomps. & L.A.S. Johnson (henceforth Cypress pine) and *Eucalyptus camaldulensis* Dehnh. (henceforth Red gum). The sites were chosen because they are important for grazing and recreation, and have provided valuable forestry resources for more than a century (Gorrod et al., 2017). Because of their areal extent and the fact that much of the upperstorey is relatively intact, they are important areas for biodiversity conservation (Horner, Cunningham, Thomson, Baker, & Mac Nally, 2012; Smith & Smith, 2014). All communities are well distributed across the study area. The climate is mediterranean and typically semi-arid (Aridity Index 0.26–0.39). Average rainfall (385–460 mm/year) and average temperatures (~18 °C) varied little across the gradient (Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016). Soil textures ranged from sandy clay loams in Cypress pine to silty loams in Blackbox and Red gum communities (Eldridge et al., 2016).

The three communities occupy different geomorphic settings within the landscape. The Blackbox community is typically found

TABLE 1 Mean, minimum and maximum tree density (trees/ha), cover (%) and basal area (m²/ha) for the three communities

Attribute	Blackbox			Cypress pine			Red gum		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Density (trees/ha)	191.8	20.0	1325.0	837.4	20.7	27733.3	363.6	75.0	1550.0
Cover (%)	31.9	0.5	91.0	31.6	2.7	81.7	47.6	2.0	87.0
Basal area (m²/ha)	2.9	0.3	10.0	12.6	0.7	194.1	6.0	2.6	25.6

on higher-level levees of deep fine-textured soils with high silt and clay levels (Eldridge, Koen, & Harrison, 2007) that flood infrequently (10–40 yrs; Smith & Smith, 2014). Red gum communities have deep, uniform soil profiles with high levels of fine sediments and flood about every 8–15 years. Blackbox and Red gum communities occur as riverine forests on the lower terraces of major river systems (Murray, Murrumbidgee and Lachlan Rivers). Cypress pine sites occur on higher-level plains of Quaternary colluvium and aeolian material that receive water solely from precipitation. Livestock grazing is the predominant land use across the study area, and large areas are reserved for conservation (national parks, nature reserves).

2.2 | Assessment of groundstorey and woody plant cover and density, and soil fertility

We surveyed 451 sites, each of 2 ha, 150 in each of Blackbox and Red gum, and 151 in Cypress pine. All sites were sampled within the same season, between late spring and early summer 2013. None of the sites showed evidence of thinning over the past 100 yrs. Within each site, we positioned a 200-m long transect along which we placed five 25 m² (5 m × 5 m) plots (hereafter "large quadrat") every 50 m (i.e. 0 m, 50 m, 100 m, 150 m and 200 m). We placed a smaller quadrat (0.5 m × 0.5 m; hereafter: "small quadrat") centrally within each large quadrat. Within the large quadrat, we recorded the cover, by species, of all vascular plants. Tree canopy cover was measured using the 200-m transect by recording how many of the 100 points located every 2 m along the transect were directly beneath the canopy of any tree. To calculate tree density and basal area, we counted and measured the DBH of all trees within a 20-m wide strip along the 200-m transect and summed the areas of all trees to obtain total basal area (m²/ha). Tree density was greatest in the Cypress pine (837 trees/ha, range: 21–27,700) and least in Blackbox (mean: 192 trees/ha, range: 20–1,325) community. Tree cover was greatest in the Red gum (mean: 48%, range: 2–87%) but similar in the other communities (~ 31%, 0.5–91%). Tree basal cover ranged from 2.9 m²/ha in Blackbox to 12.6 m²/ha in Cypress pine (Table 1).

Within each small quadrat, we collected ~500 g of soil from the top 5 cm using one undisturbed core sample. This was air-dried, passed through a 2-mm sieve and analysed for total C (using high combustion LECO CNS-2000 Analyser), available P using the Olsen method (Colwell, 1963) and soil particle size distribution (hydrometer method; Gee & Bauder, 1986).

2.3 | Assessment of grazing intensity

Along the 200-m transect, we measured the width and depth of all livestock tracks that intersected the transect. The total cross-sectional area (cm²/200 m) of livestock tracks across each site was used as a proxy of historic (long-term) grazing impacts. Tracks are typically deeply incised, last for many decades, and their density and size have been used widely as a proxy of historic grazing (Pringle & Landsberg, 2004). Dung and pellet counts were used to assess recent grazing intensity. Dung and pellets were identified and counted in both small and large plots, separately, for cattle (*Bos taurus* L.), kangaroo (*Macropus* spp.) and rabbit (i.e. rabbits and hares; *Oryctolagus cuniculus* L. and *Lepus europaeus* Pallas). Sheep (*Ovis aries* L.) and goat (*Capra hircus* L.) dung was lumped. The small quadrats were used to count small scats (rabbits, sheep/goats, kangaroos), while the large quadrats were used to count larger dung and pellets (all but rabbit pellets). We collected dung samples of each type of herbivore from each site. Samples were oven-dried at 40 °C and weighed to estimate the mass of pellets, or in the case of cattle, dung events. We used this to calculate the average mass of dung per hectare for of each type of herbivore (Table 2; see Eldridge et al., 2016). Where dung from the same herbivore was counted in both the large and small quadrats, the average mass per hectare was calculated by averaging the values calculated in small and large quadrats.

2.4 | Correlation network

For each plant community, we used correlation network ("co-occurrence networks") analysis to identify ecological clusters of strongly associated plant species using the following protocol. We calculated all pair-wise Spearman's (ρ) rank correlations among all plant taxa (%cover). We focused exclusively on positive correlations as they provide information on species that may respond similarly to different conditions of grazing or forest structure (Barberán, Fernández-Guerra, Bohannan, & Casamayor, 2012) . We considered a co-occurrence to be moderate yet statistically informative if the Spearman's correlation coefficient was >0.25 and $P < 0.01$. This cut-off has a mathematical meaning, as variables that are highly correlated (e.g. Spearman rank coefficients >0.25) are more likely to suffer from multicollinearity, indicating a mathematically plausible link between two variables. It also has a biological meaning, because we only focus on plant species that are strongly co-occurring, and

TABLE 2 Mean (±*SE*) dung loads (kg/ha) for the four herbivore types across the three communities. Sheep dung includes sheep + goats; rabbit grazing includes rabbits + European hares

Community	Cattle		Sheep		Rabbit		Kangaroo	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Blackbox	28.8	4.2	3.4	0.8	2.2	0.5	1.7	18.9
Cypress pine	142.0	39.2	12.1	3.3	12.2	2.4	3.4	52.9
Red gum	17.8	4.1	0.2	0.1	1.0	0.4	2.4	33.2

are therefore more likely to interact with each other within a given plant community. The network was visualized with the interactive platform gephi (Bastian, Heymann, & Jacomy, 2009). Finally, we used default parameters (network resolution = 1.8 in all cases) from the interactive platform gephi to identify clusters of the most strongly interacting plant species. We then computed the relative abundance of each cluster by averaging the standardized relative abundances (*z*-scores) of the species from each cluster. Standardizing the data allowed us to exclude any effect of merging data from different plant groups, for example, tree and forb. We tested our research question in three communities separately, rather than merging data from the three communities. We report on only three clusters from each community that contained the largest number of species.

2.5 | Statistical analyses

For each community, we used structural equation modelling (SEM) to build a system-level understanding of the effects of grazing and trees on the composition of the three plant clusters. Each SEM included all three plant clusters so that we could examine potential trade-offs among the three clusters, i.e. if increases in one cluster resulted in declines in another. SEM was used because it partitions direct and indirect effects of one variable upon another and estimates the strengths of these multiple effects. Unlike regression or ANOVA, SEM offers the ability to separate multiple pathways of influence and view them as parts of a system. It is useful therefore for examining complex relationships among predictors commonly found in natural ecosystems (Newman & Girvan, 2004).

We first developed an a priori model of how we expected our system to behave with increases in grazing intensity and forest structure (Supporting information Appendix S1). These expectations were based on existing knowledge of the effects of grazing on plant community composition. Using our empirical data, we tested the plausibility of a causal model, based on a priori information, in explaining the direct and indirect relationships among variables of interest.

In the a priori model, we predicted that grazing (cattle, sheep, rabbits, tracks, kangaroos), forest structure (cover, density, basal area) and soil fertility (soil C and P, silt + clay content) would have direct effects on different plant clusters, separately, and that there would be a number of indirect effects, mediated by soil fertility (Supporting information Appendix S1). Grazing has been shown to have indirect effects on plant richness via changes in soil P, soil C and soil texture (Eldridge et al., 2017), but the extent to which tree cover/density/basal area might alter composition, either directly or indirectly via soil fertility, is largely unknown.

Hypothesized pathways in our a priori model were compared with the variance–covariance matrix of our data in order to calculate an overall goodness-of-fit using the chi-square statistic. The 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. Before fitting empirical data to our a priori models, we examined the univariate correlations among all variables and standardized (z-transformed) the data. The stability of the resultant models was evaluated as described in Reisner, Grace, Pyke, and Doescher (2013). Analyses were performed using the AMOS 22 (IBM, Chicago, IL, US) software. For each of our models, those with low chi-square, high goodness-of-fit index [GFI] and high Normal Fit Index [NFI]) were interpreted as showing the best fit to our data.

3 | RESULTS

We recorded 822 different plant species across the three communities: 409 from Blackbox, 451 from Cypress pine and 356 from the Red gum communities. A total of 57% of these were forbs, 26% grasses and sedges, 13% shrubs and sub-shrubs and 4% trees. Of these, 64% of all species (523 species) occurred in only one community and only 12% occurred in all three communities. There was relatively high community fidelity, with 145 species in Blackbox, 148 in Red gum and 230 in Cypress pine communities. Across all communities, three quarters of all species were native and two thirds were perennial.

For simplicity, we focused on the top three clusters in each community that included the largest number of species. These clusters accounted for 87% of the 409 species found in Blackbox, 75% of the 451 species found in Cypress pine and 70% of the 356 species found in the Red gum community.

Using the same parameters in all communities, the network analysis discriminated four, five and six separate clusters in Blackbox, Cypress pine and Red gum communities, respectively (Figure 1). In the Blackbox (*Eucalyptus largiflorens*) community, cluster BB1 comprised mainly annual native forbs, shrubs and sub-shrubs that are grazing- and shade-intolerant, whereas BB2 comprised mainly grazing-tolerant exotic grasses and forbs (Table 3; Supporting information Appendix S2). Cluster BB3 was dominated by perennial native forbs.

Our SEM analyses allowed us to detect cluster-dependent effects of grazing intensity and tree density, including positive (winners) and negative (losers) effects on particular assemblies of plant

Blackbox

Cypress pine

Red gum
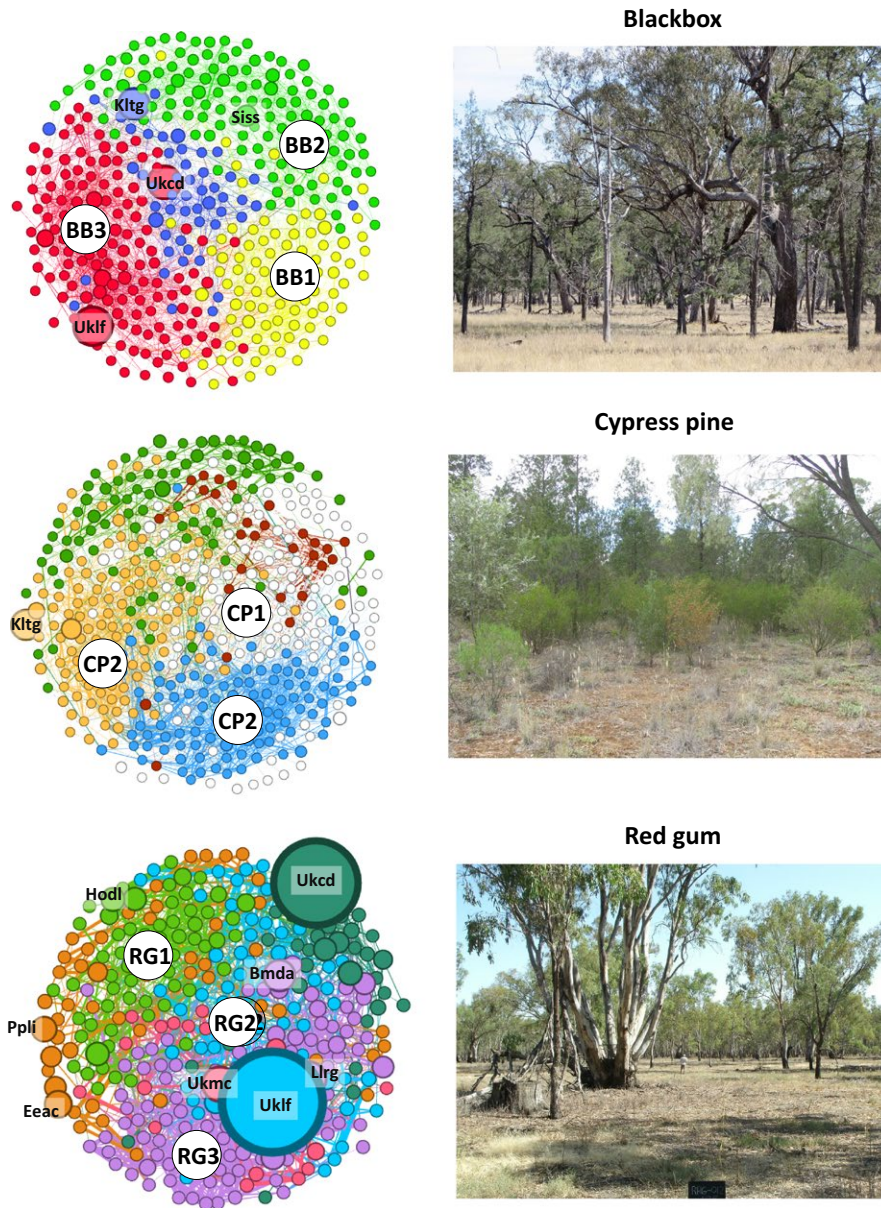
FIGURE 1 Correlation network for the three vegetation communities. Each individual point represents a node (i.e. a species). The links between nodes are based on correlations and illustrate the potential interaction among taxa. Within a community, different colours indicate separate clusters and the three main clusters in each community are indicated (e.g. BB1). Four letter codes indicate different plant species highly indicative of specific clusters. Kltg = *Callitris glaucophylla*, Uklf = *Eucalyptus largiflorens*, Ukcd = *Eucalyptus camaldulensis*, Siss = *Austrostipa scabra* subsp. *scabra*, Hodl = *Hordeum leporinum*, Bmda = *Bromus diandrus*, Ukmc = *Eucalyptus microcarpa*, Eeac = *Eleocharis acuta*, Ppli = *Paspalidium jubiflorum*, Llrg = *Lolium rigidum* [Colour figure can be viewed at wileyonlinelibrary. com]

species. In the Blackbox community, the effects of grazing and trees differed markedly among clusters. For example, increasing tree cover was negatively related to the relative abundance of BB1 and BB2, but positively related to BB3. Further, increases in any one cluster were associated with declines in the others (Figure 2a). Tree cover and density had opposite effects on clusters BB2 and BB3, and, while increasing intensity of cattle grazing was negatively related to the relative abundance of BB1, it was positively related to that of BB2. There were also some indirect effects of trees and grazing on different plant clusters. For example, increasing intensity of rabbit grazing and increasing tree density increased the suppressive effect of soil C on BB1.

Land-use intensification strongly regulated the plant community assembly of the three forest communities (Figure 2). However, the effects of grazing and forest structure on plant assemblies were also highly dependent on the specific cluster and forest community, with

no single winner or loser across all forest conditions or grazing intensities. For example, for the Cypress pine community, there was almost no effect of trees on any plant clusters other than a weak increase in cluster CP3 with increasing tree cover (Figure 2b). Overall, grazing had a larger negative direct and indirect effect on plant clusters than trees in this plant community. For example, increased rabbit grazing, and to a lesser extent cattle grazing, was negatively related, indirectly, to CP2 (native forbs) by enhancing soil P (Figure 2b). Further, increased grazing by rabbits was negative related to CP3 (dominated by perennial native forbs such as *Einadia hastata;* Table 3; Supporting information Appendix S2), indirectly, by increasing soil P, while increased tree cover and basal area increased CP3 by enhancing soil C. In the Red gum community, increasing tree basal cover, foliage cover and density directly altered cluster RG1, but increased cattle grazing suppressed RG1, which comprised mainly native forbs such as *Sclerolaena muricata* (Supporting information Appendix S2).

TABLE 3 General description of the plant ecological clusters, their response to grazing, changes in forest structure and examples of characteristic plant species

Cluster	Description	Response type	Example plant species
BB1	Annual native forbs, shrubs and sub-shrubs	Reduced by cattle grazing; suppressed by tree cover and density	*Atriplex lindleyi* *Vittadinia dissecta*
BB2	Annual exotic grasses and forbs; perennial grasses	Increased with cattle grazing and tree density; reduced by tree cover	*Echium plantagineum* *Brassica tournefortii* *Rhytidosperma caespitosum*
BB3	Perennial native forbs	No effect of grazing; increased with tree cover; reduced with tree density	*Atriplex semibaccata* *Sida corrugata*
CP1	Perennial plants	Reduced by cattle grazing; no effect of forest structure	*Wahlenbergia gracilis* *Atriplex stipitata*
CP2	Native forbs	Reduced by cattle and rabbit grazing; no effect of forest structure	*Leptorhynchos squamatus* *Ptilotus sessilifolius*
CP3	Perennial native forbs	No effect of grazing; increased with tree cover	*Einadia hastata*
RG1	Perennial grasses	Increased with cattle grazing; increased with cover and basal area; reduced with density	*Enteropogon acicularis* *Rytidosperma caespitosum*
RG2	Forbs	No grazing or forest structure effects	*Dichondra* sp.
RG3	Native forbs	No grazing or forest structure effects	*Sclerolaena muricata*

4 | DISCUSSION

We found that the relative abundance of clusters within ecological networks of plant communities was regulated by grazing, forest structure and soil fertility across the three communities. Further, the effects of grazing, forest structure and soil fertility on plants were community- and plant cluster-dependent. Few plant species within a given community declined (losers) in response to changes in the two land-use intensification drivers, while other clusters were promoted (winners) or showed no change. Our results are important because they identify those plant clusters, and their constituent taxa, that are likely to respond to different drivers, providing important insights into potential mechanisms and traits that might make plants winners or losers under different intensities of land use. Our work also suggests that, unlike traditional species-level approaches, networks allow us to identify entire groups of species that are likely to respond to changes in grazing by different herbivores or different forest management practices, thereby providing information that is important for conservation of biodiversity in these forested systems.

We found substantial variation in the response, from positive to negative or benign, of different clusters of plant species to changes in forest structure and/or grazing intensity, with effects depending on plant community type, herbivore type and plant cluster. For example, the three understorey Blackbox clusters responded differently to increasing tree density, cover and basal area, with either declines (BB1) or a mixture of increases and declines in BB2 and BB3. Similarly, there were modest but significant positive effects of tree cover, basal area and cattle grazing on RG1, but negative effects of a similar magnitude for tree density. Our catalogue of plant clusters and species within them, and their likely responses to the two drivers (Supporting information Appendix S2) provide useful information for land managers on how to use different management scenarios

to promote or enhance particular plant community assemblies or manage against others. Further, membership of a cluster was mutually exclusive, so that increases in one cluster were automatically associated with declines in another, and *vice versa*. Interrelationships among clusters were largest in the Blackbox community. We can link, therefore, management that affects one cluster with predicted changes in other clusters.

4.1 | Grazing effects on plant ecological clusters

Overgrazing is a major disturbance process in woodlands and forests (Lunt, Eldridge, Morgan, & Witt, 2007), removing grazing-sensitive species, and favouring exotic annual species (Eldridge et al., 2017; Travers et al., 2018). Grazing effects were apparent in all communities, particularly Blackbox and Cypress pine, although we observed a mixture of responses to grazing, with entire clusters of plant species that were grazing winners or grazing losers. The effects of grazing were clearly herbivore- and cluster-specific. For example, the standardized total effects of cattle grazing ranged from negative (BB1 and BB3) to positive (BB2) in Blackbox, and cattle effects were negative for CP1 and CP2 in Cypress pine, but positive for RG2 in Red gum (Table 4).

Species membership of various clusters and their responses to grazing is consistent with results of studies that have identified Australian plant species as grazing winners or losers (Friedel, 1997; Gibson & Kirkpatrick, 1989; Landsberg et al., 2003; Leigh, Wilson, & Mulham, 1979; Leigh et al., 1987; McIntyre, Heard, & Martin, 2003). For example, the abundance and cover of CP1 forbs (*Goodenia* spp. *Vittadinia cuneata* var. *cuneata*) and perennial grasses (*Rytidosperma erianthum*) decline with heavy grazing (Landsberg et al., 2003). Livestock grazing has been shown to lead to reductions in the forb *Sclerolaena diacantha* in different communities (BB1 and CP2; Leigh
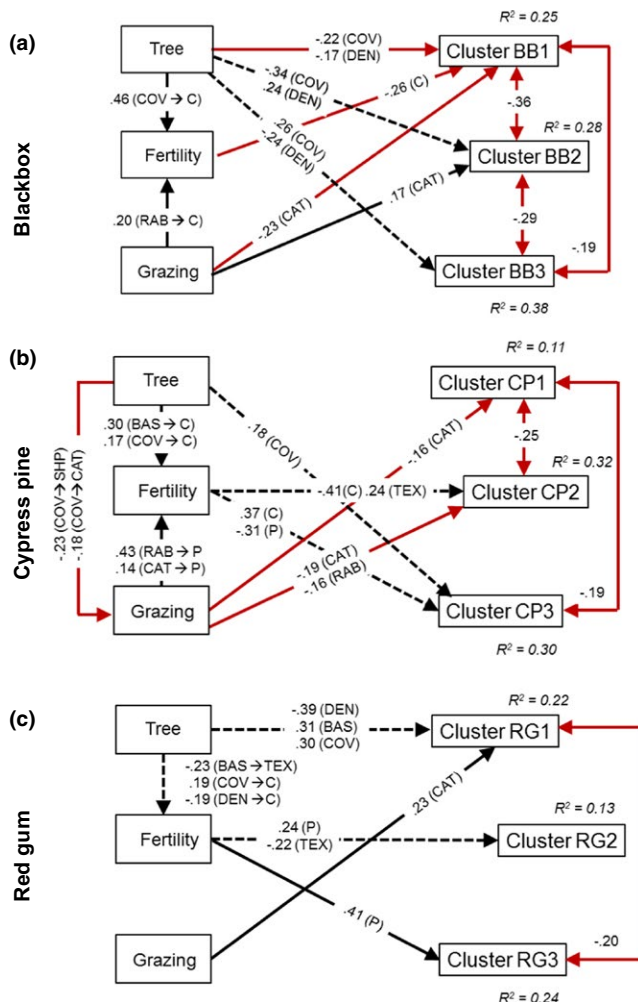
FIGURE 2 Structural equation models of the direct and indirect effects of tree, grazing and fertility on different plant clusters. "Tree" comprises foliage cover (COV), basal cover (BAS) and density (DEN); grazing comprises recent grazing by cattle (CAT), sheep (SHP), rabbits (RAB) and kangaroos (KAN) and historic livestock is represented as livestock tracks (TRA). Fertility comprises: soil texture (silt + clay content, TEX), soil P (P) and soil C (C). SEM, superimposed on arrows, are analogous to partial correlation coefficients and indicative of the effect size of the relationship. Pathways are negative (red unbroken line), positive (black unbroken line) or mixed negative and positive (black broken lines). The proportion of variance explained (R^2) in each cluster is given. Blackbox: χ^2 = 12.36, df = 12, P = 0.42, GFI = 0.981, RMSEA = 0.001, Bollen-Stine = 0.90. Cypress pine: χ^2 = 11.20, df = 12, P = 0.051, GFI = 0.984, RMSEA = 0.020, Bollen-Stine = 0.166. Red gum: χ^2 = 8.42, df = 9, P = 0.49, GFI = 0.986, RMSEA = 0.001, Bollen-Stine = 0.370 [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 1979; Landsberg et al., 2003) because it is moderately palatable to livestock (Cunningham, Mulham, Milthorpe, & Leigh, 1992). Similarly, the shrubs *Myoporum* (CP1), *Eremophila glabra* (CP1) and *Eremophila longifolia* (CP2) are known to decline under increasing intensity of livestock (Chesterfield & Parsons, 1985; Landsberg et al., 2003) and rabbit (Auld, 1993) grazing. These shrubs often reach high densities when livestock are removed (Daryanto & Eldridge, 2010).

Hypochaeris radicata (RG1) has a rosette-forming habit and responds positively to high levels of grazing (Pettit & Froend, 2001). Its prostrate habit, content of alkaloids, phenolics and saponins likely reduce its palatability to vertebrate herbivores (Senguttuvan, Paulsamy, & Karthika, 2014), and its ability to produce abundant wind-dispersed seeds, make it a grazing winner.

Interestingly, our SEMs further suggest that there are indirect, as well as direct, effects of grazing intensity and tree density on the relative abundance of particular clusters via changes in soil properties. For example, increases in the relative abundance of *Eucalyptus largiflorens* (Figure 2a) and *Callitris glaucophylla* (Figure 2b) within BB1 and CP2, respectively, were associated with increases in soil C. Soil C pools are larger close to the canopies of woody plants due to higher biological activity, seed rain and infiltration. We can view BB1 and CP2, therefore, as comprising species that favour open, unshaded sites with lower levels of soil C. Our analyses indicate that these species are predominantly a mixture of perennial and annual native, open area specialists (Supporting information Appendix S2). Cattle grazing was negatively related to BB1 and CP1, which comprised N-fixing shrubs such as *Acacia stenophylla* and *Senna artemisioides*. This has the potential to reduce soil N pools in these forests (Forrester, Bauhus, Cowie, & Vanclay, 2006), with indirect effects on plants comprising the other clusters within Blackbox (Figure 2a) and Cypress pine (Figure 2b) communities.

We also found that effects of soil fertility, particularly soil C and P, had important impacts on plant clusters, and the standardized total effects were of a similar magnitude to grazing and forest structure effects in BB1, CP2 and CP3, and RG3 (Table 4). For example, there were strong negative effects of soil C and P on CP2 and CP3, respectively, and strong positive effects of soil P on cluster RG3 (Figure 2). The results suggest to us that land management activities, such as control of rabbit grazing, are likely to have an impact on plant clusters, for example, by suppressing the negative effect of soil C on BB1 or reducing the negative effects of soil P on CP3. The mechanism for these latter two effects likely involves excavation of subsurface soils by rabbits and exposure of clay-rich sediments with higher P content.

4.2 | Forest structure effects on plant ecological clusters

Changes in forest structure such as reductions in density by thinning have been shown to produce mixed results for understorey species, with increases (Metlen & Fiedler, 2006), reductions (Wienk, Sieg, & McPherson, 2004) and a mixture of responses (Dodson, Peterson, & Harrod, 2008) in the plant community composition of dry coniferous forests. Our SEMs allowed us to examine potential effects of changes in forest structure without removing trees, allowing us to disentangle potential effects of forest structure and grazing across three forest/woodland communities by tracking naturally occurring sites with different levels of tree cover, density or basal area. Responses to different levels of forest structure varied among different clusters and plant community types. In previous studies, a lack of significant effects

TABLE 4 Standardized total effects (STE) derived from the structural equation modelling of forest structure (cover, density, basal area), grazing (cattle, sheep, rabbit, kangaroo, tracks), fertility (soil C, silt + clay content, soil P) and different plant clusters

Attribute	Blackbox			Cypress pine			Red gum		
	BB1	BB2	BB3	CP1	CP2	CP3	RG1	RG2	RG3
Forest structure									
Cover	−0.31	−0.29	0.31	0.01	−0.14	0.30	0.27	−0.09	−0.09
Density	−0.07	0.20	−0.23	0.06	0.05	−0.06	−0.33	−0.04	−0.20
Basal area	0.01	0.10	0.21	−0.15	−0.14	0.10	0.27	0.07	0.09
Grazing									
Cattle	−0.23	0.20	−0.14	−0.16	−0.19	−0.04	0.20	0.10	−0.07
Sheep	0.04	−0.06	−0.04	−0.15	0.10	−0.05	−0.10	−0.08	0.04
Rabbit	0.01	−0.09	0.11	−0.18	−0.12	−0.10	0.01	0.13	0.06
Track	−0.14	0.02	−0.15	0.04	−0.10	0.01	−0.05	−0.09	−0.14
Kangaroo	0.02	−0.01	0.11	0.01	0.06	0.14	−0.05	0.01	0.01
Fertility									
Texture	−0.21	−0.06	−0.04	0.13	0.12	0.05	−0.07	0.09	0.17
Soil C	−0.26	−0.05	0.36	0.07	−0.42	0.36	−0.08	0.11	0.19
Soil P	0.06	0.17	−0.33	−0.06	0.05	−0.30	0.00	0.03	0.02

Note. The STE is the sum of all direct and indirect effects of one attribute on a particular cluster. Large negative numbers indicate a large overall negative effect of a particular attribute on a cluster and vice versa.

in the understorey might simply have been due to increases in one cluster being offset by declines in another. For example, Horner et al. (2012) showed that native plant richness was negatively correlated with increasing density of *Eucalyptus camaldulensis* trees, but that this may have been confounded with flooding history, given that reduced flooding favours a lower density of trees (Gorrod et al., 2017) and a higher abundance of exotic plants (Stokes, Ward, & Colloff, 2010).

Plant species advantaged by densely timbered, low cover sites (BB2) included the perennial grasses *Rytidosperma caespitosum* and *Panicum decompositum* that are strongly grazing-intolerant and would be advantaged where high tree density prevents the ingress of larger-bodied herbivores. We found a negative relationship between tree cover and grazing by cattle and sheep in Cypress pine, but no significant effect for density. Although tree cover and density were weakly correlated in our study (Pearson's $r = 0.19$, $P = 0.02$), the differing responses of the clusters suggest that different mechanism may be at play. Increased tree cover suppressed BB1 and BB2 (annual forbs), likely due to competitive effects where forbs are unable to tolerate reduced light penetration due to canopy closure (Ares, Neill, & Puettmann, 2012) . However, perennial forbs (BB3) are likely better adapted to shaded conditions associated with high tree cover given that they are long-lived. This effect likely relates solely to habitat structure, given that there were few grazing effects on these groups.

5 | CONCLUSIONS

Our work provides a novel perspective on how different environmental drivers, grazing, forest structure and to a lesser extent soil

fertility, affect the abundance of clusters of plant species within ecological networks from three plant communities. Our work provides evidence that the relative abundance of ecological clusters is affected by grazing and tree density, and responds differently to changes in forest structure, and herbivore type and intensity. It also shows how increases in one cluster of species within the network is intimately linked to declines in a second cluster, reinforcing the notion that changes in grazing, forest structure and soil conditions will create a patchwork of plant winners and losers.

Our work also suggests that blanket stocking rate recommendations or management prescriptions for altering forest structure by removing trees will have markedly different effects on different groundstorey species. It is critical, therefore, to consider how different land management actions involving manipulation of grazing, control of feral herbivores or changes in forest structure might affect the groundstorey vegetation. A knowledge of how land-use drivers affect different plant clusters is important if conservation agencies are to design appropriate policies to guide the management of *Callitris* and eucalypt woodlands and forests in eastern Australia, as endangered species might be directly or indirectly involved in ecological clusters negatively responding to land-use intensification.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Structural Equation Model procedures and the *a priori* model

Appendix S2 Complete list of 938 plant species from eastern Australia classified in relation to the nine clusters, including plant origin (native, exotic), perenniality (perennial, annual), growth form (forb, grass, geophyte, sedge, shrub, subshrub, tree, vine) and status (winner, loser, no effect) under increased grazing and changes in forest structure