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More Resistant Than Resilient: Effect of 15 Years Conservation Management on Ground-Layer Vegetation Composition in Temperate Woodland and Forest

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ABSTRACT

We monitored ground-layer vegetation in permanently marked plots in a temperate grassy woodland/sclerophyll forest mosaic, after the removal of sheep, but with continuing macropod grazing. Data collection over 15 years encompassed extremes of drought and high rainfall. Plots were stratified to sample 13 subhabitats reflecting variations in vegetation type and landscape position. Species composition varied with: (i) site productivity (grassy vs sclerophyll forest), (ii) soil moisture (landscape position) and (iii) presence of tree canopies in open grassland. After 15 years, most subhabitats retained their distinctiveness, with net changes suggestive of nutrient decline under tree canopies and increasingly mesic conditions on higher slope positions. Analysis of species richness of 18 origin and life-form groups over time revealed three types of responses: (i) stable, (ii) linear increase and (iii) a quadratic response. The latter was identified for native and exotic species in all habitats, specifically for annuals and short tussocks. There were sustained linear increases in the species richness of three native life forms (geophytes, subshrubs and leafy herbs) suggesting improvements in conservation status, while most native perennial groups were stable. Large perennial native grasses (*Themeda triandra*, *Rytidosperma pallidum*, *Poa sieberiana* and *Aristida ramosa*) maintained their initial dominance, while that of *Lomandra filiformis* and *Melichrus urceolatus* increased. The level of dominance of exotics was largely sustained, although exotic annuals fluctuated in response to seasonal conditions. The frequency of exotic perennial dicots increased slightly, despite intensive control efforts. We attribute the persistence of biomass under severe drought to the high dry matter content of many ground-layer dominants, which served to protect soil and provide refuge to palatable geophytes and native herbs. Our findings are consistent with ecological models that predict that cessation of fertiliser inputs and heavy livestock grazing will promote vegetation with ecosystem attributes resistant to climate extremes.

1 | Introduction

Removal of livestock grazing is the primary management action associated with the transition of land to conservation management (Lunt et al. 2007). It may be required for the remediation of damage to soils (DCCEEW 2023) and allows for the regeneration of trees and mid-story shrubs (Briggs et al. 2008) and potential recovery of grazing-sensitive species (Trémont 1994; Lunt et al. 2007; McIntyre et al. 2018). Nonetheless, conservative livestock grazing can also be compatible with the maintenance of grasslands of high conservation value (McIntyre and Martin 2001; Zimmer et al. 2010) and destocking is not always advantageous, there being a complex legacy of past ecosystem modifications that can limit the

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potential for spontaneous improvement in ecological integrity (Neilly et al. 2021; Price et al. 2021). The most difficult restoration scenarios in temperate woodlands are where the native soils have been rendered more productive by soil enrichment, for example, fertiliser applications, additions of lime and the sowing of legumes (McIntyre and Lavorel 2007; McIntyre et al. 2017). Exotic species can outcompete natives in the presence of elevated nutrients when grazing ceases (Skinner et al. 2010; Schultz et al. 2011). While available phosphorus will decline over time, the legacy of nitrogen can be perpetuated through seasonal cycling of available nitrates via the life cycle of exotic annual species (Jones and Woodmansee 1979; Prober et al. 2002). With very little remaining grassy eucalypt woodland, and even less in excellent condition in southeastern Australia (DCCEEW 2023), sites considered for conservation and restoration invariably have some history of livestock grazing and soil eutrophication.

The nature of the landscape matrix can also influence a postlivestock trajectory. In rural areas, the removal of livestock does not necessarily mean a complete cessation of grazing or herbivory, as grazing pressure may be maintained by native and/or feral herbivores, sometimes with detrimental effects (Gordon et al. 2021; Neilly et al. 2021). In urban areas, native herbivores may be absent, fire regimes may change, and the offsite effects of a hostile matrix have been reported to reduce diversity in grassland (Williams et al. 2006). In both rural and urban landscapes, the fragmented nature of grassy woodland means that the importation of exotic propagules and an absence of native propagule dispersal are likely to inhibit improvements in vegetation condition unless carefully managed (McIntyre 2011; McIntyre, Lewis, et al. 2022). These contextual variables are important, but hard to quantify, and are not always reported in studies. For example, few studies have specifically reported a switch from livestock and macropod grazing to macropod-only grazing (Price et al. 2021), although it is likely the most common scenario for the establishment of conservation reserves in rural landscapes.

The highly complex task of predicting species dynamics in grasslands (Lunt et al. 2007; Price et al. 2019), combined with the limited number of reported observations (Price et al. 2021), and the intricacies of interpreting multiple studies, have led practitioners to use expert elicitation in an attempt to reach some consistent conclusions. In one such exercise, Dorrough et al. (2019) concluded that while there was a wide range of predictions regarding the response of vegetation to conservation management, gains in species richness were considered to be small, and most likely to occur when the starting condition of vegetation was low to moderate. While such exercises can summarise the state of our knowledge base, a recent review by Price et al. (2021) reveals a deficit of long-term studies and patchy coverage of the variety of disturbance switches that can be applied when land use is converted to conservation management. Both these are required for a systematic and consistent understanding of the consequences of management actions, one that takes into account both land use legacy and landscape contexts.

This study investigates the nature of change in the ground layer within a landscape supporting box-gum grassy woodland and dry sclerophyll forest under conservation management. We analyse plant species composition, as well as life-form and life-cycle groups within exotic and native species.

More specifically we ask:

a. Does native species diversity spontaneously increase?
b. Is there improvement in the native/exotic balance in the landscape?
c. Are compositional changes similar across all subhabitats?
d. What are the implications of the changes observed for ecosystem prospects under climate change?

We have used a before-after design (*sensu* Christie et al. 2019) to monitor permanent plots, over a 15-year period, during which extremes of drought and high rainfall occurred. Thirteen subhabitats were sampled across a 50-ha landscape of sclerophyll forest and grassy woodland, to account for variation in vegetation type, structure and landscape position. The conservation management actions applied that were most relevant to the ground-layer response at the scale reported here were: (i) the cessation of sheep grazing resulting in reduced grazing pressure by macropods only, and (ii) the ongoing control of some exotic species. Our plot results are interpreted in the context of previously reported species changes on the study site at landscape scale (50 ha, McIntyre, Lewis, et al. 2022).

2 | Methods

2.1 | Study Site

The study site is located on the western side of the Yass River valley, on the southern tablelands of New South Wales. Permanent plots were established across a single 50 ha paddock (centre 34°58′30″ S, 149°12′23″ E) covering an altitudinal range of 50 m (585–635 m). The soil parent materials are Ordovician sediments (Jenkins 2000) and the clay-loam soils are acidic (pH 4–5), nutrient-poor and highly erodible. The mean annual temperature is 20°C (maximum) and 6.5°C (minimum). Annual rainfall averages 644 mm, with monthly averages ranging from 46 mm (in May, June, July) to 66 mm (November) (From 1935, Ainslie Station 70000, http://www.bom.gov.au, Table S1). Extremely wet or dry conditions may be experienced in any month of the year, and frosts are frequent in winter.

Over the 50 ha, the vegetation comprises roughly equal amounts of (i) Southern Tableland Dry Sclerophyll Forest (hereafter sclerophyll forest), (ii) Southern Tableland Grassy Woodland (hereafter grassy woodland) (after Keith 2004) and (iii) grassland-open woodland mosaic derived from tree clearing. While there is evidence of past ringbarking, much of the now open area was subjected to pasture development in 1972–74. This involved most trees being bulldozed into windrows and burnt, followed by chisel-ploughing, superphosphate addition and sowing to *Trifolium* spp. The entire site was also burnt by wildfire in 1975. There have been no further pasture inputs, and soil sampling in 2006 indicated that available soil phosphorus had returned to 'native' levels (Colwell P, 5 mg.kg^{-1}; see

McIntyre 2008). Conversion from pastoral use to conservation use was initiated at the end of 2004 with the permanent removal of all livestock. The surrounding landscape matrix comprises pastures, large areas of sclerophyll forest regrowth and a low density of dwellings.

The study site has a 200-year history of livestock grazing. In the 25 years prior to stock removal, 100 wethers grazed the site as a single paddock. This was reduced to 65 during the Millennium Drought (2000–04). While this stocking rate of 2 Dry Sheep Equivalent/ha is midrange carrying capacity for native grassland in the region (Langford et al. 2004) one third of the study area was dry sclerophyll forest, which suggests higher grazing pressures.

2.2 | Management Regime Over the Monitoring Period

The study area, and the broader landscape, supported macropods both before and after removal of livestock. These moved freely within the 50 ha and through numerous entry points on the boundary fence. Weekly records over the 15-year monitoring period indicate Eastern Grey Kangaroos (*Macropus giganteus*) to be the most abundant of the vertebrate herbivores, regularly present as a large group of up to 40 individuals, with grazing focussed on open grassy habitats. Red-necked Wallabies (*M. rufogriseus*) were observed singly or in groups of less than 10, primarily in shrubby grassland, while *Wallabia bicolor* occurred as occasional individuals mostly confined to dry sclerophyll forest. Hares were present in very low numbers with no grazing impact evident, and rabbits were absent. These numbers, together with the estimated grazing impact of kangaroos (0.4 dry sheep equivalent; Dawson and Munn 2007) suggest overall grazing pressure to be less than half relative to livestock presence in the 25 years before sheep removal. Variations in grazing pressure were both seasonal (varying with rainfall and growth rates) and spatial. Some open areas were persistently utilised and maintained as grazing lawns throughout the study, while most of the site was lightly and selectively grazed. The low productivity of the dry sclerophyll forest, and the tendency for all macropods to camp there in daytime meant that shrub browsing was persistently severe over the monitoring period.

Conservation management of the ground-layer across the site was undertaken by the landholders (the senior authors) with academic and practical skills relating to woodland ecology. The actions were applied frequently and consistently over the monitoring period with an estimated effort of 2 days per week. The work comprised: (i) ongoing manual removal, but not eradication, of selected invasive species with sparing or no herbicide (*Rubus* sp., *Nassella trichotoma*, *Cassinia sifton*, *Cirsium vulgare*, *Erigeron* spp., *Hypericum perforatum*, *Solanum nigrum*, *Sonchus* spp. *Lactuca* sp.), (ii) surveillance of weeds and eradication of seven newly colonising exotic species, (iii) (re)introduction of native forbs and shrubs (see McIntyre, Lewis, et al. 2022), (iv) assisted dispersal of existing species within the site to new locations to increase population size and range, (v) manual thinning of eucalypt seedlings to maintain grassland for both fire safety and conservation, (vi) treatment of sheet erosion and gully erosion and (vii) small-scale cool burning of accumulated grass litter in limited areas.

2.3 | Study Design

We established 73 permanently marked plots (5 × 6 m) and assessed the ground-layer vegetation in 2005, 12 months after the removal of sheep, allowing for some growth of the closely cropped sward and more accurate identifications. Four subsequent surveys of these plots were conducted in 2010, 2013, 2016 and 2020 (intervals of 5, 3, 3, 4 years, respectively). Plot (= site) locations were stratified to sample the range of vegetation and landscape positions over the 50-ha study area. These were categorised in terms of vegetation structure, tree species and landscape position, and numbers of plots were roughly proportional to the representation of the area of the habitats, although 'Sheep Camps' were over-represented. All but the 'Forest' category were sites located in grassy woodland or derived grassland broadly associated with grassy woodland eucalypts.

1. *Forest*—in 16 ha area of sclerophyll forest with continuous tree canopy characterised by *Eucalyptus rossii* and *Eucalyptus mannifera* on the mid- and upper slopes and by *Eucalyptus macrorhyncha* and *Eucalyptus polyanthemos* on the mid and lower slopes ($n = 17$, Upper = 6, Mid = 7, Lower = 4).
2. *Open*—grass-dominated sites away from tree canopies ($n = 27$, Upper = 8, Mid = 10, Lower = 9).
3. *Tree*—under a well-developed canopy of a eucalypt (*Eucaly. macrorhyncha*, *E. polyanthemos* or *E. melliodora*) in a scattered tree or woodland setting ($n = 11$, Upper = 4, Mid = 3, Lower = 4). Habitats 2 and 3 were intermingled over an area of approximately 34 ha.
4. *Sheep Camp*—these were physically equivalent to upper slope 'Tree' habitat but carried a nutrient legacy from their previous use by sheep as locations for habitual resting (Robinson et al. 1983; Niu et al. 2009), as evident from accumulated and recent dung ($n = 4$, Upper = 4, Mid = 0, Lower = 0). Area < 1 ha.
5. *Drainage Line*—intermittent watercourses (first and second order) totalling 1.2 km in length, with scour ponds and incised sections (as described in Eyles 1977). Trees were largely absent from the drainage line sites ($n = 14$, Upper = 4, Mid = 4, Lower = 6).

For habitats 1–3, upper slopes included hill crests and shoulders, lower slopes included break of slope and flats, while mid-slopes were intermediate locations. Slope position for drainage lines was determined from the overall altitude at the study site as follows: upper (first order drainage lines, > 615 m), mid (first order, 600–615 m) and lower (second order drainage line, < 600 m).

Burning was applied to half the open and tree canopy plots 1–5 times over 15 years, depending on the rate of biomass accumulation. No burning was applied to drainage lines or sclerophyll forest plots. There were no discernible effects of fire on floristic composition, and the treatment is not reported here.

2.4 | Survey Methods and Data Generated

The choice of sampling year was flexible to ensure that observations were preceded by near-average or above-average rainfall in winter–spring. The same two people (SM, JL) did all the plot assessments. The presence of all herbaceous species (except cryptogams) and shrubs with a potential growth height of up to 1.5 m was recorded in each survey. The seasonality of sampling was fixed and involved two assessments: early spring (late September–early October) when cool season geophytes and early annuals were apparent, and late spring (late November–early December) for warm-season species. The second survey also assessed relative abundance by ranking the top 10 plant species by biomass. The two assessments were merged in the final data set, with species recorded in early spring being recorded as present or ranked if they were rated in the top 10 in the second survey.

Two forms of floristic data were used in analyses:

i. Presence/absence data. The proportion of sites present (= relative frequency), referred to in the text as *frequency*, is presented in Table S2 for all species recorded. Data were analysed as species density (number of species per 30m^2 plot) and referred to as *species richness*.

ii. Biomass rankings. These were used to determine *relative abundance* (also referred to as dominance) which was scored as follows: 1st ranked = 11; 2nd ranked = 10; 3rd ranked = 9, and so on, down to species that were ranked 11th onwards scored as 1. In grassland, this scoring method is the equivalent of an arc sine, square-root transformation of relative biomass (Mannetje and Haydock 1963). Relative abundance (Table S2) represents the relative performance of a species under the conditions prevailing at the time, and does not reflect the total amount of biomass, which varied between seasons.

2.5 | Floristic Analyses

Relative abundance data were used to create a dissimilarity matrix using the Bray and Curtis coefficient (Oksanen et al. 2022) for use in nonmetric multidimensional scaling ordinations (NMDS) for the 73 plots in each of the five surveys. The function metaMDS (Oksanen et al. 2022) was used to generate the ordination solution using the default options which implies that the function monoMDS (Oksanen et al. 2022) was used with the model set to 'global' (equivalent to Kruskal's [Kruskal 1964a; Kruskal 1964b] original NMDS). The minimum and maximum number of iterations was set to 1000 which gives a minimum number of random starts ensuring that a global rather than a local optimum solution has been found. The treatment of ties was set to be true, implying that where equal observed dissimilarities are allowed to have different fitted values. The NMDS site scores for Axes 1 and 2 were used to calculate the Euclidean distances moved by each plot from its previous position in 2010, 2013, 2016 and 2020. Centroids were plotted for each of the 13 combinations of habitat type and slope position, to illustrate the extent and direction of vegetation change over the monitoring period.

2.6 | Analysis of Species Richness by Origin and Life-Form

Species or species entities were classified initially by origin (native/exotic), and then into relevant trait groups based on life form and life cycle (Cornelissen et al. 2003) (Table 1). To determine whether there was any consistent change in species richness of these groups over the five surveys, a series of Generalised Linear Mixed Models were fitted. The fixed effect tested was Year, and the random effects were Plot to account for the repeated measures on the individual plots. The function glmmTMB from the R package glmmTMB (Brooks et al. 2017) was used to estimate the parameters of the GLMM fitted. Three models, a null model, a linear change and a quadratic change, were fitted. The best model was selected using the R package AICcmodavg (Mazerolle 2020) based on Burnham and Anderson (2002). The models were assessed by comparing the AICc using an information theoretic approach (Mazerolle 2020) and selecting the model with the lowest value. Models that differed by less than 2 units were considered to be equivalent, and the more parsimonious model was selected.

A second analysis focussed on species richness by origin (native/exotic) within each of the five habitats (over all slope positions), to determine whether the changes in richness were consistent across the five habitats. The potential predictors were Year (centred) and Habitat class. Year was fitted as a first or second order polynomial and Habitat either as an additive covariate or as an interaction with Year. As before, we fitted Plot as a random effect to account for possible correlations between observations made on the same Plot. Model comparison used the same approach as for trait groups.

3 | Results

3.1 | Seasonal Conditions and Timing of Sampling

Monthly rainfall totals, averages and long-term averages are detailed in Table S1 and rainfall conditions in the years preceding each field sampling are summarised in Table 2. Seasonal conditions varied greatly with the overall observation period bookended by drought: the Millennium Drought (1997–2009) and the record-breaking 2017–19 drought. A general indication of ground-layer condition can be gained from estimates on open, midslope sites. Measured annually between 2014 and 2020, biomass averaged 1870 kg.ha^{-1} (range 1400–2300 kg.ha^{-1}) (S. McIntyre unpublished data). The winter and spring preceding each monitoring event were consistently wet, with the exception of 2013, which experienced erratic winter–spring rainfall and a notably dry October. The two-stage sampling in early spring and late spring–summer optimised conditions for identification of geophytes, fast-developing winter annuals, as well as shrubs, Asteraceae, Fabaceae and most warm-season graminoids.

3.2 | Sampling Representativeness

A total of 251 taxonomic entities were recorded in the plots, representing 265 species (there were five multispecies groups,

TABLE 1 | Trait group classification of species based on origin (native/exotic), life cycle and life form.

		No. spp.
Native species ($n = 163$)		
Short tussock	Hemicryptophyte, graminoid, caespitose with table height < 15 cm.	16
Rosette herb	Scapose hemicryptophyte, rosette, leafless flowering scape.	10
Large tussock	Hemicryptophyte, graminoid, caespitose with table height > 15 cm.	10
Persistent herb	Chamaephyte—shoot or branch system remains within 1–50 cm of ground, nonwoody evergreen perennial forbs.	13
Shrub	Phanerophyte—shoots remain above 50 cm.	12
Subshrub	Chamaephyte—shoot or branch system remains within 1–50 cm of ground with woody stems at least at base.	19
Leafy herb	Scapose hemicryptophyte (protohemicryptophyte). Leaves do not decrease in size up the stems.	16
Partial rosette	Scapose hemicryptophyte, rosette. Leaves decrease in size up flowering stems.	10
Creeping herb	Hemicryptophyte, reptant (creeping or matted).	9
Geophyte	Produces leaves seasonally, except under adverse conditions, for example, orchids, lilies.	24
Annual	Therophyte, shoot and root system dies after seed production. Life cycle completed within 1 year.	24
Exotic species ($n = 89$)		
Perennial graminoid	Perennial, graminoid (caespitose grass, rush or sedge).	9
Annual legume	Therophyte, Fabaceae.	11
Annual graminoid	Therophyte, graminoid (caespitose grass, rush or sedge).	20
Perennial dicot	Any growth form.	11
Annual small rosette	Therophyte, includes partial rosettes, rosette diameter ≤ 10 cm.	12
Annual leafy herb	Therophyte, leaves located along stems, not decreasing in size.	18
Annual large rosette	Therophyte, includes partial rosette, rosette diameter > 10 cm.	8

Note: Definitions are after Cornelissen et al. (2003): *Phanerophyte*—grows taller than 0.50 m and whose shoots do not die back periodically to that height limit; *Chamaephyte*—mature branch or shoot system remains below 0.50 m, or grow taller than 0.50 m, but shoots die back periodically to that height limit; *Hemicryptophyte*—periodic shoot reduction to a remnant shoot system, so that buds in the 'harsh season' are close to the ground surface (e.g., many grasses and rosette forbs); *Geophyte*—annual reduction of the complete shoot system to storage organs below the soil surface; *Therophyte*—shoot and root system dies after seed production, life cycle completed within a year.
Abbreviation: No. spp., number of species in each trait group recorded in the entire survey sample.

hereafter referred to as species). The permanent plots totalled 0.22 ha (approx. 0.4% of the sampled 50 ha), but contained 72% of the 370 species that were recorded in the entire 50 ha (McIntyre, Lewis, et al. 2022). The morphologically distinct *Rytidosperma pallidum* was easily assessed in the field. The other 11 *Rytidosperma* species were difficult to distinguish in the field, and were ranked as a group (*Rytidosperma* spp.). Collections enabled individual species to be identified and contributed to the species richness data with as many as five species being recorded in a single plot. Individual species responses within *Rytidosperma* have been analysed and reported separately (McIntyre, Müller, et al. 2022). The observed relative abundance and frequency of each species in each survey is tabled in Table S2.

3.3 | Floristic Composition and Change

Plot records for the initial 2005 survey within each of the five habitats are delineated on the ordination in comparison with the samples from the subsequent four surveys (Figure 1). Except in the case of sheep camps, most of the subsequent samples fall within the original 2005 ordination space, suggesting little overall change in vegetation composition. The outlier points in the forest group represent an upper-slope site initially supporting barely any biomass, where there was no recovery and no more than two species recorded in most surveys.

A plot of the centroids representing the 13 subhabitats (habitat × slope position) better elucidates vegetation change over the four sampling intervals (Figure 2). The relative positions of the 13 centroid clusters indicate that the subhabitats generally retained their distinctiveness over the 15 years. Axis 1 suggests a gradient of site fertility, with sheep camps and drainage lines positioned furthest from the dry sclerophyll forest sites. Axis 2 suggests a moisture gradient, with the greatest differences

TABLE 2 | Summary of rainfall conditions preceding each of the five sets of field observations between 2005 and 2020.

	Rainfall conditions in years preceding sampling	Vegetation response observed
2005	Midway through Millennium Drought (1997–2009) with very dry autumn, and very wet winter and spring in 2005.	Effects of 9 years of drought
2010	Extremely dry (2006, 2009) to average years (2007–8). Autumn 2010 was very dry, winter–spring 2010 produced high rainfall.	Mixed dry and average seasons
2013	Extremely wet 2011–12. Autumn 2013 extremely dry, wet winter and erratic spring rainfall 2013.	Drought recovery
2016	2014–5 were wet-average years. 2016 was 300 mm above average, and persistently wet in winter–spring.	Post-drought consolidation
2020	Record-breaking 2017–19 drought, broken by heavy rain from February 2020 to time of sampling (November 2020).	Effects of extremely severe three-year drought

Note: Monthly totals are provided in Table S1, and drought descriptions are from http://www.bom.gov.au/climate/drought/knowledge-centre/previous-droughts.shtml .

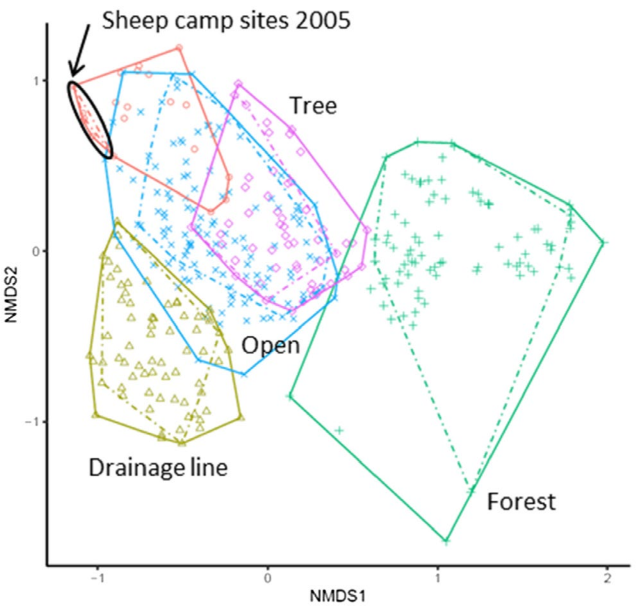

FIGURE 1 | Ordination of ground-layer vegetation (73 permanent plots sampled five times: 2005, 2010, 2013, 2016, 2020) in the first two dimensions of a three axis NMDS ordination. The five habitats sampled are delineated by broken lines (2005 observations only) and solid lines (all observations). Habitats are: *Sheep Camp* (red circles); *Drainage Line* (yellow-green triangles); *Open* grassland (blue x); *Tree* canopy (pink diamonds); dry sclerophyll *Forest* (green +). The tight cluster of sheep camp sites circled are the sites sampled in 2005.

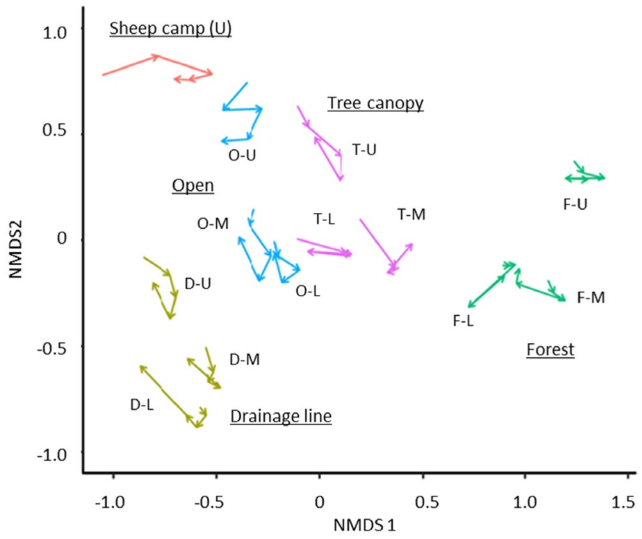

FIGURE 2 | Movement of the centroids of 13 habitat/landscape position combinations over 15 years in the space defined by NMDS Axes one and two, derived from a three-axes ordination of the year × plot × all species matrix. Arrows indicate the degree and direction of change in floristic composition between the five sampling times (2005, 2010, 2013, 2016, 2020). D, *drainage line*; S, *sheep camp*; O, *open* grassland; T, under *tree* canopy in woodland; F, dry sclerophyll *forest*; U, upper slopes; M, midslopes; L, lower slopes.

being between drainage lines on lower slopes and sites on upper slopes. There is a similar ordering of slope position within habitat types reflecting the drier nature of upper-slope positions, which are more strongly differentiated from the mid- and lower-slope sites within the habitats. Axis 3 separated open sites from those under tree canopies (not shown, see McIntyre, Lewis, et al. 2022). In summary, site productivity appears to be a major driver of plant composition, differentiating grassy from sclerophyll sites and areas of water run-on from upper slopes and hill crests.

After varying degrees of divergence, the vegetation in most subhabitats tended to return towards their original 2005 composition, especially in the 2016–20 interval (Figure 2). In both the 2005 and 2020 surveys, severe drought had preceded the sampling season and was likely the main influence on the vegetation (Table 2, Table S1). The time at which the sites were furthest from their original floristic composition varied between habitats, but half were in 2016, which had been preceded by 7 years of mostly good seasons, and the direction of trajectories is broadly consistent with these more mesic conditions. Forest upper-slope sites were the most stable of the subhabitats. The five subhabitats showing the greatest net change were:

3.3.1 | Sheep Camps (All Located on Upper Slopes)

At the time of sheep removal, sheep camps were the only habitat to be actively receiving nutrient inputs in the form of imported dung and urine and were strongly dominated by exotics. A decline in dominance of *Poa bulbosa*, *Spergularia rubra* and *Hordeum glaucum* was observed, being replaced by *Microlaena stipoides*, *Lomandra filiformis* and *Panicum effusum*. *Arctotheca calendula* and other exotic annuals fluctuated.

3.3.2 | Open Upper Slopes

Composition converged towards that of open mid-slope sites (Figure 2), namely *Poa bulbosa, Rytidosperma* spp. and *Microlaena stipoides* being displaced by *Aristida ramosa*, *Panicum effusum*, *Melichrus urceolatus*, and increases in native forbs. The movement to the right on Axis 1 represented the drought recovery period of 2010–13, when there was decreasing dominance of annuals (*Triptilodiscus pygmaeus*, *Euchiton sphaericus*, *Tolpis barbata*, *Spergularia rubra*), and increasing dominance of perennials (*Hypochoeris radicata*, *Juncus* spp., *Microtis* spp., *Luzula densiflora*, *Wahlenbergia stricta* and *Acaena echinata*). This change in dominance was reversed in the 2017–19 drought.

3.3.3 | Tree Canopy Mid-Slopes

The major change occurred in the first 5 years, over which time *Poa sieberiana* and *Dianella revoluta* increased in dominance, and *Rytidosperma* spp. declined in dominance, and exotic annuals (*Aira* spp. and *Vulpia* spp.) declined in frequency and dominance.

3.3.4 | Tree Canopy Lower Slopes

The most notable changes were sustained increases in dominance of *Lomandra* spp., *Dianella revoluta* and *Anthosacne scabra*, with net declines in dominance (and sometimes frequency) of a number of annual exotics, including *Aira* spp., *Trifolium* spp. and *Briza* spp.

3.3.5 | Drainage Line Lower Slopes

This subhabitat varied little across the first four sampling intervals, but the effects of 3 year's drought followed by a persistently wet late summer–spring prior to sampling saw substantial changes in the form of increased diversity of mainly exotic annual species in 2020. Five native and 13 exotic species not previously recorded in this habitat appeared in 2020, including species typical of drier habitats (e.g., *Cassinia sifton*, *Crassula sieberiana*, *Gamochaeta calviceps*, *Gnaphalium indutum*).

3.4 | Changes in Origin and Trait Groups Across All Sites Over Time

Native and exotic total species richness responded similarly over time, having a quadratic response identified, with the highest predicted richness coinciding with the two post-drought surveys, 2005 and 2020 (Table 3, Figure 3, Tables S3 and S4). Amongst natives, this pattern was underpinned by the short tussock and annual species, two groups that also had a quadratic response identified. Of the 89 species of exotics, 69 were annuals, and four of the five annual life forms had quadratic models fitted. The fifth group, exotic annual graminoids, included species with consistently high frequencies and relative abundance, notably species of *Briza*, *Aira* and *Vulpia* spp. (Figure 4, Table S2). There was no evidence of linear or quadratic response in this group, with the best fit model containing an intercept term only.

Most native trait groups (6/11) were constant in their species richness, while three of them increased linearly over the 15-year survey period: subshrubs, leafy herbs and geophytes (Table 3, Figure 3). The subshrub response was driven by *Melichrus urceolatus*, which also increased in dominance (Figure 4). A number of leafy herb species increased in frequency: *Euphorbia drummondii*, *Opercularia hispida* (open sites), *Einadia nutans*, *Veronica calycina*, *Scutellaria humilis* (under trees) and *Veronica gracilis* (drainage lines), while the most frequent species (*Hypericum gramineum* and *Oxalis perennans*) retained their presence. Similarly, while a large number of orchid species contributed to geophyte richness increase, the most frequent geophyte in 2005, *Drosera peltata*, did not gain in frequency. Native annuals, while most frequent after droughts in 2005 and 2020, also appeared to be increasing, with the observed richness in 2020 being 77% greater than in 2005.

None of the exotic trait groups declined linearly in species richness, and only one, the perennial dicots, demonstrated a linear increase. *Hypochaeris radicata* and *Rumex acetosella* were the most frequent species underpinning this increase, although their relative abundance varied greatly over the survey period (Table S2). Greater rates of increase might have been recorded had there not been systematic control of four species of exotic perennial dicots (*Chondrilla juncea*, *Rubus* sp., *Orobanche minor*, *Hypericum perforatum*). The quadratic frequency response observed in four of the annual exotic groups was similar to that of native annuals, with higher richness associated with postdrought rains. The most pronounced increase in 2020 was among the eight species comprising the annual large rosettes, most of which are wind-dispersed (*Erigeron* spp., *Sonchus* spp., *Cirsium vulgare*, *Lactuca*). *Arctotheca calendula* presence was maintained as a seed bank, and plants greatly increased in frequency and dominance in open habitat in 2020, as did *Erigeron* spp. and *Cirsium vulgare* (the latter two were intensively controlled throughout the observation period). There were no clear trends in richness amongst the other exotic annual groups. The species within these exotic groups varied in their frequency over the survey period, with the most important species being *Hypochoeris glabra*, *Linaria pelisseriana* and *Centaurium erythraea* in terms of frequency and dominance increases (Figure 4, Table S2).

3.5 | Species Richness by Origin Within Habitats

The detailed models fitted to (i) total native and (ii) total exotic species richness, as a function of Year and Habitat were similar

TABLE 3 | Observed species richness of trait groups within native and exotic categories as defined in Table 2.

	2005	2010	2013	2016	2020	Fitted model
Native species						
All native species	23.8	24.4	22.9	25.0	26.9	Quadratic
Partial rosette	1.0	1.1	1.1	0.9	1.2	Null
Rosette herb	1.8	1.8	1.6	1.9	1.7	Null
Large tussock	2.3	2.3	2.5	2.5	2.3	Null
Persistent herb	3.8	3.8	4.0	4.2	4.1	Null
Shrub	1.2	1.3	1.3	1.2	1.3	Null
Creeping herb	1.1	1.0	1.0	1.1	1.2	Null
Subshrub	1.1	1.2	1.4	1.3	1.3	Linear
Leafy herb	1.5	1.5	1.3	1.7	1.8	Linear
Geophyte	2.8	3.3	2.6	3.3	3.6	Linear
Short tussock	4.6	4.1	3.7	3.8	3.9	Quadratic
Annual	2.6	3.0	2.4	3.3	4.6	Quadratic
Exotic species						
All exotic species	13.7	13.4	12.0	14.3	15.6	Quadratic
Perennial graminoid	0.8	0.8	0.6	0.7	0.6	Null
Annual graminoid	4.8	4.5	4.3	5.3	4.7	Null
Perennial dicot	1.1	1.1	1.2	1.4	1.3	Linear
Annual small rosette	2.9	3.0	3.0	3.0	3.7	Quadratic
Annual legume	2.4	1.9	1.3	2.0	2.3	Quadratic
Annual leafy herb	1.3	1.7	1.1	1.6	1.9	Quadratic
Annual large rosette	0.3	0.3	0.5	0.4	1.1	Quadratic

Note: Data are means over all 73 plots (30m^2). See Figure 3 for predicted means of fitted models and model details in Tables S3 and S4.

(see Tables S5 and S6 for details of the model rankings). For both response variables, the best model was a quadratic function of time and separate intercepts for each habitat class with a common slope for all habitats. This suggests that while habitats were associated with different levels of richness, the relative change over time was constant.

3.6 | Overview

Table 4 summarises the initial vegetation and changes observed in the five habitat types. The perennial native grasses that dominated the four major habitats maintained their frequency and relative abundance even when total biomass varied with rainfall (Figure 4, Table S2). An exception was the cryptic *Rytidosperma*, a group of short tussock species that maintained their frequency (Table S2), but not their high initial relative abundance (Figure 4). Perennial exotic grasses remained a very minor component of the vegetation in contrast to annual grasses, which were the most frequent of the exotics (Table 3). The latter varied greatly in dominance, but not apparently at the expense of native grass dominance. Most of the native persistent herbs (chamaephytes) maintained their dominance, with notable increases in the abundance of *Lomandra filiformis* and *Melichrus urceolatus*. The exotic annual species displayed different responses to seasonal conditions in terms of both frequency and relative abundance (Figure 4, Table S2). In terms of overall exotic/native composition, the level of dominance of exotics was related to site productivity and largely persistent, with some decline under tree canopies (including sheep camps), consistent with the removal of livestock (Figure 5). Forest sites had a negligible exotic component.

4 | Discussion

4.1 | Did Native Species Diversity Improve Spontaneously?

Plant diversity across the entire study site was high (McIntyre, Lewis, et al. 2022), with 'reference condition' diversity (*sensu* Gibbons et al. 2008) at small scales, and 115 species in survey plots being recognised as 'important' components of critically endangered Box-Gum Woodland (i.e., grazing-sensitive, regionally significant or uncommon, DCCEEW 2023) (Table S2). Under these circumstances, changing the grazing regime could be considered unadvisable (Lunt et al. 2007), potentially disrupting the disturbance regime for many species. However, the ecological rationale for removing livestock included the need to address widespread soil erosion, depletion of the shrub layer and lack of eucalypt regeneration in the previously cleared, pasture-improved areas. The small population sizes of a number of species were an additional concern. While the scale and number of permanent plots in this study were not suited to monitoring these small populations, the responses of the native life-form groups provide some insight. Three groups had significant linear increases in species frequencies (native subshrubs, geophytes and leafy herbs), indicating population increase. As 40 of the 50 species comprising these three life-form groups were 'important' species, we conclude that there have been modest but significant gains in conservation status associated with destocking. A recent review of switches in disturbance types in grassland identified few studies comparable to ours (Price et al. 2021), but in one highly comparable woodland environment, Price et al. (2010) reported similar positive responses of

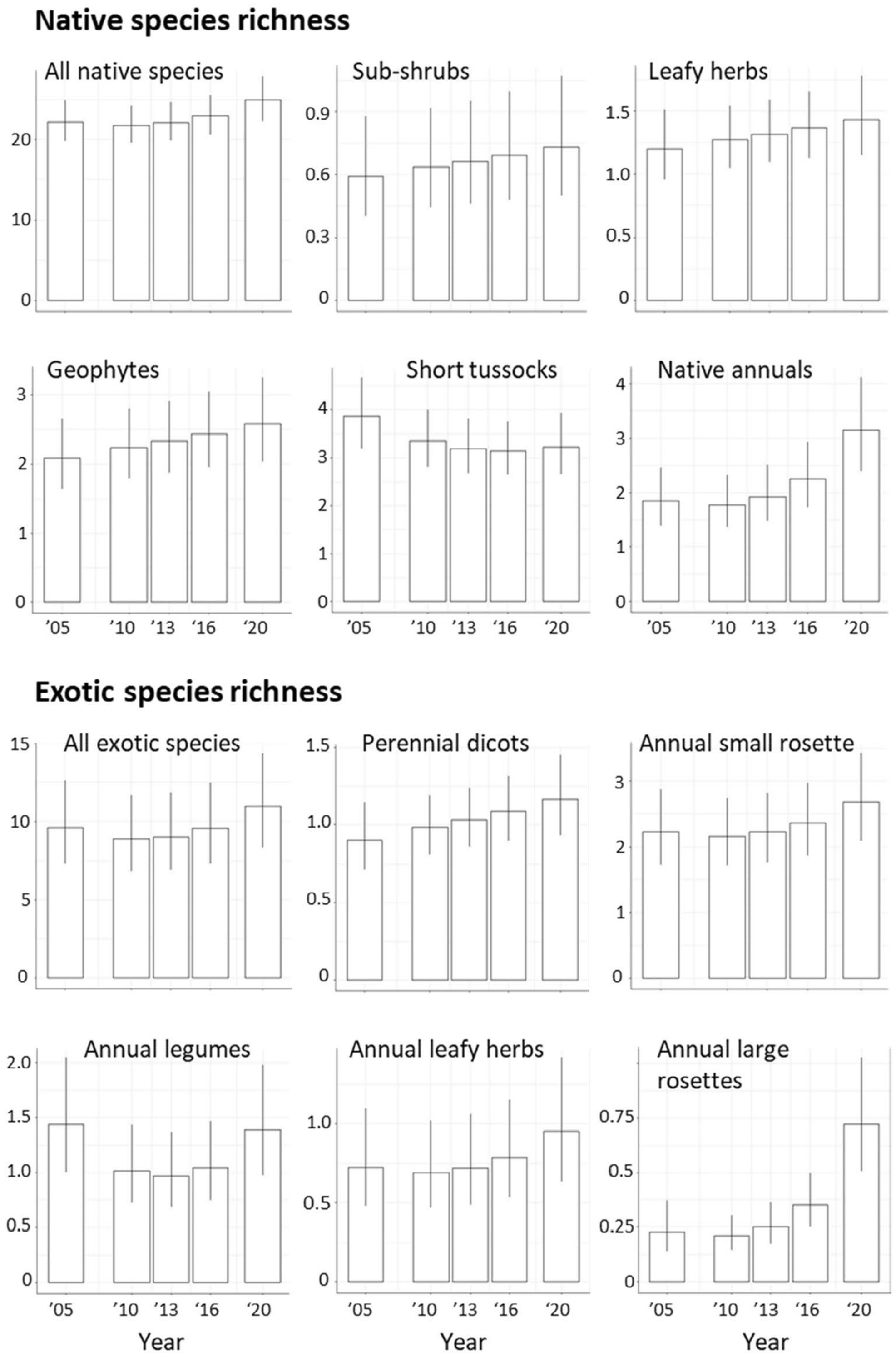

FIGURE 3 | Predicted species richness (30 m^{-2}) and 95% confidence intervals for the native and exotic trait groups as a function of year. Trait groups that did not support a linear or quadratic response, and were best described by a null model are not illustrated. Note that the y-axis scale is not constant across the panels.

native geophytes, herbs and the subshrub *Astroloma humifusum*, 20 years after transitioning from sheep to macropod grazing. Native annuals fluctuated over the monitoring period in our study, but a 37% increase in diversity during the favourable seasons of 2011–16 may have led to increase in seed populations as there was an additional 40% increase in richness after the 2017–9 drought.

Native short perennial tussocks were the only life form to decline in richness overall (Figure 3), and in the case of short tussock *Rytidosperma*, a number of species within the genus also declined in relative abundance, outstripped in biomass by shrubs and persistent herbs (Figure 4b; McIntyre, Müller, et al. 2022). Past work has shown this response would be an expected outcome of reducing total grazing pressure

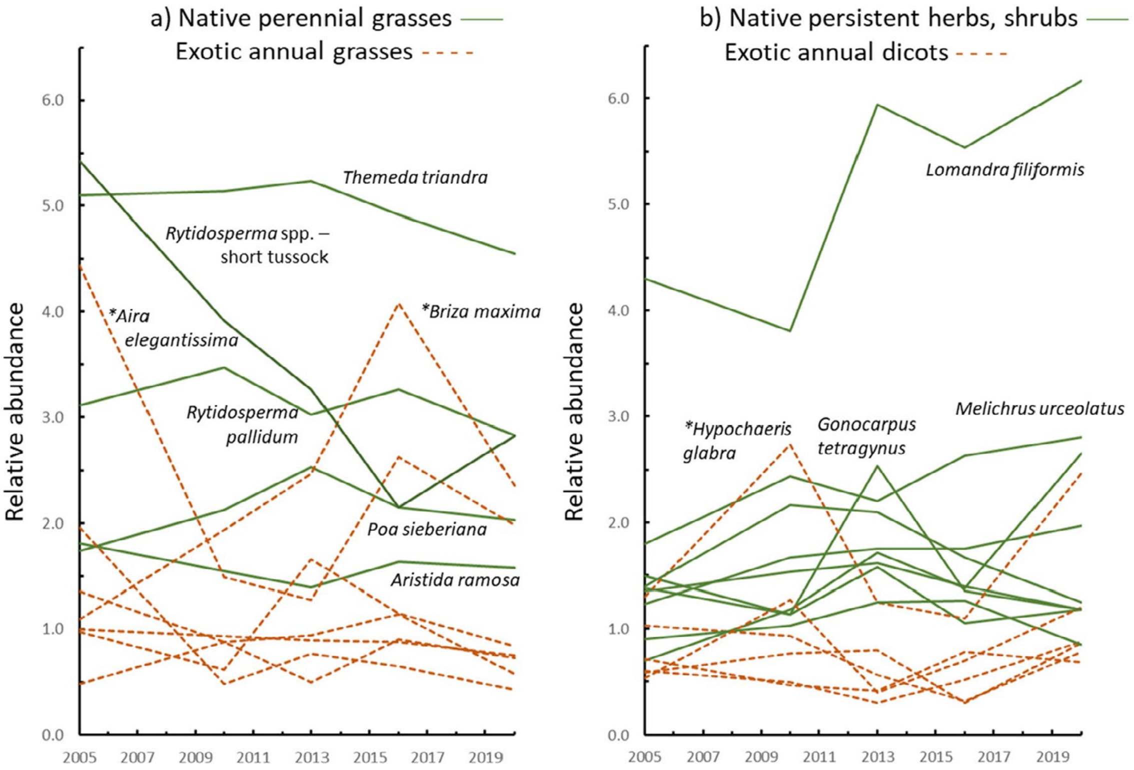

FIGURE 4 | Changes in observed relative abundance between 2005 and 2020 of: (a) the five most dominant native perennial grasses (labelled on figure) and the most dominant exotic annual grasses (in deceasing order of starting abundance: *Aira elegantissima*, *Aira caryophyllea*, *Vulpia myuros*, *Briza maxima, Briza minor*, *Vulpia bromoides*, *Bromus* spp.); (b) the most dominant native persistent (chamaephyte) herbs and native shrubs/subshrubs (in deceasing order of starting abundance: *Lomandra filiformis*, *Melichrus urceolatus*, *Gonocarpus tetragynus*, *Goodenia hederacea*, *Acacia genistifolia*, *Dillwynia phylicoides*, *Dianella revoluta*, *Daviesia leptophylla*, *Lomandra multiflora*) and the most dominant exotic annual dicots (in deceasing order of starting abundance: *Hypochaeris glabra*, *Tolpis barbata*, *Trifolium dubium*, *Petrorhagia nanteuilii*, *Trifolium arvense*, *Trifolium subterraneum*). * Denotes exotic species.

(Stuth 1991; McIntyre and Tongway 2005; McIvor et al. 2005) and may continue to vary with grazing pressure, as indicated by the quadratic response of the short tussocks and uptick in frequency in 2020. There is a need to reconcile this quadratic response with the linear increase in many notionally grazing-sensitive species among the geophytes and leafy herbs. Field observations indicate that a number of grazing-avoided species (e.g., *Melichrus urceolatus*, *Lomandra filiformis*, *Rytidosperma pallidum*, *Aristida ramosa*) provide associational defence (Milchunas and Noy-Meir 2002; Wilson et al. 2019; Caram et al. 2024) for more palatable species. As much as the change in herbivore type (sheep to macropods) and decreased grazing pressure overall may have helped recovery of native forbs, the protective nature of these unpalatable plants with high dry matter content (McIntyre 2008) was evident throughout the monitoring period (e.g., Figure 6a,b).

4.2 | Was There Improvement in the Native/Exotic Balance in the Landscape?

Monitoring started midway through the 13-year Millennium Drought, while the final set of observations captured the effect of the first wet autumn–spring after the extreme 2017–19 drought. Only two of the study's 15 years approximated average conditions, yet over that time there was no overall rainfall deficit owing to extremely wet years between the two droughts (Table S1). Rainfall after dry years in 2005 and 2020 (Table 2) increased the occurrence of all four exotic annual groups in all habitats (Figure 3). The importance of climate in driving grassland dynamics, especially annuals, is widely reported (e.g., Hobbs et al. 2007; Prober et al. 2013; McIntyre et al. 2017; Farmilo and Moxham 2019; Neldner and Butler 2021; Farmilo et al. 2023) and while the combination of bare ground and rainfall associated with breaking droughts stimulates annual plant growth generally, ecological variation within these four exotic annual groups is considerable (Symonides 1988), with fluctuations in annual populations driven by rainfall onset, duration, amount and timing (Rossiter 1966; Figueroa and Davy 1991). In our study, individual exotic species' patterns also varied, and peaks of abundance were not restricted to bare ground, post-drought scenarios. For example, *Briza maxima* increased over wet years under reduced grazing pressure, peaking in 2016, but declined in relative abundance in the drought preceding the 2020 survey (Figure 4a).

Of the 69 annual exotic species, the most important were *Aira elegantissima*, *Briza maxima* and *Hypochoeris glabra* in the sense that their relative abundances exceeded that of the most dominant perennial grasses in some years (Figure 4a). There

TABLE 4 | Summary descriptions of vegetation associated with five habitats (and slope positions), and major compositional changes synthesised from ordinations, modelling of trait groups, and individual species' frequency (freq.) and relative abundance (RA) data.

Initial vegetation–2005	**Changes 2005–2020**
Sheep camp ($n = 4$, all upper-slope, under tree canopy)	No. spp. recorded 2005–20 = 90
– Nutrient-enriched, exotic-dominated sites supporting herbaceous vegetation dominated by *Poa bulbosa*[a], *Arctotheca calendula*[a], *Hordeum glaucum*[a], *Rytidosperma racemosum*, *Spergularia rubra*[a], *Vulpia myuros*[a], *Rumex acetosella*[a].	– Increased *Microlaena stipoides*, *Lomandra filiformis*, *Hypochoeris radicata*[a], *Paronychia brasiliana*[a], *Juncus* subgen. *Genuinii*. – Decline RA of *Poa bulbosa*[a], *Hordeum glaucum*[a], *Rytidosperma racemosum*, *Spergularia rubra*[a].
– Many annual species.	– Annuals fluctuated.
Open ($n = 27$, upper- mid- and lower slopes)	No. spp. recorded 2005–20 = 182
Rytidosperma spp., *Lomandra filiformis*, *Microlaena stipoides*, *Austrostipa scabra* (U), *Poa bulbosa*[a] (U), *Aristida ramosa* (U,M), *Themeda triandra* (M,L), *Poa sieberiana* (L).	– Short tussocks (*Rytidosperma* spp., *Panicum effusum*) and annuals (*Aira* spp.[a], *Tolpis barbata*[a], *Triptilodiscus pygmaeus*, *Hypochaeris glabra*[a]) fluctuated in freq. and RA. – Increased frequency and dominance of subshrubs (*Melichrus urceolatus*), leafy herbs (*Hypericum gramineum*), geophytes (*Microtus* spp.).
Tree canopy ($n = 11$, upper- mid- and lower slopes)	No. spp. recorded 2005–20 = 140
Rytidosperma spp., *Microlaena stipoides*, *Lomandra filiformis*, *Aira caryophyllea*, *Gonocarpus tetragynus*, *Themeda triandra*, *Poa bulbosa* (U), *Austrostipa scabra* (U), *Rytidosperma pallidum* (M,U), *Aira elegantissima* (M,U), *Vulpia* spp. (M,U), *Melichrus urceolatus* (M,U), *Poa sieberiana* (M,L), *Hydrocotyle laxiflora* (M,L), *Dianella revoluta* (M,L), *Plantago varia* (L), *Geranium solanderi* (L), *Scutellaria humilis* (L).	– Decreased RA of *Rytidosperma* spp. – Decreased freq. and RA of *Aira* spp., *Vulpia* spp., *Hydrocotyle laxiflora*, *Themeda triandra*. – Increased RA *Lomandra filiformis*. – Increased freq. and RA in *Melichrus urceolatus*, *Dianella revoluta*, *Juncus* subgen. *Genuini*, *Lomandra multiflora*.
Drainage lines ($n = 14$, upper- mid- and lower slopes)	No. spp. recorded 2005–20 = 179
Themeda triandra, *Carex appressa*, *Rytidosperma* spp. (M,U), *Aira elegantissima*, *Eragrostis brownii* (M,U), *Schoenus apogon*, *Solenogyne dominii* (U), *Microlaena stipoides* (M,U), *Hypochoeris radicata* (M), *Trifolium dubium* (M,L), *Briza maxima* (M,L), *Craspedia variabilis* (L), *Poa labillardieri* (L).	– Decreased RA and freq. of short tussocks (*Rytidosperma* spp., *Eragrostis brownii*) and annual grasses (*Aira* spp.). – Increased RA and freq. of *Briza maxima*[a], *Erigeron sumatrensis*[a], *Oxalis perennans*. – Annuals increased from 2016 to 2020 (*Schoenus apogon*, *Juncus capitatus*[a], *Bromus racemosus*[a], *Isolepis levynsiana*[a], *Juncus bufonius*[a], *Trifolium dubium*[a], *Trifolium arvense*[a], *Galium divaricatum*[a], *Linaria pelisseriana*[a], *Lysimachia* spp.[a], *Lythrum hyssopifolia*).
Forest ($n = 17$, upper- mid- and lower slopes)	No. spp. recorded 2005–20 = 114
Rytidosperma pallidum, *Dillwynia phylicoides*, *Acacia genistifolia*, *Brachyloma daphnoides*, *Daviesia leptophylla*, *Dianella revoluta*, *Lomandra filiformis*, *Melichrus urceolatus*, *Aristida ramosa* (U,M), *Hibbertia riparia* (U,M), *Poa sieberiana* (M,L), *Pultenaea subspicata* (M,L), *Dichelachne rara* (L).	– Very little change on upper slopes. – Decreased RA and freq. of *Microlaena stipoides*, *Dichelachne rara*, *Aristida ramosa*. – Increased freq. of orchids (*Caleana minor*, *Diuris sulphurea*, *Genoplesium* spp., *Eriochilus cucullatus, Caladenia moschata*)

Note: More detailed initial vegetation descriptions are provided in McIntyre, Lewis, et al. (2022).

[a] Denotes exotic species. Species listed are associated with all slope positions unless indicated by U (upper), M (mid-) and/or L (lower).

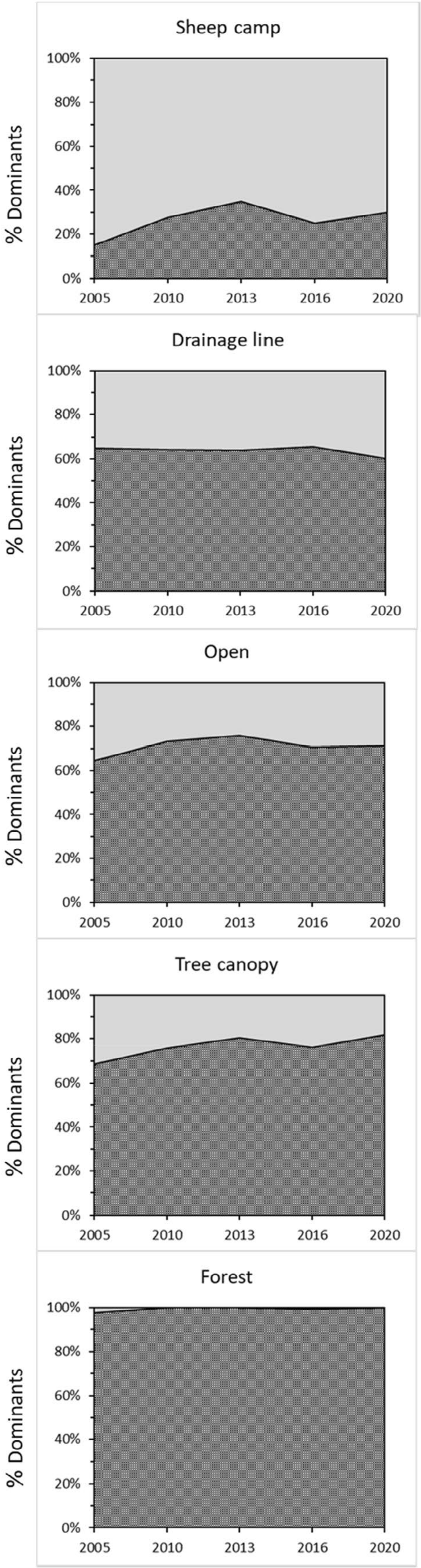

FIGURE 5 | Proportion of dominant native (dark shading) and dominant exotic species (light shading) in the five habitats surveyed between 2005 and 2020. Data are the proportion of total counts of native and exotic species that were ranked 1–10 (in terms of biomass) in 73 plots.

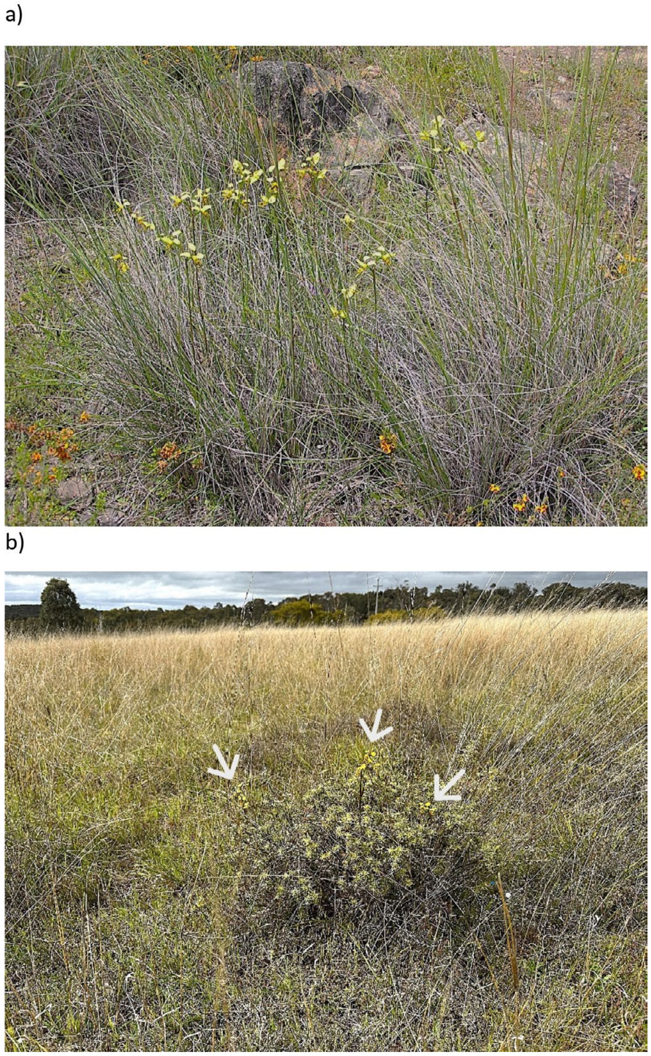

FIGURE 6 | Associational defence provided for the orchid *Diuris sulphurea* by two grazing-avoided species (a) *Rytidosperma pallidum* and (b) *Melichrus urceolata*.

was a trend of increasing frequency of exotic perennial dicots, but this was not reflected in relative abundance. Vigilant and ongoing weed control of some of this group (*Rubus* sp., *Hypericum perforatum*) as well as the perennial grass *Nassella trichotoma* may have contained dominance, but the need to control these widely dispersing species on an ongoing basis is apparent. It is also notable that a number of annual large rosette species (*Cirsium vulgare*, *Erigeron* spp., *Sonchus* spp. *Lactuca* sp.) still increased in 2020 despite systematic removal. Surveillance and eradication of new incursions are equally important and have contributed to the maintenance of the native ecosystem (McIntyre, Lewis, et al. 2022). Overall, the dominance of exotic species changed little over the 15 years, and while sheep camps showed some recolonisation by natives, they remained predominantly exotic (Figure 5). The slight reduction in the dominance of exotics under trees, especially annual grasses (Table 4) suggests that there had been some previous nutrient elevation from sheep using trees for shade and shelter, more subtle than in the sampled sheep camp habitat.

4.3 | Are Compositional Changes Similar Across All Subhabitats?

Productivity, whether expressed in terms of substrate type, landscape position, nutrient levels or water enrichment, is a primary influence on composition and exotic incursion in the grassy woodland biome (McIntyre and Lavorel 1994; Prober and Thiele 1995; Reseigh 2004; Dorrough et al. 2006, 2012; Dorrough and Scroggie 2008; McIntyre et al. 2017). Separation of these contributing factors in natural experiments is difficult, as fertiliser use often accompanies grazing and is associated with particular substrate types and topographies. However, where the influence of nutrients and water has been separated (McIntyre and Martin 2001, 2002), nutrients have been found to have a greater influence on species composition than water enrichment. This is consistent with the current study, in which the first axis in the ordination located sheep camps furthest from sclerophyll forest sites (Figures 1 and 2). The exotic component of our sclerophyll forest vegetation was negligible, highlighting the relative advantage of native species on nutrient-poor substrates (Figure 5), compared with the recently nutrient-enriched sheep camps.

Moisture relations appeared to be the second major influence on composition, differentiating drainage lines from other habitats and ordering of slope position within each habitat type (Figure 2). In all habitats, the vegetation on upper slopes (the driest part of the landscape, Rowley et al. 2024) differed most from lower and mid-slopes, a pattern also identified in grassland on the NSW northern tablelands (McIntyre and Lavorel 1994). One trend in vegetation change in open, tree canopy and drainage line habitats was for upper-slope vegetation to converge in composition towards mid-slope communities at times of high rainfall (movement down Axis 2, Figure 2). In sclerophyll forest, the upper slopes were unchanged, but mid-slope vegetation similarly converged towards lower slopes. The 2017–19 drought only partially reversed this trend, suggesting sustained improvement in rainfall interception by the grass sward, supported by the author (SM) observations of progressively decreasing runoff after rainfall events. Godfree et al. (2011) demonstrated that moister subhabitats can provide refuge in droughts, and we observed equivalent responses in lower drainage lines. The ordination trajectories and the authors' field observations suggest that mesic species can also grow higher in the landscape in wet years.

Despite the changes, all habitats retained their floristic identity after 15 years (Figure 2), due to the stability of the dominant perennial species, most notably *Themeda triandra*, *Lomandra filiformis*, *Microlaena stipoides*, *Aristida ramosa*, *Poa* spp., *Rytidosperma pallidum*, *Dianella revoluta*, *Melichrus urceolatus* (Table 4, Figure 4), suggesting a high level of resistance to change in the face of record-breaking drought (Ritman and Ashcroft 2020). Annual species were important drivers of variation in native and exotic species richness across the 15 years (Figure 3) and the shape of the response did not differ between habitats, indicating that broader-scale factors, such as seasonal conditions, were responsible for the year-to-year differences.

4.4 | What Are the Implications of the Changes Observed for Ecosystem Prospects Under Climate Change?

The large number of persistent exotic species (114) present at the site, and the spontaneous colonisation rate of 0.75 new species per annum (McIntyre, Lewis, et al. 2022) point to the likelihood of a sustained or expanding exotic component of the vegetation in the future. This would particularly be the case if there were a shift to warmer, wetter, summer rainfall conditions, which would favour already expanding C4 exotic grasses such as *Eragrostis curvula* and *Hyparrhenia hirta*. Vehicles are an important vector of exotic, but not native species (Wace 1977) so vehicle hygiene would be an important management consideration alongside an active and continuous weed control program.

An increasingly dry cool season may reduce the impact of the many winter-growing annual exotics, but it could also adversely affect native geophytes and annuals which grow actively from autumn to spring. Given the low rate of spontaneous immigration of native species at the site (0.25 species per annum), and the vulnerability of grassland forbs to loss of genetic diversity in declining populations (Prober et al. 1998; Broadhurst and Young 2007), climate-adjusted colonisation may be required to augment small populations and maintain their viability (McIntyre 2011).

A space-for-time study in the district (McIntyre 2008) established that both the removal of livestock and little or no fertiliser use contributed to grassland being dominated by species having higher leaf dry matter content, an attribute associated with slow growth rates, longer-lived leaves, slow decomposition and physical toughness (Pérez-Harguindeguy et al. 2013). Consistent with trade-offs in the economy of leaves (Reich 2014), more productive, disturbed habitats (fertilised pastures and crops) are dominated by exotic species having low levels of dry matter content (McIntyre 2008) and correspondingly fast growth rates, and short-lived, tender, fast-decomposing leaves, representing the opposite side of the economic spectrum (Montesinos 2022). The conservative strategy is associated with conditions of drought or mineral deficiency (Diaz 2004). This study has documented how a reduction in disturbance (defoliation, trampling) has maintained and increased the overall dominance and frequency of a range of conservative species represented as shrubs, persistent herbs and large perennial tussocks.

A study of soil biophysical condition in the district by Prober et al. (2014) compared *Themeda triandra* dominated patches with those dominated by short tussock *Rytidosperma* spp. or *Aristida ramosa*, finding the latter two patch types having poorer soil water relations and predicting them to be less resilient under a drying climate change scenario. By observing

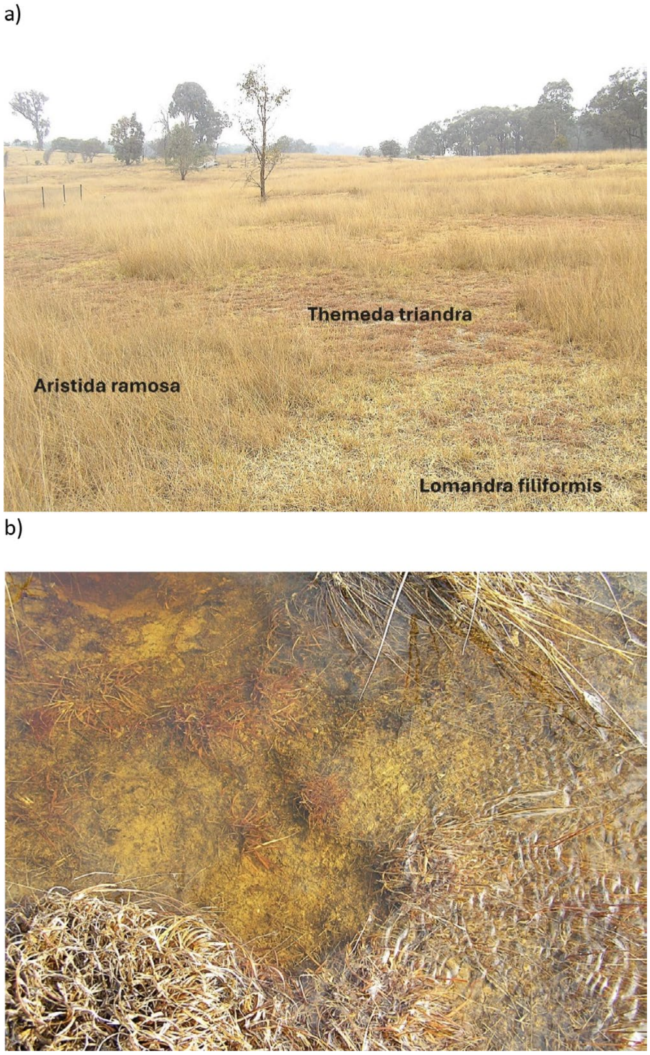

FIGURE 7 | (a) Open habitat mid-slope on January 11th 2020 near the end of the 2017–19 drought. A total of 26 mm of rain had fallen on this site in the previous 100 days. Patches dominated by *Aristida ramosa*, *Lomandra filiformis* and *Themeda triandra* are labelled. Bushfire smoke haze is evident. (b) Clear runoff from the same landscape after a fall of 67 mm in the previous 24 h (9th February 2020).

FIGURE 8 | Vegetation response in October 2020 after the 2017–19 drought. Previously dominant *Themeda triandra* tussocks have mostly died back with some resprouting. Species colonising bare ground include: native annuals (*Stuartina muelleri*, *Crassula sieberiana*, *Triptilodiscus pygmaeus*, *Isoetopsis graminifolia*, *Sebaea ovata*); native perennials (*Euchiton japonicus*, *Wahlenbergia* sp.) and exotic annuals (*Hypochaeris glabra*, *Galium divaricatum*, *Aira elegantissima*, *Gamochaeta americana*, *Petrorhagia nanteuilii*).

these species under extremes of wet and dry, we have seen a more complex picture that needs to take into account the patchy nature of the grazed landscape in both space and time. *Themeda triandra* is a large tussock grass of high productivity (Johnston et al. 1999), which is associated with fast nitrogen cycling and small nitrate pools (Prober et al. 2014) making it less prone to nitrogen loss than exotic annual grass swards (Jones and Woodmansee 1979). Large perennial tussocks generally (including *Aristida* and *Themeda*) promote soil water infiltration, soil stability and nutrient cycling (McIntyre and Tongway 2005), having deeper roots and greater accumulation of soil organic carbon (Derner et al. 1997) than short tussocks. In our study site, open sites support a mosaic of patches characterised by varying dominance of these three grasses, together with *Lomandra filiformis*. Dominance is determined by soil variations and the level of selectivity exerted by herbivores. During drought, increasing grazing pressure reduced *Themeda* patches to lawn, while *Aristida* patches were avoided (Figure 7a) and provided shaded, grazing-protected areas for some green herbage to survive (SM, JL Pers. obs.). The combined presence of *Themeda, Aristida* and *Lomandra filiformis* afforded protection to the soil during drought-breaking rain (Figure 7b). The close-cropping of *Themeda* created bare ground, with cryptogam cover, and opportunities for faster species, including native annuals (Figures 3 and 8, Table S2) many of which are considered to be declining and threatened (Sinclair et al. 2021). Thus, the dominant grasses contribute variously to productivity, diversity maintenance and soil protection under varying conditions.

Predictions of further extremes of drought and inundation (Pakdel et al. 2024) make the management of the ground layer critical to the management of grassy ecosystems, whether for animal production or biodiversity conservation. The presence of drought-resistant species with conservative growth attributes provides a greater chance of maintaining biodiversity, landscape and ecological functions (Mokany et al. 2008; Lavorel et al. 2015). Our study demonstrates that moderate macropod grazing can maintain a diversity of species, with a range of ecological strategies that maintain productivity and stability under climate stress.

5 | Conclusion

The transition from commercial livestock to lighter macropod grazing was associated with linear increases in the frequency of native life forms and species of conservation significance, while the established native perennial vegetation has been resistant to change in the face of severe drought and extremes of rainfall, and retained its high initial conservation status. Increases in the dominance of subshrubs, persistent herbs and perennial grasses have contributed to ecosystem function and diversity.

Fluctuations in the dominance and presence of annuals (exotics, and to a lesser extent native) accounted for most of the floristic variability observed over the 15 years. The level of dominance of exotic species was largely unchanged, although linear increases in the frequency of some exotics in the face of ongoing control efforts suggest possible future threats to ecosystem integrity.

Nomenclature

Nomenclature follows the Australian Plant Census: https://biodiversity.org.au/nsl/services/search/taxonomy, except *Thelymitra* which follows: Egan J., Wood T., Farrow R. & Hayashi T. (2020) Field Guide to Orchids of the Southern Tablelands of NSW Including the ACT. Inkpen Press, Canberra.

Author Contributions

Sue McIntyre: conceptualization, data curation, formal analysis, investigation, methodology, resources, validation, visualization, writing – original draft, writing – review and editing. **Jon Lewis:** conceptualization, investigation, methodology, resources, writing – review and editing. **Anthony O. Nicholls:** formal analysis, software, visualization, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.