



Grasslands of cleared woodlands have lower invertebrate diversity and different assemblages to remnant woodlands in grazed landscapes of eastern Australia

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Abstract

Clearing of woodlands is used by graziers to promote pasture production, even though understanding of impacts of clearing on native fauna is lacking. We evaluate impacts of clearing on biodiversity by comparing invertebrates associated with ground-layer vegetation of cleared woodlands (grasslands) to that of nearby uncleared woodlands. Two replicates of grasslands consisting of pastures dominated by introduced grasses were compared with two woodlands at each of four locations. The adjacent riparian forest to each grassland and woodland site allowed evaluation of the effect of woodland clearing on the adjacent riparian zone. All habitats were grazed. Invertebrates of ground-layer vegetation were sampled using three suction subsamples of 1 m² at each site. Grasslands had significantly lower order richness and abundance of herbivores, pollinators and macroinvertebrates (food for birds) than the woodlands, whereas the riparian forests closely resembled each other in all metrics. Invertebrate assemblages of grasslands also differed significantly from those of the woodlands. BEST analysis showed that groundcover and leaf-litter percentage cover correlated strongest with invertebrate composition. This study has demonstrated that grazing management relying on clearing of fertile grassy woodlands of the rangelands of Central Queensland alters invertebrate diversity and assemblage. Thus, tree clearing not only leads to biodiversity losses in the canopy layer, but also in the ground-layer vegetation.

Implications for insect conservation Pastoralists have the capacity to improve outcomes for invertebrate biodiversity by maintaining groundcover (ground-layer vegetation and litter cover) above 80%, by encouraging native pastures over introduced species such as Buffel Grass and by retaining native woodlands.

Keywords Clearing · Buffel grass · *Cenchrus ciliaris* · Rangeland management · Remnant woodland · Biodiversity · Conservation · Grassy woodlands · Invertebrates · Sustainable grazing practices

Introduction

Managed grazing of domestic livestock is the most extensive form of land use on the planet, occupying 25% of the global land surface (Asner et al. 2004). Graziers throughout the world traditionally manipulate the landscape to enhance pasture production, primarily by clearing trees (and associated woody vegetation) or altering grazing pressure by varying

stock numbers (Ash et al. 2011; Hall et al. 2016). Consequently, it is important to understand the impacts of grazing management, including those associated with land clearing, on biodiversity of native fauna of woodlands.

Clearing of woodlands generally promotes grass growth (Walker et al. 1972, 1986), primarily by increasing insolation to ground-layer vegetation (Specht and Morgan 1981). However, while there are typically substantial increases in pasture biomass in the short-term, longer-term studies suggest that these gains may not be sustainable over longer time frames (> 20 years) due to nutrient rundown (Kaur et al. 2005; Sangha et al. 2005a; Radford et al. 2007). These studies also point to other issues caused by tree clearance such as loss of biodiversity and land degradation (Rolfe 2002; Sangha et al. 2005b) and a reduction in soil nutrients and pasture quality (Jackson and Ash 1998). Besides altering

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pasture biomass, several other changes to the ground-layer vegetation are associated with removal of the tree layer. The reduction in shading of the ground-layer vegetation may raise soil temperatures, possibly influencing soil moisture (Lal and Cummings 1979; Hashimoto and Suzuki 2004). Less rainfall may be retained (Thornton et al. 2007), causing more rapid leaching of salts (Cowie et al. 2007) and elevation of soil pH with reduced nutrient availability (Sangha et al. 2005a). There is a loss of input of leaf and woody litter altering the quality of litter available (Sangha et al. 2006), potentially influencing food webs. Finally, there may be changes in plant dominance associated with colonisation by introduced pasture grasses or weeds, particularly where heavy grazing occurs (Dorrough et al. 2006; Dorrough and Scroggie 2008; Kutt and Fisher 2011; Hall et al. 2017).

In Australia, grazing is the dominant land use (40% of land mass) and in Queensland 80% of terrestrial land is classified as rangelands used for domestic livestock grazing (Department of Environment and Resource Management 2011). In Queensland, Buffel Grass (*Cenchrus ciliaris*) is one of the most important pastoral species for cattle grazing (Marshall et al. 2012). This species was introduced in the 1920s and is still widely sown. Although beneficial to graziers, Buffel Grass has the capacity to invade and expand its range into non-target habitats such as nearby woodlands (Eyre et al. 2009). Buffel Grass has been shown to reduce ground-layer plant diversity (Melzer et al. 2014; Fensham et al. 2015). Invasive grasses such as Buffel Grass have been found to affect the quantity and quality of the grass litter, altering invertebrate assemblages and diversity (Grigg 1999; Wolkovich et al. 2009).

While tree clearing will have obvious impacts on invertebrate fauna associated with the canopy layer of woodlands such as invertebrates dependent on foliage or bark of trees, impacts on those associated with the ground-layer vegetation are less obvious (Dorrough et al. 2012). However, studies have shown that clearing generally leads to a decline in invertebrate biodiversity associated with ground-layer vegetation (Green and Catterall 1998; Bromham et al. 1999; Vasconcelos 1999; Mathieu et al. 2005; Houston et al. 2015; Majer et al. 2021). Clearing may also impact on the adjacent habitat by disrupting dispersal patterns and altering the intensity of ecological processes (e.g. predation) leading to changes in faunal assemblages of adjacent vegetation (Craig et al. 2015).

Invertebrates are key components of any ecosystem but particularly for soils where they contribute to soil health by improving aeration and water infiltration and turnover of nutrients (Stork and Eggleton 1992). They also contribute to other important ecosystem services such as pollination, detritivory, herbivory and control of weed species, as well as providing food for larger animals such as birds and other vertebrates (Hallmann et al. 2017; Neilly et al. 2020).

Diets of woodland and ground-foraging insectivorous birds in Australia are typically dominated by a few prey groups including beetles, ants, spiders, bugs, flies, grasshoppers, caterpillars and lacewings (Major 1991; Gamez-Virues et al. 2007; Razeng and Watson 2012; Lindsay et al. 2014).

The objective of the study was to evaluate the influence of tree clearing on invertebrate assemblages associated with ground-layer vegetation by comparing them to nearby uncleared remnant woodlands on grazed land of the same soil type. Long-cleared sites (i.e. > 20 years) were selected to ensure that the effects of clearing had sufficient time to alter ground-layer vegetation. As cleared sites in this region were dominated by Buffel Grass, changes to the ground-layer vegetation may reflect both clearing and Buffel Grass colonisation. We compared remnant and cleared woodland in terms of biodiversity: order richness and invertebrate assemblage composition and abundance metrics: trophic structure (abundance of detritivores, herbivores and predators), food availability for insectivorous vertebrates (combined abundance of invertebrate macrofauna) and pollinator abundance. We also assess the influence of habitat structure on arthropod assemblages.

Methods

Study area

The study area straddles the Tropic of Capricorn and lies ~ 100 km from the coast to the west of Rockhampton between latitudes 22°48' and 23°35' south (spanning a distance of ~ 80 km) and longitudes 149°11' and 150°02' east (also ~ 80 km). Four cattle grazing properties representative of the grazing management in the region and at least 20 km apart were selected: Isaac/Connors Rivers (IC); Mackenzie River (MK); Melaleuca Creek (FM), a tributary of the Fitzroy River and the Fitzroy River (FR). The climate is typified by long, hot summers and mild winters (Hutchinson et al. 2005). Annual rainfall averages 653 mm at the nearest rainfall station (Riverslea TM, Australian Bureau of Meteorology), with the three summer months (December, January and February) accounting for almost half the annual rainfall. Annual pan evaporation rates in the region are high, approximately 2100 mm per year (DES 2020).

Remnant vegetation consisted of sclerophyll woodlands and forests including riparian forests (> 30% canopy foliage projective cover (FPC)) along river edges dominated by Forest Red Gum (*Eucalyptus tereticornis*) and River She-oak (*Casuarina cunninghamiana*). Bordering the riparian forests, at slightly higher elevations, were woodlands (10–30% FPC) associated with gently sloping alluvial terraces. Dominant species of the terrace woodlands were Coolibah (*Eucalyptus coolabah*), Forest Red Gum and Brigalow (*Acacia*

harpophylla). However, while a strip of riparian forest was retained along the river margins, most of the woodlands of the adjacent alluvial terraces were cleared. Typically these were well grassed and dominated in cover by an introduced pasture species, Buffel Grass.

While grazing regime varied between properties and paddocks, when cattle numbers were annualised, all paddocks were grazed at levels typical of the commercial stocking rates in the region, which range from 0.1 to 0.3 cattle/ha (Kaur et al. 2005). Overall, riparian paddocks were stocked at slightly lower levels of grazing than the adjacent alluvial terraces.

Sites and study design

At each of the four locations, four sites, separated by at least a kilometre to ensure independence, were established along 10–15 km of riverbank. Two sites were in patches with remnant terrace woodland present (TW) and two in patches where terrace woodlands had been cleared, the terrace grasslands (TP) (Fig. 1a). In addition, on the riverbank adjacent to each site, sites were established in the riparian forest: RFp if adjacent to the terrace grassland or Rfw if adjacent to the terrace woodland (Fig. 1b). To avoid edge effects, terrace sites were located at least 150 m from the edge of the riparian zone. This gave four habitat types in all, with two replicates of each at each location: terrace woodland, terrace grassland, and the adjoining riparian vegetation, either Rfw or RFp. Before clearing, terrace grasslands had similar vegetation to the terrace woodlands. The two terrace habitats (grassland or woodland) in each set had similar stocking rates, as did the two riparian habitats.

The comparison between the terrace grassland and the terrace woodland was the main interest of the study and provided the basis for establishing the influence of clearing on ground-layer invertebrates. The riparian habitats were included to evaluate the effect of woodland clearing on the adjacent riparian zone and were analysed separately.

Sampling

Surveys were undertaken in Autumn (April–May) 2007. A 200 m transect aligned parallel to the river was established at each site. Habitat attributes were measured within a 10 m radius of each of three points (0, 100 and 200 m) along the transect. Percentage projective cover of ground-layer vegetation was visually estimated for grass (including introduced grasses), leaf litter, total litter (includes both leaves and woody debris), ground-layer vegetation (combined grass, forbs and foliage of low shrubs < 0.5 m height) and groundcover (combined ground-layer vegetation and litter). Percentage projective cover of important introduced species such as Buffel Grass, Green Panic (*Megathyrus maximus*

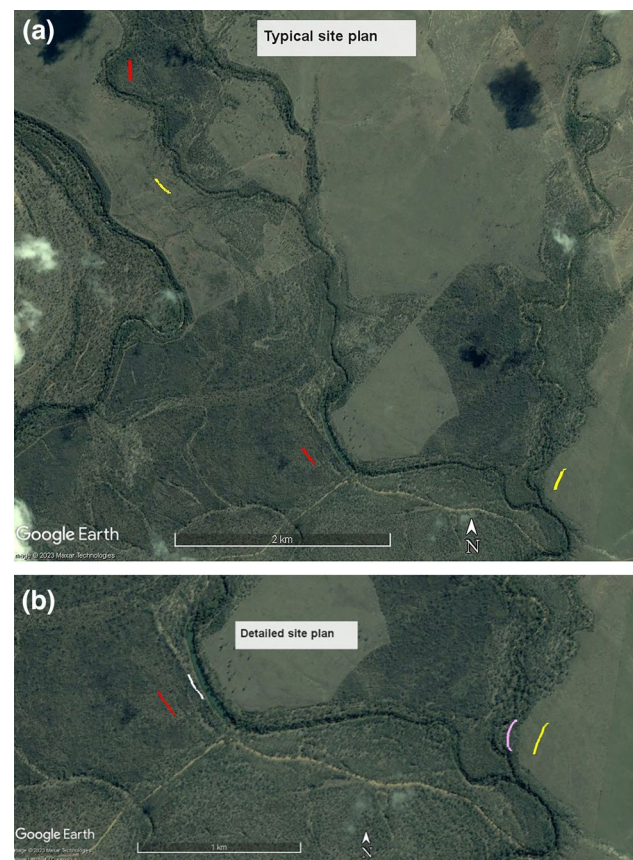


Fig. 1 **a** Example of the typical site plan showing 4 sites arrayed along the riverbank at one location, two in uncleared terrace woodlands (red transects, TW) and two in grasslands on cleared terrace woodlands (yellow transects, TP); and **b** detail of the same location showing the pairs of sites in the riparian forest and adjacent terrace habitats—TW (terrace woodland, red transect), Rfw (riparian forest adjacent to woodland, white transect) and TP (terrace grassland, yellow transect), RFp (riparian forest adjacent to grassland, pink transect)

var. *pubiglumis*) and total invasive species cover (i.e. combined Buffel, Green Panic and invasive forbs such as *Parthenium hysterophorus*) were also recorded. Grass height was estimated from a measure of the height of tallest ground-cover vegetation (cm) at 30 points spaced at 1 m intervals along 3 radii of 10 m at each point. The number of native species of ground-layer plants was also recorded in each of the three circles of 10 m radius.

To allow for the quantitative assessment of the abundance of invertebrates (numbers/m²) (King and Hutchinson 2007), soil surface, litter and grass-associated invertebrates were sampled using an MTD leaf blower acting as a suction sampler. The maximum air-flow velocity of this model (~ 70 ms⁻¹) exceeded the minimum (45.6 ms⁻¹) recommended for samplers of this type (Stewart and Wright 1995). The sampler was passed repeatedly over the vegetation and groundcover for 30 s within a randomly located 1 m² quadrat

(Cagnolo et al. 2002) at each of 3 points along the 200 m transect (0, 100 and 200m). To avoid damage, invertebrates were collected in a fine-meshed bag placed in the mouth of the suction device.

Samples were washed through a fine meshed sieve (150 μ), sorted to Order (Naumann 1991) and enumerated. The three samples from each site were averaged to provide a sample estimate for each site. Exceptions to the order-level of classification were a few groups sorted to class, Chilopoda (centipedes), Diplopoda (millipedes) and Gastropoda (snails); and Hymenoptera was split into family Formicidae (ants) and Other Hymenoptera (wasps and bees). Collembola (springtails) were categorised as elongate-bodied (orders Poduromorpha and Entomobryomorpha) or globular springtails (order Symphypleona).

To evaluate trophic structure, invertebrate taxa with relatively uniform feeding habits and dominated by one trophic category were placed in one of three groups—detritivores (mites, springtails, book-lice, cockroaches and termites); herbivores (bugs, grasshoppers, stick insects, thrips, butterflies and moths) and predators (spiders, pseudoscorpions, mantids, lacewings and wasps) (Naumann 1991; Houston and Melzer 2018). Due to a broad range of feeding habits, some taxa could not be assigned to a single trophic category (ants, beetles and flies). In addition, taxa comprising the macrofauna were summed to provide a measure of the available food for birds and other vertebrates. Macrofauna comprise invertebrates > 2 mm and include most taxa sampled except those comprising the mesofauna (i.e. invertebrates < 2 mm; mites, springtails and pseudoscorpions). In the same way, pollinating taxa: wasps and bees, flies, butterflies and moths, beetles and thrips were summed to provide a measure of pollinator capacity (Thien et al. 2000).

Analysis

To evaluate the effect of clearing on terrace woodlands, a two-way analysis of variance (ANOVA) was used to test the influence of location (four properties) and habitat (two types: terrace woodland or terrace grassland) on habitat attributes and arthropod metrics: order richness, total invertebrate abundance, abundance of each trophic category (detritivore, herbivore and predator), macrofauna, mesofauna and pollinators. A $\log_{10}(x + 1)$ transformation was used on abundance data to normalize distribution. Where applicable, a posteriori Tukey tests (for multiple pairwise comparisons) were used to identify significant differences between locations (Quinn and Keough 2002). To determine if clearing influenced bordering remnant habitat, the two riparian habitats (either adjacent to cleared or uncleared woodland) were analysed using the same ANOVA design.

Non-metric multidimensional scaling (nMDS) ordination was used to examine relationships between samples based on

the order-level invertebrate assemblages. To reduce the influence of abundant taxa, data were square root transformed and sites were compared by applying the Bray–Curtis similarity index (Clarke and Warwick 2001). Ordinations were visualised in two-dimensional space, whereby sites closer together have a more similar assemblage than those further apart.

To evaluate influence of location and habitat on order assemblages, a permutational ANOVA was applied (PERMANOVA, PRIMER-e, v7) (Anderson et al. 2008). Pairwise tests were used to identify significant differences in invertebrate assemblages between locations. Since this test is sensitive to data dispersion and may confound differences among groups with differences in scatter within groups, a multivariate homogeneity of dispersion test (PERMDISP, PRIMER-e, v7) was also applied (Anderson 2001). For all analyses, a p-value threshold of 0.05 was considered significant.

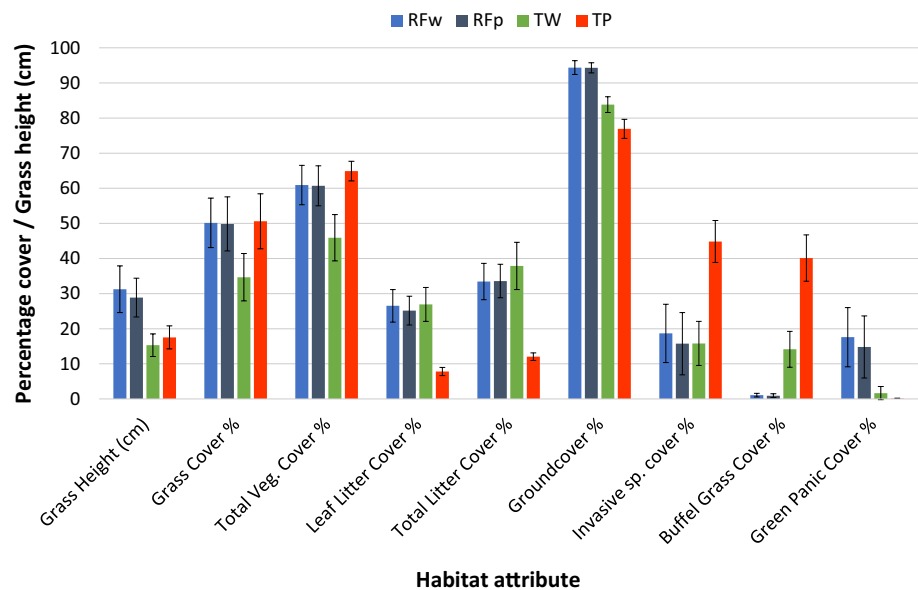
To ascertain which aspect of habitat structure (i.e., grass height, grass cover, ground-layer vegetation cover, leaf litter cover, total litter cover, groundcover, and invasive species cover) correlated with changes in invertebrate assemblage composition, a BEST analysis was applied (PRIMER-e v7) (Clarke and Warwick 2001) on all four habitats. The BEST routine seeks to choose explanatory (e.g. environmental) variables which ‘best explain’ the multivariate pattern in the response (e.g. assemblage) variables, by calculating a rank correlation coefficient (Spearman’s) between all the elements of their respective similarity matrices. Habitat attributes were normalized to correct for the different scales of measurement and Euclidean distance applied as the similarity measure. Because Buffel Grass and Green Panic were associated mainly with either terrace zones or riparian zones respectively, they were not included individually but as a component of the invasive species cover.

Results

Ground-layer attributes of the four habitats

Grasslands on cleared terrace woodlands had more grass but less leaf and woody litter than the terrace woodlands, resulting in significantly lower groundcover (76% compared with 83%; Table 1, Fig 2). Terrace grasslands also differed in being dominated by introduced species such as Buffel Grass with an average of 40% cover compared with 14% in terrace woodlands. Terrace grasslands had fewer native plant species than the terrace woodlands ($18 \pm$ standard error 2 compared with 25 ± 2 in woodlands). There were some property differences as well, mainly due to IC terrace vegetation having less grass (including Buffel Grass) and more leaf and woody litter than the other sites.

Fig. 2 Mean ground-layer attributes of the four habitat types (RFw riparian forest adjacent to remnant woodland; RFp riparian forest adjacent to cleared woodland; TW: remnant woodland on an alluvial terrace; TP: cleared woodland (grassland) on an alluvial terrace) (standard error bars shown)



In contrast to the terrace habitats, the two riparian forest habitats, irrespective of whether adjacent to woodlands or grasslands on the adjoining terrace, resembled each other in all ground-layer habitat attributes (Fig. 2), being relatively well vegetated with grass cover above 50% and more than 90% groundcover due to the combination of ground-layer vegetation (mainly grass but also forbs and low shrubs in the ground-layer), leaf and woody litter. Buffel Grass was present but comprised less than 1% of groundcover. Grass was relatively taller than in the terrace habitats (averaging 30 cm compared with 15–18 cm), partly reflecting the dominance by tall, introduced grasses such as Green Panic which averaged 15–18% cover. Native plant species richness was similar to the terrace woodland ($22-23 \pm 3$).

Invertebrate biodiversity & trophic metrics

Over 20,000 invertebrates from 24 taxa were captured during the study. Eleven taxa comprised almost 98% of the catch, with representatives of all trophic categories – detritivorous: mites (23.5%), globular springtails (9.6%), elongate-bodied springtails (5.9%) and book-lice (5.2%); herbivorous: thrips (16.9%) and bugs (11.0%); predatory: spiders (11.5%) and wasps (3.6%) and mixed: flies (4.2%), beetles (3.5%) and ants (2.8%). Remaining taxa were in low abundance (i.e. <1% of the catch) and included grasshoppers and crickets, cockroaches, moths and butterflies, mayflies, lacewings, praying mantids, pseudoscorpions, millipedes, isopods, phasmids, termites, silverfish and dragonflies.

Analysis of the biodiversity data (order richness) showed that terrace grasslands had significantly fewer invertebrate orders than the terrace woodlands (an average of 14 orders/site compared with 17), although there

was a significant interaction with location and only two of the four locations, IC and MK, had pronounced lower order richness than the nearby terrace woodlands (Table 1, Fig. 3).

Detritivorous invertebrates accounted for 45% of the overall catch, herbivores 29%, predators 15% and 11% unassigned (i.e. those orders with mixed feeding habits). Three of the four habitats had the expected abundance pattern with detritivores > herbivores > predators (Fig. 4). Terrace grasslands were the exception having similar numbers of herbivores and predators. Abundance of detritivores was similar across the four habitats.

Analysis of abundance and trophic data showed that terrace grasslands had significantly fewer herbivores than the terrace woodlands (Table 1). This pattern was consistent at all four locations. The same pattern was observed in all herbivorous taxa, Thysanoptera (thrips), Hemiptera (bugs), Orthoptera (grasshoppers) and Lepidoptera (caterpillars) indicating that it was a universal trend in this group. Predator abundance was also relatively low in terrace grasslands but not significantly lower than in terrace woodlands. These trends are illustrated for the most abundant taxa in each trophic group (Fig. 5).

Terrace grasslands had significantly fewer macrofauna than the terrace woodlands (Table 1, Fig. 6), showing that food availability for insectivorous vertebrates was reduced following clearing. Numbers of pollinators showed a similar pattern with significantly fewer pollinators in the terrace grasslands than the terrace woodlands (Fig. 6). There were also differences in location with more pollinators at IC than FM.

Although there were some differences by location, the two riparian habitats resembled each other in all invertebrate

Table 1 Results of two-way ANOVA (location x habitat) on ground-layer attributes and invertebrate metrics testing effects of clearing (terrace sites) and whether clearing affects adjacent remnant vegetation (riparian sites)—results of ANOVA on riparian habitat attributes were all non-significant with P values > 0.6 and are not shown

Metric	Location		Habitat		Location xHabitat	
	F _{3,8}	P	F _{1,8}	P	F _{3,8}	P
Habitat attributes—terrace						
Grass height (cm)	1.213	0.366	0.438	0.527	0.595	0.636
Grass % cover	35.931	0.000	20.065	0.002	0.881	0.491
Total ground-layer vegetative % cover	10.692	0.004	26.567	0.001	3.471	0.071
Leaf litter % cover	6.630	0.015	79.750	0.000	13.788	0.002
Total litter % cover	7.991	0.009	67.708	0.000	8.783	0.007
Groundcover %	5.546	0.024	10.979	0.011	1.497	0.288
Total invasive species % cover	1.526	0.281	11.968	0.009	0.175	0.910
No. native plant species	4.465	0.040	16.884	0.003	1.504	0.286
Buffel Grass % cover*	7.365	0.011	26.620	0.001	1.396	0.313
Green Panic % cover*	0.956	0.459	0.867	0.379	1.044	0.424
Invertebrates						
Terrace						
Order richness	0.800	0.528	10.800	0.011	4.489	0.040
Total abundance (no./m ²)	0.877	0.492	1.873	0.208	0.257	0.854
Detritivore abundance (no./m ²)	0.696	0.580	0.341	0.575	0.224	0.877
Herbivore abundance (no./m ²)	0.323	0.809	28.381	0.001	2.003	0.192
Predator abundance (no./m ²)	2.488	0.135	4.159	0.076	1.493	0.289
Macrofauna abundance (no./m ²)	3.010	0.095	27.878	0.001	2.994	0.096
Mesofauna abundance (no./m ²)	0.824	0.516	0.639	0.447	0.299	0.826
Pollinator abundance (no./m ²)	4.793	0.034	9.679	0.014	3.351	0.076
<i>Permanova</i>						
Order-level assemblage (998 permutations)	1.780	0.042	3.571	0.006	1.371	0.150
<i>Riparian</i>						
Order richness	0.634	0.613	0.806	0.395	3.387	0.074
Total abundance (no./m ²)	2.384	0.145	0.047	0.834	2.329	0.151
Detritivore abundance (no./m ²)	1.479	0.292	0.079	0.785	1.270	0.348
Herbivore abundance (no./m ²)	2.059	0.184	0.021	0.888	3.331	0.077
Predator abundance (no./m ²)	3.421	0.073	0.112	0.747	1.592	0.266
Macrofauna abundance (no./m ²)	4.119	0.049	0.004	0.952	3.397	0.074
Mesofauna abundance (no./m ²)	3.451	0.072	0.067	0.803	1.583	0.268
Pollinator abundance (no./m ²)	7.976	0.009	0.775	0.404	4.659	0.036
<i>Permanova</i>						
Order-level assemblage (998 permutations)	1.821	0.049	0.504	0.790	1.667	0.137

Significant results at 0.05 shown in bold

abundance and biodiversity metrics (Table 1, Figs. 3, 4, 5, 6).

Invertebrate assemblage

Although some terrace grasslands were relatively closely associated with other habitats (e.g. at FM and FR), seven of the eight grassland sites were to the right of the ordination while most sites comprising the other habitats were to the left or middle, indicating that terrace grasslands had the most distinctive invertebrate assemblage of the four habitats (Fig. 7a). PERMANOVA on square root transformed

abundance data showed that the terrace grassland assemblage differed significantly from the terrace woodland assemblage (Table 1). In contrast, riparian forests closely resembled each other in invertebrate composition; confirming that clearing has led to changes in ground-layer invertebrate assemblages but has not altered invertebrate assemblages associated with the adjacent riparian vegetation. Habitats had similar levels of dispersion (PERMDISP, homogeneity of dispersion, terrace habitats: $F_{1,14} = 1.301$, $P = 0.328$; riparian habitats: $F_{1,14} = 2.130$, $P = 0.171$), indicating that differences in taxa composition between habitats

Fig. 3 Mean order richness of the 4 habitat types at each of the 4 sampling locations (see Fig. 2 for habitat label descriptions; locations—IC: Isaac/Connors Rivers; MK Mackenzie River; FM Melaleuca Creek, a tributary of the Fitzroy River and FR: Fitzroy River) (standard error bars shown)

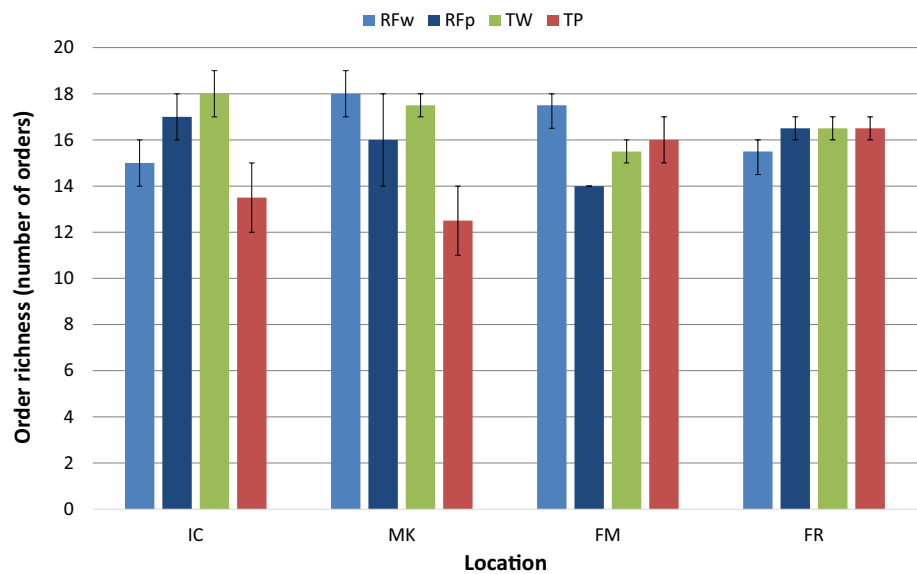
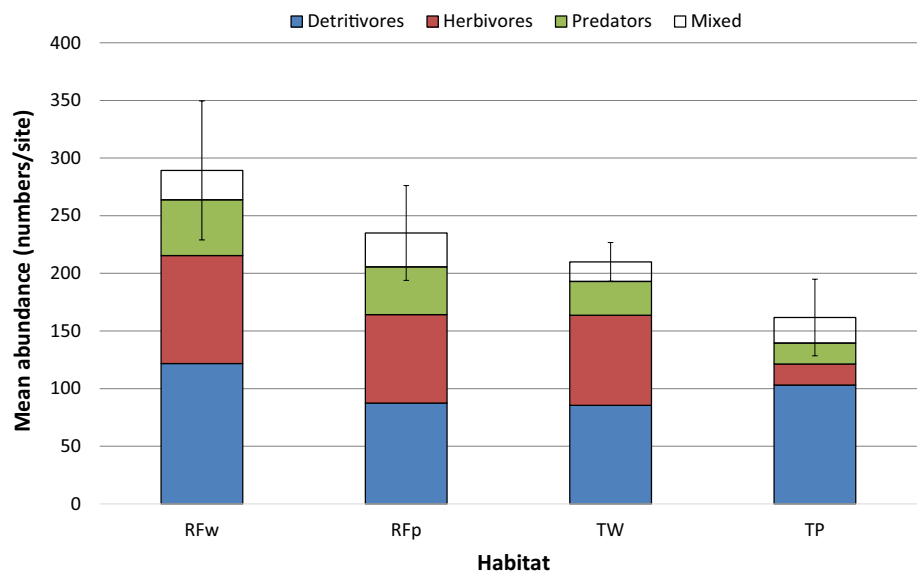


Fig. 4 Trophic structure of the 4 habitat types (RFw riparian forest adjacent to remnant woodland; RFp riparian forest adjacent to cleared woodland; TW: remnant woodland on an alluvial terrace; TP: cleared woodland (grassland) on an alluvial terrace) based on mean abundance data (standard error bars shown for overall abundance)



obtained with PERMANOVA were not due to differences in dispersion.

The BEST routine using the seven selected habitat attributes indicated that groundcover (Spearman's $r_s = 0.306$) had the highest correlation with changes in invertebrate assemblage composition, the remaining attributes being < 0.3 . The highest correlation was achieved with two attributes – groundcover and leaf litter cover (Spearman's $r_s = 0.402$). The four terrace grasslands with the most distinct invertebrate assemblage to the right-hand side of the ordination were characterised by a combination of relatively low percentage groundcover ($< 78\%$, Fig. 7b) and leaf litter cover ($< 10\%$).

Discussion

This study has demonstrated that grazing management relying on clearing of fertile grassy woodlands of the rangelands of Central Queensland leads to a reduction in biodiversity (i.e. order richness) of invertebrates associated with the ground-layer vegetation and a change in invertebrate assemblage composition. In addition, terrace grasslands had fewer herbivorous invertebrates, food available for insectivorous vertebrates and pollinating insects compared to uncleared nearby woodlands and these differences were consistent at all four properties studied. Thus, clearing not only leads to biodiversity losses in the canopy layer of vegetation and associated fauna (Dorrrough et al. 2012), but also in the

Fig. 5 Mean abundance of the most abundant orders in the herbivore and predator trophic groups shown for each of the 4 habitat types (see Fig. 2 for habitat label descriptions) (standard error bars shown)

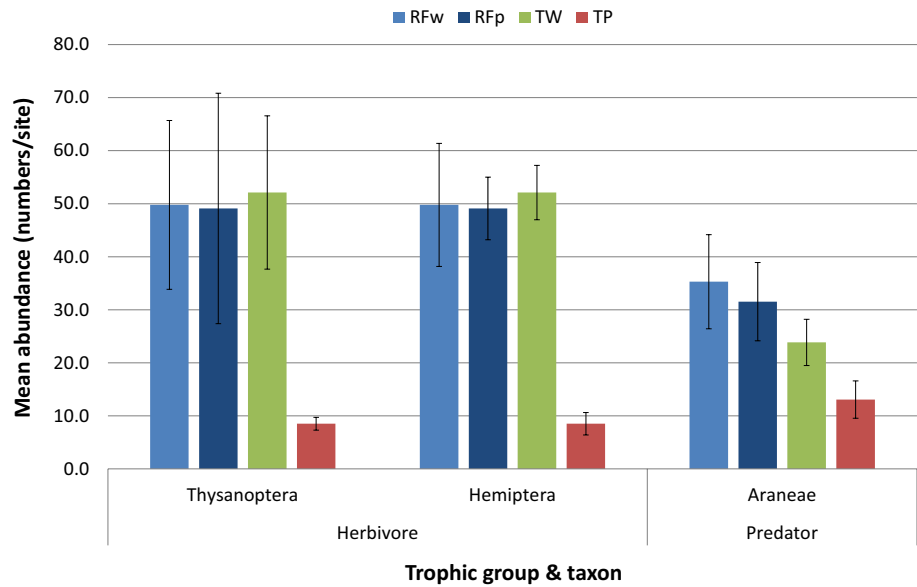
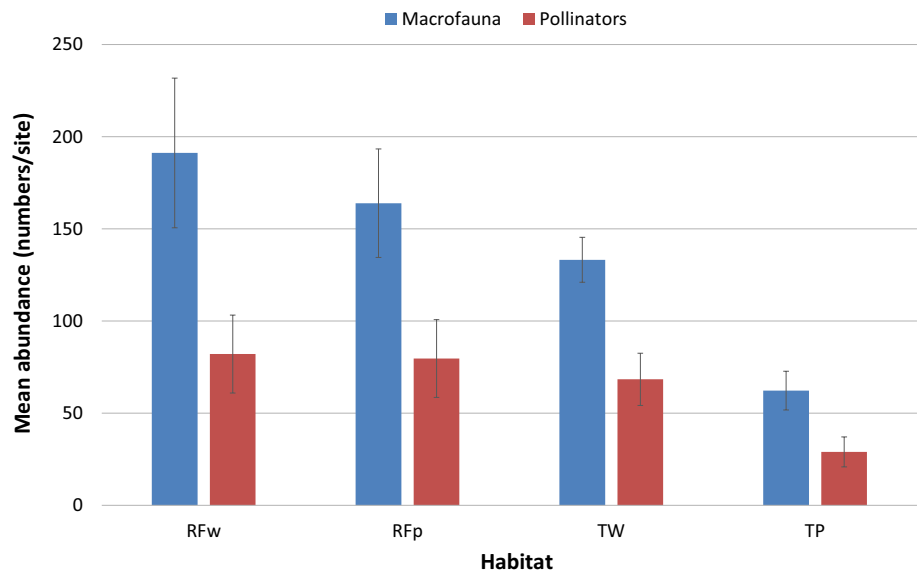


Fig. 6 Mean abundance of macrofauna (> 2 mm; spiders, bugs, thrips, book-lice, beetles, flies, wasps, ants, cockroaches, grasshoppers, moths and butterflies, lacewings, phasmids, mantids, silverfish) and pollinators (wasps and bees, flies, butterflies and moths, beetles and thrips) shown for each of the 4 habitat types (see Fig. 2 for habitat label descriptions) (standard error bars shown)



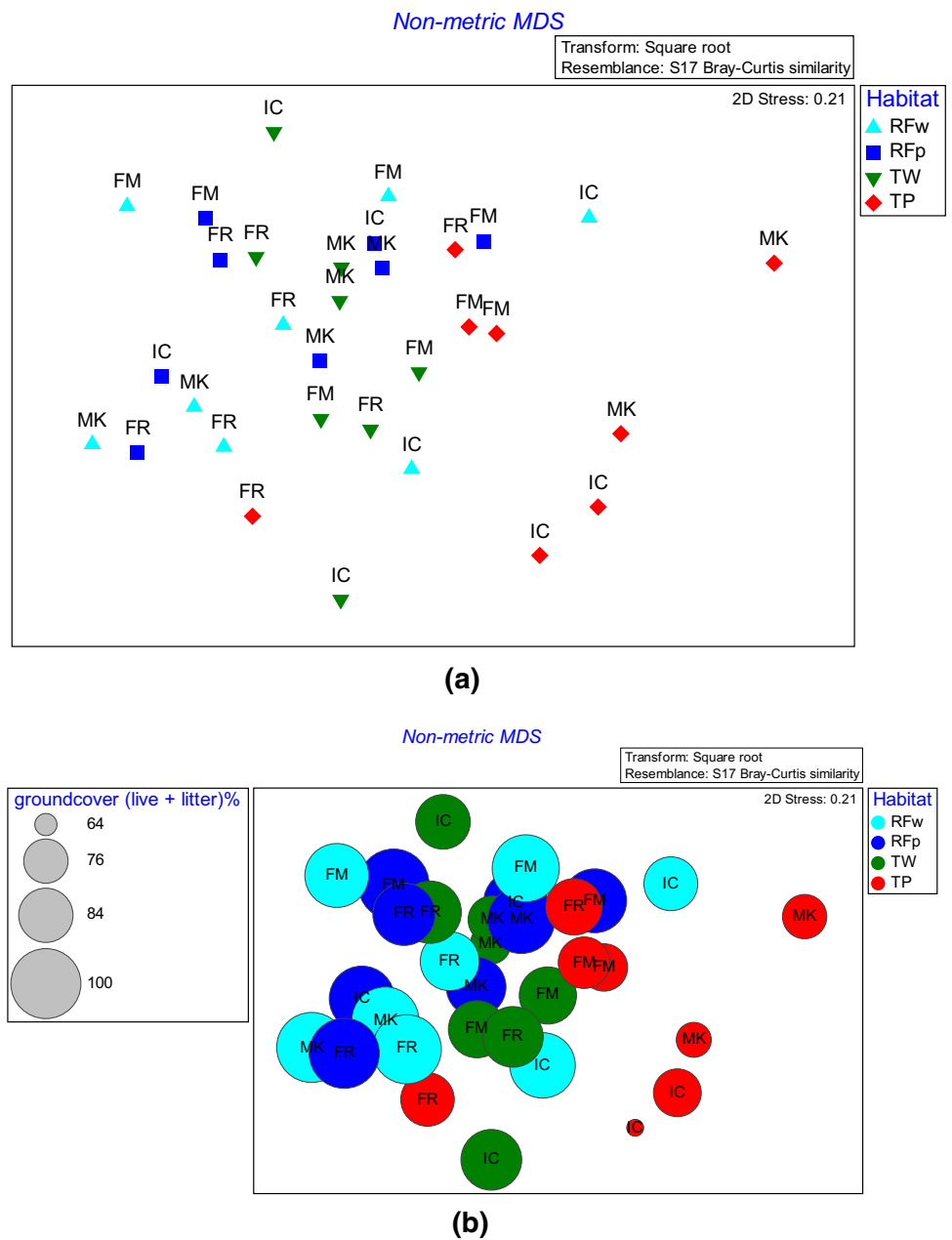
biodiversity and resource base of the invertebrate fauna associated with the ground-layer vegetation. Implications for sustainability of such changes need to be considered within the wider context that has identified rundown of pasture productivity following clearing over longer time frames (Kaur et al. 2005; Radford et al. 2007).

However, while clearing led to changes in ground-layer invertebrate assemblages, there was no apparent change in invertebrate assemblages associated with the adjacent riparian vegetation. This suggests that fauna of adjacent riparian vegetation remains relatively intact following clearing and that retention of even thin strips of remnant riparian forest helps sustain biodiversity on farm properties.

Soil and ground-layer vegetation invertebrates are known to have important roles in supporting grazing production systems (Stork and Eggleton 1992). In particular, greater biodiversity of invertebrates has been shown to be associated with improved soil health and enhancing nutrient availability (Kemmers et al. 2013), indirectly supporting grass and cattle production. Lower diversity of invertebrate fauna was implicated in slower rates of litter decay in pastures compared with nearby woodlands (Grigg 1999).

Retention of woodland patches in the landscape matrix provides ecosystem functional benefits by promoting the abundance of macrofaunal invertebrates and pollinators. These provide a number of ecosystem services such as pollination, biocontrol of insect pests of pastures and weed

Fig. 7 Nonmetric multidimensional scaling (nMDS) ordination, using Bray–Curtis similarities on square-root transformed data, comparison of invertebrate assemblages based on order-level abundance from pitfall traps **a** Ordination of sites and **b** bubble plot with bubbles proportional to percentage groundcover (see Fig. 3 for location label descriptions)



outbreaks, benefitting both graziers and any crops grown in the vicinity (Potts et al. 2006; Holland et al. 2017; St. Clair et al. 2022). In addition, by enhancing the food available for insectivorous vertebrates, woodlands help support food webs and birds, which indirectly also benefit agricultural systems through predation on insect pests of crops and pastures, and controlling pest outbreaks (Gamez-Virues et al. 2007; Peng et al. 2020).

Reasons why clearing has led to a grassland that supports a reduced number of herbivorous invertebrates have not been determined. Another study, also using suction samplers, found no effect of clearing on biodiversity (order richness), total abundance, abundance of trophic groups

or composition of invertebrate assemblages (Houston and Melzer 2018). However, that study took place in recently cleared paddocks (< 5 years) with native pastures of comparable biomass that resembled the composition of the ground-layer vegetation of the original woodlands (Hall et al. 2016). In contrast, clearing in the current study had occurred many years ago (> 20 years) and grasslands were dominated by introduced pasture grasses such as Buffel Grass. Thus, it appears that tree clearing per se does not necessarily lead to changes in associated ground-layer invertebrates; but relate to further changes associated with the consequences of the clearing.

One possible explanation for the observed changes in biodiversity, trophic structure and invertebrate composition may relate to the relatively greater dominance by Buffel Grass in the terrace grasslands than the uncleared terrace woodlands in the current study—40% cover compared with 14% in terrace woodlands and 1% in riparian forests. Another study also reported lower invertebrate diversity in Buffel Grass pastures (Grigg 1999). A North American study of rangelands colonised by Buffel Grass found that the invaded paddocks had less invertebrates, particularly ants, beetles and spiders than native grasslands (Flanders et al. 2006). Most Australian studies were focussed on ant functional groups with mixed results, some ant groups declining, some increasing and others showing no change (Smyth et al. 2009; Williams et al. 2012; Bonney et al. 2017).

Consistent with other studies, Buffel Grass was found to be associated with lower native plant diversity in pastures (Melzer et al. 2014; Fensham et al. 2015). It is possible that this may have flow-on consequences for dependent fauna such as herbivores with specialist feeding preferences. A study of minesite rehabilitation pointed to such an impact. Corresponding with lower plant diversity than nearby native woodlands, there were fewer species of plant-feeding insects such as Hemiptera (bugs) in the rehabilitated habitat (Moir et al. 2010; Orabi et al. 2010). Further, it is possible that Buffel Grass, as an invasive non-native species, has relatively fewer endemic herbivorous insect species feeding on it compared to native grasses (Cappuccino and Carpenter 2005), although further studies are needed to evaluate this.

Other explanations for the reduced numbers of herbivorous invertebrates in cleared woodlands compared to uncleared woodlands may relate to the quality of the grass. Graziers in northeastern Australia have long been aware of issues of “nutrient tie-up” in Buffel Grass pastures where productivity typically declines over time from the ‘tying-up’ of plant available nitrogen in the crowns, roots and organic matter of old grasses, resulting in reduced carrying capacity for cattle production (Peck et al. 2011; Clewett et al. 2021). Further, long-cleared pastures are prone to reduced nutrient availability and impacts on grass productivity and quality (Jackson and Ash 1998; Kaur et al. 2005, 2007; Sangha et al. 2005a). Irrespective of the cause, as well as impacts on cattle production, pasture rundown is likely to lead to less nutritious pasture grasses for herbivorous insects.

Differences in biodiversity and invertebrate assemblage of terrace grasslands and terrace woodlands were most pronounced in the two properties that used traditional grazing management approaches (i.e. continuous or long session grazing). In contrast, the two properties in which the terrace grasslands resembled the terrace woodlands

in biodiversity attributes employed more modern grazing management approaches such as rotational grazing that improved grass productivity (Eaton et al. 2011). It is possible that the style of grazing management may have positive impacts on biodiversity outcomes, although more detailed studies are needed (McCosker 2000; Dorrough et al. 2002; Lindsay and Cunningham 2009; Eaton et al. 2011).

Management applications

Our results show there is a link between retaining more groundcover and enhanced invertebrate biodiversity. Thus, pastoralists have the capacity to improve outcomes for invertebrate biodiversity by maintaining groundcover above 80%. In general, greater levels of ground-layer cover are recommended as a way to enhance sustainability of rangeland cattle production systems (Beutel et al. 2021). In another study in Northern Australia, heavy grazing reduced grass cover and land condition, leading to lower profitability and reptile diversity compared with moderately grazed paddocks (Neilly et al. 2018). Rotational grazing practices that typically involve resting of paddocks from cattle grazing for part of the year may also promote conservation of biodiversity (Dorrough et al. 2002; Eaton et al. 2011; Houston et al. 2013; Houston and Black 2016) and profitability (Neilly et al. 2018), although not always (Dorrough et al. 2012).

Graziers interested in improving biodiversity on their property should consider encouraging native pastures over introduced species such as Buffel Grass. Most likely this would only be possible on a small scale due to the known capacity of Buffel Grass to colonise disturbed habitats.

Maintaining woodlands rather than clearing is another option, particularly where the benefits in grass and cattle production are ambiguous as suggested by longer-term studies in some vegetation types (Jackson and Ash 1998; Kaur et al. 2005; Sangha et al. 2005a; Radford et al. 2007). The terrace woodlands of this study had greater biodiversity, more pollinators and macroinvertebrates, and a more natural assemblage and trophic structure (i.e. comparable to the riparian forests) than the terrace grasslands. Retention of woodlands in the landscape enhances ecosystem services such as pollination, pest and weed control, including indirectly by supporting insectivorous birds and other vertebrates (Crisol-Martínez et al. 2016). Graziers could consider retaining a matrix of intact woodlands and cleared patches as a way of promoting biodiversity benefits and cattle productivity.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

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