

REVIEW ARTICLE

Land-use legacies limit the effectiveness of switches in disturbance type to restore endangered grasslands

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Temperate native grasslands in Australia have been decimated across their range since European colonization (>200 years ago), and the few remaining remnants are mostly fragmented and degraded. Changes in disturbance type, particularly the removal of Indigenous fire and the introduction of livestock grazing, resulted in the local extinction of fire-dependent and grazing-sensitive native species, and led to an increase in exotic species. Recently, native grasslands have been acquired to improve the reservation status of the threatened community and management strategies have been implemented that involve the removal of livestock grazing and the reintroduction of fire or other biomass reduction methods. Here, we examine if the change in disturbance type—a disturbance switch—improves the native composition of grasslands. We review literature that reports instances where there has been a change in disturbance type to examine how grasslands respond to disturbance switching. We found mostly no change in native and exotic species richness when management changed from stock grazing to fire (at least in the short term, ≤10 years). Positive outcomes for other disturbance shifts (grazing → mowing, or cultivation → grazing) occurred when the disturbance type was accompanied by seed addition, or in landscapes where dispersal from nearby remnant sites was possible. This suggests that seed- and/or dispersal-limitation may limit passive restoration outcomes in fragmented landscapes. It is necessary to determine the longer-term impacts of switches in disturbance regimes, and whether recovery thresholds have already been crossed.

Key words: Australian temperate grasslands, conservation management, fire, passive restoration, regeneration, seed limitation, species richness

Implications for Practice

- Temperate grasslands have a disturbance requirement (specifically fire) for the maintenance of species richness. The removal of an exogenous disturbance (introduced stock grazing) had varied impacts on species richness and the outcomes partly depended on productivity.
- Passive recovery of native species is uncommon with the removal of introduced stock grazing and the reintroduction of fire, suggesting recovery is limited by agricultural land-use legacies in the grassland sites and surrounding landscape (seed and/or dispersal limitation).
- Active restoration in the form of seed addition will likely improve restoration outcomes for these endangered communities, but the longer-term prognosis is largely unknown (including determining optimal ongoing disturbance management).

Introduction

Disturbance promotes species diversity in temperate grasslands globally by constraining biomass, and hence the competitive effects of dominant species on subordinate species (Collins 1992; Grace 1999; Lunt & Morgan 2002; Prober et al. 2013; Koerner & Collins 2014). Much of the focus in grassland conservation management and restoration has therefore centered on identifying appropriate disturbance regimes to maintain and

recover diversity (e.g. Olff & Ritchie 1998; Morgan & Lunt 1999; Price et al. 2019). However, different disturbance types (e.g. fire vs. grazing) can have fundamentally different impacts on native biodiversity, and hence they are not necessarily interchangeable (Price et al. 2019). Exposure to an endogenous (historic) disturbance regime likely fosters ecosystem resilience, whereas exogenous disturbances can have substantial (negative) impacts on plant communities (Hobbs & Huenneke 1992; Yates et al. 2000).

Many grassland studies have compared the effects of different disturbance types on native diversity and composition (e.g. Collins et al. 1998; MacDougall & Turkington 2007; Tardella et al. 2020; Vermeire et al. 2020). While often the historical management regime is seen as desirable, there may be

Author contributions: JNP, NLS, JAH, MAC, JWM wrote and edited the manuscript.

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doi: 10.1111/rec.13271

practical limitations to implementation and/or the ecosystem may have shifted significantly such that historical management is no longer optimal (MacDougall & Turkington 2007; Valkó et al. 2014). In some cases, different disturbances are substitutable as they affect diversity through the same mechanisms, i.e. alleviating light limitation (Collins et al. 1998; MacDougall & Turkington 2007; Tardella et al. 2020), whereas in other studies this has been not the case (Catorci et al. 2014; Vermeire et al. 2020). In many cases, the reintroduction of traditional management that has been abandoned is compared with other practical alternatives. For example, many studies have considered the reintroduction of fire in ecosystems that have a history of regular fire, and compared fire with other management options (especially where there are practical limitations with implementing fire disturbance) (MacDougall & Turkington 2007). In Europe, fire has been explored as a substitute for the traditional management of grazing and mowing because it may be more practical (Valkó et al. 2014). Hence, there is an understanding that historical disturbance types may not be the best, or the most practical, management for improving native composition; hence other disturbances are explored as substitutes.

The first step in restoration is often the removal of the degrading force (which may be an exogenous disturbance) and reinstating historical disturbances (Aronson et al. 1993; Hobbs & Norton 1996; Gann et al. 2019). In the absence of other interventions, community recovery after the removal of an exogenous disturbance might be expected if successional processes dictate the recovery of communities (Aronson et al. 1993; Suding et al. 2004). Indeed, passive restoration has been successful in many regions in Europe (e.g. Fagan et al. 2008; Řehouňková & Prach 2008; Öster et al. 2009). However, land-use legacies associated with introduced stock grazing, and other agricultural practices such as cultivation, can make some degraded systems resistant to passive recovery (McIver & Starr 2001; Suding et al. 2004). Additionally, fragmentation creates dispersal barriers further limiting passive restoration (Johanidesová et al. 2015; Prach et al. 2015). Models of alternative ecosystem states that incorporate system thresholds and feedbacks are more relevant in these cases (Westoby et al. 1989; Suding et al. 2004; Cramer et al. 2008). Whether grasslands recover with passive restoration, such as the removal of an exogenous disturbance and its replacement with historical disturbance regimes, will depend on thresholds such as abiotic changes, exotic species invasions, loss of native species pools, shifts in species dominance, and propagule availability (Suding et al. 2004).

Prior to European colonization, Australian temperate native grasslands were burnt by Indigenous peoples for hunting and to promote food plants (Morgan & Williams 2015). Jones (1969) coined the phrase “fire-stick farming,” arguing that Aboriginal burning widely reported at the time of European arrival was part of a continuum going back to the earliest inhabitants. The soil disturbance created from Indigenous people collecting roots of food plants is likely to have also influenced the local dynamics of grasslands (Gott 1982; Gott 1983; Gott 2005). Bioturbation by digging mammals (such as bettongs and bandicoots), now largely extinct in much of their previous range, also provided

regular, small disturbances (Fleming et al. 2014; Valentine et al. 2017). While temperate grassland distributions in Australia are mostly driven by “bottom up” processes (Morgan et al. 2017), it is likely that regular disturbance maintained alpha diversity, particularly in high productivity grasslands (Price et al. 2019).

Changes to disturbance regimes following European colonization had dramatic and rapid effects on grassy ecosystems—removal of fire and the introduction of livestock grazing resulted in the local extinction of grazing-sensitive and fire-dependent native species (Stuwe & Parsons 1977; Lunt 1997; Lunt et al. 2007). Introduced livestock negatively affected native species which did not have an evolutionary history to grazing by large herds of ungulates, and favored many exotic species (which were commonly from regions with a long evolutionary history of ungulate grazing) (MacDougall & Kirkpatrick 1993). As grazing intensity increased, grasslands shifted from dominance of tall, C4 native perennial grasses to short, C3 native perennial grasses; at even higher grazing intensities, the flora shifted to dominance by exotic C3 annual grasses (Moore 1970). Additionally, grasslands have been heavily cleared for agriculture and urban development (MacDougall & Kirkpatrick 1993; Williams et al. 2005), and all temperate grasslands in southern Australia are endangered or critically endangered (Morgan et al. 2017).

In many new grassland conservation reserves that have been acquired to improve the reservation of this endangered ecosystem, stock have been removed and (sometimes) burning reintroduced to favor native species over exotic species (Williams et al. 2006; Williams 2007; Wong & Morgan 2012; Zeeman et al. 2017). Substituting one disturbance regime with another has obvious appeal—native grassland species did not evolve with grazing by ungulates, but did evolve with fire. But rarely has the success of such a strategy been assessed. If there is a legacy of the past management, grazing may have eliminated grazing-sensitive native species and there may be very few native species that can then take advantage of a new regime; they have been lost from the species pool. Further, it is unclear if grassland species rely on fire to maximize germination through effects of heat and smoke, or if fire promotes recruitment by reducing light limitation, and hence whether fire is substitutable (Hodges et al. 2019; Price et al. 2019). It remains unclear if changes in disturbance type can enhance conservation outcomes, by promoting native species that are currently suppressed or disadvantaged, while simultaneously reducing exotic plant cover and richness.

Study Aims and Questions

The aim of the review was to examine the response of native plant diversity and species composition in temperate native grasslands of southeastern Australia to shifts in disturbance type. We first explore the importance of disturbance per se for maintaining alpha native diversity in native grasslands (i.e. outcomes of abandonment). We then ask if species composition improves (i.e. increases in native species richness and reductions in exotic species richness) with a switch in

disturbance type. Disturbance types can have fundamentally different impacts on vegetation; grazing is a “press” disturbance (sensu Lake 2000) and is selective, fire is a “pulse” disturbance which consumes all biomass and has direct effects on seed germination for some species, and slashing generally leaves some litter on the ground. In addition to these differences in disturbance type, the *status quo* management may have legacy effects that restrict recovery after removal; hence ecosystems may be in a stable, but degraded, state.

Literature Review

We reviewed peer-reviewed studies reporting plant responses to a shift in *disturbance type* (abandonment or from one disturbance to another) in lowland temperate grassy ecosystems (grasslands and grassy woodlands) in southeastern Australia. Two criteria determined study eligibility: (1) the paper studied a native grassy ecosystem (grassland or grassy woodland); and (2) it reported on plant responses to a shift in disturbance type, including one disturbance to another, or no disturbance to a disturbance (and vice versa).

We used ISI Web of Science and Scopus to search for papers that explored a switch in disturbance type. We used the following search terms: (grass* OR woodland*) AND (disturbance* OR fire OR graz* or mow* OR slash* OR cultivat*) AND (temperate OR semiarid) AND Australia*. The search produced 778 unique references that were initially screened for inclusion based on the titles to determine if they met the scope for inclusion. From this list, 73 papers were retained for abstract screening to determine suitability. The main reasons for exclusion were that studies were outside the geographic scope, or agricultural studies (crops and pastures), or detailing fauna impacts, or focused on impacts of disturbance rather than a switch. From this, 50 papers were retained that required further investigation of the full paper to determine suitability. A further 20 papers were excluded at this stage, mostly because they were outside of the geographic scope or did not report on a disturbance switch. The final number of papers suitable for data extraction were 30 (resulting from systematic review) and 14 which were found through additional searches or through authors' knowledge (some were unpublished theses or reports). In total, 44 studies met our criteria.

Results and Discussion

We found 45 switches in disturbance type in grassy ecosystems reported from 44 studies (Table 1). We grouped shifts into four main classes: (1) abandonment of disturbance (18 cases); (2) the introduction of disturbance where there was no disturbance in recent history (fire or mowing; eight cases); (3) switches from one disturbance to another (14 cases); and (4) old field succession (a switch from cultivation to grazing; five cases). “No disturbance” refers to no active disturbance management, but can include grazing from native macropods and lagomorphs. The grazing exclusion studies vary in the type of herbivores excluded; for our purposes we are interested in stock grazing, but exclosure studies likely also excluded native vertebrate

herbivores, whereas space-for-time chronosequences only exclude stock.

Studies were conducted at a range of spatial and temporal scales. The longest temporal sequences included the space-for-time-substitution studies (all of the old fields, and many of the fire abandonment studies, Table 1). Several studies used revisitation surveys to compare richness with shifts in management through time and space (e.g. Williams et al. 2006). Most of the grazing abandonment studies used experimental exclosures for various lengths of time (3–16 years, Table 1). Most of the switches from one disturbance type to another were experimental studies, in which a new disturbance type was imposed on a site with an existing legacy—commonly a legacy of stock grazing to fire or mowing. Most experimental studies report short-term responses to a change in disturbance type (typically within 1–3 years of the change), and often involve the reintroduction of a single fire (Lunt 1990; Prober et al. 2004; Sinclair et al. 2014; Bryant et al. 2017).

Abandonment

The relaxation of fire from grasslands historically exposed to regular fire (“abandonment” sensu Grime 1979) tends to decrease diversity in productive temperate grasslands, with localized (i.e. site-level) extinctions reported (Williams et al. 2006; Moxham et al. 2016) (Table 1). All of the studies addressing this outcome were conducted in C4 *Themeda*-dominated grasslands; hence, we cannot determine if the same pattern occurs in other less productive C3 grasslands (i.e. if it is dependent on annual net primary productivity, ANPP). Most of the studies were also space-for-time substitutions which tend to report on longer time frames, and all studies reported responses >10 years after abandonment.

The effects of herbivore exclusion differed from fire abandonment, indicating the disturbance requirement depends on disturbance type, among other factors (Table 1). The majority of cases found no change in native or exotic richness (seven studies) with grazing exclusion, suggesting limits to passive recovery after removal (Table 1). Most of the studies report on short-term responses (approximately 3 years, Table 1). Three studies found reductions in richness with grazing exclusion; these were high productivity sites and studies were mostly long term (>10 years) (Tremont 1994; Schultz et al. 2011; Mavromihalis et al. 2013). Productivity is likely to be an explanatory factor; one study conducted at multiple sites (across a mean annual precipitation gradient of 272–960 mm/year in Victoria) found species richness decreased with herbivore exclusion at sites with higher phytomass accumulation, but had neutral or positive responses at sites with lower phytomass accumulation (Schultz et al. 2011). Further supporting this notion, most of the studies that found increases in native richness were conducted at lower rainfall or low biomass sites (Foreman 1996; Price et al. 2010). Reductions in exotic richness were only found in one study (Price et al. 2010), with most reporting no change in richness. We found no evidence that grazing exclusion increases exotic species richness (although some exotic species increased in cover, Table 1).

Table 1. Shifts in disturbance type divided into four groups of transitions: those that represent (1) abandonment of disturbance; (2) introduction of disturbance where there was none; (3) a switch from one disturbance type to another; and (4) old field succession. The method described in the table refers to the specific aspect of the original study that revealed the outcome of the change in disturbance type, and does not necessarily summarize the overall methods used in the original study. For example, plots described as control plots in the table may not have been considered control plots in the original study, but they serve as controls for the comparison being made in the table. Rows have multiple references when multiple studies reported on different aspects of the same experiment. Studies that tested more than one shift are presented on different rows. Prober et al. (2004) and Lewis et al. (2010) had grazing removed 5 and 6 years, respectively, prior to introduction of other disturbances (fire and mowing), but we have considered these as transitions from grazing due to the legacy effects of a long history of stock grazing. We have included the “Infrequent fire → Frequent fire” transition with the studies that introduce a disturbance where there was none before; we deemed this the most suitable classification of these studies.

Dominant Genera (and Photosynthetic Pathway)	Method	Native SR Response	Exotic SR Response	Describe Response to Shift in Disturbance	Mean Annual Precipitation (mm)	Scale of Observation (m ²)	Reference
Transitions that represent abandonment of disturbance							
Fire → No disturbance							
<i>Themeda</i> (C4)	Revisitation (16 years)	Decreased	NA	Unburnt sites had up to twice the local extinction rate of annually burnt remnants	500–750	4.5 × 10 ⁵	Williams et al. 2005; Williams et al. 2006
<i>Themeda</i> (C4)	Space-for-time: time-since-fire (up to 11 years)	NA	NA	<i>Themeda</i> grasslands reached a “tipping point” without fire; dominant tussocks die and system is transformed to exotic-dominant state	568	0.25	Morgan & Lunt 1999
<i>Themeda</i> (C4)	Plots left undisturbed for 12 years in site previously burnt every 4–8 years; burnt control plots (different frequencies)	Decreased	NA	<i>Poa</i> abundance increased without burning. Total cryptogam cover, abundance and richness were lower in undisturbed plots than in all three burn frequencies	600	25	Prober et al. 2007; O’Byrne et al. 2009; Prober et al. 2013
<i>Themeda</i> (C4)	Space-for-time: time-since-fire (up to 10 years)	Decreased	Increased	Decreased native richness with time-since-fire at both spatial scales. Increased exotic richness only at larger spatial scale, though some exotic species declined with time-since-fire	641	0.25 and 100	Moxham et al. 2016
Grazing → No disturbance							
Various perennial grasses (C3 and C4)	Grazing exclusion (5–16 years)	Various	NA	Decreased species richness with grazing exclusion at highest productivity sites. No change in species richness at lower productivity sites, except at the lowest productivity site, where species richness increased	272–960	1	Schultz et al. 2011
Various native perennial grasses (C3 and C4) and exotic grasses (C3)	Space-for-time: time-since-grazing removal (1–10 years)	Increased	NA	Overall species richness increased with grazing exclusion, and positive correlation between native species richness and time-since-exclusion	550–800	400	Briggs et al. 2008

Table 1. Continued

Dominant Genera (and Photosynthetic Pathway)	Method	Native SR Response	Exotic SR Response	Describe Response to Shift in Disturbance	Mean Annual Precipitation (mm)	Scale of Observation (m ²)	Reference
Grazing → No disturbance (continued) Herb-rich woodland (C3)	Space-for-time: grazing removal (up to 24 years)	Increased	Decreased	Increased exotic richness in continuously grazed sites compared with intermediate and recently ungrazed sites. Compositional shift in absence of grazing	687	16	Price et al. 2010
<i>Themeda</i> (C4) and <i>Rytidosperma</i> (C3)	Grazing exclusion (4 years)	No change	No change	No change in total species richness, but native forb diversity and abundance increased	568–732	225	Zimmer et al. 2010
<i>Dichanthium</i> (C3) and <i>Astrelia</i> (C4)	Grazing exclusion (8 years)	No change	No change	No difference in total species richness between exclusion plots and grazed controls	550	2	Lewis et al. 2008
Mix of perennial grasses (C3 and C4)	Grazing exclusion (16 years)	Decreased	No change	Many species unique to both grazed and ungrazed treatments, but species richness significantly lower in ungrazed plots	788	0.25	Tremont 1994
<i>Rytidosperma</i> (C3)	Grazing exclusion (3 years)	No change	No change	Grazing exclusion favored some exotic species, abundance of some natives declined as bare ground decreased	370–437	4	Foreman 1996
Mix of perennial grasses (C3 and C4)	Grazing exclusion (2.5 years)	No change	No change	No evidence of species establishing in the exclusion plots that were not in grazed controls	604–819	400	Schultz et al. 2014
Mix of perennial grasses (C3 and C4)	Grazing exclusion (4 years)	No change	NA	No change in total species richness at either spatial scale	666	1 and 625	Allcock & Hik 2003
Mix of perennial grasses (C3 and C4)	Grazing exclusion (up to 17 years)	NA	NA	Some changes in species composition with grazing exclusion, but very limited convergence with reference condition, and unrelated to time-since-exclusion	594–805	400	Sims et al. 2019
Mix of perennial grasses (C3 and C4)	Grazing exclusion (4 years)	No change	No change	Exclusion of high-density kangaroo grazing had no effects on species richness or live-plant basal area	629	0.25	McIntyre et al. 2017
Mix of perennial grasses (C3 and C4)	Grazing exclusion (3 years)	Decreased	NA	Rate of decrease in species richness correlated with rate of phytomass accumulation	620–730	0.25	Mavromihalis et al. 2013

Table 1. Continued

Dominant Genera (and Photosynthetic Pathway)	Method	Native SR Response	Exotic SR Response	Describe Response to Shift in Disturbance	Mean Annual Precipitation (mm)	Scale of Observation (m ²)	Reference
Grazing → No disturbance (continued)							
<i>Austrostipa</i> (C3)	Grazing exclusion (4 years)	No change	No change	Cover of native and exotic species increased	439	1	Souter & Milne 2009
Mix of perennial grasses (C3 and C4)	Space-for-time: time-since-grazing removal (up to 50 years)	NA	NA	Cover of biological soil crust increases with time-since-exclusion, plateauing after 20 years	370–410	0.25	Read et al. 2011
Transitions that introduce disturbance where there was no disturbance before							
No disturbance → Fire							
<i>Themeda</i> (C4) and <i>Poa</i> (C3)	Burnt plots (different frequencies in autumn) in long-unburnt area; unburnt control plots over 12 years	Decreased	NA	Native forb cover declined after fire and required approximately 3 years to recover to levels of unburnt plots. Native species generally favored by nil to little disturbance	600	25	Prober et al. 2013
Mix of perennial grasses (C3 and C4)	Burnt (single burn only) and unburnt plots monitored over 4 years	NA	NA	No change in total species richness, and no difference in composition of dominant species between burnt and unburnt plots	629	0.25	McIntyre et al. 2014; McIntyre et al. 2017
<i>Rytidosperra</i> (C3), exotic grasses (C3 and C4)	Spring burn and autumn burn plots (burnt annually), and unburnt plots, monitored over 4 years	No change	NA	Native perennial <i>Rytidosperra</i> cover increased with both burn regimes, and exotic grass cover decreased	670	NA	Prober et al. 2009
<i>Bothriochloa</i> (C4), exotic annual grasses (C3)	Burnt sites (spring burns in two consecutive years) and unburnt plots monitored over 3 years	NA	NA	Cover of perennial grasses generally increased and cover of exotic grasses decreased in burnt plots compared to unburnt control	650	NA	Prober et al. 2005
Infrequent fire → Frequent fire							
<i>Themeda</i> (C4)	Comparison of grasslands after several years of divergent management (1–7 years since fire)	NA	NA	High co-existence of perennial species at small spatial scale in frequently burnt grassland	520–700	0.25	Morgan 1999
<i>Themeda</i> (C4) and <i>Rytidosperra</i> (C3)	Resurvey plots after 10 years and an increase in fire frequency	Increased	Increased	Increase in abundance and frequency of rare native forbs	592	15	Kirkpatrick 1986
No disturbance → Mowing							
Mix of perennial grasses (C3 and C4)	Comparisons of mown plots (cut to 10 cm annually for 10 years; slash removed) to undisturbed controls	Increased	Increased	Increase in richness of most native functional groups. Richness of native grasses increased with mowing in C3 grasslands but not <i>Themeda</i> grasslands. Cover of exotic perennial grasses decreased	629	4	Smith et al. 2018

Table 1. Continued

Dominant Genera (and Photosynthetic Pathway)	Method	Native SR Response	Exotic SR Response	Describe Response to Shift in Disturbance	Mean Annual Precipitation (mm)	Scale of Observation (m ²)	Reference
No disturbance → Mowing (continued) <i>Themeda</i> (C4)	Comparison of mown plots (cut annually, slash removed) with undisturbed plots over 2 years. Rare (decreaser) or widespread (increaser) species added to plots	Increased	NA	No differences in survival of decreaser or increaser species between mown and undisturbed plots; decreaser species increased in growth in annually disturbed plots	540	1	Zeeman & Morgan 2018
Transitions from one disturbance to another Grazing → Fire <i>Rytidosperma</i> (C3)	Comparison of two burn treatments to unburnt controls (± sheep grazing)	No change	Decreased	Some native annuals decreased in abundance with fire (annual burning tended to be negative)	370–437	4	Foreman 1996
<i>Austrostipa</i> and <i>Rytidosperma</i> (C3)	Opportunistic comparison of burnt and unburnt plots (>1 year post fire)	NA	NA	High mortality of native grasses after fire (between 90–95%), but with evidence of recruitment	532	1	Sinclair et al. 2014
<i>Austrostipa</i> and <i>Rytidosperma</i> (C3)	Opportunistic comparison of three burn regimes and unburnt control (1 and 2 years post fire)	Increase/No change	NA	Forb richness was greater than unburnt control for summer burn, but not autumn burn. Burning increased native tussock grass cover and abundance. Generally, exotic abundance reduced by summer burn but increased by autumn burn	481	100	Bryant et al. 2017
<i>Austrostipa</i> (C3)	Comparison burnt plots with grazed control (up to 3 years post fire)	No change	No change	Native species abundance higher in burnt plots than in control. Transient decrease in exotic abundance after fire	325–410	0.25	Wong & Morgan 2012
<i>Themeda</i> (C4)	Grazing removed and fire re-introduced (no controls); Surveyed 10 years after grazing removed, with variable fire history (max. intervals of 4–11 years within the site)	No change	No change	Whilst no significant change in native or exotic richness, total species richness increased over 10 years. Increase attributed to ruderals that easily disperse by wind. Composition was not on a trajectory towards high quality remnants	568	15	Lunt & Morgan 1999
<i>Themeda</i> (C4)	Comparisons of burnt plots (annual spring burns for 3 years) compared with unburnt controls with grazing history	No change	No change	Large reduction of exotic annual grass richness and abundance, but not other exotic species. No effects of fire on native forb and grass abundance	590	NA	Prober et al. 2004

Table 1. Continued

Dominant Genera (and Photosynthetic Pathway)	Method	Native SR Response	Exotic SR Response	Describe Response to Shift in Disturbance	Mean Annual Precipitation (mm)	Scale of Observation (m ²)	Reference
Grazing → Fire (continued) <i>Themeda</i> (C4)	Comparison of plots before and after fire, and to unburnt control plots (>1 year post fire)	No change	No change	No composition difference pre- and post-fire. No change in native forb and perennial grass species richness. Some exotic species increased in abundance	568	15	Lunt 1990
<i>Astrebula</i> (C4) and <i>Dichanthium</i> (C3)	Comparison of burnt plots (two burn treatments) to unburnt controls in area with no disturbance (but a history of stock grazing), monitored for 2 years	No change	No change	Some short-term declines in species richness in response to fire, but effect did not persist; no effect of either burn treatment on native or exotic species richness	550	32	Lewis et al. 2010
<i>Austrostipa</i> and <i>Rytidosperma</i> (C3)	Comparison of burnt and unburnt plots in sites with legacy of stock grazing (<1 year post-fire)	No change	No change	Fire changed structural and environmental variables (increased light and reduced biomass) but had no impact on any richness values	425	1	Cleland 2019
<i>Austrostipa</i> and <i>Rytidosperma</i> (C3)	Burn in long-unburnt grassland; survey tussock survival and resprouting after 7 weeks	NA	NA	C3 grasses had low mortality, and resprouted. Tiller regrowth was similar to regularly burnt <i>Themeda</i> grassland. Smaller tussocks had higher rate of mortality	550–615	NA	Morgan & Salmon 2020
Grazing → Mowing <i>Poa</i> and <i>Rytidosperma</i> (C3)	Frequent mowing (slash removed), compared to grazed plots. Grazing removed and mowing commenced 12 years before sampling	Increased	Increased	Perennial species (native and exotic) favored in mown plots, but less total exotic cover in mown plots; annual species favored in grazed plots	610	25	Verrier & Kirkpatrick 2005
<i>Themeda</i> (C4)	Thinning of grass tussocks with glyphosate and seed addition (sampling >1 year after treatment applications)	No change	NA	Increase in species richness with thinning and litter removal, but only when seed added. Exotic forb abundance increased with tussock thinning	650	0.56	Johnson et al. 2018
<i>Astrebula</i> (C4) and <i>Dichanthium</i> (C3)	Comparison of mowed plots (four mowing treatments) to undisturbed controls, in an area previously undisturbed with a legacy of stock grazing	No change	No change	Some short-term effects of mowing, but no difference in species richness between undisturbed plots and any mow treatments at final monitoring	550	32	Lewis et al. 2010

Table 1. Continued

Dominant Genera (and Photosynthetic Pathway)	Method	Native SR Response	Exotic SR Response	Describe Response to Shift in Disturbance	Mean Annual Precipitation (mm)	Scale of Observation (m ²)	Reference
Fire → Mowing <i>Themeda</i> (C4) and <i>Poa</i> (C3)	Biennial mowing (slash retained) at site previously burnt every 4–8 years. Monitored for 12 years, comparison with burnt control.	No change	NA	Native species richness was similar in mowed plots and burnt controls. Total cryptogam cover, abundance and richness were lower in mowed plots than in all three different burn frequencies	600	25	O'Bryan et al. 2009; Prober et al. 2013
Transition from cultivation to grazing (old field succession) Cultivation → Grazing							
<i>Austrostipa</i> and <i>Rytidosperma</i> (C3)	Space-for-time: management units with different time-since-cultivation (up to >100 years since cultivation)	Increased	Increased	Slow recovery of native species richness with time since cultivation. Increase in exotic species richness with time since cultivation, but decline in exotic species dominance	395	100	Wong et al. 2010
<i>Austrostipa</i> and <i>Rytidosperma</i> (C3)	As above (up to approximately 100 years since cultivation)	Increased	No change	Slow recovery of species richness and decrease in exotic annual grass richness with time since cultivation	395	0.25	Scott & Morgan 2012b
<i>Austrostipa</i> and <i>Rytidosperma</i> (C3)	As above (up to approximately 60 years since cultivation)	Increased	Decreased	Recovery of native species richness and decrease in exotic species richness with time since cultivation	400	0.02	Flaim 2014
Various perennial grasses (C3 and C4)	As above (up to approximately 55 years since cultivation)	Increased	No change	Recovery of species richness with time since cultivation considerably faster than in the other studies	595–874	400	Schultz 2011
<i>Austrostipa</i> and <i>Rytidosperma</i> (C3)	Space-for-time: management units with different time-since-cultivation (up to approximately 90 years)	NA	NA	Cover of biological soil crust variable across cultivation history, but significantly lower in recently cultivated sites. Cyanobacteria recovered quickly	395	0.25	Briggs & Morgan 2012

Switches From “No Disturbance” to Disturbance Management

When *status quo* management changed from “no disturbance” (or infrequent fire) to fire or mowing, we found mostly positive responses (either increases in native richness or cover, Table 1). Increases in native richness were found in *Themeda*-dominated grasslands (Kirkpatrick 1986; Smith et al. 2018; Zeeman & Morgan 2018), and also in C3-dominated grasslands (Smith et al. 2018). Decreases in native species richness were found with the introduction of fire in a long-unburnt grassy woodland where competition from trees limits understory biomass (Prober et al. 2013). Hence, the disturbance requirement for maintaining alpha diversity might not be ubiquitous across the range of grasslands. Indeed, in subtropical grasslands, no change in native richness was found when mowing and fire were introduced in previously undisturbed sites, likely due to lower rates of biomass accumulation compared to temperate grasslands (Fensham et al. 2017). Introducing disturbance into undisturbed sites also increased exotic richness (Kirkpatrick 1986; Smith et al. 2018), but most studies did not explore this (Table 1).

Transitions From Stock Grazing to Fire

The removal of stock grazing and reintroduction of fire had mostly no effect on native species richness (Table 1; Lunt 1990; Foreman 1996; Lunt & Morgan 1999; Prober et al. 2004; Wong & Morgan 2012; Bryant et al. 2017). Such muted responses may be because both grazing and fire maintain species richness via the effects of biomass removal. Shifting from one disturbance to another may have comparable impacts on light availability (Lunt 1990; Prober et al. 2004; Wong & Morgan 2012), and hence opportunities for species coexistence of the incipient community (Schultz et al. 2011). Exotic species richness was also largely unaffected by the switch from grazing to fire. No negative effects on native species richness were found (Table 1).

The negligible effect of disturbance switching on alpha diversity in grasslands (grazing → fire) is likely because stock grazing has removed many (palatable) native species, and vegetation responses to fire were seed-bank and/or dispersal-limited. Increased species richness might be expected where colonization is by ruderals with long-distance dispersal ability (Lunt & Morgan 1999). Many of the disturbance switching studies here occur in the landscape context of remnants being small, isolated, and embedded in an agricultural or urban matrix, where native species typically have small persistent or transient soil seed banks (Lunt 1995; Williams et al. 2006; Scott & Morgan 2012a). Despite the lack of native richness response, positive compositional changes were commonly reported, with increased cover and abundance of native species (Table 1). All of the studies reported on short-term responses (≤10 years), and hence richness improvements may take longer than the study duration. The grazing exclusion studies which tended to report on longer-term changes support the idea that passive recovery from stock grazing takes longer than the approximately 3 years of most studies.

There were few negative effects found when switching from livestock grazing to fire. However, some caution is needed for

employing this management across all grasslands. Some native species may be susceptible to fire (e.g. C3 grasses, Moore et al. 2019), with responses depending on the location of regenerating buds (Pausas & Paula 2020). Resprouting capacity, particularly for C3 species, may also be negatively impacted by drought (Prober et al. 2004; Moore et al. 2019). Some exotic plants benefit in the short term from the shift (Wong & Morgan 2012). The timing of fire also determined the response of exotics—summer fires reduced exotic abundance, but autumn fires increased exotic abundance (Bryant et al. 2017) and, in a grassy woodland, spring burns controlled few exotic plants (Prober et al. 2004). Hence, the best fire regime for promoting natives and minimizing exotics under different contexts needs further understanding.

Transitions From Grazing or Fire to Slashing

Few studies explored switches from either grazing or fire to some mechanical means of biomass removal (mowing, slashing, or tussock thinning); most reported no change in native species richness (Table 1). Positive richness responses occurred when biomass (slash) was removed after cutting or when seed was added (Verrier & Kirkpatrick 2005; Johnson et al. 2018). If litter is left on the ground, it can smother small-statured species, including cryptogams (O’Byrne et al. 2009). The height of slash affects the outcomes; if the grass tussocks are mown too low, mortality occurs due to loss of the regenerative parts of plants (Morgan 2015). A mowing height of 10–15 cm was found to be necessary to minimize mortality of perennial grass tussocks (Prober et al. 2013; Smith et al. 2018). Only one study found increases in exotic species with mowing (Verrier & Kirkpatrick 2005), but exotic responses were not reported consistently (Table 1).

Old Field Succession

Five studies observed grassland recovery with old field succession (cultivation → grazing), and all found increases in native species richness (Table 1). The rate at which species reestablished in old fields varied among the studies; on the north-west slopes of New South Wales, Schultz et al. (2011) observed rapid recovery of species richness, with similar richness to that observed in uncultivated paddocks after 10–25 years. Other studies have found comparatively slower recovery. For example, in Victoria’s northern riverine plains, Wong et al. (2010) found that species richness recovered along a linear trajectory with time-since-cultivation, but estimated that it may take >100 years to reach the species richness of nearby uncultivated native pastures. Rapid reestablishment of plant diversity was observed by Schultz et al. (2011) in relatively productive sites that were surrounded by species-rich native pastures (>70% of the agricultural area; Lodge et al. 1991). Slow recovery occurred in regions with low total cover of grasslands in the landscape, poor connectivity, and lower productivity (Wong et al. 2010; Scott & Morgan 2012b).

Spatial Scale

One consequence of disturbance switches not addressed is the impact of different disturbances on ecological processes acting at larger spatial scales than those observed by the studies reviewed here. The primary response to a disturbance shift recorded is the change in native species richness at local scales (Table 1). Grazing has been shown to reduce native species richness at landscape scales through removal of species from the local species pool despite increasing native richness at local scales (Dorrough et al. 2007; Schultz et al. 2016), but it is still unclear if removal of grazing, or a switch from grazing to fire could reverse such a trend. For example, will species that are grazing-sensitive and/or spatially restricted in the landscape find additional recruitment opportunities as a result of disturbance switches? If so, there might be conservation benefits regardless of the impact on local native species richness. Testing this will require studies conducted at both longer temporal scales and larger spatial scales. Nevertheless, the potential for the impacts of disturbance switches on larger-scale processes is acknowledged, and should be considered by future studies.

Switches in Disturbance Type Indicate Passive Recovery Occurs but Is Limited by Land-Use Legacies

Temperate native grasslands do appear to have a disturbance requirement, as evidenced by a reduction in species richness with abandonment; this is particularly true for grasslands where the removal of fire occurs in areas that have been historically burnt. This outcome likely depends on site productivity—all the fire abandonment studies have been conducted in productive *Themeda*-dominated grasslands where ANPP is high (Groves 1965; McDougall 1987). Studies that introduced a new disturbance (fire or mowing) into sites lacking disturbance management reported a range of native richness responses. The grazing exclusion studies support the contention that site productivity governs the response to disturbance, with reductions in richness with grazing exclusion only occurring at higher productivity. However, many studies report no change in richness with grazing exclusion indicating that grasslands may be in a stable, but degraded state.

The main switch in disturbance type involved the removal of stock grazing and the introduction of fire or mowing. In these cases, the common response was no change in native richness, supporting the idea that grazing legacies are persistent. However, improvements in species composition were commonly reported, such as increases in native species cover or abundance. Most of the studies, however, were short term and it is unclear if passive recovery will occur with longer time-since-grazing removal, or if more fire events are needed. Recovery could potentially be expedited with seed addition (Johnson et al. 2018).

The most modified temperate grasslands in this study were the old fields where cultivation has been part of their recent history; in all cases, passive restoration improved native richness. As these are the most degraded sites considered here, increased richness compared to the recently cultivated state is likely to occur; but what is more important here is the trajectory to a

reference site. These studies were all space-for-time chronosequences; hence longer-term recovery was reported and, for most studies, recovery towards a reference state took a long time, and was faster for sites that had native propagules available in the surrounding landscape. Typically, studies on old field recovery support the “grazing to fire” outcomes—when missing species are dispersal-limited, seed addition will be necessary to take advantage of new establishment opportunities associated with changes in disturbance type, and may help expedite recovery. These studies accord with the global literature on old field succession (e.g. Török et al. 2011).

Seed and Dispersal Limitation: A Key Barrier to Restoration Under Shifting Disturbances

Reintroduction of locally extinct species is a key goal of restoration, but achieving this passively is often limited by propagule availability (Seabloom et al. 2003; Pinto et al. 2014). This is clearly illustrated by seed addition experiments that increase alpha diversity, regardless of disturbance regime, suggesting native grasslands are inherently recruitment-limited (Johnson et al. 2018; Zamin et al. 2018). Grassland species may be poor dispersers; hence, species may fail to recolonize recently disturbed sites because the distances between remnant grasslands exceeds their natural dispersal ability (in many cases it is <1 m, Scott & Morgan 2012a). Additionally, even when species are present in the site, seed may be absent from the seed bank and unable to take advantage of reduced competition for light and resources post-disturbance (i.e. seed-limitation, Münzbergová & Herben 2005). This may occur because of short seed longevity (Long et al. 2015) and/or heavy seed predation which is often symptomatic of grassland species (Lunt 1995; Dudenhöffer et al. 2016).

The *type of matrix* in fragmented landscapes appears to be important for determining if passive restoration is a viable option for recovery of degraded grassland. For example, old field recovery was rapid in regions of Australia where the matrix consisted of native pastures (Lewis et al. 2010; Schultz 2011), whereas in urbanized regions, local extinction of grassland plants was related to fire suppression and urbanization in the surrounding matrix (Williams et al. 2006). As such, the amount of natural vegetation in the surrounding matrix is likely to be a strong determinant of whether seed addition is required for successful restoration (Řehounková & Prach 2008; Török et al. 2011; Shackelford et al. 2017; Zirbel et al. 2019).

The common disturbances reviewed in this study are likely to have similar (albeit not synonymous) effects on microsite conditions via the removal of biomass. For many grassland species, fire-related germination cues (such as smoke and heat) promote germination (Vening et al. 2017; Carthey et al. 2018; Hodges et al. 2019). For such species, substituting grazing and mowing for fire is unlikely to promote germination. For other species, where germination is linked to gap-detection and rainfall, any biomass-reducing disturbance that provides sufficient gaps in the canopy is likely to be sufficient to stimulate recruitment. Hence, consideration of the germination requirements of species is necessary when

considering if disturbance switches will improve native species richness.

Climate Change Impacts on Disturbance Transitions

Temperate grasslands in Australia are sensitive to changes in the dominant processes that regulate distributions and productivity (e.g. rainfall, temperature; Morgan et al. 2016) and, in the future, climate change is likely to drive significant changes to those processes. Regional climate projections suggest that grasslands in southeastern Australia likely face warmer temperatures, reduced water availability (especially in winter), higher evaporation and increases in heavy precipitation events such as storms and periodic flooding. In particular, predicted increases in the frequency and severity of droughts and heatwaves are likely to have a significant impact on the productivity and composition of native grasslands (Hodgkinson & Müller 2005; Godfree et al. 2011). With climate change, drier conditions are likely to slow biomass accumulation rates in many types of grassland, potentially reducing the need for disturbance—and disturbance switching—to maintain diversity. The greatest effects would most likely be evident in marginal environments where species exist at their physiological limits, and where recruitment probability after disturbance may be compromised. Such predictions need to be robustly assessed in the field, as it will likely create opportunities in some landscapes for grassland enhancement, while challenge ongoing persistence in others.

Final Remarks and Further Research

Passive restoration, after disturbance switching, in Australian temperate native grasslands is likely limited by seed availability because of agricultural land-use legacies. Hence, active restoration is necessary to restore the full suite of species that occurred in the predisturbed state. The evidence suggests temperate grasslands are in a stable but degraded state, and that switching disturbances—from exogenous (e.g. stock grazing) to endogenous (e.g. fire)—has little capacity to recover native species (at least in the short term). Seed addition, however, is unlikely to be a panacea for restoration as seedling emergence and survival are not always reliable (Lodge 1981; Cole & Lunt 2005; Gibson-Roy et al. 2010b). Sourcing seed required for large-scale restoration will be challenging given remnants are typically small; seed production areas are necessary to scale up the availability of seed (Gibson-Roy et al. 2010b). Sites that are heavily degraded (dominated by exotic species and fertilized) may not be suitable for restoration, without much greater inputs (e.g. scalping or topsoil removal, Gibson-Roy et al. 2010a).

Increased knowledge around seed dormancy and germination requirements are necessary, as are improvements to restoration practice (e.g. through seed technologies to maximize establishment, Perring et al. 2015). Diverse seed mixtures increase the costs of restoration (Palma & Laurance 2015), and cost-effective approaches are needed. One approach can be to use species-poor seed mixtures at the site scale, and patchily apply more diverse mixtures that enable natural dispersal around the site (Török et al. 2011; Kiss et al. 2020). Experiments are needed to test

these approaches under different disturbance types and regimes. In some cases, pretreatment of seed with smoke may reduce the necessity to burn, but this requires further investigation, and may only be suitable for low productivity sites that do not require biomass removal.

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Guest Coordinating Editor: Peter Török

Received: 15 January, 2020; First decision: 25 February, 2020; Revised: 29 July, 2020; Accepted: 15 August, 2020