

Multivariate drivers of diversity in temperate Australian native grasslands

Jodi N. Price^{A,G}, Megan K. Good^B, Nick L. Schultz^C, Lydia K. Guja^{D,E} and John W. Morgan^F

^AInstitute of Land, Water and Society, Charles Sturt University, Albury, NSW 2640, Australia.

^BSchool of BioSciences, The University of Melbourne, Vic. 3010, Australia.

^CSchool of Health and Life Sciences, Federation University Australia, Ballarat, Vic. 3350, Australia.

^DNational Seed Bank, Biodiversity Science Section, Australian National Botanic Gardens, Canberra, ACT 2601, Australia.

^ECentre for Australian National Biodiversity Research, CSIRO, Canberra, ACT 2601, Australia.

^FDepartment of Ecology, Environment and Evolution, La Trobe University, Bundoora, Vic. 3083, Australia.

^GCorresponding author. Email: joprice@csu.edu.au

Abstract. Disturbance has been considered essential for maintaining biodiversity in temperate grassy ecosystems in Australia. This has been particularly well demonstrated for inter-tussock plant species in *C*₄ *Themeda*-dominated grasslands in mesic environments. Disturbance is also thought crucial to maintain the structure of preferred habitat for some animals. Relationships between disturbance and diversity may be contingent on ecosystem productivity, but little is known about the generality of the disturbance-promoting-diversity paradigm across the range of temperate grasslands. To date, the disturbance-promoting-diversity paradigm has taken a univariate approach to the drivers of biodiversity; rainfall is seen as a key driver of productivity, which then drives diversity, mediated by disturbance. We argue that this framework is too simplistic as biodiversity drivers are multivariate. We suggest that the accumulation of phytomass (live and dead plant material) is an important determinant of diversity in grassy ecosystems and that phytomass accumulation is governed by multiple drivers (of which disturbance is just one). For fauna, it is structure – not biomass – that determines habitat suitability, and this can be moderated by both abiotic and biotic drivers. The assumption that there is a consistent effect of disturbance on diversity through the range of temperate grassland settings in southern Australia ignores the likelihood that biodiversity also responds to other factors such as spatial heterogeneity in the environment, resource availability and climatic variation. We developed a conceptual model of the multivariate drivers of grassland diversity that explores mechanisms underpinning patterns of species richness. Despite four decades of research, it is clear that our understanding of the multivariate drivers of diversity across the range of temperate grasslands in Australia is still incomplete. Further research into the conditions under which disturbance is required to maintain biodiversity in grasslands is integral to conservation planning in these endangered systems.

Additional keywords: beta diversity, biomass, disturbance, fire, grazing, regeneration, resources, spatial scale.

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Introduction

Disturbance theory has served as the primary framework for understanding species coexistence in temperate grasslands in Australia (Lunt and Morgan 2002; Prober *et al.* 2013) and elsewhere (e.g. Grime 1973; Huston 1979; Collins and Steinauer 1998; Fynn *et al.* 2004). In highly productive environments, large dominant species (usually grasses) can monopolise resources (such as light) and competitively exclude other species (Grime 1973; Grace 1999; Harpole *et al.* 2016), as well as regulate many ecosystem functions including nutrient cycling, population dynamics and animal habitat (Knapp and Seastedt 1986; Lunt 1997a; Morgan and Lunt 1999). Disturbances such as fire can promote species

diversity by constraining biomass and hence, the competitive effects of dominant species. In unproductive environments, plants tend to recover more slowly after disturbance, leading to slower rates of competitive exclusion. Hence, disturbance-promoting-diversity is thought to be contingent on productivity. Rates of biomass accumulation are dictated by the rates of primary productivity and decomposition, both of which are regulated by climate (Knapp and Smith 2001; O'Halloran *et al.* 2013) and, at smaller scales, by soil fertility (Harpole *et al.* 2016). Hence, productivity gradients controlled by climate and edaphic factors are likely to regulate the degree to which disturbance is necessary in grasslands to maintain diversity and ecosystem function.

The temperate grasslands of southern Australia are among the nation's most well studied ecosystems (see synthesis by Williams *et al.* 2015) and biomass accumulation is known to be rapid in some parts of the range (McDougall 1989; Morgan and Lunt 1999; Prober *et al.* 2007; Schultz *et al.* 2011). As a consequence, moderate to high-frequency fire regimes typically promote plant species coexistence in productive grasslands (Morgan 1999), whereas infrequently-burned grasslands have lower plant species density (Stuwe and Parsons 1977). Such findings underpin management recommendations that have promoted frequent burning as necessary to maintain plant biodiversity, particularly in those sites that have a long-history of fire. Indeed, Williams *et al.* (2006) found that local extinction of plants was highest in native grasslands where burning regimes were relaxed, an outcome also observed in tallgrass prairie (Leach and Givnish 1996).

Prior to European colonisation, Australian temperate grasslands were burnt by Indigenous peoples for hunting and to promote food plants (Gott 2005). The details of the pre-European fire regime (i.e. frequency, intensity) are largely unknown in southern Australia due to the history of colonial invasion which meant Indigenous people had few opportunities to remain on their country and maintain traditional practices (Neale *et al.* 2019). It is generally thought that lowland grassland distributions are mostly driven by bottom-up processes (resource-constrained) rather than top-down (disturbance-driven) (Morgan *et al.* 2017). However, it is likely fire played a role in promoting plant diversity in these ecosystems. The disturbance created from Indigenous people collecting roots of food plants is likely to have also influenced the dynamics of grasslands (Gott 2005). Changes in disturbance regimes following European colonisation had dramatic and rapid effects – the removal of fire and introduction of livestock grazing resulted in the local extinction of grazing-sensitive and fire-dependent species. Additionally, grasslands have been heavily cleared and degraded by agricultural and urban development (McDougall and Kirkpatrick 1993), and all temperate grasslands in southern Australia are now endangered or critically endangered (Morgan *et al.* 2017).

A common assumption is that native grasslands require frequent disturbance to remove accumulated biomass (i.e. live + dead plant material = phytomass) in order to maximise local species diversity. In the absence of disturbance, perennial grass phytomass accumulates as annual leaf production by the dominant grass adds to the previous year's litter which is slow to decompose. The diverse array of species occupying the inter-tussock spaces decline because of the direct relationship between phytomass, light availability and plant competitive interactions (Grace 1999). In temperate grasslands in south-eastern Australia, kangaroo grass (*Themeda triandra*) tussocks create a thatch of dead leaves over the soil surface that decomposes slowly (Morgan and Lunt 1999), shading out inter-tussock species (Morgan 1997, 1998b), smothering seedlings (although quantitative data are lacking) and contributing to the decline of plant diversity (Williams *et al.* 2006). However, the applicability of this model to other ecosystems is less well documented.

For fauna, disturbance has also been thought crucial to maintain habitat suitability of grassland species. The plains-wanderer (*Pedionomus torquatus*), for example, is sensitive to

grassland biomass – as it affects structure – which can either be too dense or too open (Baker-Gabb *et al.* 2016), whereas the striped legless lizard (*Delma impar*) is thought to be suited to a complex grassland structure that develops with increasing time since disturbance (Dorrrough and Ash 1999; Howland *et al.* 2016). Howland *et al.* (2014) showed that reptile richness and abundance are positively related to grass cover. Although disturbance-diversity relationships are often invoked to explain faunal habitat suitability, the mechanisms underpinning such relationships are rarely explored, nor are how these relationships change over a species' range.

A simplified model summarising over 40 years of research on disturbance-diversity relationships in lowland temperate Australian grasslands is presented in Fig. 1. The approach to understanding drivers of biodiversity has been univariate, largely focussed on rainfall as the key driver of biomass, and disturbance as the single factor that modifies biomass, which then governs small-scale richness. A more nuanced model incorporating some of the contingencies in this relationship (e.g. species identity, resource availability) has not been incorporated into the disturbance-promoting-diversity paradigm (although see Clarke 2003; Prober *et al.* 2013 for notable exceptions). Such nuances are necessary when making predictions about the need for, and type of, management interventions to maintain biodiversity.

We developed a conceptual model of the multivariate drivers of grassland diversity that explores mechanisms underpinning patterns of species richness. Overwhelmingly the grassland literature in temperate Australia has come from one type of grassland (*Themeda*-dominated), at one spatial scale (small), in one bioregion (Victorian Volcanic Plains). Hence, these findings are unlikely to be generalisable to other grasslands, particularly more xeric ecosystems. Despite this, disturbances (fire, grazing or slashing) are being employed as a biomass reduction management tool in many temperate grasslands, with little understanding of the effects on biodiversity (especially at large spatial scales) and often without a clear theoretical underpinning for doing so.

We review the literature from lowland temperate grasslands in southern Australia and use examples from other grasslands to

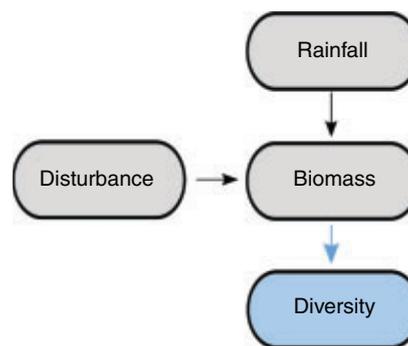


Fig. 1. The univariate model developed from literature in grasslands in southern Australia, in which rainfall is the main driver of biomass, and biomass determines diversity which is mediated by disturbance. The problem with this simple paradigm is that it misses both the multivariate and mechanistic nature of the factors that determine biodiversity, as well as their causal relationships.

understand the mechanisms governing diversity and how they may vary in space and time. In particular, we explore the limitations of focusing on small-spatial scales and α diversity for understanding the relationship between disturbance and diversity (see section ‘The scales at which grasslands have been studied limit generality about landscape patterns’), the multivariate drivers of phytomass accumulation (see section ‘Phytomass accumulation is governed by multiple drivers; disturbance is just one of them’), the importance of grassland structure for plants and animals (see section ‘Grassland structure – more than just biomass’), multivariate drivers of grassland function (see section ‘The need to account for multivariate drivers of grassland function’), and if disturbances are substitutable (see section ‘Disturbances are not substitutable: on the need to understand why disturbance affects function differently’). We then identify key research questions that must be addressed to advance the conservation management of these endangered ecosystems (see section ‘Future research directions’).

The scales at which grasslands have been studied limit generality about landscape patterns

Most ecological research in Australian temperate grasslands has been conducted at small spatial scales, limiting our ability to understand relationships that occur at larger scales. As a result, many management interventions are focussed on maximising plant and animal diversity at the plot or (less typically) the site scale. Yet, we know that average plant size increases with biomass (Oksanen 1996), and fewer individuals can occur in small plots at high biomass, even if there are no ecological interactions. As a result, species density (the number of species in an area of fixed size) inevitably will decline with increasing time-since-disturbance, even if species richness does not. The focus on maximising small-scale plant richness (α diversity), typically by promoting forb species over grass cover, has come at the expense of understanding the complex, interacting drivers of diversity (such as climate, species identity, disturbance, regeneration) of this ecosystem across its range. Of the 21 published studies reporting fire effects on temperate grassy ecosystems in Australia between 1977 and 2017, all use plots ≤ 20 m² to describe compositional, structural or functional response to fire (see Supplementary Material table S1 available at the journal’s website). Hence, an important and as yet unanswered question is: do small plots adequately describe the effects of long-term fire regimes on species persistence in temperate native grasslands in southern Australia, or are these regime effects scale-dependent?

Similarly, the effects of grazing on grassland diversity have predominantly been observed at small spatial scales (0.01–400 m²), with the common conclusion being that moderate grazing can promote species diversity at local scales by negating competitive exclusion (Tremont 1994; Fensham 1998; McIntyre and Martin 2001). However, grazing can reduce plant species diversity at the landscape or regional scale by removing grazing-sensitive species from the species pool, or by favouring grazing-tolerant species (Lunt 1997a; Landsberg *et al.* 2002; Dorrrough *et al.* 2007; Schultz *et al.* 2016). Grassland management often aims to create a structure that accommodates the highest diversity of species, but the

landscape configuration that most effectively conserves the highest proportion of the local species pool may include a variety of grassland structures, some of which may be relatively species poor (Schultz *et al.* 2016; Shahan *et al.* 2017; Abraham and Morgan 2018).

At larger spatial scales, species richness in less-frequently disturbed temperate grasslands may be comparable to frequently-disturbed grasslands due to within-community habitat heterogeneity which can promote species coexistence (Harper *et al.* 1965; Grace 1999). Environmental heterogeneity occurs due to spatial variation in soil properties (Harrison *et al.* 2003; Lundholm and Larson 2003; Price *et al.* 2017), animal disturbance (Hobbs and Mooney 1985; Martin 2003), topographic and edaphic factors (Fuhlendorf and Engle 2001) and variable competitive interactions among plant species (Aarssen 2001). Hence, frequent disturbance is perhaps only necessary to maintain small-scale (e.g. 1–100 m²) richness in productive grasslands, by allowing mechanisms such as species packing to operate (Oksanen 1996). In tallgrass prairie, Collins (1992) found that heterogeneity was significantly negatively related to burning frequency, perhaps because nitrogen-limitation is higher in frequently burned areas (Seastedt *et al.* 1991; Collins and Steinauer 1998). Collins (1992) also found a significant positive relationship between heterogeneity and species diversity and total species richness. Hence, if unburned grasslands develop patchiness based on topography and edaphic factors, high diversity might be permitted at larger scales despite dominance by tussock grasses that constrain small-scale diversity. In Australia, moderate to high disturbance is not consistently beneficial for plant diversity; rather, diversity can depend on management history and spatial heterogeneity (Prober *et al.* 2013).

Fauna-habitat relationships are also likely to be influenced by spatial scale, but for most fauna that occur in grasslands, there is little information on their habitat requirements. Globally, studies of fauna–habitat relationships have also suffered from a lack of acknowledgement of the effects of spatial scale on the observed patterns (Levin 1992; Shahan *et al.* 2017).

Phytomass accumulation is governed by multiple drivers; disturbance is just one of them

We argue that it is the accumulation of phytomass and the arrangement of biomass (see section ‘Grassland structure – more than just biomass’), not productivity *per se*, that indirectly affects grassland diversity (Fig. 2). Data on phytomass accumulation rates in temperate grasslands are sparse (Morgan *et al.* 2017); this is perplexing given biomass is thought to be a key driver of local species richness. Phytomass in mesic *Themeda*-dominated grassland increases after fire (Groves 1965; McDougall 1989); increases are linear because annual leaf production of *Themeda* subsequently contributes to accumulation of dead leaves that fail to decompose quickly (see fig. 1 in Morgan and Lunt 1999). Phytomass of up to 4.6 t ha⁻¹ has been recorded within 2 years of burning a *Themeda* grassland in southern Australia (Morgan and Lunt 1999), and 2.5 t ha⁻¹ has been recorded within 2.5 years in subtropical *Themeda* grasslands in north-western Australia (Bennett *et al.* 2003). At regional scales, Schultz *et al.* (2011) found phytomass accumulation in ungrazed grasslands varied from 28 to 944 g m⁻², increasing with

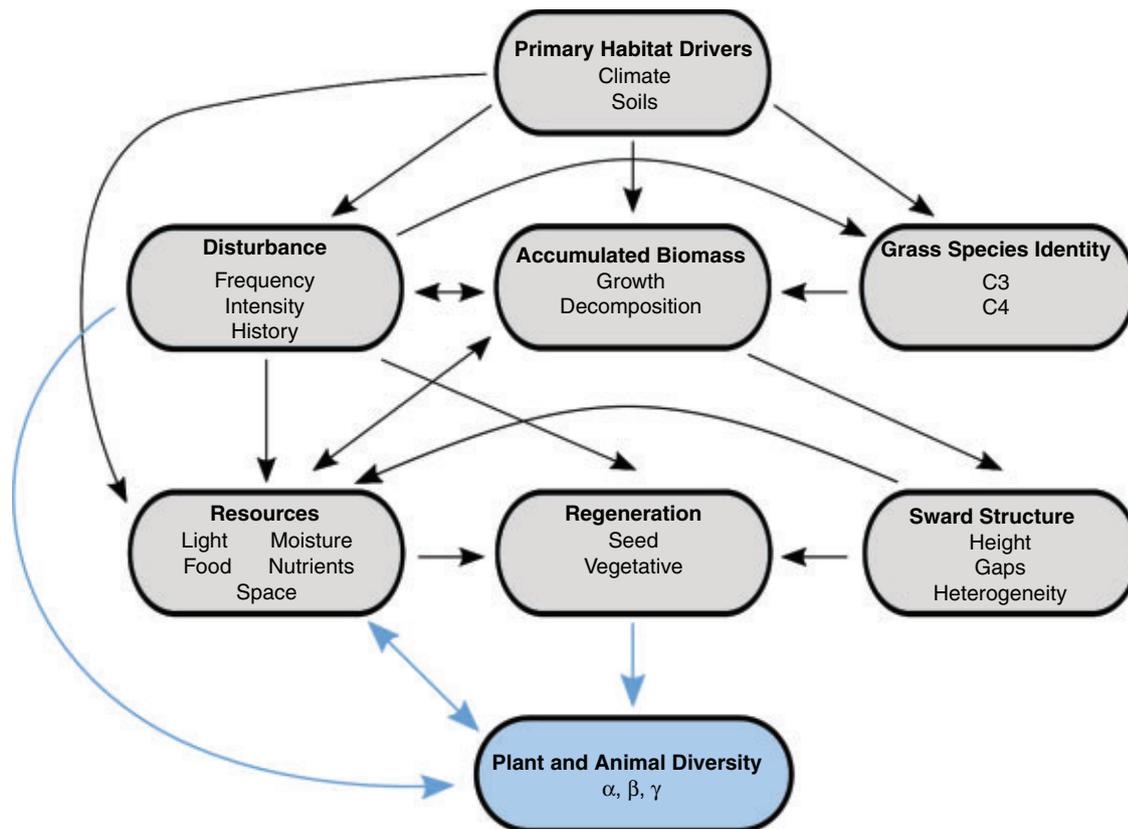


Fig. 2. The multivariate and mechanistic nature of the factors that determine biodiversity, as well as their causal relationships, are outlined in our conceptual model. Our model highlights the paucity of direct drivers of diversity (blue arrows). A key difference with the univariate model presented in Fig. 1 is the lack of a direct link between biomass and diversity; rather this is mediated through the effects of accumulated biomass on resources and sward structure which influences regeneration. We expect disturbance type to effect these responses and this is discussed in section ‘Disturbances are not substitutable: on the need to understand why disturbance affects function differently’.

mean annual rainfall (independent of time-since-grazing exclusion). In low rainfall grasslands (<500 mm annual rainfall), rates of biomass accumulation were slow (Schultz *et al.* 2011).

Most grass leaves have short lifespans, so accumulated phytomass is mostly comprised of dead leaf material produced in earlier years. Undisturbed *Themeda* grasslands in mesic regions, for example, accumulated large quantities of dead grass; 88–93% of phytomass in long unburnt (11–14 years) *Themeda* and *Themeda–Poa* grasslands was dead material (Morgan and Lunt 1999; Prober *et al.* 2007). Environmental controls on litter decomposition are typically related to differences in litter quality (e.g. N, C:N, lignin content) and local climate (precipitation) (Brandt *et al.* 2010; Gaxiola and Armesto 2015). These factors modulate the activity of microbes and other decomposers. The effects of photodegradation (UV radiation during rainless periods) also contributes to differences in decomposition rates (Austin and Vivanco 2006). Photodegradation is greater in arid than in mesic ecosystems, and in litter that is more recalcitrant to microbial decomposition (with high lignin concentrations) (Brandt *et al.* 2010).

In subtropical and semiarid ecosystems, low biomass accumulation might reflect high decomposition rates (Fensham *et al.* 2017) or erratic production (e.g. tied to above-average

rainfall; Austin and Williams 1989). Importantly, phytomass accumulation does not follow a linear function of time-since-disturbance, i.e. it is decoupled from disturbance (Fensham *et al.* 2017). Lewis *et al.* (2008, 2010) found in arid (*Astrelba*) grasslands, with a highly variable climate, that recent rainfall events were far more important for sward density than disturbance. In drier grasslands, litter accumulation is also negligible over long periods; either it decays quickly or gets blown away (Lewis *et al.* 2008; Morgan and Williams 2015). For example, Conway (2000) found that litter cover declined from over 50 to <10% in a single year during drought conditions in northern Victoria. Thus, low levels of accumulated biomass in semiarid grasslands probably reflect high decomposition rates as well as low productivity.

Given that phytomass accumulation varies in different grasslands, disturbance may only promote small-scale richness in areas where phytomass accumulation is substantial. Indeed, Schultz *et al.* (2011) found diversity in Victorian grasslands declined when biomass was >500 g m⁻². Disturbances are thought to maintain richness in these high productivity sites because the removal of the phytomass produced by the dominant grass species frees up resources (light, space, nutrients and moisture) for subordinate species to germinate, grow or persist in the ecosystem (Fig. 2). Lunt and Morgan

(2002) found light availability was reduced to less than 10% beneath *Themeda* tussocks when phytomass exceeded 4 t ha^{-1} . This level of phytomass can accumulate within just 2–4 years after burning (Morgan and Lunt 1999). Phytomass accumulation is also influenced by disturbance history and species identity (Fig. 2). For example, Prober *et al.* (2013) found declines in richness with increasing time-since-fire in sites with a recent history of tree clearing and burning and with high biomass ($>600 \text{ g m}^{-2}$), a response that was not reported in uncleared sites without a recent history of fire and with low biomass (314 g m^{-2}). These sites have similar rainfall to mesic *Themeda*-dominated grasslands in Victoria, which highlights the importance of considering multiple drivers of phytomass accumulation (Fig. 2). Although *Themeda* recovers rapidly after fire, other dominant grasses require more time to return biomass to pre-disturbance levels (Prober *et al.* 2007).

Given that we identify phytomass accumulation (and decomposition) as a key indirect driver of species diversity in grasslands (Fig. 2), it is crucial that data be obtained to test this relationship. Additionally, we need studies from xeric sites dominated by other species, as most studies in south-eastern Australia are primarily from *Themeda*-dominated grasslands (Stuwe and Parsons 1977; Lunt and Morgan 2002; Lunt *et al.* 2012), in which fast accumulation of phytomass smothers inter-tussock species and reduces light availability. In particular, uncoupling the effects of species identity and climate on phytomass accumulation should be a priority. This can be done experimentally (e.g. standardised decomposition rates using teabag protocols, Didion *et al.* 2016) and by field studies coupled with models (Grace 1999).

Grassland structure – more than just biomass

The horizontal and vertical arrangement of biomass – not just the quantity of biomass – has profound effects on ecological processes in grasslands, particularly as it affects light interception, microclimate, plant–soil interactions, canopy gap availability and animal behaviour (Baker-Gabb 1988; Lunt 1997b; Zehm *et al.* 2003; Baker-Gabb *et al.* 2016). Biomass *per se* is a poor measure to capture the spatial (i.e. horizontal and vertical arrangement), temporal and functional aspects of

grassland swards. Light penetration may vary according to a combination of factors including phytomass, but also plant architecture (Fig. 3). High biomass grasslands can provide abundant gaps if the sward is open (Fig. 3b), whereas a closed sward with high biomass is unlikely to provide safe sites for recruitment (Fig. 3a). Conversely, low biomass (when comprising a closed sward) may provide limited safe sites for establishment (Fig. 3c). Currently, few examples exist that document the variation in temperate grassland structure as a function of climate variation (i.e. temporal rhythmicity) and disturbance processes (but see Lunt 1997b for an exception).

Measures of grassland structure that include multiple variables, such as grass height and cover (or grass volume, Howland *et al.* 2014; Schultz *et al.* 2017), likely provide a better estimate of the vegetation profile than biomass, and might capture attributes of grass swards that plants and animals respond to (e.g. habitat complexity, light availability). There are other approaches for measuring grassland structure and heterogeneity, including variance in biomass (Dorrough and Ash 1999), point quadrats to capture height and canopy distribution (Lunt 1997b), the ‘golf ball method’ to provide an integrative measure of vegetation density, height and heterogeneity (Schultz *et al.* 2017), and horizontal photography to measure vertical arrangement of vegetation (Zehm *et al.* 2003). Measuring the amount of bare ground, cryptogamic crust, and soil cracks is also important as these attributes affect seed germination of native (Briggs and Morgan 2011) and exotic species (Morgan 2006), provide important refuges for fauna (Hadden 1995; Bourke *et al.* 2017), and are responsive to management interventions (Morgan 2004; Wong and Morgan 2012). Indeed, it is likely that structure (and its complexity and heterogeneity) may be a more important driver of small-scale richness than biomass *per se* through impacts on regeneration (Fig. 2).

We poorly understand the habitat preferences of most grassland fauna, but structure (not biomass *per se*) is typically invoked as a key attribute of grasslands that needs to be manipulated to maximise selected faunal taxa (Supplementary Material table S2). Habitat suitability for grassland birds is directly related to the structural environment provided by the dominant tussock grasses, with some species preferring short and

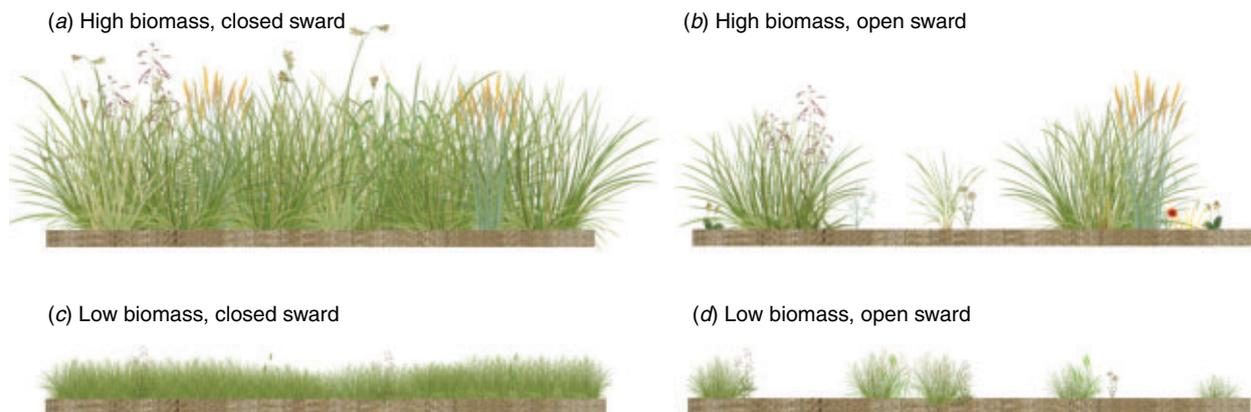


Fig. 3. Biomass poorly captures the spatial (i.e. horizontal and vertical arrangement) aspects of grassland swards. Here, we illustrate that (a) high biomass in a closed sward provides limited opportunities for seedling recruitment and animal movements, whereas (b) high biomass in an open sward may provide safe sites for recruitment and faunal habitat use. Low biomass can provide safe sites for recruitment if the swards are open (d) but might not if closed (c).

sparse grassland (Baker-Gabb *et al.* 2016) while others utilise denser, closed swards (Antos and Williams 2015). Clearly, some species are more abundant in closed than open swards e.g. stubble quail (*Coturnix pectoralis*) and Richard's pipit (*Anthus richardi*) (Neave and Tanton 1989) – hinting that a 'one size fits all' approach to biodiversity conservation has limited application. At landscape-scales, a range of different sward structures is required to maintain habitat for a range of different species (McIntyre 2005). Reptiles typically require a grass canopy to avoid heat stress and predation (Howland *et al.* 2014), but also need a degree of canopy openness to permit sufficient sunlight for metabolic function. Some reptiles, however, are found across a range of grassland structures and respond to other habitat elements. The abundance of the hooded-scaly foot (*Pygopus schraderi*), for example, is determined by the cover of cryptogams and the incidence of spider holes and soil cracks (Brown and Scroggie 2012), whereas the earless dragon (*Tympanocryptis pinguicolla*) requires access to holes excavated by arthropods (Stevens *et al.* 2010).

For many faunal species, the effects of grassland structure may be mediated by indirect factors such as food resource availability (i.e. invertebrates, seeds). King and Hutchinson (1983) showed that the biomass and diversity of invertebrates declined with increasing intensity of sheep grazing in the New England Tablelands, and similar trends have been demonstrated in grasslands elsewhere (Dennis *et al.* 1998; McCracken and Tallowin 2004). Typically, there are fewer decomposers in a grassland system when a greater proportion of the biomass is removed (King and Hutchinson 1976), and the life cycle stages of invertebrates are disrupted by biomass removal (McQuillan 1999). Ant composition, however, shows a different trend, and is mostly determined by grassland structural complexity. High ant diversity has been demonstrated across a range of grassland habitats and conditions (New 2000), although ant abundance is generally higher in heavily grazed, low-biomass sites (Hutchinson and King 1980). Phytophagous species such as the golden sun moth (*Synemon plana*) and morabine grasshopper (*Keyacris scurra*) appear to respond more to the presence of particular food plant species than to grassland structure (O'Dwyer and Attiwill 1999; Griffith and Nano 2011; Richter *et al.* 2013). While the abundance and diversity of invertebrates in grasslands is assumed to influence grassland food webs, we do not have a good understanding of how invertebrates influence grassland ecosystem function (Abraham and Morgan 2018).

The need to account for multivariate drivers of grassland function

Univariate drivers of diversity, such as those presented in the simplified model (Fig. 1), underplay the complex processes that affect biodiversity in grasslands (Grace 1999; Harpole *et al.* 2017). Biodiversity is invariably influenced by, and interacts with, multiple drivers through both direct and indirect pathways. To account for this complexity, models of ecological dynamics need to be developed that incorporate these multivariate drivers of diversity. We introduce a conceptual model of temperate grassland dynamics that proposes the key multivariate drivers that underpin diversity in grasslands (Fig. 2). Here, accumulated

biomass governs the structure of grasslands and this, in turn, affects diversity through its effects on resource availability. Regeneration opportunities are influenced by species-specific responses to disturbance regimes, resources and structure (Fig. 2). We outline the key direct drivers of diversity in temperate grasslands – disturbance, resources and regeneration – in an effort to better understand how grasslands vary ecologically across their range, and why structure, function and diversity are more than outcomes of the amount of biomass singularly.

Species identity

Despite four decades of research, we actually know very little about most grassland species. Hence, our understanding of grassland dynamics comes from a small subset of the species pool. Grassland management has mostly focussed on the ecology of the dominant grass (*Themeda triandra*), a limited number of forbs from (mostly) the Asteraceae, and a suite of highly threatened species, while the literature on land-use intensification has identified those species sensitive to nutrient addition and grazing (Vesk and Westoby 2001; Clarke 2003; Dorrrough *et al.* 2004). Plant functional traits have been used to generalise responses to disturbance (e.g. McIntyre and Lavorel 1994) and management (Williams *et al.* 2006). For example, Zeeman and Morgan (2018) found that grassland habitat suitability varies with plant species and can be predicted by traits affecting competition such as height. Native species that increase in little disturbed grasslands (after being absent from frequently disturbed grasslands) typically comprise tall, wind-dispersed species, while those native species that decline are often short, rosette forming species. Studies of faunal responses are generally limited to charismatic threatened species such as plains wanderer (*Pedionomus torquatus*), striped legless lizard (*Delma impar*) and golden sun-moth (*Synemon plana*). Similarly, little is known about the role of species identity in ecosystem function (Abraham and Morgan 2018) and how the loss of rare species affects ecosystem function (Mokany *et al.* 2008).

What is clear is that species respond differently to disturbance, a point poorly articulated in the simplified model (Fig. 1). Stuwe and Parsons (1977) showed that native grasslands in grazed areas support a different suite of species, not just a subset of those in ungrazed and burnt grasslands. For example, *Glycine latrobeana* (Fabaceae) and *Comesperma polygaloides* (Polygalaceae) are disadvantaged by frequent fire regimes, their occurrence being favoured in unburnt and/or grazed areas (Scarlett and Parsons 1982). There are also many examples of grassland species that do well under anthropogenic disturbance regimes (Kirkpatrick 2007). Lunt (1997a) coined this process 'habitat segregation' and found evidence for different species complements in ungrazed, burnt railway verges compared with grazed, unburnt forests. Hence, species responses to disturbance are more nuanced than is depicted in the current simplified model of grassland function. As a case in point, Sinclair *et al.* (2014) showed that long-unburnt C₃ grasses such as *Austrostipa* (spear grasses) did not recover by vegetative resprouting after a summer fire, despite the general temperate grassland literature suggesting that grasses are resistant (via resprouting) to fire. Moore *et al.* (2019) showed that temperate C₄ grasses had higher probabilities

of surviving fire relative to C_3 grasses, and that drought plays a role in the ability of native grasses to vegetatively recover after fire. This has implications for understanding the persistence of species in landscapes where fire management is practiced. Hence, models need to specify which species are advantaged or disadvantaged by a given disturbance regime, and identify the mechanisms that underpin such responses.

Regeneration opportunities

It is commonly thought that fire promotes regeneration indirectly – by removing biomass and providing gaps for recruitment – rather than directly stimulating germination. As such, much of the grassland literature has focussed on the importance of biomass removal in promoting diversity (Fig. 1). However, studies have mostly examined particular plant groups (mostly Poaceae and Asteraceae, e.g. Morgan 1998a; Clarke and French 2005) and few studies have directly explored the effect of fire-cues on germination. Disturbances such as fire, grazing and bioturbation can cause a myriad of changes in abiotic and biotic conditions that can affect seedling recruitment. We expect germination cues to be related to gap formation and resource availability, or to fire-related cues such as heat or smoke (Fig. 2). Hence, we require an understanding of the factors that directly affect germination as a result of gap formation e.g. nutrient changes, light intensity changes, temperature changes, temperature during fire (dormancy removal), soil changes (disturbance/compaction) and cryptogam cover, and how the effects of these factors may also vary with species identity.

Germination of some grassland forbs are promoted by fire-cues (Vening *et al.* 2017; Hodges *et al.* 2019) and restoration practitioners have also identified many difficult-to-germinate species from grassy ecosystems, indicating seed dormancy may be more prevalent than previously recognised. As such, fire may directly promote germination or remove dormancy for grassland species, as found in other fire-prone ecosystems (Bell 1999). Many herbaceous species have types of dormancy (physiological or morphological) that often require a combination of cues to remove dormancy and enable germination (Merritt *et al.* 2007; Baskin and Baskin 2014). Some species may only become responsive to fire-cues once dormancy has been removed and may therefore require a combination of dormancy removal and fire-cues to enable germination (Ooi *et al.* 2006; Thompson and Ooi 2010; Long *et al.* 2011). For example, *Dianella revoluta* had highest germination when subject to warm stratification (dormancy removal treatment) and smoke (fire-cues) in combination (Hodges *et al.* 2019), and further investigations of such treatments are required to determine if other grassland species have a similar strategy. Determining the processes involved in gap-driven germination is important for understanding the effect of disturbance type and timing on seedling recruitment. For example, if fire directly promotes seed germination, then fire may promote diversity regardless of biomass accumulation and this has implications for considering if disturbances are substitutable (see section ‘Disturbances are not substitutable: on the need to understand why disturbance affects function differently’). Resource variation and the environmental

conditions during seedling emergence and establishment are also critical for recruitment success.

Below ground, whether species are able to form persistent soil seed banks that survive the disturbance interval is relatively unstudied, but vital for understanding recruitment potential after different disturbance types. Seed persistence or longevity across the diversity of species in grasslands is likely to have a much greater range than the transient soil seed banks known for a select few daisies and forbs (Lunt 1995), and requires further investigation.

Resource variation

Temperate grasslands exist over a range of climates as a consequence of their wide distribution across latitude, distance to coast and altitude (Fig. 4). Importantly, grasslands also differ in their seasonality of precipitation (uniform to distinctly winter-dominated), frequency of drought (return interval), and the severity of drought (duration) throughout the range of climates that support temperate grasslands. As a result, gradients in rainfall quantity and seasonality, as well as temperature, drive turnover in plant species composition (McDougall and Kirkpatrick 1993), and long-term ecological dynamics as driven by exposure to different disturbance regimes (Morgan *et al.* 2017).

Availability and use of water by plants is one of the dominant forces influencing the phenology and productivity of ecosystems, and deserves greater recognition in temperate grasslands. Interannual variation in precipitation, for instance, has been shown to be a strong determinant of yearly primary productivity in Australian temperate grasslands (e.g. Groves 1965; McDougall 1989; Morgan *et al.* 2017) and elsewhere (Knapp and Smith 2001). Year-dependent effects on primary production are particularly important in Australian grasslands because the El Niño–Southern Oscillation cycles cause large inter-annual variation in precipitation (Vines *et al.* 2004). This introduces the potential for significant variation in the rates of canopy recovery after disturbance, seedling recruitment opportunities, as well as species coexistence processes. Elsewhere, temporal variation in water availability influences community composition in grasslands (Pitt and Heady 1978; Hamilton *et al.* 1999; Corbin *et al.* 2005) and herb-rich savanna (Myers and Harms 2011).

Grassland productivity is also influenced by soil nutrients, either singly or via co-limitation (Elser and Bracken 2007; Harpole and Ngai 2011; Fay *et al.* 2015). Temperate grasslands generally occur on fine-textured soils (Fensham *et al.* 2015), but soil nutrients vary substantially as a function of parent material and age. Temperate grasslands are mostly associated with cracking clay vertisols derived from recent deposits of basalt and alluvium, although in some regions, such as the Monaro Tablelands, grasslands also occur on clays derived from a greater range of parent rocks including limestone, fine-grained sedimentary rocks and even granite (Benson 1994). Such differences in soils likely play a role in the rate at which competitive exclusion occurs. Multiple nutrient limitations have also been shown to structure plant diversity and composition in grasslands, independently of changes in light and biomass (Harpole *et al.* 2017). Indeed, in the global NutNet

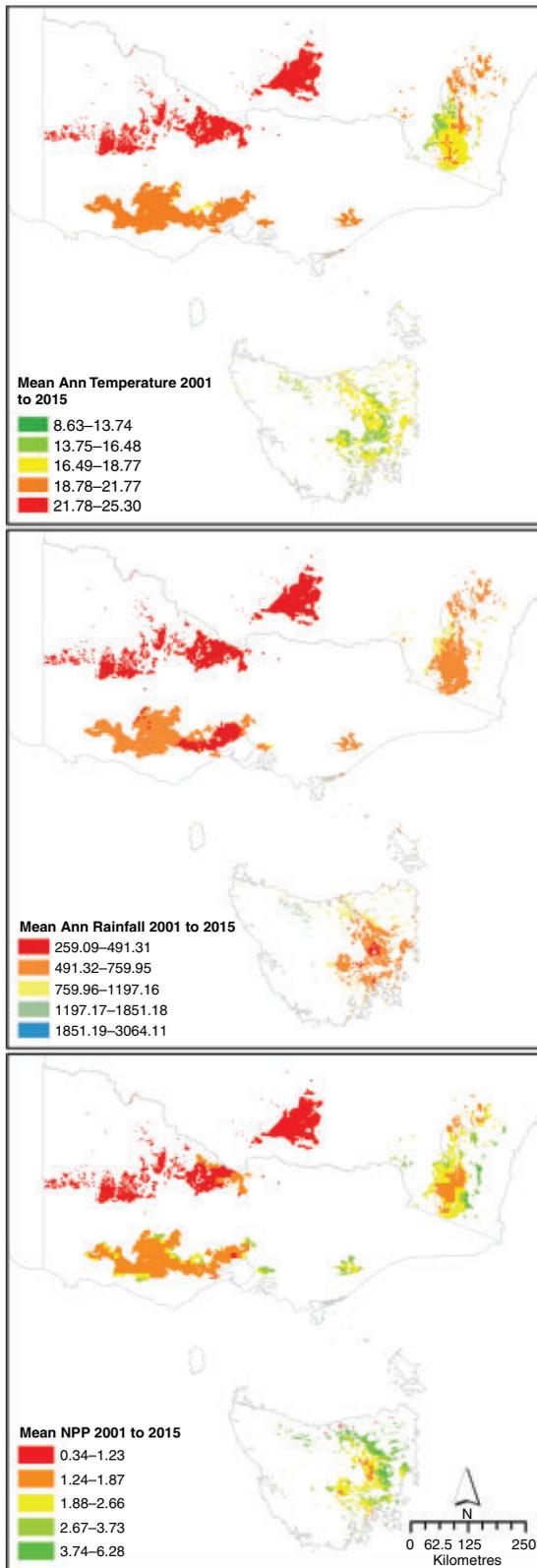


Fig. 4. The extent of temperate grasslands in south-eastern Australia in relation to MAT (mean annual temperature, °C), MAP (mean annual precipitation, mm), and how this affects net primary productivity. The rainfall and temperature layers were produced by averaging the Bureau of

experiment examining drivers of plant diversity in grasslands (which includes temperate grasslands from south-east Australia; Morgan *et al.* 2016), many sites showed no significant increase in biomass with nutrient addition, yet lost diversity when nutrients were added (Harpole *et al.* 2017). Hence, although light limitation can be an important contributor to diversity loss in grasslands, it is not always a causal mechanism. Additionally, the magnitude of the nutrient addition effect in grasslands increases with increasing plant available water, i.e. nutrient addition interacts positively with growing season precipitation (Prober and Wiehl 2012; Dwyer *et al.* 2015). A robust assessment of the extent to which water and nutrient availability limit productivity in Australian temperate grasslands under present climatic conditions is needed. Variation in rainfall and soil nutrients in time and space, likely modifies species' responses to disturbance and competitive exclusion and it can be predicted that patterns of diversity will respond in non-linear ways to these key drivers; hence the need for their inclusion in updated models of grassland function (Fig. 2).

Disturbances are not substitutable: on the need to understand why disturbance affects function differently

The 'state' of a grassland (e.g. species composition, degree of invasion by exotic species, life form representation) has typically been regarded as a function of its long-term management history, i.e. its disturbance regime (Stuwe and Parsons 1977; Lunt 1997a; McIntyre and Lavorel 2007). Based on this, the literature often recommends maintaining the *status quo* in relation to disturbance regimes to manage grasslands (Fig. 1; Ross 1999; Wong and Morgan 2007). This is based on the idea that maintenance of the processes that gave rise to the patterns of diversity is viewed as the best way of maintaining those patterns. For example, cessation of fire results in local extinction of native forbs from temperate grasslands that previously had a history of frequent fire (Williams *et al.* 2006; Zeeman *et al.* 2017). Maintaining the *status quo*, however, may no longer be an option with global climate change (Harris *et al.* 2015).

Little is known about whether different disturbance types are substitutable, i.e. moving beyond the *status quo*. Disturbance, as defined by Grime (1977), is any event that removes biomass, but disturbance type can have fundamentally different outcomes on vegetation; grazing is selective, fire consumes all biomass, and slashing generally leaves litter on the ground. This will have impacts on the post-disturbance ecosystem that is created, with consequent effects on the biota that utilise grassland habitat. Such changes are already occurring as land management practices change with rural population decline (Williams 2007), urbanisation (Williams *et al.* 2006; Zeeman *et al.* 2017) and conservation covenanting (Wong and Morgan 2012). Changing long-term regimes might lead to instability in the system (in the

Meteorology's annual rainfall and temperature grids for 2001 to 2015 in ESRI's Arcmap ver. 10.5. The NPP (net primary productivity) layer was produced by averaging the annual net primary productivity grids produced by NASA (reference https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MOD17A2_M_PSN, accessed 31 August 2018) 2001 to 2015 in ESRI's Arcmap. The grids were clipped to the grassland study regions as defined by the grassland layers supplied by D. Keith (from Morgan *et al.* 2017). The layers were then symbolised.

short term), but to improved conservation outcomes because it ultimately favours more species (at landscape scales). Legacy effects will influence the response of grasslands to new disturbances. Species identity is likely to be an important determinant of how grasslands respond to different types of disturbances (Kirkpatrick *et al.* 2005). For example, high mortality has been observed in C₃ tussock grasses when reinstating fire into a long unburnt site (Sinclair *et al.* 2014), and C₄ grasses are more resilient to burning than C₃ grasses (McDougall 1989; Moore *et al.* 2019). Additionally, two types of disturbances applied concurrently can have different impacts than a single disturbance type. For example, fire and grazing can benefit the striped legless lizard but concurrent application of both disturbances may trigger population collapse (Scroggie *et al.* 2019).

Fire is a 'pulse' disturbance (Bender *et al.* 1984), typically destroying all plant material in a relatively homogenous way, but it can vary in intensity both spatially and temporally (Morgan 1999). The effects of fire and fire regimes on grasslands are generally well described, particularly for plants (Lunt and Morgan 2002; Morgan *et al.* 2017). For invertebrate species, abundance and richness are reduced after fire, but can recover relatively quickly to pre-fire levels (Greenlade 1997; Abraham and Morgan 2018). Among vertebrates, reptiles can suffer elevated mortality from fire, with mortality influenced by the season of burning (Griffiths and Christian 1996) and burrow use (Fenner and Bull 2007). Marsupials like fat-tailed dunnarts aim to evade fire; they can arouse from torpor when they detect smoke, increasing their likelihood of evading an approaching fire (Stawski *et al.* 2015; Nimmo *et al.* 2019), suggesting that the presence of unburnt refuges, and the speed of an approaching fire front may influence mortality. For soil fungal communities, fungal diversity and composition were influenced by fire regime (long-term fire frequency), but not time-since-fire (Egidi *et al.* 2016). It is clear that removing fire has negative effects for many species (Williams *et al.* 2006; Zeeman *et al.* 2017), but there has been little quantification of (1) the time that grasslands can remain unburned before irreversible declines in diversity occur, and (2) how substituting other disturbances in place of fire may mitigate such declines.

Livestock grazing can reduce vegetation cover, with substantial reductions persistent over time in many areas (i.e. a 'press' disturbance *sensu* Bender *et al.* 1984). Grazing is used as a management tool because it can maintain species richness (at high numbers in small quadrats)—based on the idea that competitive exclusion reduces small scale diversity (Fig. 1). Although α diversity is high, β diversity across the landscape may be low when grazed (Schultz *et al.* 2016) and fire-cued recruitment opportunities will be lost. Conservation managers are loathe to remove stock from native grasslands because they are acutely aware that destocking might lead to declines in α diversity. This fails to recognise that destocking might lead to increases in β diversity if it promotes heterogeneity via microsite differentiation. So far, the evidence for effects of changing disturbance – such as moving from a grazing to fire regime, abandonment, or altering the *status quo* grazing regime – is mixed, with positive, neutral and negative impacts on plant,

invertebrate and bird diversity observed (Hadden 1995; Kirkpatrick *et al.* 2005; Zimmer *et al.* 2010; Wong and Morgan 2012). If a grassland has a long history of grazing, it is likely that grazing-sensitive plant species have been lost from the system (Price *et al.* 2010). Hence, reinstating fire or grazing removal is unlikely to recover those species without further management interventions such as seed addition and could lead to loss of species that require some disturbance (Kirkpatrick *et al.* 2005; Johnson *et al.* 2018; Zamin *et al.* 2018). Little is known about the effects of native marsupial grazing on Australian temperate grasslands; a few studies have explored impacts of over abundant native animals, and high selectivity has been observed (Leonard *et al.* 2010).

In general, mowing promotes greater native richness than grazing (Verrier and Kirkpatrick 2005), but reduced richness compared with fire (Prober *et al.* 2013). Slashing is comparatively a fairly homogenous disturbance, particularly if applied frequently, as it generally encourages low-biomass, closed grassland structure (Prober *et al.* 2008; Fig. 3c). Mowing can result in aggregated litter which can have negative consequences unless slash is removed (Verrier and Kirkpatrick 2005; Morgan 2015). Slashing is generally viewed as unfavourable in temperate grasslands (Kirkpatrick 1986), particularly for taller species, but Smith *et al.* (2018) show that annual mowing can have positive influences on plant diversity, and may promote structural heterogeneity when applied patchily, and can also favour some rare species (Gilfedder and Kirkpatrick 1997). Mowing increased cover of native species (including some rare or threatened species) and reduced exotic grass cover compared with grazing in Tasmania (Verrier and Kirkpatrick 2005). In degraded grasslands in the ACT, tussock thinning and litter removal favoured native forbs, but only when seeds were added (Johnson *et al.* 2018). Positive effects of slashing at small spatial scales (α diversity), might not translate to larger scales (β diversity) (Smith *et al.* 2018).

Bioturbation is another disturbance type that has been understudied, particularly in the context of Australian temperate grasslands. Burrowing mammals are recognised globally as ecosystem engineers in grasslands, increasing biodiversity and habitat heterogeneity (Davidson *et al.* 2012). In Australian ecosystems, the ecological roles of digging animals are best understood in semiarid and arid ecosystems, where digging by burrowing bettongs (*Bettongia lesueur*) can suppress shrubs and increase the cover and diversity of perennial grasses by altering soil characteristics, trapping litter and water, and enhancing seed germination (Noble *et al.* 2007; Eldridge and James 2009). In Australia's temperate grasslands, bioturbation by digging animals such as eastern-barred bandicoots (*Perameles gunnii*) could perform similar or other ecological roles, but such animals have been lost from temperate grasslands (Dufty 1994; Reading *et al.* 1996). A recent study highlights the potential for bettongs (*Bettongia gaimardi*) to enhance soil processes in degraded temperate woodlands (Munro *et al.* 2019). We predict that digging might provide a relatively low-intensity disturbance that could have ecological benefits in the more xeric temperate grasslands that do not require frequent disturbance.

Future research directions

Despite four decades of research in temperate grasslands, much remains unknown about the multivariate drivers of animal and plant diversity as outlined in Fig. 2. Using this model as a starting point for future research, we believe there are five key questions that need to be urgently addressed.

1. What are the rates, and drivers, of phytomass accumulation in different grasslands?

Rates of phytomass accumulation across the range of temperate grasslands are likely to be influenced by climate, dominant grass species identity, and decomposition. Understanding how these processes vary in space and time would allow us to predict phytomass accumulation in a given location enabling better prediction of the disturbance requirements for promoting diversity, and hence more tailored management decisions.

2. Under what conditions is disturbance required for recruitment?

More research is required on seed persistence, dormancy and germination cues for many grassland plant species. From a management perspective, identifying responses to fire-cues for many component species is required to determine if fire *per se* is required to promote diversity, or simply the removal of biomass. We also need to explore the ability of species to form persistent soil seed banks and the effect of other disturbance types on seedling regeneration, e.g. soil disturbance, animal diggings.

3. What are the impacts of changing from long implemented management regimes (*status quo*) to alternative disturbance regimes?

Little is known about whether a switch from one long-term management regime (the *status quo*) to another management regime (e.g. fire to grazing and *vice versa*) has positive, negative or neutral outcomes for diversity. Responses of plants and animals will depend on land-use legacies and if sites are stable under the current management regime.

4. Do small plots adequately describe the effects of long-term disturbance regimes on species persistence?

We require a better understanding of the drivers of β and γ diversity in grasslands, as well as the drivers of spatial and temporal variation in composition. There is almost no data to address these questions, both of which logically flow to landscape-scale conservation planning.

5. How does disturbance influence faunal assemblages and habitat?

More research is needed on the effect of disturbance on habitat provision and food resources for most grassland fauna. In particular, we need to understand the relationship between faunal diversity and grassland structure, and how habitat diversity and disturbances might affect different faunal food webs.

Conflicts of interest

The authors declare no conflicts of interest.

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