NEW ZEALAND JOURNAL OF ECOLOGY

Predicting ecological change in tussock grasslands of Aotearoa New Zealand

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Abstract: Natural grasslands are among the most threatened biomes on Earth. They are under pressure from land cover change including afforestation, farming intensification, invasive species, altered fire regimes, and soil amendments, all of which impact native biodiversity and ecosystem functioning. In Aotearoa New Zealand, tussock-dominated native grasslands expanded due to increased fire activity during waves of human settlement. These areas have subsequently been maintained as modified grasslands by agricultural pastoral land management practices and effects of introduced feral mammals. Despite many decades of research on biodiversity in tussock grasslands, we need greater fundamental understanding of many processes causing change in their biodiversity and ecosystem functioning in order to predict how future global change will impact this important and increasingly threatened biome. In this perspective forum article, we present five key research questions that, if answered, would greatly enhance our understanding of connections between tussock grassland biodiversity, ecosystem functioning, and associated ecosystem services: (1) What are the relative impacts of domesticated and non-domesticated mammals on indigenous biodiversity in grasslands? (2) Where will invasive plants undergo range expansion? (3) Will future fires tip tussock grasslands into alternative vegetation states? (4) What are the implications of woody thickening by native or non-native species? (5) What are the impacts of global change, and vegetation change in particular, on soil processes and ecosystem functioning? We provide recommendations for research to address and integrate across these questions using both existing and new data. This work would build on our current knowledge and lead to a framework to better understand the ecological impacts of ongoing global change in tussock grasslands.

Keywords: carbon, *Chionochloa*, drought, ecosystem functioning, fire ecology, *Festuca novae-zelandiae*, global change, invasion, soil, vegetation change, woody thickening

Introduction

Grassland ecosystems around the world are severely threatened by global change, resulting from direct and indirect human-induced changes operating at various spatial and temporal scales (Sage 2020; Bardgett et al. 2021). Indigenous grasslands of Aotearoa New Zealand (NZ) are experiencing many of the same global change pressures as elsewhere in the world, including increased droughts, fires, continued land management changes such as altered grazing regimes, afforestation efforts, and increased pressure from invasive animals and plants (Fig. 1). While effects of losses or changes in grasslands on ecosystem functioning and associated ecosystem services

have been quantified in some grassland systems around the world (Lavorel et al. 2015; Farley & Bremer 2017; Lark et al. 2020; Bardgett et al. 2021) more information on this is urgently needed in NZ.

Tussock grasslands are an iconic vegetation type in NZ with research dating back many decades. As a result, we have a good understanding of plant community structure in relation to environmental gradients in tussock grasslands (Connor & Vucetich 1964; Connor 1965; Cockayne 1967; Wardle 1991; Day & Buckley 2013) and plant invasions (e.g. Treskonova 1991; Day & Buckley 2011; Steer & Norton 2013). However, understanding the ecological and functional implications of global change processes on tussock grasslands is comparatively
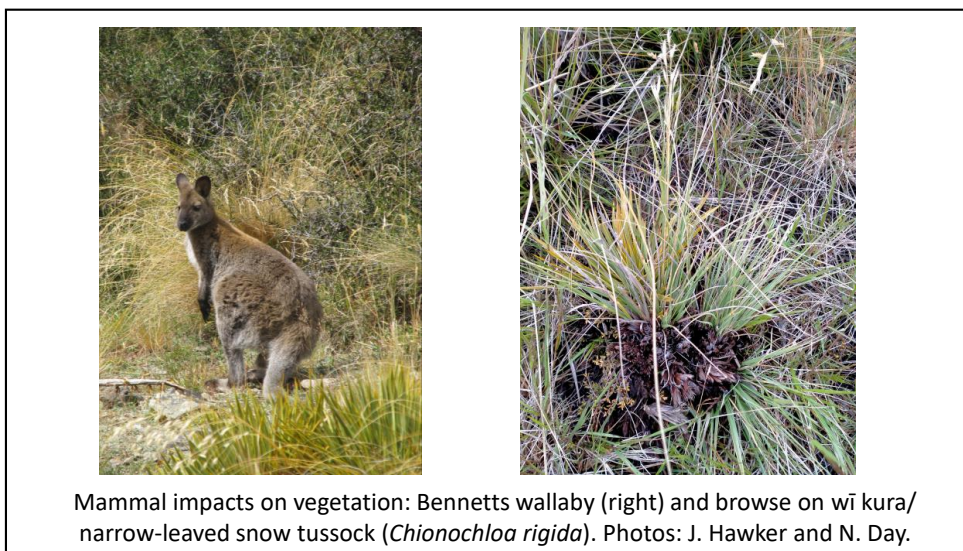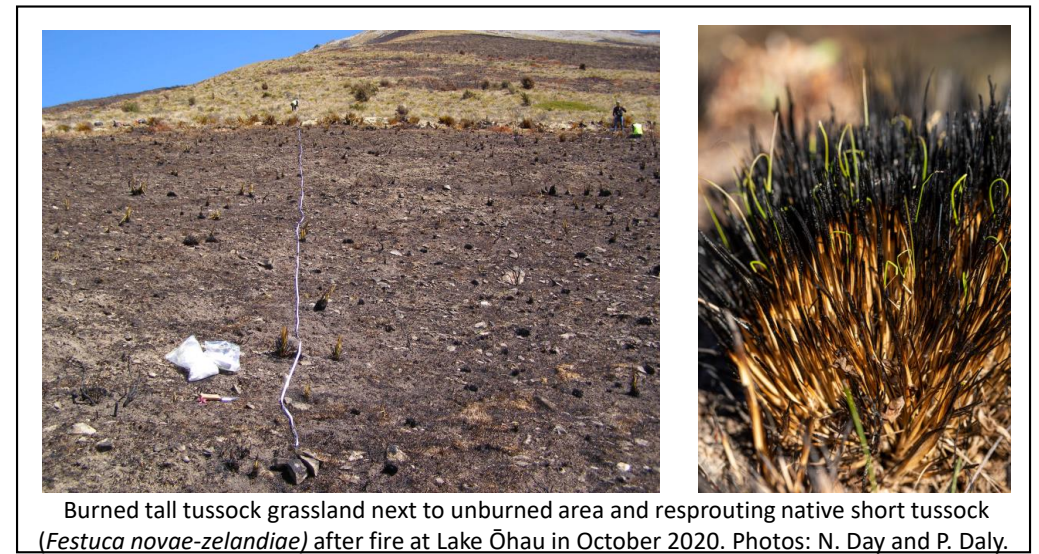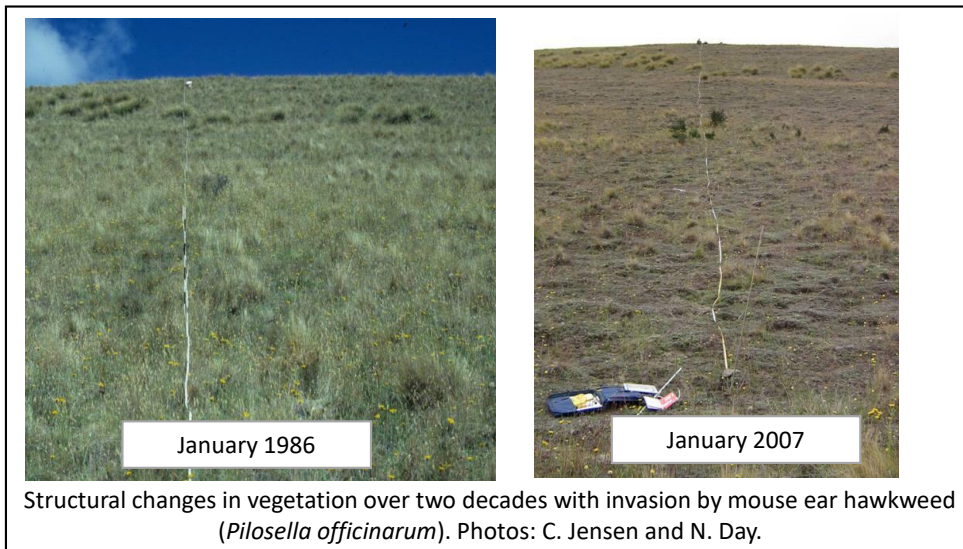
Structural changes in vegetation over two decades with invasion by mouse ear hawkweed (*Pilosella officinarum*). Photos: C. Jensen and N. Day.

January 1986

January 2007

Burned tall tussock grassland next to unburned area and resprouting native short tussock (*Festuca novae-zelandiae)* after fire at Lake Ōhau in October 2020. Photos: N. Day and P. Daly.

Mammal impacts on vegetation: Bennetts wallaby (right) and browse on wī kura/ narrow-leaved snow tussock (*Chionochloa rigida*). Photos: J. Hawker and N. Day.

Example of woody thickening in Central Otago. Photo: D. Norton.

Figure 1. Examples of global change processes impacting tussock grasslands of Aotearoa New Zealand.

limited, including the effects of land use change (Weeks et al. 2013), fire (Barratt et al. 2009, 2019; Payton & Pearce 2009), invasive feral mammals (Whitehead et al. 2014; Cruz et al. 2017), and changes in soil properties (Wakelin et al. 2013; Adair et al. 2019). We lack key information at the temporal and spatial scales necessary to be able to predict the ecological and functional effects of global change across the environmental extent of tussock grasslands (i.e. conditions in elevation, aspect, drainage, management, pest densities). Predictions are further challenged by likely legacy effects of past management regimes common over 100 years ago, such as burning and oversowing of pasture species, and high stocking densities well above those used now in at least some areas of the high country (O'Connor 1982; Morris 2013).

The aim of this forum article, a perspective piece, is to outline what we consider to be critical research questions that need to be addressed to predict future responses of our native grasslands to global change processes and their interactions. We identified the research questions by combining literature searching (Web of Science) and our cumulative knowledge of native grassland research in NZ and globally to overview the current status and challenges in tussock grassland ecology. Through this, we identified areas we need to better understand how global change processes will impact biodiversity and ecosystem functioning in tussock grasslands in the coming decades, with a focus on four key areas of global change: mammal impacts, plant invasions, changing fire regimes, and woody thickening. We then suggest research directions to better understand ecosystem functioning and associated ecosystem services in tussock grasslands. This forum article is not a comprehensive literature review of tussock grassland ecology and these can be found elsewhere (e.g. Wardle 1991; Mark et al. 2013). Rather it provides a framework from which we can build research approaches to assess ecosystem properties over time and under different management regimes.

Background

Aotearoa New Zealand indigenous grasslands encompass many rare (Williams et al. 2007) and threatened (Holdaway et al. 2012) ecosystem types. Grasslands dominated by tussock (bunch) grasses were distributed above and below altitudinal treeline prior to human arrival, becoming more extensive at lower elevations through burning associated with human settlement (Molloy et al. 1963; O'Connor 1982; McGlone 2001; Walker et al. 2004; Perry et al. 2012). Together with subsequent introductions of browsing and grazing mammals, this led to dramatic losses of native biodiversity across grasslands both above and below altitudinal treeline, and the formation of broadly different grassland types with diverse ecological and social values (Cockayne 1967). Despite these impacts, tussock grasslands currently still retain and support a wide taxonomic range of native biodiversity, including many rare plants, invertebrates, reptiles (Mark et al. 2013), and essential ecosystem functions and services, such as carbon storage (Ross et al. 1997a; Holdaway et al. 2014), nutrient cycling (Wakelin et al. 2013), and hydrological processes (Mark & Dickinson 2008; Michel et al. 2013).

Tussock grasslands fall into a few types (Mark et al. 2013). Above treeline (1200–1500 m a.s.l.), where only limited areas have been subject to intensive livestock grazing, snow or tall tussocks in the *Chionochloa* genus (Poaceae) dominate (Mark et al. 2013). *Chionochloa rubra* is common below treeline

on the volcanic plateau in the North Island and localised moist areas throughout NZ (Mark et al. 2013). Below natural treeline, short tussock grasslands dominated by *Festuca novae-zelandiae* and *Poa* spp. (Poaceae) that expanded with historical burning and deforestation were, and still are, exposed to more intense grazing and pastoral management than those at higher elevations (Mark et al. 2013; Cieraad et al. 2015). The majority of plants associated with these grasslands are long-lived perennials, so changes in plant communities over decades are slow (e.g. Day & Buckley 2013).

A pervasive paradigm in NZ is that grasslands below the natural treeline are unnatural, induced ecosystems, and of little ecological or social value (Mark et al. 2013). We believe this ignores the idea that woody and non-woody ecosystems were likely dynamic in the past, as they are today, due to disturbance events such as fire altering vegetation patterns, especially east of the divide in the South Island. Mark et al. (2013) present strong evidence that pre-human grasslands were distributed along wide elevation gradients. While pollen, fossil, and charcoal studies have provided invaluable insight into pre-human vegetation, these studies are necessarily localised and restricted to areas suitable for preservation (e.g. Molloy et al. 1963; McGlone 2001). Initiatives such as the Lakes380 project has the potential to greatly enhance our understanding of pre-human vegetation across the broader landscape (https://lakes380.com/).

A large proportion of tussock grasslands are on public conservation land. With 125 of the 303 pastoral lease properties having completed tenure review under the Crown Pastoral Land Act 1998, 302 554 ha of land has been taken out of farming operations, mainly livestock grazing (New Zealand Cabinet 2019). The majority of these areas were transferred to public conservation title, where there are limited resources for adequate pest control; or to freehold title, where the risk of losing indigenous land cover is high (Mark & McLennan 2005; Weeks et al. 2013; Brower et al. 2020). Approximately 1.4 Mha, or 58%, of snow tussock grasslands are now in the conservation estate to be managed by the Crown (Manaaki Whenua Landcare Research 2020). Additionally, 227 000 ha (14%) of low-producing grassland that contains exotic sward species and indigenous short tussock species such as hard tussock (*Festuca novae-zelandiae*), blue tussock (*Poa colensoi*), and silver tussock (*Poa cita*), are currently in public conservation land (as opposed to freehold or pastoral lease; Manaaki Whenua Landcare Research 2020). The practice of tenure review has now ceased. However, given that so much area of tussock grasslands is now public lands, the Government of New Zealand has a responsibility to manage these grassland systems in a way that reduces degradation, enhances native biodiversity and ecosystem functioning, and optimises their contribution to global climate change mitigation and adaptation (Brower et al. 2020). Here are some suggestions for research areas that could add to our understanding to support management decisions for lands dominated by tussock grasslands across land tenures.

Research question 1: What are the relative impacts of domesticated and non-domesticated mammals on indigenous biodiversity in grasslands?

Current understanding

Introduced grazing and browsing mammals are having a large novel impact on indigenous grassland ecosystems because native tussock grassland plant species in NZ evolved in the absence of grazing mammals and instead evolved with large avifauna (many recently extinct). Removing livestock grazing can facilitate local recruitment of *Chionochloa* spp. and other native plants (Lee et al. 1993; Walker et al. 2016), but can lead to dominance by exotic grasses in more modified short-tussock grasslands in some situations (Lord 1990). Exclosure studies across grassland types suggest there is no substantial impact on plant community structure when grazing is removed over relatively short time frames of 5–16 years (Primack 1978; McIntosh & Allen 1998; Grove et al. 2002; Rose & Frampton 2007; Norton & Young 2016) and no significant changes in soil chemical properties (Lord 1990; McIntosh & Allen 1998). Increases in native woody cover after many decades of low or no domesticated grazing have been observed in short- (Rose et al. 2004) and tall-tussock grasslands (Young et al. 2016). However, 30 years without grazing at Black Rock Reserve showed woody thickening was highly localised, resulting in a grassland-shrubland mosaic (Mark & Dickinson 2003); this emphasises the importance of spatial scale and environmental gradients when assessing impacts of grazing removal. In fact, a comprehensive review suggested that there is seldom a clear transition of grassland to shrubland after grazing cessation, even after many decades (Ewans 2004). Variation in vegetation responses to grazing could be due to spatial or temporal scale of measurements, site-to-site variation in microclimates associated with elevation and aspect, ongoing effects of feral grazing and browsing, differences in initial vegetation, changes in the local environment (loss of soil, increased transpiration), and/or lack of propagule sources. Additionally, legacy effects of past management regimes may take decades to be fully realised (O'Connor 1982).

There are few quantitative data on the relative effects of managed domesticated livestock compared to feral introduced animals on tussock grassland ecosystem structure and functioning. Teasing apart these effects is complex because even in cases where historical grazing data can be obtained from landowners at the scale of a paddock or run, this may not reflect within-paddock variability and does not account for population dynamics of feral mammals or possible similarities in their diet with domesticated animals. A study where sheep (*Ovis aries*; Bovidae) were fitted with Global Positioning System (GPS) collars in one valley in Canterbury showed most grazing occurred in short tussock grasslands on flat, low slopes, while night camping occurred at higher elevations (Steer 2012). Even at a paddock scale, knowledge of stocking densities for more than a few decades is difficult to obtain, leading to uncertainty in the effects of lag or legacy effects of past management regimes. Moreover, which mammal species are present will likely cause different effects on vegetation due to dietary preferences for particular plant species or traits (e.g. Lloyd et al. 2010).

Given that current stocking rates of domesticated sheep are typically quite low in tussock grasslands (< 1 sheep ha^{-1}), we may assume the largest impact of mammalian herbivory on vegetation is by non-domesticated mammals; notwithstanding the huge impacts caused by cattle (*Bos taurus*; Bovidae), and deer (Cervidae), and legacy effects of previously high stocking rates (O'Connor 1982). Recent estimates of tahr (*Hemitragus jemlahicus*; Bovidae) densities range from 0.01–0.03 ha^{-1} (Ramsey & Forsyth 2018). Brown hares (*Lepus europaeus*; Leporidae) reached as many as 8 ha^{-1} in tussock grasslands in Southland in 2003–2004 (Wilson et al. 2006), and there were as many as 1000 ha^{-1} rabbits (*Oryctolagus cuniculus*; Leporidae) in parts of Otago in 2022 (Parkes 2022). Macropods (Macropodidae), mustelids (Mustelidae), Canada geese (*Branta canadensis*; Anatidae), and pigs (*Sus scrofa*; Suidae) are emerging threats as they expand above and below treeline. In observational studies it is difficult to disentangle effects of different types of grazers from other agricultural effects, such as fertiliser (Whitehead et al. 2014), and potential legacy effects of high sheep stocking rates and feral deer and rabbit densities in the past (O'Connor 1982; Nugent & Fraser 1993). Hare impacts on vegetation are difficult to estimate because there have been few studies excluding these mammals. However, hares are widely distributed, relatively unselective in vegetation preferences, and they impact recruitment of native grasses and herbs (Wong & Hickling 1999). As omnivores, possums (*Trichosurus vulpecula*; Phalangeridae) may also have wide-ranging effects on populations and communities of plants and invertebrates (Parkes & Forsyth 2008). Trampling effects of large ungulates, such as tahr and deer, likely impact grasslands. We are unaware of any studies that have quantified this, although historic deer trails are evident in many alpine areas. Further, whether reductions in predators, such as those targeted by the Predator Free 2050 effort, i.e. rats (*Rattus* spp.; Murinae), stoats (*Mustela erminea*; Mustelidae), and possums (https://predatorfreenz.org/), affects the density or impacts of feral herbivores in the future is uncertain.

Research needs

More long-term investment in monitoring, maintaining, and potentially establishing new grazing exclosures to also exclude lagomorphs and macropods would provide exceptionally useful information on the roles of different types of grazing and browsing on tussock grasslands. A major challenge is that lagomorph exclosures are particularly prone to snow damage (e.g. Norton & Young 2016) so need regular maintenance and therefore consistent investment in people and materials. Grazing removal studies need to have targeted funding for > 10 years since results from shorter studies on plant communities or tussock densities are inconclusive (e.g. Meurk et al. 2002; Norton & Young 2016). Providing land managers with financial incentive to maintain exclosures and monitor animals, plants, and soils should be a goal to obtain a more complete ecological picture across grassland types and environmental gradients. Monitoring a broad range of variables describing aspects of ecosystem functioning, such as soil carbon or nutrient levels, would maximise the value of exclosure plots. Moreover, combining exclosure plots with other experimental and situational treatments, such as burning (Payton & Pearce 2009), irrigation (Rodrigues et al. 2017), or planting woody species would enhance their value by enabling evaluation of interactive effects of multiple factors.

Animals with GPS collars can be tracked to understand their local and landscape level behaviours, which can then be related to plant community data (Steer 2012). More research like this is required across the full suite of herbivores present in NZ grasslands. Pairing exclosure studies with knowledge

of animal population densities, or better still, experimentally manipulating animal densities inside or outside study areas, would allow rigorous assessment of the relative impacts of different types of mammals on plant species and ecosystem functions. To be successful, we need to develop approaches to overcome the limitations associated with subsequent animal movement and the complication that lagomorph exclosures also exclude ungulates. Remote sensing studies paired with ground-truthing in areas where domesticated grazing has been removed or non-native animal densities are known would enhance broad knowledge of their effects in different contexts, such as initial vegetation conditions, aspects, and soil conditions. This will help us know which mammals have the greatest impacts, how they impact different processes, and aid management goals and decision-making.

Research question 2: Where will invasive plants undergo range expansion?

Current understanding

Common invasive exotic plants in tussock grasslands have likely been present for many decades, as NZ's strict biosecurity regulations and vigilance at the border are relatively recent with the introduction of the Biosecurity Act in 1993. Priority invasive plants in the high-country landscape are hawkweeds (mainly *Hieracium* spp. and *Pilosella officinarum*; Asteraceae) and wilding conifers (Pinaceae), which reduce both conservation and pastoral values where they invade. Hawkweeds appear to be both a symptom and a cause of degradation (Treskonova 1991; Rose & Frampton 2007; Day & Buckley 2011), while wilding conifers and deliberate planting of exotic trees are considered a cause of degradation (Peltzer 2018). Conifers and hawkweeds can also impact ecosystem functioning by altering soil microbial communities (Dickie et al. 2010; Morman 2021). Generally, exotic and invasive plants are most abundant at low elevations and in disturbed areas, which corresponds with dominance of short tussock grasslands and where management is most intensive (Day & Buckley 2011, 2013). With changing climates, there is potential for new plants to become invasive and for present invasive plants to expand their ranges and spread upslope (e.g. Steer & Norton 2013). However, this assumes the distribution and abundance of invasive plants in our grasslands are temperature-limited, which is not the case at this point in time; both wilding conifers and hawkweeds are limited by their dispersal ability, not their environmental tolerances, at least in the initial phases of invasion (Miller et al. 2015; Wyse & Hulme 2021). Hawkweeds spread to higher elevations in the last two decades of the 20th century (Day & Buckley 2011) and we expect other invasive plants will follow this pattern due to propagule pressure, regardless of climatic change. Moreover, hawkweeds and conifers are both reliant on mutualistic mycorrhizal fungi in the soil to obtain nutrients to grow and compete with other plants (Downs & Radford 2005; Dickie et al. 2010). Therefore, interactions among species' dispersal ability, niches, climate change, and mutualisms need to be better understood to predict future abundance and distributions of invasive plants in alpine areas. How invasive vertebrates and invertebrates may impact, or be impacted by, changing plant distributions is unknown.

Research needs

Long-term monitoring is key for understanding changes in distributions of invasive plants and predicting where they may expand or contract under climate change (Day & Buckley 2011; D'Antonio & Flory 2017). Pairing ground data on population distributions and densities with modelling and experiments to assess changes in ranges of invasive plants will be invaluable. For example, the FATE-HD model (Functional Attributes in Terrestrial Ecosystems) of vegetation change combines knowledge of plant-plant interactions, dispersal, and climate filtering to predict future changes in vegetation or plant functional groups (Boulangeat et al. 2014). In the French Alps, simulations from FATE-HD showed drought intensity and frequency had greater impacts on grassland-forest ecotone shifts than scenarios of land use change (Barros et al. 2017) and promoted significant expansion of invasive woody plants (Carboni et al. 2018). In some cases, impacts of invasive plants decline over time (Dostál et al. 2013; D'Antonio & Flory 2017), though given that there are many exotic plants in tussock grasslands that are clearly in the range expansion phase, we expect impacts of invasive plants at higher elevations will be an ongoing challenge.

Research question 3: Will future fires tip tussock grasslands into alternative vegetation states?

Current understanding

Charcoal dating has suggested there were five distinct periods where fire return intervals changed across the country: (1) c. 11 000 years before present (BP): fires every c. 200 years, (2) c. 3000 years BP: every c. 50 years, (3) c. 1000 years BP: every c. 14 years, (4) c. 700 years BP (Māori arrival): every c. 10 years, and (5) c. 200 years BP (European settlement): every c. 14 years (Ogden et al. 1998). This shows that there was some long-term variability in fire frequency in NZ, but does not allow us to assess fire frequency at local scales where it could select for fire adaptations in particular populations of species (Bond et al. 2004). It is therefore generally thought that most of the native flora is poorly adapted to fire (Ogden et al. 1998; McGlone et al. 2014; Perry et al. 2014), but little work has been done to empirically test this hypothesis among and within species.

While NZ plants with adaptations to fire may have needed to survive for long periods without it (Ogden et al. 1998), many native plants in tussock grasslands are able to survive and resprout after fire, such as narrow-leaved snow tussock (*Chionochloa rigida*), matagouri (*Discaria toumatou*; Rhamnaceae), harakeke/flax (*Phormium cookianum*; Asphodelaceae), and several mountain daisies (*Celmisia* spp., Asteraceae; Mark 1965; Daly 1967; Calder & Wardle 1969; Allen & Partridge 1988). While some native plants may survive and resprout following fires, competition with invasive species and adverse climatic conditions have also caused their decline in burned areas (Payton & Pearce 2009). Further evidence is accumulating that traits have evolved in response to fire in many native plant species, such as geographic and habitat variation in serotiny in *Leptospermum scoparium* (Myrtaceae; Bond et al. 2004; but see Battersby et al. 2017), while plants with traits that confer high flammability can be found in species from both fire-prone and relatively fire-free environments in NZ (Cui et al. 2020). These studies suggest further research and debate on the role of fire in the evolution of native flora is warranted in order to predict ecological responses to future fires.

One of the most comprehensive studies on fire behaviour and fire impacts on the ecology of tussock grasslands were the experimental burns conducted in the early 2000s at two sites in Otago: Deep Stream on the Lammerlaw Ranges and Mt Benger on the Old Man Range (Barratt et al. 2009, 2019; Payton & Pearce 2009; Pearce et al. 2009). While summer burning caused the highest mortality of *Chionochloa rigida* (Payton & Pearce 2009), populations of litter-dwelling amphipods (Crustacea: Amphipoda), the invertebrate taxon most severely affected by fire, took longer to recover after spring-burning because of the unusual intensity of the spring fire and resulting removal of the litter layer (Barratt et al. 2019). This demonstrates the value in regularly monitoring burned sites for over a decade after fire and studying a wide range of taxa. The Deep Stream experimental site recently re-burned in a wildfire in spring 2019. Other recent major burns in tussock grasslands, specifically the 2020 Pūkakī and Lake Ōhau fires, occurred in early spring when historically conditions were considered too wet to be at risk of fire. Recent (and current) unusual fire activity anecdotally suggests we are now observing effects of long-term dry conditions, as projected by modelling (Pearce et al. 2011; Lawrence et al. 2022).

Whether increased wildfire frequency and severity will lead to sustained changes in plant community structure in NZ, as seen in the past (Perry et al. 2012) and in grasslands outside of NZ (e.g. D'Antonio & Vitousek 1992), is unknown. This is a pertinent area of research if we wish to predict tussock grassland cover and ecosystem functioning under scenarios of global change. Exotic plants with low stature may have low flammability, so are less likely to burn (Padullés Cubino et al. 2018), which may facilitate faster recovery to outcompete native plants. Alternatively, small-seeded, easily dispersed plants may rapidly colonise burned areas. Mortality of *Chionochloa* tillers is higher if grazed in the immediate years after fire (Gitay et al. 1992), so while spelling (i.e. removing domesticated grazing) of domestic stock has been advocated for in the past, recovery of tussocks may also benefit from an increase in feral mammal management in the years following fires. While there is evidence from overseas that grazing can reduce fire frequency and intensity in grasslands (Foster et al. 2020; Rouet-Leduc et al. 2021), this effect likely varies depending on the type of grassland (Leonard et al. 2010). For example, in Tasmanian grasslands grazing of herbivore-maintained lawns reduced fuel loads, but grazing in low-palatability tussock grasslands led to higher proportions of dead fuel (Leonard et al. 2010). Tussock grasslands in NZ may exhibit similar relationships between grazing and fuel loads, but there are no data explicitly testing this.

Research needs
Although many natural grasslands in NZ below treeline have expanded in extent through the effects of fire after human settlement (Perry et al. 2012), interactions of fire with climate change, grazing pressure from feral animals, and range expansion of exotic invasive weeds, especially woody ones, suggest recovery of grasslands after fire is perhaps not predictable. Targeted work on fire behaviour with pre- and post-fire (or "space-for-time"/ chronosequence) sampling of plant community structure, tussock cover, and soil properties is required. We need more quantitative information on which native plants can recover from fire, how they do so (e.g. seeding or resprouting), and the role of grazing by domesticated and non-domesticated mammals in recovery. Recent government-funded research on understanding fire behaviour in rural landscapes is providing much-needed knowledge and awareness of spatial patterns of fire (https://www.ruralfireresearch.co.nz/), though the ecological component is limited. Some trait-flammability links are theoretically predicted but still need to be empirically tested. For example, a laboratory study combined with field data suggests high abundance of low-stature forbs reduces community-level flammability (Padullés Cubino et al. 2018), so assessing whether these forbs actually reduce fire intensity and spread at a site scale could facilitate predictions of fire behaviour. Research on wildfires and vegetation that spans multiple scales, from individual plants to landscapes, will lead to predictions of where wildfires are likely to occur, their fire intensity and severity, how they will spread, and what this means for ecosystem recovery.

Research question 4: What are the implications of woody thickening by native or non-native species?

Current understanding
Woody thickening, an increase in native or exotic woody plant density, is increasing in some areas of tussock grasslands due to plant invasions, changing fire regimes, and land management decisions, including retirement from grazing, and active tree planting (Young et al. 2016; Ropars et al. 2018). Pressures from deliberate exotic afforestation potentially leads to additional sources of wilding/invasive trees, losses of local biodiversity, changes to soil microbial communities, and altered fuel loading and fuel structure. Succession to vegetation dominated by native woody species may occur naturally in areas that were likely dominated by forests below treeline where seed sources and conditions allow (e.g. Rose et al. 2004; Mark & Dickinson 2003). For example, experimental studies suggest varying success of woody germination due to variations in soil biota and microclimatic conditions (Williams et al. 2011; Rodrigues et al. 2017), suggesting woody thickening in future drier climates needs to be considered. In our opinion, emphasis on afforestation efforts in grasslands of NZ neglects evidence that some areas in lowlands may not have supported closed forest in the past (Molloy et al. 1963; McGlone 2001; Walker et al. 2004) and therefore needs to be carefully considered in each case.

If woody thickening occurs, then native woody species may be preferable to exotic species; however, the functional and successional implications of these changes are yet to be fully assessed. Using soils collected from tussock grasslands in Canterbury, one study showed lodgepole pine (*Pinus contorta*) altered biogeochemical cycling to favour establishment of exotic graminoids and hawkweeds, even after the trees were removed (Dickie et al. 2014). Further, soils under the pine trees reduced ectomycorrhizal colonisation of the native early successional woody species kānuka (*Kunzea ericoides*; Myrtaceae), which could reduce plant nutrient acquisition. In some situations, exotic woody species, such as nitrogen-fixing broom (*Cytisus scoparius*; Fabaceae), can act as a nurse species to provide an environment that promotes germination and growth of other species (Burrows et al. 2015; Allen et al. 2020). However, successional trajectories under gorse differed compared to those facilitated by kānuka or mānuka (Sullivan et al. 2007). These studies, albeit all at low elevations, highlight long-term implications of woody thickening depending on the initial colonising species.

Woody thickening or succession towards native forests would lead to greater carbon sequestration aboveground (Holdaway et al. 2014). Soils in tussock grasslands hold 1.4 times more microbial carbon than soils in native Nothofagaceae forests (Ross et al. 1997a) and may even be able to sequester more carbon under conditions associated with climate change (Krna 2015). Moreover, native trees may mitigate predicted increases in fire activity because many native NZ tree species are low in flammability (Wyse et al. 2016) and species in late-successional native forests are less likely to burn than early successional forests (Perry et al. 2014).

Research needs

Aerial and/or satellite imagery are powerful tools for assessing broad changes in tussock cover or woody thickening, at least of larger shrubs, over decades (Weeks et al. 2013; Hua & Ohlemüller 2018). Some species are able to be differentiated using satellite imagery, such as matagouri, a widely distributed yet understudied native nitrogen-fixer (Day 2020). Combining satellite imagery with mesocosm or field experiments that focus on ecological functions, such as the ones cited, will further knowledge of the implications of woody thickening in grasslands by different species across spatial scales. Studies assessing impacts of planting different woody species in grasslands on successional processes and ecosystem functions in different grassland types would greatly enhance our ability to plan land management in the future. In particular, experiments with different woody species in projected drought conditions would be highly informative.

Research question 5: What are the impacts of global change, and vegetation change in particular, on soil processes and ecosystem functioning?

Here we outline what is known about ecosystem functioning in tussock grasslands and discuss implications in relation to the global change factors overviewed in the previous sections. A large proportion of research in NZ's tussock grasslands has focussed on biodiversity, without explicit links with, or understanding of, ecosystem functioning or associated ecosystem services; unfortunately this information is also limited for grasslands globally (Bardgett et al. 2021). While soils have long been valued in tussock grasslands from an agricultural perspective, we need greater understanding of soil ecology and biogeochemistry in tussock grassland types and gradients. Research that has been done confirms international evidence (Bardgett et al. 2021) that nutrient cycling and water yields are greater in unmodified grasslands, where tussock cover is high, compared to modified grasslands or pine forests (Mark & Dickinson 2008; Dymond et al. 2012; Wakelin et al. 2013). Conservation of soil and soil processes should therefore be integral in all management decisions for tussock grasslands, including management of weeds and pests and woody thickening.

Carbon Storage

Carbon storage is high in tussock grasslands, particularly in soils (Ross et al. 1997a). Aboveground, carbon has been shown to accumulate faster on north-facing slopes compared to south-facing slopes after retirement from grazing over two decades, which was partly attributed to woody thickening (Holdaway

et al. 2014). Schipper et al. (2017) tentatively suggest fertiliser and irrigation may increase soil carbon in tussock grasslands, but note a general lack of data on soil carbon in these systems. Moreover, legacies of past management and vegetation can play a large role determining carbon storage in tussock grasslands both above- (Holdaway et al. 2014) and below-ground (Li et al. 2019a), making broad predictions on carbon sequestration and storage potential challenging (Schipper et al. 2017). Carbon in soil is also more protected during disturbances that can reduce aboveground carbon, such as fire, so may represent more stable long-term sequestration compared to carbon in aboveground vegetation. Transitions from grassland to exotic plantation forestry may enhance aboveground carbon in the short-term but reduce soil carbon (Li et al. 2019b), a pattern supported in a recent global meta-analysis in tropical savannas that showed most soil organic carbon is derived from grasses with overall small increases in soil carbon with increased tree cover (Zhou et al. 2023). Where feasible, restoration of native woody vegetation would increase aboveground carbon while maintaining or enhancing biodiversity values. This highlights trade-offs when considering multiple ecosystem functions and the need for rigorous studies measuring multiple attributes of ecosystem functioning to be able to make clear predictions.

Soil biota and functioning

Predicting global change impacts on soil biota and associated functioning is challenging because patterns are often context-dependent and interact with other factors. This is true in tussock grasslands, which occur across a wide range of elevations, aspects, and associated gradients in soil and climate conditions. In one of the only *in situ* experimental studies in tussock grasslands, artificial warming caused shifts in functional potential of soil bacterial communities towards more energetically-conservative traits that could reduce carbon sequestration (Adair et al. 2019). This effect was thought to be caused by lower soil moisture in the warmed soils. In the same experiment, invertebrate herbivore biomass increased under warming, but plant and parasitoid biomass did not, suggesting increasing temperatures associated with climatic change could lead to relative increases in herbivory rates (de Sassi & Tylianakis 2012). These results tell us that community responses to global change factors differ by trophic level, and belowground responses may not be obvious, or even predictable, from aboveground patterns.

Increasing anthropogenic modification in NZ grasslands leads to declines in overall soil microbial functioning and increased abundances of plant pathogens (Sarathchandra et al. 2005; Wakelin et al. 2013). Globally, fires tend to negatively impact mutualistic mycorrhizas, reducing their richness and colonisation of plants (Dove & Hart 2017). However, a lab-based study subjecting soils from tussock grasslands to temperatures simulating fires had no measurable effects on arbuscular mycorrhizal fungal community structure (Morman 2021). On the other hand, increased soil pH after fire (Ross et al. 1997b; Certini 2005) indirectly impacts soil biota by altering nutrient availability and is a major driver of soil microbial communities in tussock grasslands (Wu et al. 2017; Wakelin et al. 2021) and globally (Tedersoo et al. 2014). The strong pH gradients with elevation in tussock grasslands, which are probably linked to management practices, likely somewhat explain turnover in soil bacterial communities along an elevation gradient (Day & Buckley 2013; Wu et al. 2017; Wakelin et al. 2021). Using attributes like pH, that are easy to measure and do not change in the short term at

a site scale, are therefore highly informative and likely link well with understanding soil functional capacity in tussock grasslands (unless there are point sources of urine or fertiliser, for example). More work in this area would be beneficial.

Plant-soil interactions

Plant community structure and dominant plants impact soil microbial communities and subsequent ecosystem functioning, such as aboveground net productivity and nitrogen cycling (Grigulis et al. 2013; Flombaum et al. 2017). We therefore expect that large, sustained shifts in plant community composition or functional groups, such as those observed during plant invasions, will significantly impact soil communities and nutrient cycling (Grigulis et al. 2013; Morman 2021). High tussock cover may facilitate ecosystem resilience through global change. For example, we hypothesise that canopies provided by large or dense tussocks prevent soil carbon losses by providing cool microclimates that reduce microbial respiration observed in high temperatures (Graham et al. 2014). Bryophytes are often neglected but may play a key role in reducing carbon losses by mitigating temperature fluctuations in soils, retaining water and enhancing ecosystem recovery. Bryophytes are particularly important in dry areas by being among the first plants to colonise after disturbances in tussock grasslands (Michel et al. 2013). These feedbacks between plants and soil impact functionality, such as moisture retention and nutrient cycling, and therefore provide opportunities for valuable research.

Relating species traits to ecosystem functioning

Trait-based ecology can be used to quantify change in ecosystem functioning across types of grasslands and spatiotemporal scales (Lavorel & Garnier 2002; Boeddinghaus et al. 2019; Hanisch et al. 2020), but these data are highly limited for NZ grassland species. Measuring microbial traits and linking these to function is relatively novel but provides an opportunity to make broad predictions on the impacts of global change (Piton et al. 2020; Zanne et al. 2020; Leizeaga et al. 2021). Recent gains in knowledge in root traits highlight how incorporating belowground plant attributes is essential to linking plant and microbial functions (Carmona et al. 2021). In Europe, plant and microbial traits can be strongly linked to grassland functioning and resilience to global change factors (Grigulis et al. 2013; Pommier et al. 2018; Piton et al. 2020). Limited knowledge of fundamental natural history and trait information for many grassland species in NZ makes the assessment of functional implications of vegetation change challenging. We therefore believe research on plant traits in grasslands across a range of environments should be a priority, including root and reproductive traits and assessments of intraspecific trait variation. Collecting information about microbial communities and functions would further enhance our understanding of these interactions.

Tussock cover as a potential indicator of biodiversity and ecosystem functioning

Tussock cover is relatively easy to measure either on the ground or using remote sensing technology. Relating tussock cover to other components of biodiversity and ecosystem functions could enhance understanding of impacts of vegetation change at spatial scales larger than plots or transects (Hua & Ohlemüller 2018; West 2019). For instance, there may be non-linear relationships between tussock cover and native plant diversity where high cover provides microclimates for native plants but too much cover may reduce diversity due to competition for soil resources (Adair et al. 2019) or shading effects (Rodrigues et al. 2017). Native plant diversity may affect other trophic groups by altering resources for native herbivores, pollinators, and seed dispersers, such as invertebrates, birds, and skinks (Patterson 1992; de Sassi & Tylianakis 2012; Young et al. 2012; Wotton et al. 2016), but such effects are difficult to predict with current data. If we can use tussock cover to accurately reflect ecosystem processes, such data could be combined with knowledge of drivers of past changes in tussock cover or densities to predict where ecosystem changes will occur in future.

Conclusions and recommendations

Effective management of tussock grasslands can be improved by better understanding the nature and quality of ecosystem functions in tussock grasslands, and how they vary along environmental gradients and spatiotemporal scales in different types of grassland. In areas where woody thickening by native species is a realistic aim for the future, this will likely not be achieved by removing grazing alone because invasive vertebrate pests are widespread, soils have been highly modified (or depleted), seed sources have been lost, and there are few suitable microsites for seeds to germinate and seedlings to establish (Rodrigues et al. 2017). Ecosystem functions cannot be maximised across all ecosystem components, so we believe research on trade-offs, values, and across scales in time and space is crucial.

All tussock grasslands in NZ are at some stage of change since human arrival and anthropogenic disturbance, with biodiversity values of some indigenous grasslands in decline (Cieraad et al. 2015). Current ecosystem dynamics can be considered legacy effects that will determine how land cover and biodiversity will be impacted by future global change; short-term or small-scale studies are not able to detect these long-term impacts. Addressing the above research questions requires new approaches, particularly greater support to establish and maintain large-scale, long-term ecosystem experiments along key environmental gradients encompassed by tussock grasslands. This may require searching archives and researcher records for documentation needed to facilitate relocation and remeasurement and the willingness of the original researchers or parent organisations to support this process. Efforts and support should therefore be provided to facilitate open data and data sharing, including archiving metadata to facilitate remeasurements (Table 1).

We can also apply new approaches to existing datasets (Table 1) to develop or apply modelling, which is the only way to project longer-term responses and explore a range of scenarios, such as combining climate scenarios with management responses. Our knowledge will be maximised by determining measures that are broadly useful across all research questions outlined and for multiple users. For example, tussock cover, density, or biomass indicate both aboveground carbon storage (Holdaway et al. 2014) and soil microbial community structure and functioning (Sarathchandra et al. 2005; Wakelin et al. 2013). We believe the research gaps and opportunities highlighted above would benefit by focussing on:

(1) valuing and enhancing knowledge of natural history, including open and accessible trait data,

(2) increasing use of remote sensing that includes past data

Table 1. Framework for potential approaches to address the identified research questions and contributing sources of data and knowledge. Integrating knowledge across all research questions in a way that focuses on ecosystem functioning will best enable the prediction of impacts of global change on tussock grasslands.

Research question	Potential sources of existing data or knowledge	Possible frameworks
What are the relative impacts of domesticated and non-domesticated mammals on indigenous biodiversity?	• National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz/) • Farmers • Hunters • Regional Councils • Grey literature • Published literature • Local and national databases, such as DOC's monitoring and reporting system, tier one plots, wild animal spatial distribution maps • Wallaby database (https://www.mpi.govt.nz/biosecurity/exotic-pests-and-diseases-in-new-zealand/long-term-biosecurity-management-programmes/controlling-pest-wallabies-in-nz/)	• Increased long-term investment in monitoring, maintaining, and potentially establishing new grazing exclosures to also exclude lagomorphs and macropods • Multi-decadal funding to mammalian herbivore removal studies • Pairing herbivory addition/exclusion studies with knowledge of animal population densities and animal behaviour, such as using GPS collars • Combining exclosure plots with other experimental and situational treatments, such as burning (Payton & Pearce 2009), irrigation (Rodrigues et al. 2017), or woody thickening
Where will invasive plants undergo range expansion?	• National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz/) • Satellite imagery (https://data.linz.govt.nz/layer/106279-nz-10m-satellite-imagery-2020-2021/) • TRY Plant Trait Database (https://www.try-db.org/TryWeb/Home.php) • Wilding Conifer Information System (https://wildpines.linz.govt.nz) • Published floras • Mana whenua • Photopoints • Grey literature • Published literature • Local and national government weed databases Weed identification guides (e.g. https://www.doc.govt.nz/nature/pests-and-threats/weeds/identifying-weeds/)	• Pairing long-term ground data with remote sensing modelling and experiments to assess changes in invasive plant ranges • Collect data to parametrise models to quantitatively predict impacts of global change factors, such as drought, on invasive plant populations and plant communities, e.g. FATE-HD • Integrate data on trait distributions of invasive plants with environmental gradients to assess invasion potential • Use remote sensing that includes past data sources such as aerial photos to assess and predict plant invasion rates in different environments • Investigate which invasive plants and what type of data can be gained via photopoints
Will future fires tip tussock grasslands into alternative vegetation states?	• Climate Change forecasting models (e.g. NIWA: https://niwa.co.nz/our-science/climate/information-and-resources/clivar/scenarios) • Fire risk forecasting (e.g. Scion, NIWA) • Fire and Emergency New Zealand reports on past fires (https://www.fireandemergency.nz/research-and-reports/) • Regional Councils • National Vegetation Surveys database • Farmers • Mana whenua • Grey literature • Published literature	• Pre- and post-fire sampling of plant and invertebrate community structure, tussock cover, and soil properties • Quantitative studies on which native plants can recover from fire, how they do so (e.g. seeding or resprouting), and the role of grazing by domesticated and non-domesticated mammals in recovery • Integration of ecological data into fire behaviour studies • Empirical tests of results from lab-based studies on flammability traits to field studies to better predict flammable landscapes • Integration of photopoints, remote sensing, and aerial photos to assess aspects of recovery of plant communities from fire • Compilation of fire occurrence datasets

Table 1. Continued.

Research question	Potential sources of existing data or knowledge	Possible frameworks
What are the functional implications of woody thickening?	• Photopoints • Remote sensing datasets • Satellite imagery • Wilding Conifer Information System (https://wildpines.linz.govt.nz) • Weed identification guides (e.g. https://www.doc.govt.nz/nature/pests-and-threats/weeds/identifying-weeds/) • Grey literature • Mana whenua • Published literature • Historical photos	• Quantitative studies assessing functional and successional implications of woody thickening by native vs exotic species, or by functionally different species (e.g. N-fixing) • Combining aerial or satellite imagery of woody thickening, by different species if possible, with mesocosm or field experiments that focus on ecological functions and climate scenarios
What are the impacts of global change, and vegetation change in particular, on soil processes and ecosystem functioning?	• National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz/) • Soil maps (S-map: https://smap.landcareresearch.co.nz/) • Regional councils soil and vegetation survey results • Mana whenua • Grey literature • Published literature	• Soil ecology and biogeochemistry in tussock grassland types and across gradients • Quantification of soil carbon in different grassland types and environmental gradients • Natural history of soil biota and plants, including morphological and functional traits above and belowground • Understanding of drought impacts on water relations and species interactions

sources such as aerial photos,

(3) continued investment in long-term monitoring that include measures of functional aspects of grasslands, particularly soil processes, and feral and domesticated animal population densities at meaningful scales,

(4) developing methods to gain quantitative information on ecosystem states and monitoring by developing standard protocols for easy-to-use tools such as repeated photopoints (Michel et al. 2010) or using Unmanned Aerial Vehicles to assess long-term broad changes in vegetation.

All research questions identified in this article to predict and prepare for ongoing global change in tussock grasslands require greater investment in research and people. In general, tussock grassland ecological research lacks a cross-disciplinary and collaborative, co-design approach with iwi, farmers, conservationists, and hunters. It is encouraging that there are some regional programmes to integrate conservation efforts and mana whenua in some areas, such as Te Manahuna Aoraki (https://www.temanahunaaoraki.org). However, in our experience, research and management of tussock grasslands has been siloed in the past and economically driven, and there appears to be little regular communication or engagement among researchers, stakeholders, and iwi. One way to address disparate regional approaches could be to re-establish a research capability equivalent to the former Tussock Grasslands and Mountain Lands Institute focussed on research for better scientific and social understanding to translate into sustainable management of our grassland ecosystems. Perhaps a comprehensive gap analysis could be undertaken to contextualise some of the research needs among interested parties. Goals for grassland management will likely differ depending on who is involved, which is why integration across different interest groups will bring the greatest value.

Acknowledgements

Additional information and declarations

Data and code availability: There is no data or code associated with this paper.

Ethics: N/A

Conflicts of interest: The authors declare no conflicts of interest.

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