Natural history features of the high-country and drylands of the South Island, New Zealand

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Abstract
The high-country and dryland zone of the South Island of New Zealand includes the Southern Alps and eastern mountains and basins. Formed by post-Pliocene tectonic, glacial and alluvial processes, these areas contain a range of landforms across extreme climatic gradients. Diverse habitats support plants and animals which have a distinctive and long natural history. New Zealand's short (*c.* 700 years) history of human land use has been highly disruptive for indigenous biodiversity. We have misunderstood the eco-evolutionary vulnerabilities of the native biota, the extent of environmental limits, and the impacts of introduced weeds and pests. Recent large-scale capture of water and addition of nutrients for agriculture are excluding indigenous biodiversity in many ecosystems. Predicted climate change and competition for water resources will exacerbate agricultural impacts, but the remaining indigenous biodiversity can be resilient if representative areas are protected.

Keywords: indigenous biodiversity, land use, conservation

Introduction
The upland and dryland environments of the central and eastern South Island, encompassing some of New Zealand's most iconic landscapes, are currently undergoing profound changes. In this opinion piece I focus on the natural values of the high-country and some of the distinctive habitats and special adaptations of the plants and animals they support. Our forest- and alpine-focussed perspectives in New Zealand frequently overlook the importance of non-forest habitats below regional treelines. These open habitats have created much of the diversity and novelty of the New Zealand biota, especially over the last 5 million years when climate regularly restricted forest growth. I will briefly describe the history and major features of the high-country before assessing the impacts of human land-use activities and identifying the challenges we face to sustain our natural biological heritage in these areas. Although I come from a dairy farming background in the Waikato, my experience of the high-country is as a conservation ecologist researching the past and present patterns of indigenous biodiversity, managing threats, and developing approaches to biodiversity assessment. I cover some of the main research findings that have shaped my view of the high-country.

The diversity of the land
Landform diversity: Over the past 5 million years tectonic processes have led to impressive uplift along the Main Divide and eastern foothills, producing for the first time persistent alpine environments. Discrete block-faulted mountains have extended these environments to the east. During the past 2 million years, Pleistocene glacial and interglacial activities on a massive scale have carved U-shaped valleys and basins with over-steepened slopes, now flanked with rock falls, moraines, terraces and extensive outwash fans dissected by channelised and braided rivers. Much of the hill-country is draped with loess, fine silt produced from glaciers and rivers that has blown across the landscape. Complex faulting, tectonic patterns and the regional-scale dominance of different lithologies (schist, greywacke and limestone) have created extraordinary physiographic diversity in the high-country.

Environmental diversity: Rain shadow areas east of the Southern Alps induce strong climate gradients, forming some of the most extreme environments in New Zealand, with hot summers, cold winters and declining rainfall at lower elevations and increasing distance from the Main Divide. Nearly half the Land Environments of New Zealand are represented in the high-country. In addition, semi-deserts associated with mosaics of glacial and alluvial derived landforms in the drylands are an exclusive and striking feature of the inland basins in the South Island.

Biodiversity: The tall, evergreen forests characteristic of much of New Zealand were also once an important part of the high-country and drylands, but their evolutionary significance in the high-country has been surpassed by the proliferation and diversification of biota in other biomes, particularly the scrublands and grasslands, non-forested habitats below and above the regional treeline where disturbance, climate or soils have severely limited the growth of trees. Lowland and montane open habitats have been a major engine room for speciation in the New Zealand flora,

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especially amongst shrubs (e.g. *Coprosma*, *Olearia*, *Dracophyllum*, *Carmichaelia*), forbs (e.g. *Aciphylla*, *Leptinella*, *Gentiana*) and grasses (e.g. *Rytidosperma*, *Poa*), providing the lineages from which much of our alpine flora is also derived. These large-scale adaptive radiations involving the proliferation of species into new niches reflect the importance of non-forest habitats for the evolution of the New Zealand biota. Along the Southern Alps intense glacial activity removed all vegetation at times, but in the east, landscapes supported grassland and scrubland habitats, where endemic species arose and remain due to geographical isolation or the presence of peculiar habitats and environments that limit forest encroachment.

During interglacial periods native biodiversity was augmented by immigrants from southern and northern parts of the South Island, as well as local endemics. Similar patterns are found in lizards, moths and invertebrate detritivores, highlighting the importance of open habitats for many different groups of organisms. In general, the most endemic and ancient terrestrial biodiversity is in streams and rivers, where stoneflies, dragonflies and crayfish have lived since the Cretaceous. They also support a diversity of fresh water fish, including galaxiids and drought-hibernating mudfish, species whose DNA is revealing the story of population linkages lost and gained with changing river courses responding to the uplift of mountains and hills.

Of the many special aspects of high-country biodiversity, I want to highlight four features that have emerged in recent decades that emphasise the importance of these areas. Lizards, with probably over 100 endemic species, are a key group of organisms persisting in the high-country and drylands. Geckos favour forests and scrublands, while skinks occupy diverse open habitats, including screes, grassland and scrubland, extending into the alpine zone. Stunningly coloured lizards remain in many grasslands and shrublands across the high-country, and we know little of their distribution and habits.

The second feature is the presence of representatives of our meagre spring-annual flora in these environments, often associated with highly disturbed and nutrient-rich microsites. These tiny plants (e.g. *Myosurus minimus*, *Ceratocephala pungens*), with boom/bust population fluctuations and foliar nutrient levels similar to ryegrass, persist in depleted and degraded landscapes because of their special life history and ecology.

Third, we have fascinating dryland specialists, again often very small cryptic plants (e.g. *Convolvulus verecundus*, *Raoulia monroi*) with exaggerated floral displays that occupy the driest environments found in New Zealand. They access moisture at depth but tend to die back in summer when conditions really dry out. Most commonly they occupy glacial outwash on free-draining silty soils, and today are sparsely distributed across the few remaining suitable habitats.

The fourth feature of interest is the diversity and ecological and evolutionary importance of shrublands in the high-country. Colloquially termed "grey scrub", they contain a range of plant and animal lineages that have diversified in New Zealand to occupy non-forest habitats that currently often represent the last vestiges of woody vegetation in the landscape. This includes notable tree genera that have evolved open habitat representatives (e.g. *Sophora prostrata*, *Aristotelia fruticosa*). Grey scrub represents notable convergent evolution, with the dense, twiggy (divaricate) growth form and wiry shoots co-existing with a range of shade-adapted forbs and grasses. Many lizards, moths and beetles – important elements of New Zealand's biota – are dependent on the presence of these shrub species.

The diverse high-country biota also reflects an extraordinary array of different habitats, such as river scroll plains, saline patches, inland dunes, limestone sink holes and bluffs, frost flats, moraines, boulder fields, and river terraces, each of which has an unusual suite of plants and ecologies. Over the past decade I have investigated the workings of ephemeral wetlands, naturally rare ecosystems associated with hummocky moraine topography created by deposits from retreating glaciers at the end of the Pleistocene. Largely rain-fed, the depressions are typically swamps in winter and deserts in summer. Plants occupying these habitats represent around 20% of the total flora and are extraordinarily small, usually less than 5 cm tall. They have swollen, air-filled roots that enable them to cope with being underwater, and die back aboveground in the summer when water is scarce. These sites have moderate soil nitrogen levels, and consequently are favoured by native and introduced birds that graze the turfs when accessible, producing novel "avian lawns". Their diverse composition depends on size, substrate texture and precipitation, and the local vegetation type is generally controlled by ponding regimes over the previous 4-5 years. They are threatened by wilding conifers, and weed and nutrient spill-over from adjoining agricultural areas.

Origin of the current grasslands

Globally, natural grasslands in benign climates are the product of abiotic factors preventing tree growth in some way, usually assisted by grazing mammals. Wind, water, salt spray, frost, nutrient limitation and lightning fires can all prevent tree dominance and facilitate grasslands. In New Zealand, these have been the major causes of the establishment of primary grasslands below the regional tree limit. The extensive tussock grassland landscapes that greeted European settlers in the 19th century were largely created by Polynesian burning of beech and conifer-hardwood forests. From modelling ranges based on the current distributions of trees, it is likely that tall forest could potentially cope with the full range of environmental conditions occurring in inland basins today. However, evidence from analysis of moa coprolites (fossil dung) and pollen spectra in bogs indicates that on the valley floors and outwash plains these forests may have given way to scrubland mosaics of diverse *Olearia* and *Coprosma* species on more fertile soils, and bog pine and *Dracophyllum* on less fertile areas where tall forest was restricted because of drought or nutrient limitation. Mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea* spp.), widespread today where forest is absent, may have occupied intermediate sites.

Amongst a wooded landscape, primary grasslands would also have occupied regularly disturbed habitats, areas near the coast, on flood plains and active fans, as well as shallow soils on terrace scarps and bluffs, waterlogged soils, frost flats and habitats created by natural fires. These may have been extensive in some areas, but were definitely present throughout most catchments and provide the source biota for early successional communities on newly available slopes following forest clearance by fire in the 13th and 14th centuries. The short-tussocks (*Festuca*, *Rytidosperma*, *Poa*) appear to have advanced into these new niches rapidly, reflecting their relative recent colonisation (*c.* 10 million years) of New Zealand and pre-adaptation to disturbance.

Tall-tussocks (*Chionochloa*), which have been here much longer (*c.* 30 million years), also expanded into deforested areas: *Chionochloa rigida* in the southern South Island, *C. flavescens* in the northern South Island, and *C. rubra* and *C. macra* throughout. These species were all growing east of the Main Divide and were therefore best positioned to expand their distribution when the opportunity arose. The dominance of the tussock or bunch-grass form amongst indigenous grasses may reflect a long history on low-nutrient soils, competition with taller shrubs, and/or the absence of mammalian grazers. However, the persistence, longevity and productivity of the tussock growth form in New Zealand is remarkably similar to that of a forest.

The lack of strong fire adaptations amongst native woody species saw them disappear from much of the eastern South Island. Where fire was infrequent, secondary grasslands would have been succeeded by shrublands and eventually forest, depending on seed source proximity. However, in most places regular burning constrained forest re-establishment. The composition of these secondary fire-induced grasslands may have resembled similar communities during past glaciations, but this is unlikely given the strong filtering effect of regular fire. They more likely represent novel communities dominated by the tussock grasses best able to regrow after fire. Many forbs are found in both primary and secondary grasslands, and it is unclear whether traits or geography has been most important in their presence in the new communities after fire. Amongst *Rytidosperma* we have recent evidence that chromosomal doubling, or polyploidy, has facilitated diversification into more drought-prone environments.

The role of past herbivores in creating indigenous grasslands is becoming clearer with the application of molecular techniques to determine diets. The results indicate that moa were not akin to grazing mammals. DNA analyses of moa droppings from a range of habitats indicate a very generalist diet of forbs and shrubs, with little evidence of tussock grass in moa diets. The lack of big foragers is also evident in the morphology of native grasses, where leaf shedding that exposes functional, nutritious leaves is over-expressed in New Zealand compared to elsewhere, suggesting vertebrate foliar herbivory was not a strong selective factor in their evolution.

Outside of grasses, the dense, tangled, wiry (divaricate) shrubs widespread in the high-country, the extreme camouflage of some plants, occasional leaf and stem spines and the diverse tiny herbs are all potential legacies of the moa and do confer modest levels of resistance to certain types of mammalian herbivory. However, overall, the avian-dominated evolutionary history of New Zealand has poorly prepared the native biota for the browsing and grazing deer, cattle, sheep, goats and rabbits that arrived in abundance following European settlement.

Agricultural history

Polynesian settlers utilised rivers, wetlands and fernlands across inland environments for seasonal food, but it was their fires that transformed the landscape, removing forest and shrublands and creating extensive secondary indigenous grasslands. These grasslands presented a tantalising resource for early European settlors with home-country pastoral experience and aspirations. In their view, the high-country appeared destined to support cattle and sheep, but in only a few decades stock numbers clearly exceeded available forage. The declining state of the grasslands was exacerbated by frequent fire used to promote nutritious regrowth of tussocks and suppression of scrubland. The outcome in the montane basins was extensive desertification, erosion and weed invasion. Oversowing and topdressing were required to improve pasture quality, especially soil phosphorus levels to sustain the establishment and growth of pasture legumes. In recent decades the shifting of water, addition of nutrients and advent of forage crops have driven a further wave of direct land-use intensification, with generally increased stocking rates in the high-country.

Agricultural attempts at land management in this zone are far from exemplary. They have been punctuated by major ecological over-reach, particularly over-hunting, over-burning and over-grazing, creating a near-desert landscape in the early 20th century that was invaded by hawkweed, briar, rabbits and wilding conifers. These actions have all endangered indigenous biodiversity, which has become further reduced in recent decades as flat land is developed, water captured from distant natural areas, and high levels of imported nutrients applied.

Conservation approaches

The long co-existence of extensive pastoral farming and the persistence of indigenous biodiversity have led to the application of numerous models or frameworks to sustain environmental and social outcomes for the high-country. During my career there has been "catchment planning", "multiple use", "integrated catchment management", "sustainable management", "adaptive management", "balanced approaches" and more, but all have failed to deliver anything like the level of protection required to enable native biodiversity to persist across the landscape. The security and opportunities associated with tenure review have seen an expansion of public conservation land at higher elevation and the freeholding of montane areas, generally for more intensive agricultural development and occasionally subdivision and settlement. The net results for conservation have been equivocal, with alpine gains and major montane losses, but there is no doubt that the topographic limits of land-use intensification are expanding, to the detriment of indigenous biodiversity.

Currently, a European concept is being considered in New Zealand as an option for the sustainable co-existence of agriculture and native biodiversity: land-sharing and land-sparing. Successful land-sharing is severely inhibited in New Zealand by the evolutionary vulnerabilities of the majority of native plants and animals. Mammalian grazing, cropping, irrigation and nutrient addition expose the low growth rates, low fecundity and poor competitive ability of the native biota and drive ecosystems towards dominance by introduced species. As agriculture develops down these pathways, land-sparing appears to offer better options for indigenous biodiversity, with steep slopes, gully and riverine systems providing excellent opportunities at the farm scale to maximise multiple ecosystem services; and at the catchment scale the possibility of gaining representative and effective natural networks.

At larger scales there is a need to protect representative areas across a range of landforms if we are to sustain the special biodiversity of the region. Environmental limits are being recognised as a framework for land-use decisions, but in my view, even if they can be determined and agreed upon, they only capture half the story. We need in the 21st century to be recognising biodiversity limits, with land-use decisions accommodating the persistence of indigenous-dominated ecosystems and native species in the landscape.

For indigenous biodiversity the high-country is entering a critical phase that will test planning and regulatory frameworks around private property rights in New Zealand. Throughout most of the 20th century native biodiversity persisted in this region, where extensive grazing, oversowing and topdressing were the dominant modes of farming. However, the recent increase in stocking rates facilitated by higher-yielding crops and irrigated pasture has dramatically changed the risk profile for native habitats, leaving little space for viable indigenous habitats and communities.

Indigenous biodiversity resilience

The human transformation of extensive areas from forest to scrubland and tussock grassland in much of the high-country began a process of habitat change associated with biomass removal that continues to the present. For around the first 500 years these changes all involved native species, plants and animals, favouring those pre-adapted for reproduction, dispersal, colonisation and growth under regular fire regimes. With European settlement the degree of degradation and the context for recovery of the vegetation changed radically. The biota expanded to include grazing mammals, a myriad of new weeds were introduced, and ecosystem degradation occurred with some areas supporting little vegetation and having apparently few options for recovery. When established in 1987, the Tekapo Scientific Reserve represented arguably the most degraded landscape in New Zealand. Bare soil and extensive hawkweed dominated, with sparse native shrubs, grasses and herbs having less than 1% cover in microsites on the old moraines, outwash surfaces and terraces. However, fenced and free of rabbits for 25 years, the vegetation of the reserve now shows remarkable signs of recovery towards indigenous dominance, especially on the more productive soils.

The high-country frequently represents the last opportunity to protect representative examples of native communities, especially shrublands, grasslands and wetlands, where much of the endemic biota remains. These also coincide with places where indigenous biodiversity can provide the most assistance, filtering sediments and nutrients, sequestering carbon, and moderating water flows to deliver regular clean water for freshwater biodiversity and downstream activities. Many biological scars of previous actions will remain (e.g. loss of moa and forest), but the restoration envelope for recovering the dominance of indigenous plants and animals in appropriate habitats is still possible. This will happen at different rates in different environments, but will require the cessation of degrading factors: usually fire and mammalian grazing; wilding conifers for plants; predatory mammals for birds, lizards and invertebrates.

Conclusion

The high-country and drylands of New Zealand include iconic landscapes with a globally distinctive and complementary natural biota and history. The indigenous flora and fauna contain elements that have adapted over millions of years to new opportunities as diverse scrublands and grasslands intermittently prevailed over large areas. Resilient components remain following human settlement but are further threatened by intensive agriculture that monopolises resources and landforms. A representative network of protected areas of indigenous biodiversity would enable the reassembly of native plants and animals in these changing environments, and facilitate the provision of valued and enduring ecosystem services for future generations.

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