Long-term impacts of grazing on indigenous forest remnants on North Island hill country, New Zealand

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Abstract: Small isolated patches of native forest surrounded by extensive pastoral grasslands, characteristic of many New Zealand rural landscapes, represent an important reservoir of lowland biodiversity. Improved management of them is a major focus of biodiversity conservation initiatives in New Zealand. We quantified the long-term impacts of grazing on indigenous forest remnants in hill country at Whatawhata, western Waikato, North Island. Structure and composition were compared between forest fragments grazed for >50 years and nearby ungrazed continuous forest. Grazed fragments had shorter and less shady canopies, sparser understoreys, tree populations with larger mean diameters, and ground layers with lower cover of litter and higher cover of vegetation and bare soil than continuous forest. Fragments also had lower indigenous-plant species richness, especially in sapling and seedling populations, and almost no palatable indigenous shrubs, terrestrial orchids, and ferns that require high humidity (e.g. *Hymenophyllum* spp.), but contained many indigenous and adventive herbaceous species. A transition appears to be occurring in grazed fragments from tall, long-lived trees like *Beilschmiedia tawa* and *Dysoxylum spectabile* to short and shorter-lived trees like *Kunzea ericoides*, *Melicytus ramiflorus*, *and Dicksonia squarrosa*. Because grazing inhibits most regeneration processes, unfenced remnants of conifer–broadleaved forest are unlikely to be maintained in grazed pasture in the long term.

Introduction

The New Zealand Biodiversity Strategy (Department of Conservation & Ministry for the Environment 2000) has among its goals the enhancement of individual and community understanding of biodiversity, and halting the decline of indigenous biodiversity by maintaining and restoring a full range of natural habitats and of indigenous species across their natural ranges. Since large-scale clearance for pastoral agriculture of the extensive low-altitude steeplands ('hill country') of New Zealand some 80–120 years ago, remnants of the previously continuous tall forest cover have been a persistent and distinctive feature of the landscape. Although valued by farmers for stock shelter, their ecological integrity has been widely compromised by fragmentation, livestock grazing, feral browsing and elevated fertility (e.g. Stevenson 2004), and their long-term survival is uncertain. In many widely cleared districts (e.g. Waiapu; Leathwick et al. 1995), such forest fragments are the only reservoirs of indigenous vascular plant diversity left over large areas and represent one of the only prospects for its survival. They are also 'stepping stones' for the movement of biota across grossly modified landscapes (Gilpin 1980).

Despite the fact that most remnants of the original forest cover surviving in lowland pastoral landscapes in New Zealand are grazed by domestic stock, there have been few quantitative studies of grazing impacts. In alluvial forest in south Westland, cattle grazing favoured regeneration of some species such as *Pseudowintera colorata* (horopito), eliminated others such as *Schefflera digitata* (patē), and appeared to have no impact on many others (Timmins 2002) (Nomenclature follows http://nzflora.landcareresearch.co.nz/). Only qualitative descriptions of degradation sequences, e.g. Moore & Cranwell (1934), Esler (1978), exist. Degradation can be defined as the reduction or change to a lower-quality state of a characteristic or function, and forest remnants can be degraded in a variety of ways. The diversity of the plant community can be reduced and the regenerative ability (viability) of plant populations can be compromised. Forest structure can be altered. There may also be lower diversity and quality of habitat (e.g. less food available, fewer and poorer nesting sites) for different types of fauna (e.g. beetles: Harris & Burns 2000). The ability of forest fragments to provide ecosystem services such as water purification, erosion control, and carbon sequestration can be compromised. Lastly, the ecosystem may be

less resistant to invasive introduced organisms through, for example, changes in understorey density at edges (Cadenasso & Pickett 2001).

A forest fragment study was initiated in 2000 in a catchment at the Whatawhata Research Centre in the western Waikato hill country. The initial aim of our study was to assess quantitatively the condition of forest fragments exposed to the effects of pastoral land use, and later to explore the long-term recovery of indigenous biodiversity given a range of restoration approaches. The study aims to provide a focus for policy and industry initiatives to improve biodiversity management in productive landscapes. We examined a typical set of forest fragments and compared them with nearby ungrazed continuous forest. Our objectives were to (1) quantify the effects of pastoral land use (incorporating the suite of effects noted previously) on the structure and composition of indigenous forest remnants within it; and (2) verify the utility of standard forest descriptors that may be used to monitor relative degradation and recovery.

Methods

Study area

The study area occupies steeply dissected hill country at altitudes of 50–370 m a.s.l. in the catchments of the Whakakai and Mangaotama streams, tributaries of the Waipa River (Fig. 1). Soils are a complex mosaic of Allophanic Soils (yellow-brown loams) derived from very old tephras on gentle to moderately steep slopes, and Brown Soils (yellow-brown earths and their steepland variants) derived from a variety of sedimentary basement rocks on moderately steep to steep slopes (Bruce 1978). Podzols (podzolised yellow-brown earths) derived from carbonaceous shales and grits occur in places (I.L. Baumgart & A.C.S. Wright, unpubl. data). Climate is warm-temperate and humid, with a mean annual rainfall of 1600 mm, a winter maximum and a summer minimum. Mean annual temperature is 13ºC with a January (midsummer) mean of 18ºC and a July (midwinter) mean of 8ºC. Screen frosts (air temperatures below 0ºC) occur
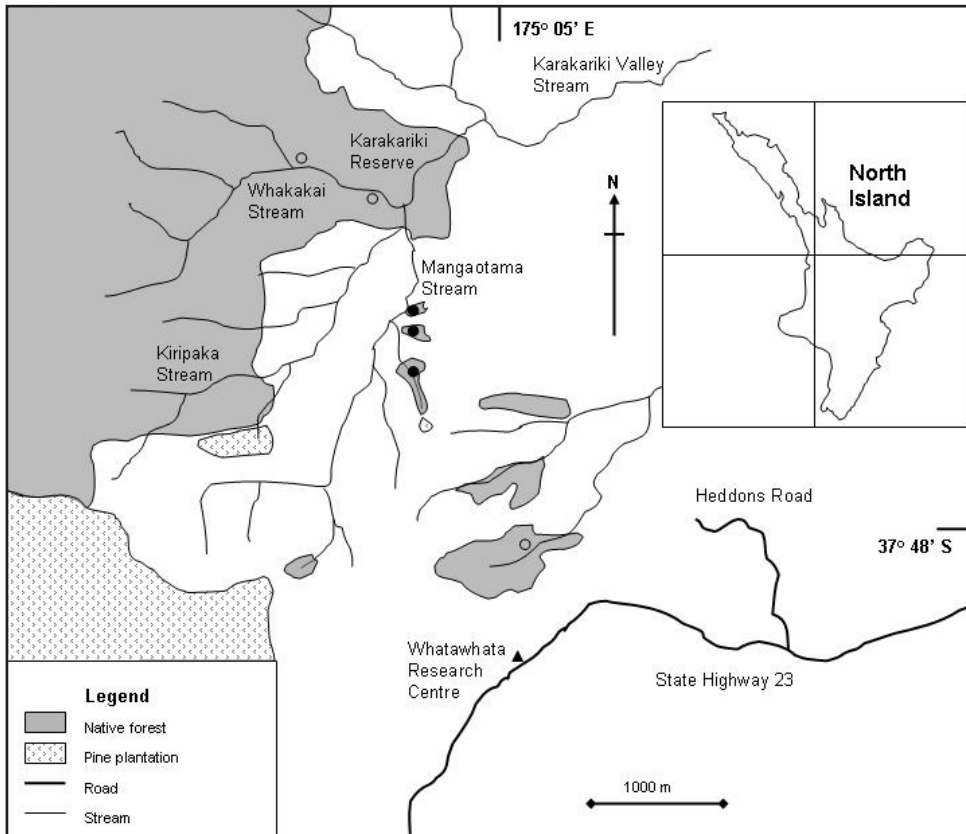

Figure 1. Location of study sites at Whatawhata, western Waikato, New Zealand. ○ ungrazed forest; ● grazed forest fragments.

on an average of 12 days per annum (New Zealand Meteorological Service 1973).

Before European settlement, the predominant primary forest cover of the area consisted of scattered *Dacrydium cupressinum* (rimu), *Prumnopitys ferruginea* (miro), and occasional *Metrosideros robusta* (northern rātā) emergent over dense broadleaved tiers dominated by *Beilschmiedia tawa* (tawa) and *Dysoxylum spectabile* (kohekohe), with scattered *Knightia excelsa* (rewarewa), *Litsea calicaris* (mangeao), and *Cyathea medullaris* (mamaku). *Laurelia novae-zealandiae* (pukatea) was common in gullies; *Dacrycarpus dacrydioides* (kahikatea) was common on riparian sites, *Prumnopitys taxifolia* (matāī) less so. *Melicytus ramiflorus* (māhoe), *Cyathea dealbata* (silver fern/ponga), and *Rhopalostylis sapida* (nīkau) were common in the subcanopy, with scattered *Hedycarya arborea* (pigeonwood/porokaiwhiri), *Olearia rani* (heketara), *Myrsine australis* (māpau), and *Quintinia serrata* (tawheowheo) (National Forest Survey, unpubl. data). Understoreys were probably dominated by *Schefflera digitata*, *Macropiper excelsum* (kawakawa), *Coprosma grandiflora* (kanono), and *Alseuosmia quercifolia*.

The exact date of forest clearance on the property is unclear, but was certainly well before the Second World War (Farrelly 1986). The general history of the district suggests that most was probably undertaken in c. 1900–1920. Forest class maps of the region (Nicholls 1979) suggest that all surviving forest on the property and in the vicinity is likely to have been selectively logged earlier last century, involving the removal of almost all larger conifers. When the property was purchased for research purposes in 1949, former pasture had largely reverted to *Leptospermum scoparium* (mānuka) scrub and *Pteridium esculentum* (bracken) fernland in early stages of secondary succession back to tall forest. Despite intensive redevelopment for agriculture from 1950 onward (Farrelly 1986), aerial photos taken from the 1940s onward show that linear fragments of the primary indigenous forest cover have persisted in many first-order catchment gullies and on some south-facing hill slopes, and these are the focus of our research.

Introduced brushtail possums (*Trichosurus vulpecula*) were liberated in the western Waikato in 1925 and 1929 (Pracy 1962), so have probably been present throughout the Whatawhata property for over 50 years. Feral goats (*Capra hircus*) have been present in the district since at least 1975 (Parkes 2005), probably earlier, but are only present in neighbouring ungrazed forest. Feral pigs (*Sus scrofa*) have probably been present for at least 150 years (McIlroy 2005) and are likely to be more common in neighbouring ungrazed forest.

Study design

Two forest categories were monitored for a range of structural attributes, with three unblocked replicate sites selected for each forest category (Fig. 1).

Grazed forest fragments: The three fragments were 2.6 ha, 1.2 ha, and 0.7 ha in area. In recent years, grazing has been characterised by a stocking rate of c. 10 stock units per hectare, mainly sheep (*Ovis aries*) but with occasional cattle (*Bos taurus*) grazing. Phosphatic fertilisers, at a typical rate of 20–30 kg ha^{-1}, have been applied annually by topdressing to the research farm, and observations suggest that fertiliser application is seldom interrupted during flight over narrow forest fragments.

Ungrazed continuous forest: The three ungrazed sites consisted of a 27-ha tract of forest to the north of the research centre and two sites within the Karakariki Scenic Reserve, part of an extensive tract of forest (>5000 ha) on the northern boundary of the research farm. Although the reserve was logged in the 1940s (Department of Lands and Survey 1984), there was no evidence of such disturbance within the sampled areas.

Data collection

Between three and five transects were established at each site at intervals of approximately 100 m, placed so as to cover the full range of topography at each site. Ten plots (5 × 10 m) were placed at approximately 50-m intervals distributed along the transects at each site. Therefore, a total of 30 plots were placed in grazed forest and 30 in continuous forest. On each transect, additional plots were placed outside the forest fragment in the surrounding grassland, for future assessment of regeneration following stock exclusion.

In each plot, percentage species cover in predetermined height tiers (Ground: 0–0.3 m; Understorey: 0.3–2 m; Subcanopy: 2–5 m; Canopy: 5–12 m; Emergent: >12 m; Allen 1992) was visually estimated. All trees with diameter at breast height (dbh) > 3 cm were permanently tagged and diameters measured. Tree ferns were measured for dbh but not tagged. Saplings (>30 cm tall, <3 cm dbh) were tallied by species. Seedlings of woody species (<30 cm tall) were tallied by species in three subplots (1 × 1 m) spaced at 0–1 m, 4–5 m, and 9–10 m along the uphill plot boundary. All other vascular species present were recorded. Percentage ground cover was recorded in the following categories: litter, vascular vegetation, bare soil, rock, and bryophytes. All visible superficial roots > 5 cm in diameter crossing uphill and downhill boundaries and a central parallel line were tallied. Fallen tree ferns, trunks, and branches crossing these lines were measured for diameter.

Total canopy shade was estimated by measuring diffuse, non-intercepted light (DifN) on each plot and at a reference site outside the forest, using an LAI 2000 Plant Canopy Analyser (Welles 1990). Canopy shade was calculated as $(1 - (DifN[plot]/DifN[ref])) \times 100$ and expressed as a percentage, where 100% equals full canopy shading and 0% equals no canopy shading.

A species–area curve was derived for the indigenous flora of each forest type by merging the species lists for consecutive plots in a cumulative fashion, to create species lists for areas of 50 m^2, 100 m^2, 200 m^2, 400 m^2, 800 m^2, and 1600 m^2.

Data analysis

Compositional and structural parameters of vegetation (vascular indigenous species richness, mean percentage cover in each tier and total canopy cover, basal area, ground layer composition, superficial root densities, incidence of coarse woody debris) were compared by unpaired t-tests between grazed forest fragments and ungrazed continuous forest sites.

Results

Vascular plant species richness

Grazed forest fragments had fewer indigenous plant species than ungrazed continuous forest when compared over all plots combined (Table 1). In particular, there were fewer tree and shrub, epiphytic fern, and orchid species. However, grazed fragments had considerably more indigenous herbaceous species and more adventive species than the reference forest. No adventive species were recorded in plots there. Also, at a different scale, grazed fragments had significantly lower indigenous species richness within sites than continuous forest sites ($t = -2.98$, d.f. = 4, $P = 0.041$). The species–area curve for indigenous species in grazed fragments tracks at a lower level than for continuous forest (Fig. 2), again indicating lower indigenous floristic richness in grazed fragments.

Forest structure

Grazed forest fragments had less cover in almost all tiers than continuous forest, significantly so in the understorey (0.3–2 m) and emergent (>12 m) tiers (Fig. 3). As well,

total canopy shade was less (at 92.2%) in grazed fragments than in ungrazed forest (98.8%; $t = 4.6$, d.f. = 4, $P = 0.01$). Therefore, grazed fragments effectively have a shorter canopy and much sparser and lighter understoreys than continuous forest. Grazed fragments tended towards lower mean basal area (49 m^2 ha^{-1}) than continuous forest (65 m^2 ha^{-1}) and lower mean tree dbh (grazed: 16.0 cm cf. continuous: 19.9 cm) though neither was significantly different. Mean tree density was similar (grazed: 2013 stems ha^{-1} cf. continuous: 2060 stems ha^{-1}).

Canopy and understorey composition

Forest canopy cover was dominated by *Beilschmiedia tawa*; subcanopy cover by *Melicytus ramiflorus* and *Hedycarya arborea* (Table 2). *Dysoxylum spectabile* was locally important in canopies. *Dicksonia squarrosa* (wheki) and *Cyathea dealbata* dominated the understorey cover of grazed fragments, while *Cyathea dealbata* and *C. smithii* (soft tree fern/kaponga) dominated continuous forest understoreys. Other important canopy cover species in grazed fragments were *Dacrycarpus dacrydioides* and *Knightia excelsa*, and *K. excelsa* in continuous forest. Terrestrial *Asplenium bulbiferum* (hen and chickens fern) was a notable component of ground layers in continuous forest only. The terrestrial and epiphytic fern *Blechnum filiforme* was common only in grazed fragments.

In terms of stem densities, *Knightia excelsa*, *Hedycarya arborea*, *Beilschmiedia tawa*, and *Cyathea smithii* were much less common in grazed fragments than in continuous forest, and *Kunzea ericoides* (kānuka) and *Dicksonia squarrosa* much more common (Table 3).

Saplings were almost absent from grazed fragments (Table 3). A variety of canopy (*Knightia excelsa*), subcanopy (*Melicytus ramiflorus*, *Rhopalostylis sapida*, *Hedycarya arborea*, *Olearia rani*), and understorey (hangehange (*Geniostoma rupestre*), *Cyathea dealbata*, *C. smithii*, *Coprosma grandiflora*, and *Dicksonia squarrosa*) tree and shrub saplings were widespread in continuous forest. Only three tree species occurred

Table 1. Indigenous and adventive vascular plant species richness by life form in 1500 m^2 (30 plots, 10 × 5 m) in grazed forest fragments and ungrazed continuous forest at Whatawhata, western Waikato, New Zealand.

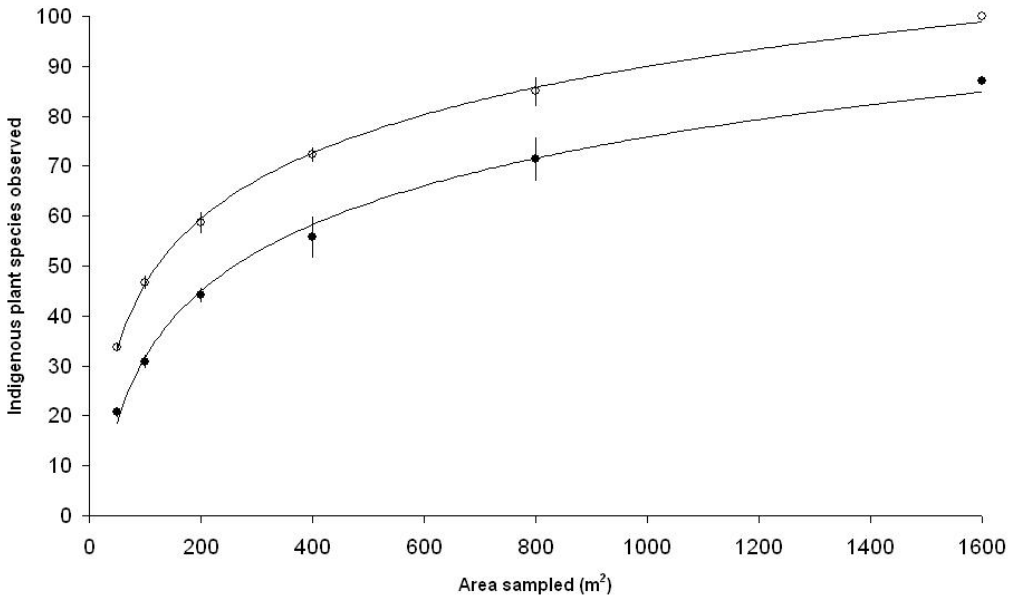| Life form	Grazed forest fragments		Ungrazed continuous forest	
	Indigenous	Adventive	Indigenous	Adventive
Trees and shrubs	28	3	35	0
Lianes	9	0	9	0
Ferns (epiphytic)	10	0	16	0
Ferns (terrestrial)	18	0	17	0
Herbs	20	22	9	0
Orchids	1	0	4	0
Total	86	25	90	0

Figure 2. Species-area relationships for indigenous forest sites at Whatawhata, New Zealand. ○ = ungrazed forest (fitted line $y = 18.9ln(x) − 40.8$, $r^2 = 0.99$); ● = grazed forest fragments (fitted line $y = 19.2ln(x) − 56.5$, $r^2 = 0.99$). Bars represent standard errors.
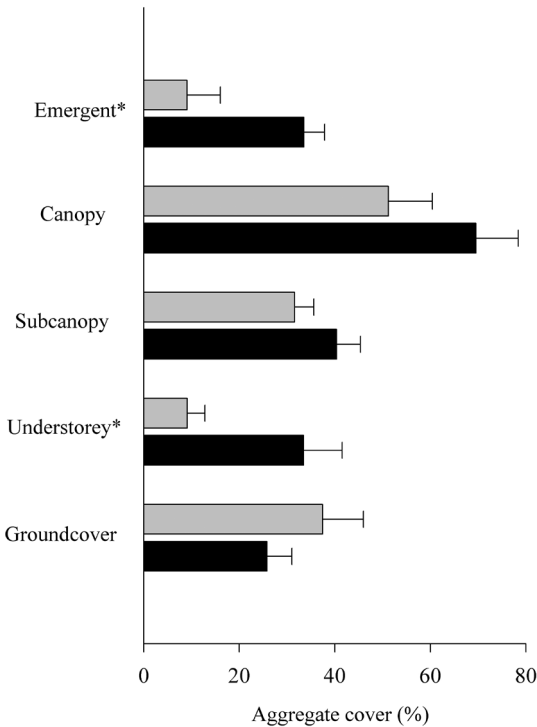

Figure 3. Aggregate cover (%) of each height tier in grazed forest fragments (grey bars) and ungrazed continuous forest (black bars) at Whatawhata, New Zealand. Bars represent standard errors. Means of each tier were compared using a t-test (d.f. = 4), with the emergent ($t = −2.98$, $P = 0.04$) and understorey ($t = −2.78$, $P = 0.05$) tiers significantly different.

Table 2. Mean cover scores aggregated over all tiers of major vascular indigenous species per block in grazed forest fragments and ungrazed continuous forest at Whatawhata, New Zealand (standard errors in parentheses). Means compared using t-tests. NS = non-significant ($P > 0.05$)

Species	Fragments ($n = 3$)	Continuous ($n = 3$)	t-test d.f. = 4	P
Asplenium bulbiferum	0.1 (0.1)	3.3 (0.6)	−5.21	0.006
Beilschmiedia tawa	14.9 (6.9)	58.3 (7.1)	−4.41	0.012
Blechnum filiforme	5.0 (0.6)	1.2 (0.6)	4.35	0.012
Cyathea dealbata	12.4 (4.2)	30.3 (2.8)	−3.57	0.023
Cyathea smithii	0.8 (0.4)	8.3 (0.9)	−7.49	0.002
Dacrycarpus dacrydioides	5.7 (5.1)	0.3 (0.2)	NS	
Dicksonia squarrosa	15.1 (4.1)	2.4 (0.7)	3.09	0.037
Dysoxylum spectabile	12.1 (9.2)	9.1 (8.8)	NS	
Geniostoma rupestre	0.1 (0.06)	1.4 (0.6)	NS	
Hedycarya arborea	2.5 (1.0)	8.1 (5.2)	NS	
Knightia excelsa	4.8 (3.7)	7.1 (2.9)	NS	
Kunzea ericoides	2.0 (2.0)	0 (0)	NS	
Melicytus ramiflorus	15.5 (1.5)	7.1 (2.2)	3.12	0.035

Table 3. Density (stems ha^{-1}) of trees and shrubs (>3 cm dbh), saplings (>30 cm tall, <3 cm dbh), and seedlings (<30 cm tall) in grazed forest fragments (F, $n = 3$) and ungrazed continuous forest (C, $n = 3$) at Whatawhata, New Zealand. Means (standard errors in parentheses except where frequencies are < 5) compared using t-tests (d.f. = 4) and results presented when $P < 0.05$.

Species	Trees				Saplings				Seedlings			
	F	C	t	P	F	C	t	P	F	C	t	P
Beilschmiedia tawa	80 (12)	307 (116)			0	27			111	111		
Dysoxylum spectabile	167 (120)	227 (197)			0	80 (53)			0	333		
Knightia excelsa	33 (18)	180 (42)	−3.24	0.03	0	260 (142)			556 (401)	2667 (1528)		
Melicytus ramiflorus	340 (92)	220 (31)			7	1280 (375)			12333 (3272)	5667 (2009)		
Hedycarya arborea	27 (13)	120 (61)			0	867 (325)			1556 (801)	10667 (2694)	−3.24	0.03
Cyathea dealbata	333 (97)	447 (85)			0	387 (127)	−3.04	0.04	0	0		
Dicksonia squarrosa	573 (101)	80 (23)	4.77	0.01	13	213			0	111		
Cyathea smithii	40 (23)	240 (35)	−4.80	0.01	0	193			0	0		
Kunzea ericoides	187	0			7	0			111	0		
Rhopalostylis sapida	7	33			0	1187 (485)			2667 (1262)	7556 (2312)		
Geniostoma rupestre	0	0			0	873 (233)	−3.74	0.02	0	2222	−2.86	0.05
Olearia rani	20	13			0	500 (336)			333	444		
Coprosma grandifolia	0	40			0	273 (160)			0	667		
Schefflera digitata	0	7			0	120 (64)			0	333		
Myrsine australis	0	13			0	20			2556	556		
Dacrycarpus dacrydioides	20	0			0	7			2333 (2000)	222 (111)		
Others	127 (24)	93 (24)			0	427 (119)	−3.60	0.02	2222 (1556)	5222 (1176)		

as saplings in grazed remnants with never more than one species per plot. In continuous forest, 30 species occurred as saplings at a mean of 7.1 species per plot. Mean sapling densities were two orders of magnitude lower (27 ha^{-1}) in grazed fragments than in continuous forest (c. 6700 ha^{-1}).

Seedlings of only six tree species (*Melicytus ramiflorus, Hedycarya arborea, Rhopalostylis sapida, Knightia excelsa, Myrsine australis, Dacrycarpus dacrydioides*) were common throughout. *Melicytus ramiflorus* seedlings tended to be more common in grazed fragments than in continuous forest and *Hedycarya arborea* and *Geniostoma rupestre* seedlings less common (Table 3). Total and mean species richness of seedling populations were both lower in grazed remnants (13 species in total; two species per plot) than in intact forest (27; 4; t = −2.78,

d.f. = 4, P = 0.05). Mean seedling densities in grazed fragments (c. 25 000 ha^{-1}) were not significantly different than in continuous forest (c. 37 000 ha^{-1}).

The mean diameters of *Dysoxylum spectabile*, *Knightia excelsa*, and *Melicytus ramiflorus* were larger in grazed fragments than in continuous forest (Table 4). Those of *Beilschmiedia tawa* and *Hedycarya arborea* were similar in both.

Ground layer and coarse woody debris

Ground layers of grazed fragments had lower cover of litter, and higher cover of vegetation and bare soil, than those of continuous forest (Table 5). Grazed fragments and continuous forest contained similar basal area of coarse woody debris and exposed roots (Table 5).

Table 4. Mean diameter of trees (>3 cm dbh) of major canopy and subcanopy species in grazed forest fragments and ungrazed continuous forest at Whatawhata, New Zealand. Means (standard errors in parentheses) compared using *t*-tests (d.f. = 4). NS = non-significant (*P* > 0.05).

Species	Fragments (*n* = 3)	Continuous (*n* = 3)	*t*	*P*
Beilschmiedia tawa	24.6 (1.2)	26.3 (2.3)	NS	
Dysoxylum spectabile	18.3 (2.2)	6.7 (1.5)	3.87	0.031
Hedycarya arborea	21.2 (2.5)	15.4 (2.3)	NS	
Knightia excelsa	37.5 (6.5)	15.3 (2.1)	3.27	0.031
Melicytus ramiflorus	16.2 (0.6)	11.7 (0.9)	4.28	0.008

Table 5. Ground cover (by percentage) in different categories, mean number of exposed roots, and coarse woody debris (m^2 ha^{-1}) in grazed forest fragments and ungrazed continuous forest at Whatawhata, New Zealand. Means compared using *t*-tests (d.f. = 4). NS = non-significant (*P* > 0.05).

Ground cover	Fragments (*n* = 3)	Continuous (*n* = 3)	*t*	*P*
Litter	43.6 (4.7)	70.3 (8.4)	−3.00	0.03
Vegetation	39.7 (4.3)	20.3 (4.6)	3.05	0.03
Bare soil	14.3 (1.9)	4.5 (1.5)	3.75	0.01
Rock	0.2 (0.1)	0.9 (0.6)	NS	
Bryophytes	2.2 (0.2)	4.0 (2.3)	NS	
Mean number of exposed roots/plot	12.1 (5.4)	13.9 (6.0)	NS	
Basal area (m^2 ha^{-1}) of coarse woody debris	6.9 (2.8)	11.1 (4.8)	NS	

Discussion

Reduced indigenous-plant species richness in grazed remnants is attributable to the *direct* effects of grazing, severely reducing or exterminating populations of highly palatable understorey shrubs such as *Alseuosmia quercifolia* and ground layer species such as *Asplenium bulbiferum* (Jane 1983), and to the *indirect* effects of reduced humidity within fragments severely reducing or eliminating species such as epiphytic filmy ferns (*Hymenophyllum* spp., *Trichomanes* spp.) that are dependent on forest interior microclimates of ameliorated temperature and humidity (Norton 2002). Young & Mitchell (1994) and Denyer et al. (2006) found that gross microclimatic edge effects penetrated for approximately 50 m into small forest remnants, regardless of their size. Despite some reduction, indigenous species richness in grazed forest remains high for a relatively long time, although populations of some species can become critically small (Esler 1978). Increased adventive species richness reflects the presence of herbaceous pasture species in ground layers, resulting from the elevated light levels beneath shorter, lighter canopies and from open edges and high edge-to-area ratios. It may also reflect elevated soil fertility (Stevenson 2004).

Largely through its influence on microclimate, topography exerts a major influence on the survival of forest remnants. Aspect also has a significant bearing on forest composition (e.g. Leathwick et al. 1988) and so the pervasive persistence of primary forest remnants only in gullies and on south-facing slopes means that, regardless of their integrity, they are unlikely to encompass the full spectrum of biodiversity once present in the landscape. These are also likely to be the dampest sites (soil moisture content under pasture is typically 5–10% higher on south-facing slopes; Bircham & Gillingham 1986), mitigating to some extent the lowered humidity typical of forest fragments.

The universal dominance of *Beilschmiedia tawa* and *Dysoxylum spectabile* shows that the canopies of remnants and continuous forests still retain strong affinities with those of the earlier pre-clearance forests. These species both have long life spans, in excess of 350 years (Smale et al. 1986; authors unpubl. data), so most existing canopy trees are likely to pre-date the general clearance a century or so ago. The larger average size of some important species, e.g. *Dysoxylum spectabile*, *Knightia excelsa*, and *Melicytus ramiflorus*, in grazed fragments than in continuous forest may indicate aging population structures resulting from impaired regeneration in remnants. But it may also indicate faster growth rates from the increased soil fertility under fragments (see below). *Dacrycarpus dacrydioides* is an exception; trees on fragment edges are typically only 50–60 years old (T. Newton unpubl. data), dating from the most recent clearance.

The shorter canopies of grazed remnants may reflect partial loss of the tallest (emergent) tier through increased exposure, and perhaps decreased wind-firmness from chronic damage to root systems by domestic stock, although there is no evidence of a higher incidence of stumps in remnants. With high edge-to-area ratios from their finger-like shape, grazed fragments are subject to far more exposure than intact forest tracts such as Karakariki Scenic Reserve.

Understoreys and ground layers accessible to stock have undergone the most change; the narrow shape (all < 100 m wide) of remnants at Whatawhata means that grazing impacts are dispersed throughout them. Like red deer (*Cervus elaphus*), sheep are selective grazers and have similar dietary preferences (Wardle 1984). Some highly unpalatable shrubs like *Pseudowintera colorata* that could replace lost palatable species, as has happened elsewhere (e.g. Smale & Kimberley 1993), are absent here.

Seedlings and saplings represent crucial stages in the regeneration niche of all major canopy and subcanopy species at Whatawhata. Despite substantial seedling populations of some existing canopy species, the virtual absence of saplings in grazed fragments indicates an almost complete regeneration gap. Only some understorey shrubs, such as *Schefflera digitata* and *Coprosma grandiflora*, also have epiphytic regeneration modes that allow them to bypass these stages, but reduced humidities in small remnants, particularly grazed ones, may diminish the viability of this regeneration mode as well.

Major shifts in the structure and composition of grazed forest remnants are inevitable, with species falling into three fragmentation response categories: *decreasers*, *increasers*, and *newcomers*. Both current canopy dominants at Whatawhata, *Beilschmiedia tawa* and *Dysoxylum spectabile*, are decreasers, *B. tawa* much reduced in the canopies of grazed remnants, and both species failing in their regeneration niche. *Knightia excelsa* and *Hedycarya arborea* are also decreasers, reduced in the canopies of grazed remnants and, despite reasonably plentiful seedlings, virtually absent in larger sizes. *Cyathea smithii* is also a decreaser. *Melicytus ramiflorus*, *Dacrycarpus dacrydioides*, and *Dicksonia squarrosa* are increasers, more common in grazed remnants; *M. ramiflorus* saplings do occur in grazed remnants but are rare. *Kunzea ericoides* and the adventive *Ligustrum lucidum* (shining privet) are newcomers, only recorded in grazed remnants.

These categories reflect varying exposure tolerances among species. *Beilschmiedia tawa*, a highly shade-tolerant species, is very sensitive to exposure, seedlings particularly so (Knowles & Beveridge 1982). *Dysoxylum spectabile* seedlings are also highly shade-tolerant (Court & Mitchell 1988). Despite its shade-tolerant seedlings and role as a subcanopy tree, *Melicytus ramiflorus* is an exposure-resistant species that outlives most others in grazed fragments (Esler 1978) and is more common here

in grazed remnants than in continuous forest. *Dicksonia squarrosa* is a common early-successional species on moist sites, *Kunzea ericoides* on drier ones (Wardle 1991); both have clearly benefited from the increased exposure on the edges of grazed stands.

Differing palatability to domestic stock and feral possums and altered soil fertility – and perhaps modified seed dispersal regimes – in remnants may also be involved. The palatability of native tree seedlings to sheep is unknown. Soils under grazed remnants at Whatawhata have greatly elevated plant-available phosphorus levels compared with those under continuous forest (Stevenson 2004).

In summary, major differences exist in composition and structure between grazed fragments and continuous reference forest. Despite the persistence of much of the original biodiversity of indigenous vascular plants, after c. 50 years of grazing, unprotected remnants are in advanced stages of degradation. Understoreys are virtually absent, there is almost no replacement of existing canopy species, and a transition appears to be underway – from the outside in – from canopies of tall, long-lived trees like *Beilschmiedia tawa* and *Dysoxylum spectabile* to short, ephemeral ones like *Kunzea ericoides* and *Dicksonia squarrosa*. While still typical of conifer–broadleaved forest in the middle North Island (authors' unpubl. data), lower basal area in grazed forest than in continuous forest suggests a progressive loss of basal area over time. Since basal area is a surrogate for biomass (Carron 1968), biomass is also likely to decline over time in grazed fragments. Although fragmentation and grazing are both involved in forest degradation, grazing appears the paramount influence here, compounding the effects of fragmentation.

In the absence of management, the outlook is bleak for grazed remnants at Whatawhata and across a wide swathe of the middle North Island where similar tree species are dominant. Long-term maintenance of unfenced remnants of conifer–broadleaved forest in grazed pasture is not a viable option. Fencing is the single most important measure that managers can take to improve the longer term viability of such fragments (Smale et al. 2005; Dodd & Power 2007); continued monitoring of recovery in fenced remnants at Whatawhata should reveal the time frame within which responses can be expected. However, the value of management measures additional to fencing remains to be demonstrated. Standard forest descriptors such as species richness, species cover in vertical tiers, basal area, and density are useful and appropriate indicators of degradation of forest remnants.

Acknowledgements

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