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Past and future trajectories of forest loss in New Zealand

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ABSTRACT

Historically, New Zealand was dominated by forest below the alpine treeline, but about 1000 years of Polynesian and European colonisation has resulted in the destruction of nearly three-quarters of the indigenous forest cover. In this study, the historical patterns of deforestation and forest fragmentation were assessed in relation to major topographical, climatic and anthropogenic variables that may drive forest loss. Deforestation has occurred almost equally on the two main islands, the North and South Islands, although the remaining indigenous forest is more fragmented in the North Island. Most deforestation has occurred in regions with a high-density of road networks, although gradients in climatic water availability and soil fertility also had weak effects. Deforestation rates over the period 1997–2002 were very low (nationwide deforestation rate of just −0.01% p.a.), but varied widely among political districts. Expansion of plantation forestry was the single most important driver of recent deforestation. Only 10 of 73 political districts are afforded long-term protection of native forest cover (having more than 30% forest cover that is managed by the Department of Conservation). Forest cover in the majority of New Zealand landscapes has been reduced below the level of an expected 'extinction threshold' (*circa* 30% native habitat cover) in 55 political districts, and long-term trajectories predict that ongoing deforestation threatens to force another five districts below the critical threshold within the next 45 years. Except for the most heavily deforested regions, relatively modest annual rates of habitat restoration could bring forest cover back above the extinction threshold by the year 2050.

1. Introduction

Three thousand years ago, forest covered virtually the entire land surface area of New Zealand below the alpine treeline (McGlone, 1989), but the arrival of the early Maori people about 1000 BP initiated widespread forest destruction. The Maori burned significant areas of lowland forest to encourage the growth of bracken fern (*Pteridium aquilinum*) that was used

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as a food source, to make cross-country travel easier and also as a strategy for hunting moa (Stevens et al., 1988). Maori were, however, not the sole cause of deforestation during this time, as climatic change, volcanism and naturally ignited fires have all been implicated as factors driving Holocene vegetation change in New Zealand (Fleet, 1986; McGlone, 1989). As a result of these combined factors, forest cover had been reduced to an estimated 68% of the land surface by the time European settlers arrived in the early 1800s (Salmon, 1975), and about half of the lowland forests had been destroyed (Stevens et al., 1988; McGlone, 1989).

The first European settlers in the early 19th Century initially cleared forest at a relatively slow rate (Arnold, 1994). However, with a growing population, improvements to roads and a new rail system, large-scale clearance of forest on the plains began in earnest in the 1870s (Arnold, 1994). Early New Zealand landholders were required by law to improve their land, and many achieved this via the simple act of burning the forest (Salmon, 1975). Primary forest clearance continued into the mid-20th century, and after the Second World War increasing amounts of forest in the mountain ranges were converted to farmland (Stevens et al., 1988) or fast-growing exotic plantations (Fleet, 1986). The net result of Maori and European exploitation of New Zealand's indigenous forest was the destruction of approximately three-quarters of the forest, reducing it from 82% to 23% of the land surface area (Fleet, 1986; Leathwick et al., 2003b, 2004).

1.1. Conservation implications of historical deforestation

In New Zealand, it is often assumed that clearing of primary native forests is no longer of significant concern and that the conservation issues associated with forest loss are no longer relevant to threatened species management (Craig et al., 2000; Clout, 2001). However, the historical effects of forest loss are frequently recognised as one of the greatest threats to endangered species (Tilman et al., 1994; Sala et al., 2000), and there is an emerging recognition of the role that historical landuse change has in structuring present-day species assemblages (Harding et al., 1998). Moreover, theoretical developments on the nature of extinction debts (Tilman et al., 1994), extinction thresholds (With and King, 1999), and synergistic interactions between forest loss and invasive species (Didham et al., 2005a,b; Ewers and Didham, 2006), advise caution in adopting the overly simplistic interpretation that historical deforestation is not relevant to present-day conservation.

First, extinction debts create a long-term decline in species richness for generations following the isolation of habitat remnants, and illustrate the long-term conservation implications of historical forest loss. The term extinction debt was coined by Tilman et al. (1994) and describes a time lag between the process of habitat loss and the eventual collapse of populations. Extinction debts are paid through time as communities in remnant habitats gradually relax to a new equilibrium number of species (Ewers and Didham, 2006). Community relaxation approximates an exponential decay with a half-life from 25 to 100 years for birds (Brooks et al., 1999), whereas for long-lived canopy trees the debt may still be current more than a century following deforestation (Turner et al., 1996; Vellend et al., 2006).

Second, much research has been focused on landscape and extinction thresholds in fragmented landscapes (Ewers and Didham, 2006). Landscape thresholds are the result of "rapid changes in the size and isolation of patches at critical proportions of habitat in the landscape" (Andrén, 1994), and are predicted to occur at approximately 30% remaining habitat cover (Andrén, 1994). Below this value, there is often an abrupt increase in the gap structure of landscapes, a marked discontinuity in dispersal between isolated sub-populations and a sharp decline in the probability of metapopulation persistence (Hanski, 1998; Hanski and Ovaskainen, 2002), at which point an extinction threshold has been passed. The extinction threshold compounds the risks posed by forest destruction, as even a small loss of habitat near the threshold may result in a precipitous decline in the probability of species persistence (With and King, 1999).

Third, many invasions do not propagate through undisturbed habitats and invasion risk increases disproportionately following anthropogenic habitat loss (May and Norton, 1996; Lonsdale, 1999; Hobbs, 2001). A growing body of evidence now shows that landscape context may be a critical determinant of local-scale predation intensity exerted by invasive species (Robinson et al., 1995; Hartley and Hunter, 1998; Ohlemüller et al., 2006). Furthermore, forest edges are focal points for invasions of remnant habitat (Wiser et al., 1998). In small fragments that consist completely of edge-affected habitat, invasive plant species like *Tradescantia fluminensis* (Commelinaceae) can influence the long-term viability of forest remnants by dramatically reducing the species richness, abundance and survival rates of native seedlings (Standish et al., 2001), as well as reducing invertebrate diversity and altering invertebrate community composition (Toft et al., 2001).

1.2. Goals of this study

There has been no extensive analysis of patterns of deforestation in New Zealand, nor an investigation into the natural and anthropogenic drivers of those patterns. The purpose of this study was to determine historical patterns of deforestation and describe current patterns of forest fragmentation. These variables were assessed in relation to major topographical and climatic features. Furthermore, because humans have been the dominant force behind the loss of native forests worldwide, correlations between human population density, recent changes in human population size and proximity to highways (a spatial indicator of human activity) were assessed as potential drivers of forest loss. Finally, the amount of extant indigenous forest that is currently included in the New Zealand protected areas network was quantified, and predictive equations were used to model the likely future of forest resources, with an emphasis on forecasting when landscapes will pass below an expected extinction threshold of 30% forest cover in the landscape. For regions that have already fallen below the threshold, restoration goals to restore those landscapes by the year 2050 are presented.

2. Methods

The New Zealand archipelago consists of several hundred islands spread across 2.2 million km^2 of the southern Pacific Ocean. For the purposes of this study, forest loss estimates were restricted to the two main islands, the North and South Islands, for which reliable data were available. The two islands combined represent 97% of the total land area of the archipelago and support over 99% of the total human population. The North and South Islands were divided into grid squares of 10×10 km for statistical analysis (Trzcinski et al., 1999) and a geographic database of historical and current forest cover, as well as climatic, geomorphological and anthropogenic variables was compiled for each grid square using Arc View 3.2 and Spatial Analyst software. A list of all variables and data sources used in this study is presented in Table 1, and full details of how variables were calculated are available in the Supplementary Information.

Table 1 – List of variables, codes, data transformations and data sources used in the analysis of New Zealand deforestation patterns

Variable	Code	Units	Transform	Data source or formula
Forest cover				
Pre-human forest cover	FOR_{hist}	%	asin(sqrt(x))	Leathwick et al. (2004)
1850 Forest cover	FOR_{1850}	%	log[asin(sqrt(x + 1))]	McGlone (1989)
1989 Forest cover	FOR_{1989}	%	log[asin(sqrt(x + 1))]	New Zealand TopoMap
1997 Forest cover	FOR_{1997}	%	log[asin(sqrt(x + 1))]	New Zealand Landcover Database ver.2
2002 Forest cover	FOR_{2002}	%	log[asin(sqrt(x + 1))]	New Zealand Landcover Database ver.2
Total forest change	FORCHA	%	log(x + 101)	$=((FOR_{2002} - FOR_{hist})/FOR_{hist}) \times 100$
Recent forest change	$FORCH_{97-02}$	%		$=((FOR_{2002} - FOR_{1997})/FOR_{1997}) \times 100$
1997 Exotic forest cover	EXO_{1997}	%	log[asin(sqrt(x + 1))]	New Zealand Landcover Database ver.2
2002 Exotic forest cover	EXO_{2002}	%	log[asin(sqrt(x + 1))]	New Zealand Landcover Database ver.2
Recent exotic forest change	$EXOCH_{97-01}$	%		$=((EXO_{2002} - EXO_{1997})/EXO_{1997}) \times 100$
Fragmentation metrics				
Length of forest edge	EDGE	km		New Zealand Landcover Database ver.2
Forest edge: area ratio	EDGEAREA	km km^{-2}	log(x + 1)	$=EDGE/FOR_{2002}$
Number of forest fragments	NUMFRAG	#	log(x + 1)	New Zealand Landcover Database ver.2
Fractal dimension	FRACTD	Dimensionless		New Zealand Landcover Database ver.2
Ordination axis 1	DCA_{frag}	Dimensionless		=DCA on above 4 metrics
Geomorphological variables				
Altitude	ALTIT	m	log(x + 1)	New Zealand 25 m Digital Elevation
Land evenness	EVEN	Std. Dev. in m	log(x + 1)	New Zealand 25 m Digital Elevation
Soil calcium	CALCIUM	Arbitrary		Leathwick et al. (2003b)
Soil phosphorus	PHOSPH	Arbitrary		Leathwick et al. (2003b)
Chemical limitations	CHEMLIMS	Arbitrary		Leathwick et al. (2003b)
Soil particle size	PSIZE	Arbitrary		Leathwick et al. (2003b)
Soil drainage	DRAIN	Arbitrary	sqrt(x + 0.5)	Leathwick et al. (2003b)
Ordination axis 1	DCA_{psize}	Dimensionless		=DCA on above 7 metrics
Ordination axis 2	DCA_{phos}	Dimensionless		=DCA on above 7 metrics
Ordination axis 3	DCA_{cal}	Dimensionless		=DCA on above 7 metrics
Climatic variables				
Mean annual temperature	TEMP	°C		New Zealand 25 m Temperature Model
Winter minimum temperature	MINTEMP	°C		Leathwick et al. (2003b)
Solar radiation	SOLRAD	MJ m^{-2} day^{-1}		Leathwick et al. (2003b)
Annual rainfall	RAIN	mm		New Zealand Forest Service
October vapour pressure deficit	VPD	kPa		Leathwick et al. (2003b)
Annual water deficit	DEFICIT	mm	log(x + 1)	Leathwick et al. (2003b)
Ordination axis 1	DCA_{moist}	Dimensionless		=DCA on above 6 metrics
Ordination axis 2	DCA_{temp}	Dimensionless		=DCA on above 6 metrics
Anthropogenic variables				
1996 Population density	$POPD_{1996}$	# km^{-2}	log(x + 1)	Statistics New Zealand Census 1996
2001 Population density	$POPD_{2001}$	# km^{-2}	log(x + 1)	Statistics New Zealand Census 2001
Recent population change	$POPCH_{96-01}$	%	log(x + 101)	Statistics New Zealand Census 1996, 2001
2001 Property value	RENT	\$ km^{-2} yr^{-1}		Statistics New Zealand Census 2001
2001 Personal income	INCOME	\$ person^{-1} yr^{-1}		Statistics New Zealand Census 2001
Road density	ROADDENS	km km^{-2}		New Zealand TopoMap
Distance to highway	ROADDIS	km	log(x + 1)	New Zealand Forest Service

For full details on the calculation of variables refer to the text.

2.1. Forest cover and forest fragmentation

Data on forest cover were obtained for five time periods; pre-human (about 1000 years before present), 1850, 1989, 1997 and 2002 (Supplementary Methods). Three metrics were calculated for each grid square to reflect patterns of forest fragmentation in 2002 (Table 1); the number of fragments, the edge:area ratio of indigenous forest, and the fractal dimension of the landscape. Data on indigenous scrub cover were also obtained for 1997 and 2002, as scrub represents an important stage in the process of forest regeneration and may be considered immature forest (Supplementary Methods).

2.2. Climatic and geomorphological variables

Data for six climatic and five geomorphological variables were obtained to represent abiotic features of the landscape that may influence patterns of forest cover (Supplementary Methods). These variables fell into four categories: (1) energy availability; (2) water availability; (3) landforms; and (4) suitability of the land for agriculture.

2.3. Anthropogenic drivers of deforestation

Total human population density (rural and urban population combined) was obtained from the Statistics New Zealand national census' in 1996 and 2001, as were data on land values and personal income levels (see Supplementary Methods). Road density and the distance from each quadrat to the nearest main highway were calculated.

Current and future deforestation are limited by the amount of forest under conservation protection, so maps of protected forest from the Department of Conservation National Conservation Units dataset (September 2003) were obtained. There were 86,436 km^2 of land in New Zealand represented in the National Conservation Units dataset, of which 84,620 km^2 (32% of total land area) is managed by the Department of Conservation (Supplementary Methods).

2.4. Statistical analysis

The analysis of forest change was conducted in four parts: (1) a regional analysis of current forest cover, (2) a grid square analysis of cumulative deforestation patterns (pre-human to 2002), (3) a grid square analysis of forest fragmentation, and (4) regional predictions of long-term trajectories in deforestation rates. Where necessary, variables were transformed to meet assumptions of normality (Table 1). Grid squares with less than 80 km^2 land area (i.e. grid squares intersecting lakes and coastlines) were excluded from the analysis (Laurance et al., 2002). To account for problems of spatial autocorrelation between grid squares, the linear, quadratic and cubic combinations of longitude and latitude of the centre of each 10×10 km grid square were included as co-variates in all analyses (Legendre, 1993; Davies et al., 2003).

2.4.1. Current status of forest cover

Summary tables of forest metrics were compiled for the 73 political districts of New Zealand. For each district, the amount of historical deforestation and the amount and degree of fragmentation of the current forest cover were assessed. The proportion of each district that was classified as plantation forest and indigenous scrub (analogous to regenerating forest) was also summarized. Annual deforestation rates were calculated over the period 1997–2002 using a compounding interest formula:

$$r = [(FOR_{2002}/FOR_{1997})^{1/t} - 1] \times 100$$

where r is the rate of change in forest cover (% yr^{-1}) and t is the time in years over which the rate of change is calculated ($t = 5$).

2.4.2. Predictors of forest loss

Forest loss was only calculated where forest was historically present, thus grid square analyses were restricted to grid squares with more than 80% of the total grid square area in forest before the arrival of humans. Preliminary correlation analyses showed that many of the climatic and landform variables were intercorrelated, so separate detrended correspondence analyses (DCA) were used to identify statistically independent gradients in the two groups of variables using CANOCO version 4.02 software (ter Braak, 1995). First, the six climatic variables were reduced to two axes explaining 98% of the variation in the climatic data set (Supplementary Table S1 a). The first axis reflected a moisture gradient (DCA_{moist}), and the second a temperature gradient (DCA_{temp}), as indicated by the high correlations between these variables and site ordering along axes 1 and 2 respectively (Supplementary Table S1 a). Second, the seven geomorphological variables were reduced to three axes that explained 94% of the landform variation (Supplementary Table S1 b). DCA Axis 1 was most strongly correlated with soil particle size (DCA_{psize}), Axis 2 with soil phosphorus levels (DCA_{phos}) and Axis 3 with soil calcium (DCA_{cal}). The identified gradients ($2 \times$ climatic and $3 \times$ geomorphological) were used in subsequent regression analyses.

Multiple regression in R software (R Development Core Team, 2004) was used to investigate the effect of these five axes plus the five anthropogenic variables on historical forest change (FORCHA). Multicollinearity amongst the predictor variables was assessed with correlation analysis. Because significance tests are sensitive to the number of replicates, and this analysis had a large sample size ($n = 1984$), parameter significance was tested with a randomisation test based on power analysis (Supplementary Methods).

ANOVA was employed to assess the drivers of recent forest loss ($FORCH_{97-02}$). Prior to analysis, grid squares with no forest cover in 1997 were excluded from the dataset. The data were divided into two sets: those grid squares in which deforestation occurred ($N = 129$) and those where there was no change in forest cover ($N = 1665$). ANOVA was used to test for differences in the values of 13 predictor variables between the two groups. As with the analysis of historical forest cover, parameter significance was tested with a randomisation test (Supplementary Methods).

2.4.3. Analysis of forest fragmentation

The three fragmentation metrics were strongly intercorrelated, so a DCA was used to identify statistically independent gradients in the metrics (ter Braak, 1995). Furthermore, fragmentation metrics are commonly tightly correlated with forest cover in the landscape (Trzcinski et al., 1999; Fahrig, 2003). Consequently, FOR_{2002} was factored in as a covariable in the DCA to obtain a measure of current fragmentation patterns that was independent of forest cover (Trzcinski et al., 1999). Prior to analysis, grid squares with no forest cover in 2002 were excluded from the dataset. The resulting partial DCA reduced the three fragmentation metrics to two axes that explained nearly all of the variation in the data (Supplementary Table S2). The first axis (DCA_{frag1}) was used as a surrogate index of forest fragmentation as this axis alone accounted for 99% of the variation in the fragmentation metrics. The signs of the DCA_{frag1} values were reversed to give a more intuitive index, with the gradient from negative to positive values reflecting a gradient from low to high fragmentation. A multiple regression approach (as described above for the analysis of historical forest cover, utilising the randomisation test detailed in the Supplementary Methods) was employed to determine the significant drivers of forest fragmentation.

2.4.4. *Long-term trajectories of forest change*

Long-term patterns of forest change in political districts were assessed by fitting an exponential curve through four points, FOR_{18750}, FOR_{1989}, FOR_{1997} and FOR_{2002}. An exponential curve was chosen on the *a priori* assumption that deforestation rates were greatest soon after colonisation and have decreased through time, and was invariably a good approximation to the empirical data. Because the likelihood of an extinction threshold occurring increases greatly when forest cover decreases below about 30% of a given landscape (Andrén, 1994), the exponential curves were used to estimate the year in which forest cover is predicted to decline below this threshold level within each district. Districts were classified into one of four categories according to the amount of forest in the landscape, the amount of that forest that is protected by the Department of Conservation, and the estimated year in which the 30% landscape threshold will be reached (Table 2). For districts that have already passed the 30% threshold (Critical category), the area of forest that would need to be restored annually for the landscape to become 30% forested by the year 2050 was calculated. Restoration targets were calculated in two ways: (1) excluding indigenous scrub and considering mature forest only, and (2) including indigenous scrub as regenerating forest.

Table 2 – Criteria for classifying landscapes according to future deforestation scenarios

Category	Forest cover	Department of conservation protected forest	Predicted date at threshold
Protected	–	>30%	–
Stable	>30%	<30%	>2050
Threatened	>30%	<30%	<2050
Critical	<30%	–	–

3. Results

3.1. *Historical forest loss*

Eighty-two percent of pre-human New Zealand was covered in indigenous forest (North Is. 96%, South Is. 72%; Leathwick et al., 2004), and this figure has dropped to 24%; a total reduction in area of some 14,000,000 ha, or 71% of the original forest (Fig. 1, Table 3). An approximately equal amount of land area has been deforested on the North and South Islands (about 7,000,000 ha), although the remaining forest in the North Island has been divided into many more fragments with an average area approximately five times smaller than that of the South Island (Table 3). Deforestation has occurred non-randomly within the two main islands, with the East Coast of the South Island and much of the low-lying North Island being almost completely denuded of forest (Fig. 1). Some of these areas have been replaced with exotic plantation forestry (notably in the North Island), but most of the deforested land has been converted into urban, horticultural or agricultural land uses. Deforestation within political districts ranged from a low of 13% in Buller to over 99% in Central Otago, Banks Peninsula, Timaru and the cities of Christchurch, Napier, Tauranga and Wellington (Table 3). Of the 73 political districts (Supplementary Table S3), 30 (two-fifths) have experienced greater than 90% deforestation.

3.2. *Drivers of forest loss and fragmentation*

The 13 predictor variables explained 35% of the variation in total forest change (Table 4a; Fig. 2), although the randomisation test indicated that only road density had strong statistical significance, with DCA_{moist} (a climatic moisture gradient) and DCA_{cal} (a soil fertility gradient) also weakly significant. Road density was the most important predictor, and reflected a trend for greater deforestation in grid squares with dense road networks. Historical forest loss was also associated with DCA_{moist}, with dry areas experiencing greater deforestation than wet areas. However, there was significant collinearity among many of the predictor variables (Supplementary Table S4), so although road density and DCA_{moist} were the most significant predictors, it is likely that other variables also played an indirect role in determining historical patterns of deforestation.

As with historical deforestation, road density was the strongest predictor of forest fragmentation, DCA_{cal} was weakly significant, and population density was not significant with $P = 0.056$ (Table 4c). Overall, forest fragmentation was greatest where road density and soil calcium were at their lowest. The multiple regression explained 38% of the variation in the fragmentation index across the 13 parameters, but road density was the only parameter that individually explained more than 5% (Table 4c).

Randomisation tests indicated that change in the amount of exotic forest cover was the only strong predictor of recent deforestation between 1997 and 2002 (Table 4b). Grid squares where indigenous forest cover was lost were strongly associated with recent increases in the cover of exotic forest (mean ± 95% CI for annual percentage change in exotic forest cover was 0.98 ± 0.14 for grid squares that

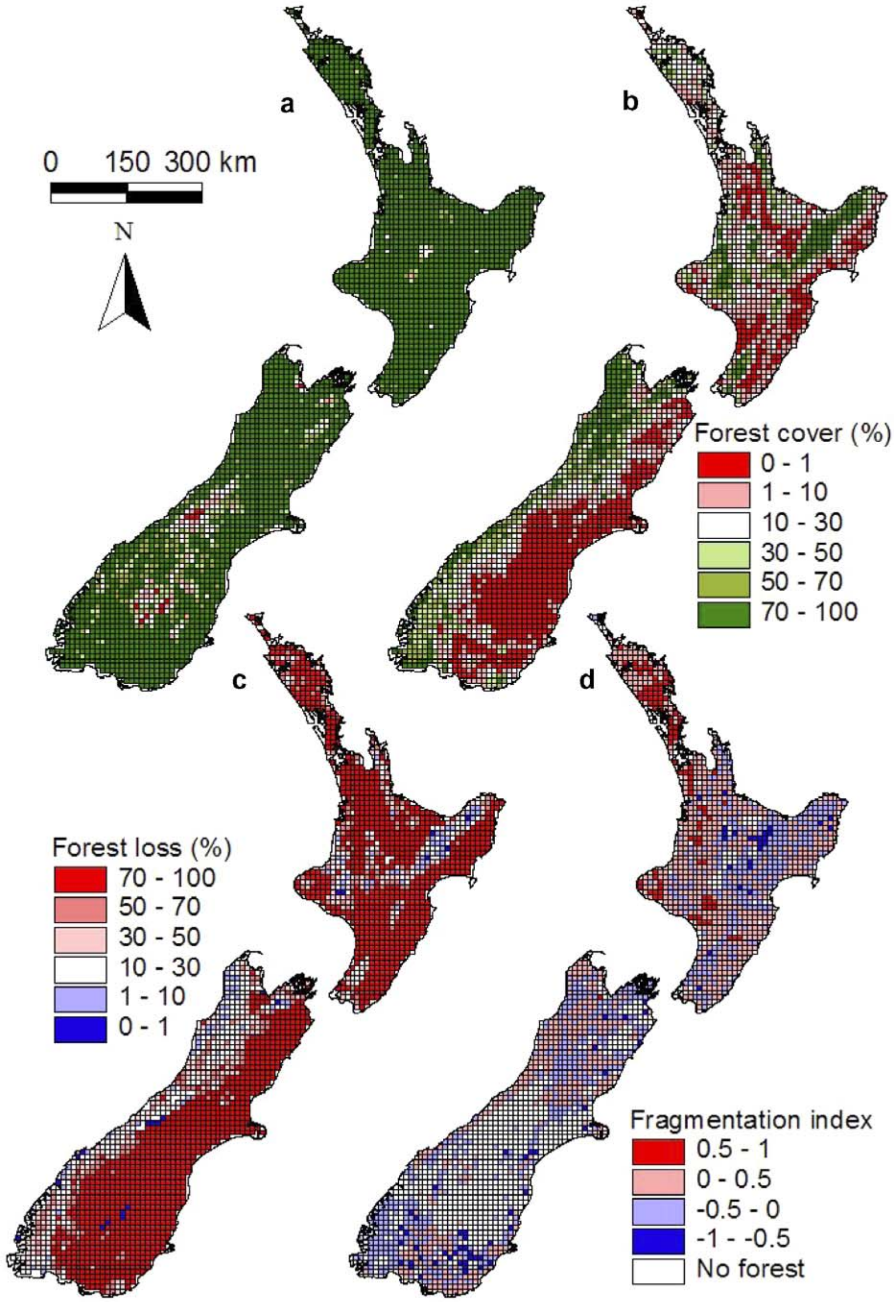

Fig. 1 – Patterns of forest change in New Zealand: (a) pre-human forest cover, (b) 2002 forest cover, (c) total forest loss and (d) forest fragmentation. The fragmentation index in (d) was calculated with a DCA ordination on number of fragments, forest edge to area ratio and fractal dimension of the landscape, after partialling out variation in total forest cover (DCA_{frag1} in Supplementary Table S2).

experienced deforestation, versus 0.53 ± 0.04 for those that did not).

3.3. *Regional trends in recent deforestation rates*

Between 1997 and 2002, 2344 ha of native forest was destroyed, equivalent to an annual deforestation rate of just −0.01% (Table 3, Supplementary Table S3). At the same time, a further 12000 ha of indigenous scrub was cleared (−0.14% yr^{-1}), with 53 of the 73 districts contributing to the net decline in scrub cover. The majority of the deforestation (1569 ha) was in the North Island, with more than half of that being cleared from the Northland region alone, and a further 24% cleared from the Waikato region. In the South Island, deforestation was greatest in Southland where nearly 500 ha were cleared. Deforestation rates varied throughout the country, with the political districts of the Far North and North Shore experiencing the highest recent rates of −0.09% p.a. However, the North Shore had only 1200 ha of forest in 1997, so the amount deforested was small in absolute terms

Table 3 – Regional assessment of past, current and likely future forest cover for the 16 political regions in New Zealand

Political region	Pre-human forest cover (ha, %)	2002 Indigenous forest (ha, %)	Total forest change (%)	Forest change ’97–’02 (ha, % yr^{-1})	2002 Indigenous scrub (ha, %)	Scrub change ’97–’02 (ha, % yr^{-1})	2002 Plantation forest (ha, %)	No. forest frags	Ave. frag. area (ha)	Edge Dens (km km^{-2})	DoC protected forest (ha, %)	Stable, protected, or threatened	Critical: (ha yr^{-1}, excl. and incl. scrub)
Northland	1,383,360 (92)	275,568 (18)	−80.08	−868 (−0.06)	150,937 (10)	−1361 (−0.18)	368,219 (24)	14,069	20	1.67	105,161 (07)		3909 (547)
Auckland	327,396 (93)	45,994 (13)	−85.95	−6 (0.00)	26,278 (07)	−17 (−0.01)	130,986 (37)	2264	21	1.10	2875 (01)		1331 (747)
Waikato	2,458,399 (94)	577,781 (22)	−76.50	−377 (−0.01)	167,380 (06)	−340 (−0.04)	778,618 (30)	8207	196	0.83	344,070 (13)		3453 (0)
Bay of Plenty	994,973 (97)	475,986 (46)	−52.16	−28 (0.00)	53,546 (05)	−238 (−0.09)	655,813 (64)	1608	564	0.84	329,088 (32)	Protected	
Gisborne	827,506 (99)	132,237 (16)	−84.02	−2 (0.00)	123,311 (15)	−936 (−0.15)	395,936 (47)	1659	523	0.60	63,024 (08)		2635 (0)
Taranaki	574,964 (99)	177,010 (31)	−69.21	−184 (−0.02)	50,505 (09)	−695 (−0.27)	37,281 (06)	2850	121	1.28	96,510 (17)	Threatened (2016)	
Hawke’s Bay	1,692,048 (98)	292,202 (17)	−82.73	−49 (0.00)	161,950 (09)	−954 (−0.12)	273,802 (16)	3748	240	0.62	183,368 (11)		3194 (0)
Manawatu-Wanganui	1,922,797 (98)	438,293 (22)	−77.21	−52 (0.00)	172,851 (09)	−1194 (−0.14)	269,247 (14)	6600	236	0.90	264,481 (13)		1678 (0)
Wellington	787,829 (98)	158,374 (20)	−79.90	−2 (0.00)	110,205 (14)	−1378 (−0.25)	119,443 (15)	1187	157	0.71	97,896 (12)		1837 (0)
Tasman	847,945 (88)	532,979 (55)	−37.14	−64 (0.00)	68,729 (07)	−1227 (−0.35)	104,715 (11)	2153	713	1.27	466,861 (48)	Protected	
Nelson	41,220 (97)	12,930 (31)	−68.63	−6 (−0.01)	5928 (14)	−1 (0.00)	12,078 (29)	93	2113	1.22	4489 (11)	Threatened (2048)	
Marlborough	796,733 (78)	208,865 (20)	−73.78	0 (0.00)	137,490 (13)	−3038 (−0.44)	73,118 (07)	806	336	0.72	166,945 (16)		2173 (0)
Canterbury	3,231,290 (67)	286,022 (06)	−91.15	−53 (0.00)	210,965 (04)	−72 (−0.01)	128,066 (03)	4282	216	0.38	189,269 (04)		5610 (17,685)
West Coast	1,848,727 (79)	1,438,453 (62)	−22.19	−145 (0.00)	85,136 (04)	−419 (−0.10)	42,520 (02)	2882	690	1.36	1,230,965 (53)	Protected	
Otago	1,744,739 (60)	181,326 (06)	−89.61	−8 (0.00)	103,079 (04)	−91 (−0.02)	127,368 (04)	2239	542	0.36	137,421 (05)		5310 (11,511)
Southland	2,250,040 (76)	1,077,089 (36)	−52.13	−499 (−0.01)	65,702 (02)	−190 (−0.06)	83,636 (03)	2993	391	0.93	942,596 (32)	Protected	
North Island	**10,969,272 (96)**	**2,573,444 (23)**	**−76.54**	**−1569 (−0.01)**	**1,016,962 (09)**	**−7114 (−0.14)**	**3,029,345 (27)**	**41,927**	**61**	**0.93**	**1,486,473 (13)**		**14,252 (0)**
South Island	**10,760,694 (72)**	**3,737,664 (25)**	**−65.27**	**−775 (0.00)**	**677,028 (05)**	**−5038 (−0.15)**	**571,499 (04)**	**15,304**	**244**	**0.72**	**3,138,546 (21)**		**17,104 (0)**
New Zealand	**21,729,965 (82)**	**6,311,107 (24)**	**−70.96**	**−2344 (−0.01)**	**1,693,990 (06)**	**−12,152 (−0.14)**	**3,600,844 (14)**	**57,231**	**110**	**0.81**	**4,625,019 (18)**		**31,356 (0)**

Data are arranged by regions from north to south, and figures in brackets are percent of district area. See text and Table 1 for details on data sources. Regions are assigned to one of four conservation categories according to the criteria in Table 2 (Stable, Protected, Threatened or Critical). For regions assessed as ‘Threatened’, the year at which forest cover is projected to fall below an extinction threshold of 30% forest cover in the landscape is presented. For ‘Critical’ regions, the figure represents the area that would need to be converted to indigenous forest annually to meet an arbitrary goal of 30% land area forested by the year 2050. The amount is presented under the assumptions that native scrub is not considered to be forest and, in brackets, that native scrub is considered to be forest. An extended version of this table that presents the same summary information for each of the 73 political districts of New Zealand (where political districts are land units that are nested within the political regions presented here) is provided in Supplementary Table S4.

Table 4 – Effects of 13 predictor variables on patterns of forest loss and fragmentation in New Zealand, after partialling out spatial autocorrelation

Variable	Linear regression or ANOVA			Randomisation test	
	df	MS	F	F (95% CI)	P (F > F_{crit})
(a) Historical forest loss (pre-human to 2002)					
EXO_{2002}	1	10.34	46.20***	4.86 (00.07, 20.22)	0.403
$POPD_{2001}$	1	23.82	106.44***	12.26 (02.06,33.97)	0.081
RENT	1	11.63	51.98***	5.70 (00.05, 23.48)	0.356
ROADDIS	1	15.61	69.76***	7.07 (00.38, 25.67)	0.285
ROADDENS	1	69.95	312.58***	34.87 (14.00, 63.92)	<0.001***
DCA_{psize}	1	6.99	31.21***	3.14 (00.02, 13.76)	0.584
DCA_{phos}	1	9.65	43.11***	4.73 (00.06, 19.32)	0.433
DCA_{cal}	1	28.71	128.32***	13.96 (03.19,33.17)	0.047*
DCA_{moist}	1	28.05	125.35***	14.91 (03.40, 36.00)	0.034*
DCA_{temp}	1	19.59	87.52***	7.88 (00.56, 25.84)	0.227
EVEN	1	14.03	62.67***	0.48 (00.00,05.15)	0.947
ALTIT	1	2.54	11.35***	7.32 (00.49, 21.60)	0.223
INCOME	1	0.27	1.23	0.52 (00.00, 06.27)	0.925
Residual	1970	0.22			
(b) Recent forest loss (1997–2002)					
$EXOCH_{97-02}$	1	1.698	28.05***	15.06 (07.37,26.33)	0.002**
$POPCH_{96-01}$	1	0.028	0.47	1.47 (00.07, 03.96)	0.974
RENT	1	0.045	0.74	0.28 (00.00, 02.89)	0.990
ROADDIS	1	0.015	0.24	0.17 (00.00,01.85)	0.998
ROADDENS	1	0.044	0.73	2.64 (00.08, 09.75)	0.670
DCA_{psize}	1	0.107	1.77	0.37 (00.00, 03.02)	0.991
DCA_{phos}	1	0.025	0.41	0.16 (00.00,01.80)	0.998
DCA_{cal}	1	0.169	2.79	0.45 (00.00, 03.39)	0.982
DCA_{moist}	1	0.017	0.29	2.00 (00.03, 07.68)	0.793
DCA_{temp}	1	0.006	0.10	0.13 (00.00,01.44)	0.999
EVEN	1	0.023	0.38	1.12 (00.00,06.16)	0.898
ALTIT	1	0.164	2.72	0.41 (00.00, 03.04)	0.986
INCOME	1	0.039	0.64	0.26 (00.00, 02.59)	0.995
Residual	1780	0.061			
(c) Forest fragmentation (2002)					
EXO_{2002}	1	11.66	58.86***	7.49 (00.20, 23.37)	0.257
$POPD_{2001}$	1	22.91	115.60***	14.66 (02.31,38.71)	0.056
RENT	1	12.25	61.81***	7.31 (00.04, 26.07)	0.283
ROADDIS	1	17.86	90.12***	10.05 (01.32,29.52)	0.124
ROADDENS	1	63.65	321.16***	39.32 (16.43,72.63)	<0.001***
DCA_{psize}	1	4.10	20.71***	2.17 (00.00,12.99)	0.672
DCA_{phos}	1	14.37	72.53***	9.02 (00.61,28.40)	0.177
DCA_{cal}	1	28.32	142.90***	16.25 (03.64,35.75)	0.029*
DCA_{moist}	1	15.49	78.18***	10.89 (01.37,29.76)	0.124
DCA_{temp}	1	10.73	54.14***	4.95 (00.07, 19.69)	0.387
EVEN	1	12.70	64.08***	0.50 (00.00, 05.49)	0.940
ALTIT	1	1.63	8.23**	7.56 (00.67, 22.29)	0.199
INCOME	1	1.00	5.04*	0.83 (00.00,07.11)	0.876
Residual	1780	0.20			

The response variables are (a) historical forest loss (%), (b) forest loss between 1997 and 2002 (%), and (c) the fragmentation index DCA_{frag1} for forest cover in 2002. The models in (a) and (c) were tested with multiple regression, and model (b) with ANOVA. Parameter significance for all models was assessed with randomisation tests that were based on power analysis. F = median value of F-statistic as generated from multiple linear regression on 1000 randomly sampled subsets of the data (±95% CI). $P_{(F>F_{crit})}$ = probability that any given F-value from the randomisation test is greater than the critical F-value. Abbreviations as in Table 1.

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

(6 ha *vs* 719 ha cleared in the Far North). Notably, no districts experienced net native afforestation, and only two had small increases in scrub cover.

Deforestation events were typically very small, with an average of just 4.9 ha destroyed at any given location (95% CI: 3.3–6.5 ha). Over 80% of the deforested areas were classified as being harvested, but this does not necessarily imply that it was felled for forestry purposes (Thompson et al., 2003). Individual scrub clearances were also small (mean ± 95% CI = 17 ± 4 ha). The majority of scrub that was

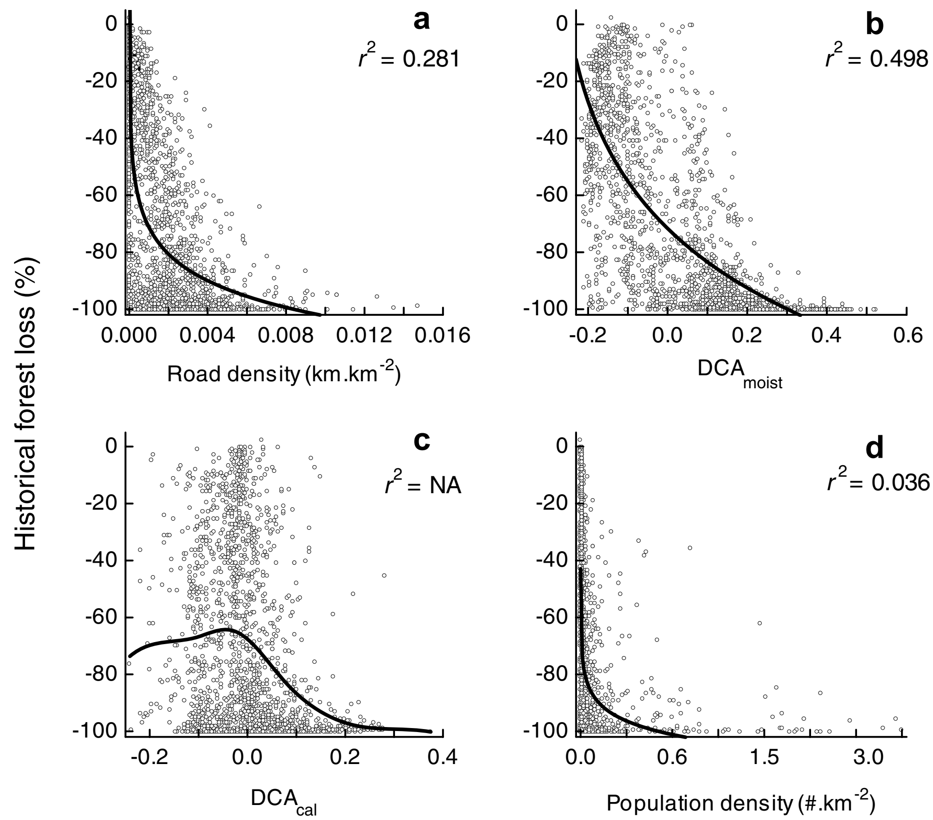

Fig. 2 – Predictors of total forest change in New Zealand: (a) road density, (b) climatic moisture, (c) soil calcium, and (d) human population density. Negative forest change values indicate deforestation, positive values indicate afforestation. DCA$_{moist}$ reflects a gradient from wet (negative values) to dry climates, and DCA$_{cal}$ a gradient from low to high soil calcium. Formulae for the fitted lines are (a) $Y = -160.12 - 34.05 \times \log_{10}(X)$; (b) $Y = -120.78 - 93.94 \times \log_{10}(X + 0.3)$; (c) distance-weighted least-squares; and (d) $Y = -112.29 - 15.91 \times \log_{10}(X)$.

cleared was converted to plantation forestry (69%), and these clearings tended to be much larger than the overall mean clearance size (35 ± 16 ha). A further 27% of cleared scrub was converted to high or low producing grassland (927 and 2541 ha, respectively).

By 2002, 55 of the 73 political districts had already passed below the extinction threshold of 30% forest cover in the landscape (Table 3, Supplementary Table S3). Of the remaining 18 that have retained significant forest resources, 10 have conservation protection in place for more than 30% of the landscape (Supplementary Table S3), and predictive models indicated that three are stable (Waitakere City, Lower Hurt City and Upper Hurt City) and five are threatened (Waitomo, Western Bay of Plenty, New Plymouth, Ruapehu and Nelson). Several districts recognised as in imminent risk of declining below the extinction threshold had experienced negligible forest change in the last 5 years, but are within 3% of the threshold value, justifying their classification as threatened landscapes. Four of the five threatened districts are in the North Island. The exception, Nelson, was far less fragmented than the North Island districts, with an average fragment area more than five times greater than any of the other threatened landscapes (Supplementary Table S3).

Annual restoration rates required for districts to meet the arbitrary restoration target of 30% forest cover by the year 2050 varied widely (Fig. 3), from less than 50 ha yr^{-1} to more than 6000 ha yr^{-1} (mean = 126 ha; 95% CI = 62–258 ha). Most (31 of 55) districts that had less than 30% forest cover required the establishment of less than 1000 ha yr^{-1} of new forest to exceed the extinction threshold by 2050 (Supplementary Table S4). For 10 of the 55 districts, the inclusion of existing indigenous scrub as regenerating forest was enough to increase their level of forest cover above the extinction threshold without requiring additional restoration.

4. Discussion

4.1. *Drivers of deforestation and forest fragmentation*

Deforestation is a non-random process that reflects the particular history and conditions of a given location. For instance, North American forest loss occurred primarily along the coast and at low altitudes (Seabloom et al., 2002), whereas in the relatively flat Amazonian Basin deforestation has principally occurred along paved highways, with human population density and climate also being important drivers (Laurance et al., 2002). By contrast, the cumulative pattern of deforestation in New Zealand was most strongly associated with the density of road networks, a climatic moisture gradient and soil fertility.

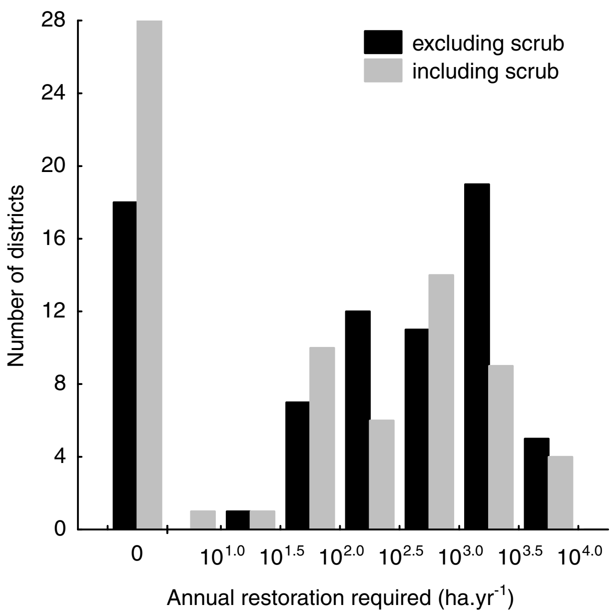

Fig. 3 – Frequency distribution of restoration rates required for the 73 political districts to meet an arbitrary goal of 30% forest cover by 2050. Districts are grouped according to the amount of forest regeneration they would need to meet the restoration target, and the area of required regeneration is calculated with scrub both included and excluded. Including indigenous scrub as regenerating forest greatly reduces the number of districts that require the establishment of more than 1000 ha of forest per year.

Road density was the strongest predictor of cumulative forest loss and fragmentation in New Zealand, as it is in much of the rest of the world (e.g. Chomitz and Gray, 1996; Cropper et al., 1999, 2001; Alves, 2002; Laurance et al., 2002; Agarwal et al., 2005). This pattern was apparent even though the measure of historical deforestation lumped pre- and post-European effects. Pre-European deforestation occurred in the absence of roads, so must have been driven by other factors. However, it appears that the tendency for post-European deforestation to occur in areas with high road densities has been so strong that it has overwhelmed the pre-European patterns. Roads form an integral component of modern commerce and can act as a surrogate variable for human landuse pressure, with high-density road networks representing intensive use of the landscape. As such, it is not surprising to find that areas with the highest density road networks, such as cities and suburbs, had the highest rates of deforestation in New Zealand, and that areas with few roads were left relatively unscathed. However, a number of grid squares that had few roads were also heavily or completely deforested (Fig. 2a), indicating that the absence of roads is not, in itself, enough to guarantee forest persistence and that other factors are responsible for causing deforestation patterns in these areas.

High rates of forest loss were also correlated with low annual rainfall, high vapour pressure deficit and high annual water deficit. This does not, however, mean that dry climates *per se* are driving forest loss. Rather, it is the human response to climate that is the ultimate cause of deforestation. The correlation between forest loss and a climatic moisture gradient probably reflects the fact that early peoples used fire as the most common method of clearing forest (Stevens et al., 1988; McGlone, 1989; Arnold, 1994), with the dry, eastern forests burning more readily and extensively (Molloy, 1969; Leathwick et al., 2003a).

Surprisingly, there was a non-significant correlation between forest loss and human population density. In other studies of deforestation rates, population density is often cited as a significant driver of forest clearance (Laurance, 1999; Pfaff, 1999; Bhattarai and Hammig, 2001; Cropper et al., 1999; Geist and Lambin, 2002). These studies are typically conducted in tropical, developing nations, where forests are converted to agricultural land to feed rapidly growing human populations which are often widely dispersed through large rural areas (Laurance et al., 2002; Seabloom et al., 2002). By contrast, New Zealand is a temperate, developed nation with a small population growth rate (1.2% p.a.), a largely urban population (86%), and an emerging trend for farmers to protect, rather than clear, privately owned forest (Queen Elizabeth II Trust, 1984; Ministry for the Environment, 2000; Davis and Cocklin, 2001).

A second reason for the non-significant relationship between historical deforestation and population density is a difference in the temporal scale of observations. The population distribution in 2001, which was the variable used in this analysis, does not necessarily reflect the population distribution at the actual time that deforestation occurred in any given area, as New Zealand has seen dramatic population movements in response to colonisation schemes, gold rushes and the eventual growth of large urban centres around major ports (Boddington, 2003). Moreover, multicollinearity amongst variables may also have weakened any direct link between human population density and historical deforestation. Population density was significantly correlated with all other predictor variables with the exception of exotic forest cover. It was most strongly correlated with road density, strengthening the assertion that road density acts as a surrogate for human landuse intensity.

There were also surprisingly weak effects of the geomorphological variables on deforestation. In particular, a strong effect of altitude on historical forest loss had been expected, as topography strongly influenced the patterns of human settlement and forest burning in New Zealand (Molloy, 1969), and most of the lowland plains are almost completely denuded of native forest (Ewers et al., 2005). That it did not show up in the analysis probably reflects the intercorrelated nature of many of the drivers. Both altitude and land evenness were strongly negatively correlated with road density ($r = -0.55$ and -0.54 respectively) and human population density ($r = -0.35$ and -0.27 respectively), a pattern also shown by Seabloom et al. (2002), and indicates that the effects of topography were encompassed within these intercorrelated relationships.

4.2. *The impact of exotic forestry on recent deforestation rates*

In contrast to patterns of historical forest loss, recent forest loss over the period 1997–2002 was associated solely with increases in the amount of exotic forest cover. This indicates that in many locations indigenous forest has been destroyed to make way for exotic plantations, and demonstrates that there is a strong role played by the forestry industry in driving current patterns of deforestation (Walker et al., 2006). Furthermore, a large proportion of the indigenous scrub that was cleared was converted to exotic plantations. The amount of land covered by exotic forestry in New Zealand has been increasing steadily since the end of the Second World War, and the fact that recent expansion of forestry operations is still associated with the loss of small indigenous forest remnants is of concern.

4.3. *Protection of indigenous forests*

Of the forested land that remains in New Zealand, three-quarters (46,250 km^2) is Crown owned and protected from clearance and development through administration by the Department of Conservation. However, the distribution of that protection is uneven between political districts. Most of the landscapes with >30% forest fell into the protected category, indicating that where abundant forest exists, the Department of Conservation administers a significant proportion of the forests for conservation purposes. Unfortunately, though, landscapes with low amounts of forest cover, where surviving remnants are of proportionately greater conservation value, also tend to have the lowest proportion of protected forest (Leathwick et al., 2003a; Walker et al., 2005, 2006).

The districts that are underrepresented in terms of the remaining Crown-owned indigenous forests managed for conservation are predominantly in the lowlands and cities (Awimbo et al., 1996; Norton, 2000), where land prices are inevitably high. This trend has been emphasized during the tenure review process of high country lands that was initiated in the 1990s in New Zealand, where historic crown leasehold land is in the process of being converted to either conservation estate or freehold farmland (Mark et al., 2003). The net result of this pattern is an extensive, but non-representative conservation estate – a problem shared by many nations in the world (Pressey, 1994). We suggest that future forest protection priorities in New Zealand should now be in two new directions.

The first priority for conservation protection is the targeting of landscapes that are at risk of forest cover declining below the 'extinction threshold' of 30% forest cover. The extinction threshold poses a considerable threat to metapopulation persistence in deforested landscapes. As the threshold is passed, dispersal between forest fragments is disrupted to the extent that extinction rates of isolated populations increases and vacant fragments are not recolonised (Kareiva and Wennergren, 1995). The loss of even a small amount of forest near the threshold may, therefore, result in an irreversible decline in species persistence (With and King, 1999). If these landscapes can be maintained above the extinction threshold by preemptive conservation measures, it may be possible to avoid future declines in the populations of native species, thereby negating the need for expensive, single-species management which becomes more costly the rarer a taxon becomes (Garnett et al., 2003). However, we stress that habitat loss is only one of many factors that interact to cause species declines (Didham et al., 2005a,b, 2006), and that preventing future habitat loss will not, in itself, guarantee the persistence of all species.

The second priority for conservation protection is the targeting of forest fragments in landscapes with very low amounts of forest cover. These landscapes can be combined with the Land Environments of New Zealand categories to assign simple priority values to fragments that are not yet protected, based on two variables: (1) the proportion of protected forest in the landscape in which the fragment is located; and (2) the proportion of protected forest in the Land Environments of New Zealand category within which the fragment is classified. This simple ranking system has the potential to provide a clear, ecologically relevant priority system for land acquisitions.

One important consideration in developing a strategy like this is that the land must be available for conservation purposes; this may not be the case for much of the forest that remains in the most threatened land environments of New Zealand. The large majority of these fragments are located on private land that is not for sale, and is not likely to be sold in the foreseeable future. Thus, effective conservation management in these areas may rely more on private land covenants through institutions such as the Queen Elizabeth II National Trust (Queen Elizabeth II Trust, 1984) than on official government protection through the Department of Conservation.

4.4. *Recent and future deforestation*

The spatial distribution of recent deforestation was clumped in several political regions at opposite ends of the nation, of which Northland and Southland were the most notable. Nearly 40% of all forest loss that occurred in New Zealand from 1997 to 2002 occurred in Northland, which also contains some of the most fragmented forest in New Zealand. Although the Northland deforestation rates are still the highest in the country, it is notable that they have been greatly reduced over the past 20 years, when indigenous forest was being cleared at 1.5% yr^{-1} (Anderson et al., 1984). Deforestation rates in Southland are also relatively high, reflecting the impact of logging activities on land owned by indigenous groups. Southland is home to almost half of the forest granted to named Maori people under the South Island Landless Natives Act 1906, and these remain today as the only privately owned forests in New Zealand that are not required to have Sustainable Forest Management Plans under the 1993 Forests Act (Ministry of Agriculture, 2001). As a consequence, it has been recognised that there is potential for ongoing unsustainable harvesting of indigenous forest in this area (Ministry of Agriculture, 2001).

Future forest loss scenarios were predicted using exponential decline curves rather than extrapolating current deforestation rates into the future, because deforestation rates are not static through time (Bhattarai and Hammig, 2001; Laurance et al., 2001). Forest destruction occurred extremely rapidly following the 1870s after establishment of European settlements in New Zealand (Arnold, 1994) and as the forest has receded, so has the rate at which further clearance has been made. To account for these changes through time, a regression approach was used that smoothed out short-term variation in deforestation rates and allowed us to determine long-term trajectories in forest cover. Because of the uncertainties implicit in any regression analysis and the unpredictable way in which year-to-year deforestation rates can vary, the dates at which the landscape threshold is predicted to be exceeded should be interpreted solely as an indication of the relative threat to different landscapes. By contrast, the restoration targets provide a clear indication of the magnitude of the conservation effort required by the individual political districts.

For heavily deforested regions, such as in Canterbury and Otago, the restoration effort required is considerable, with many districts needing to restore between 2000 and 6000 ha of forest each year. Encouragingly though, 6% of New Zealand landcover is currently classified as indigenous scrub, which, if left undisturbed for long enough time periods, should regenerate into indigenous forest, and so could be considered "forest-in-waiting." When scrub is considered in this manner, the restoration targets for many districts become more achievable. It is also encouraging that when taken as a whole, New Zealand has 30% of its total land area in either indigenous forest or indigenous scrub that should eventually regenerate into forest. However, data from the LandCover Database shows a nationwide trend for declining native scrub cover, suggesting that large areas of this landcover type are not being allowed to regenerate into mature forest before being cleared. Furthermore, only 162 ha of new scrub cover regenerated between 1997 and 2002. Of course, it is also possible that the LandCover Database has underestimated the amount of scrub regeneration that is occurring, because the early encroachment of native scrub into grasslands is unlikely to be recorded as a transition from grassland to scrub due to the minor changes in the spectral signatures of the vegetation cover at these early stages. To detect increases in scrub cover at the early stages of regeneration, finer remote sensing techniques, such as those employed by the EcoSat Project (Dymond et al., 2004), may be required.

Obviously, the process of forest regeneration in a temperate nation is slow and the final target of 30% landcover of mature forest can not realistically be achieved by 2050. However, the land required to meet this set of district-level targets could certainly be set aside by 2050, because relatively modest annual additions to the conservation estate will be enough for many districts to attain the eventual goal of restoring the New Zealand landscape to the point where the historical impacts of habitat loss are minimised.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2006.06.018.

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