The woody vegetation of Central Otago, New Zealand: its present and past distribution and future restoration needs

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S. Walker, W.G. Lee, G.M. Rogers

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S. Walker[1], W.G. Lee[1], G.M. Rogers[2]

[1]Landcare Research, Private Bag 1930, Dunedin, New Zealand
email: WalkerS@LandcareResearch.co.nz
[2]Department of Conservation, P.O. Box 5244, Dunedin, New Zealand

ABSTRACT

A spatial database of extant woody plant species and environmental information is used to describe the present and past woody vegetation of Central Otago, inland eastern South Island, and its relationship to environmental and historical factors. Fourteen present-day associations of woody plants are described that are principally related to elevation and disturbance by historical fires and grazing. Generalised additive models of the present-day distributions of woody species are used to predict the potential distributions of native woody species on a 1-km^2 grid across the study area. Twelve biogeographic zones of pre-settlement woody vegetation are identified by a classification of the predicted distributions of 15 potential former canopy dominant species that are still most common in Central Otago. The likely woody species composition of each zone immediately prior to human settlement is described on the basis of the predictions of the models and the fossil record. Potential future distributions of woody weeds in each zone are also predicted. We propose the twelve pre-settlement woody vegetation zones as a framework to guide the placement and design of a representative network of public conservation areas for the restoration of woody vegetation in Central Otago. We determine the present area of public conservation land within each zone. Up to 20% of high-elevation pre-settlement woody vegetation zones in Central Otago are currently within public conservation lands, whereas < 2% of mid- and low-elevation zones are represented. To better represent the range of natural habitats, ecosystems and indigenous species in Central Otago, more land at low elevations should be reserved for long-term succession to native woody vegetation and recovery of associated fauna. Pre-settlement vegetation patterns should be used to inform the broad goals for these conservation areas; native woody vegetation restoration efforts should be accompanied by research; and partnerships with local authorities, conservation organisations and the public should be sought.

Keywords: pre-settlement forest and shrubland, woody species asssociation, deforestation, prediction, regression, species-environment relationships, potential vegetation pattern, vegetation zone, restoration

1. Introduction

Biological studies and conservation efforts worldwide have historically been directed towards protecting areas that are less modified and richer in native species, while those that are more economically productive, and modified by human land-use, have been ascribed lower priority. The rainshadow areas to the east of the main axial ranges of the South Island, New Zealand, fall within the latter category. Here, anthropogenic impact since the arrival of Polynesian people 800 yr BP has transformed substantial areas of forest and woodland to novel, induced grassland and shrubland vegetation types. The seral (successional) woody plant communities that occur in eastern South Island today are among the most overlooked and least understood of all New Zealand vegetation types. Because so little intact native woody cover remains, inland eastern South Island environments were not covered in the National Forest Survey (Newsome 1987) and have been omitted from published estimates of potential pre-settlement forest cover (Newsome 1987; Leathwick 2001; Leathwick et al. 2003). Recently, knowledge of vegetation patterns in deforested regions of the eastern South Island has increased with initiatives such as the Protected Natural Areas Programme (Kelly & Park 1986) and Tenure Review (Crown Pastoral Land Act 1998), and through research directed towards threatened plants and ecosystems (e.g. Rogers et al. 2000). Nevertheless, much remains to be added to increase understanding of the woody component of the vegetation of inland eastern South Island.

A very small part of the area (< 2%) and biodiversity of dry, lowland eastern South Island land environments is presently protected in conservation reserves (Leathwick et al. 2002a, b). It is recognised that there is a need to add to New Zealand's public conservation lands those habitats and ecosystems that are currently poorly represented in protected areas (Ministry for the Environment and Department of Conservation 2000 p. 41). However, the advanced state of vegetation modification in under-represented regions of dry, lowland eastern South Island means that few or no examples of pristine or intact ecosystems remain. Therefore, conservation goals for ecosystems and habitats in these deforested areas will need to incorporate concepts of successional change and ecosystem restoration, rather than the maintenance of existing states. As a basis for these goals, a more thorough understanding of the present, past, and potential future woody vegetation of eastern South Island ecosystems is required.

In this study, we catalogue information on extant woody species distributions, and collate current climate surfaces and soil data, for Central Otago, one of the driest inland rainshadow regions of New Zealand. We use the resulting plant species and environmental databases to describe the regional environmental pattern, and the present-day associations of both indigenous and exotic woody species in relation to the environment. We identify 12 biogeographic zones that may have supported similar woody species compositions immediately prior to human settlement, when the climate was similar to that of the present day. We assess the likely pre-settlement woody vegetation composition of each zone on the basis of both predictions from generalised additive models and available evidence from the subfossil record, and show how the present woody vegetation relates to these. We also predict the minimum potential future distributions of woody weeds within these zones, based on their present distributions.

Finally, we discuss the conservation management implications of this work. We propose the twelve pre-settlement woody vegetation zones as a framework to guide the placement and design of a representative network of public conservation areas for the restoration of native biodiversity in Central Otago, and highlight priorities for woody vegetation conservation, restoration and research.

2. Background

Considerable changes in the vegetation of Central Otago occurred through the Holocene Period (10 000 yr BP to present) as a consequence of climatic variations. In the early Holocene, the climate may have been drier than at present, and initial postglacial afforestation may have been slower than in other parts of New Zealand. Towards 7000 yr BP, the climate became more favourable and low forest replaced shrubland and grassland. As westerly airflows and El Nino conditions became more prevalent from c. 5000 yr BP, wetter, cooler winters were experienced in the uplands (McGlone & Moar 1998; McGlone 2001). However, at low elevations, the westerly airflows may have promoted more droughty, windy summer conditions, which may have led to somewhat higher natural fire frequencies (with return times from > 1000 to several hundred years) and more open vegetation canopies from this time on. The spread of silver beech (*Nothofagus menziesii*) onto the range slopes of Central Otago occurred relatively late in the Holocene, perhaps around 4000 yr BP, while the spread of *fusca*-type beeches (e.g. *Nothofagus solandri* var. *cliffortioides*) was even more recent (from c. 2000 yr BP; McGlone et al. 1996).

Profound vegetation changes occurred with the arrival of humans in Central Otago. A major reduction in the extent of forest and shrubland vegetation resulted from clearance fires lit by Polynesian hunter-gatherers (Molloy et al. 1963; McGlone 2001; Wardle 2001b). Fire-sensitive woody species may have been eliminated from extensive areas of valley floors, hillslopes, dry interfluves and range crests in the first wave of human occupation. However, more fire-tolerant species and those protected in dissected habitats may have resprouted and sourced secondary successions in areas with longer fire-return times. In the era of pastoralism (the last 150 years), the combined effects of more frequent fires and mammalian grazing and browsing have limited secondary succession in many woody species, and further restricted their distributions to inaccessible refugia in steep gorges, rock outcrops and screes that occur mainly on dissected range slopes. In this report, we describe the current distribution and composition of woody vegetation and the main environmental and historical factors that account for it.

Relatively little woody vegetation remains in inland eastern South Island regions today to provide clues to their previous vegetation composition. Pollen and charcoal evidence, together with log fragments and the presence of forest dimples and buried podzols, have so far provided only coarse-resolution estimates of the previous woody vegetation types (e.g. Molloy et al. 1963; Molloy 1969; McGlone & Moar 1998; McGlone 2001; Wardle 2001a, 2001b). Nevertheless, in parts of Central Otago, remnants of pre-settlement forests and shrublands survive today as single trees or small stands of indigenous woody plants. Recent advances in landscape-scale mapping of environmental variables (Leathwick & Stephens 1998) and recently developed statistical tools (e.g. Lehmann et al. 2002) allow the current distributions of relict woody species to be modelled with respect to environmental factors, and for their potential pre-settlement extent to be predicted across the landscape. However, estimates of potential distributions from remnant populations can be misleading, and conservative, since surviving trees and shrubs tend to be concentrated in steep, sheltered fire-refugia or on screes that may not be typical of the wider landscape or representative of their former ranges. Furthermore, relict stands tend to be modified by fire, mammalian grazing and fragmentation, so that their composition is biased towards more disturbance-tolerant species, and some constituents of former woody communities may be missing altogether from the region today. Therefore, estimates of pre-settlement distributions based on relicts must be carefully evaluated against other sources of evidence. Records of subfossil wood, charcoal, and pollen are crucial for calibrating and augmenting models of potential vegetation that extrapolate from living plant distributions. We use both approaches to estimate the likely pre-settlement composition of Central Otago, and we acknowledge that much work remains to be done to refine these estimates.

An understanding of present, past, and potential future woody vegetation provides a basis for conservation goals for ecosystems in eastern South Island rainshadow environments. The perception that vegetation recovery should advance only towards some defined primeval goal is probably unrealistic, given the extent of ecosystem change that has occurred since human settlement. Nevertheless, better information on the pre-settlement vegetation patterns can guide effort to protect areas across a representative spectrum of now deforested pre-settlement native woody vegetation zones, and can provide broad long-term restoration goals for these areas, as well as suggest specific indigenous species that might be suitable candidates for restoration trials. Greater understanding of vegetation potential (that is, of what might be achievable in terms of restoring succession towards native woody vegetation in deforested areas) will promote efforts to increase indigenous biodiversity through encouraging native woody successions.

Detailed consideration of the past and present composition of herbaceous vegetation (including grassland) and its changes since human settlement, is outside the scope of this report, which focusses on exclusively on the woody component. We make the broad ecological generalisation that where the environment is capable of supporting indigenous trees and shrubs, these would have been competitively superior to shorter herbaceous species, which would have accounted for lower proportions of the vegetation cover. There has been some debate on the extent of woody vegetation in Central Otago immediately prior to human settlement c. 800 yr BP (Molloy et al. 1963; McGlone 2001). However, it is generally understood that forest and woodland covered the range slopes up to the lower limits of the alpine zone, that woody vegetation was far more extensive and grasslands were far less widespread than today, both above treeline and on the driest floors of the inland basins (McGlone et al. 1995; 1997; McGlone & Moar 1998; McGlone 2001). More subfossil evidence, and a better understanding of the tolerances of New Zealand plant species to environmental extremes, will be needed before the proportions of woody vegetation cover can be confidently estimated above and below the zones of tall, closed-canopied pre-settlement forests of Central Otago's range slopes. However, in this report, we make some preliminary assumptions in order to estimate the likely percentage loss of woody vegetation cover from different natural vegetation zones in Central Otago since human settlement; i.e. that valley floors comprised 25% tall or low forest, 25% shrubland, and 50% herbaceous non-forest vegetation. We believe that this under-estimates the former extent of woody cover below treeline, since indigenous woody plants survive in the most extremely drought- and frost-prone environments on the valley floors today, and we therefore expect that our estimates of lowland woody vegetation loss are conservative. In forest zones, and in shrubland zones above treeline, we assume that 5% of the total land area would have been covered by herbaceous non-forest vegetation, bare rock, or bare soil. We expect that these preliminary assumptions will be refined through future research.

3. Objectives

- To classify existing woody vegetation (both native and exotic) within Central Otago.
- To describe the current distribution and composition of woody vegetation and the main environmental and historical factors that account for it.
- To determine how well the diversity of woody vegetation is currently represented within the lands administered by the Department of Conservation (DOC).
- To comment on the implications of these results for conservation management in terms of future changes in composition of both the native and exotic components of mixed systems.

4. Study area description

The inland region of Central Otago in the southern South Island (Fig. 1) represents one of the extremes of the New Zealand climatic spectrum. Here, an almost continental climate is produced by a combination of distance from coastal maritime influence and the rainshadow effect created by the Southern Alps to the west (Maunder 1965). The geological basement of much of the

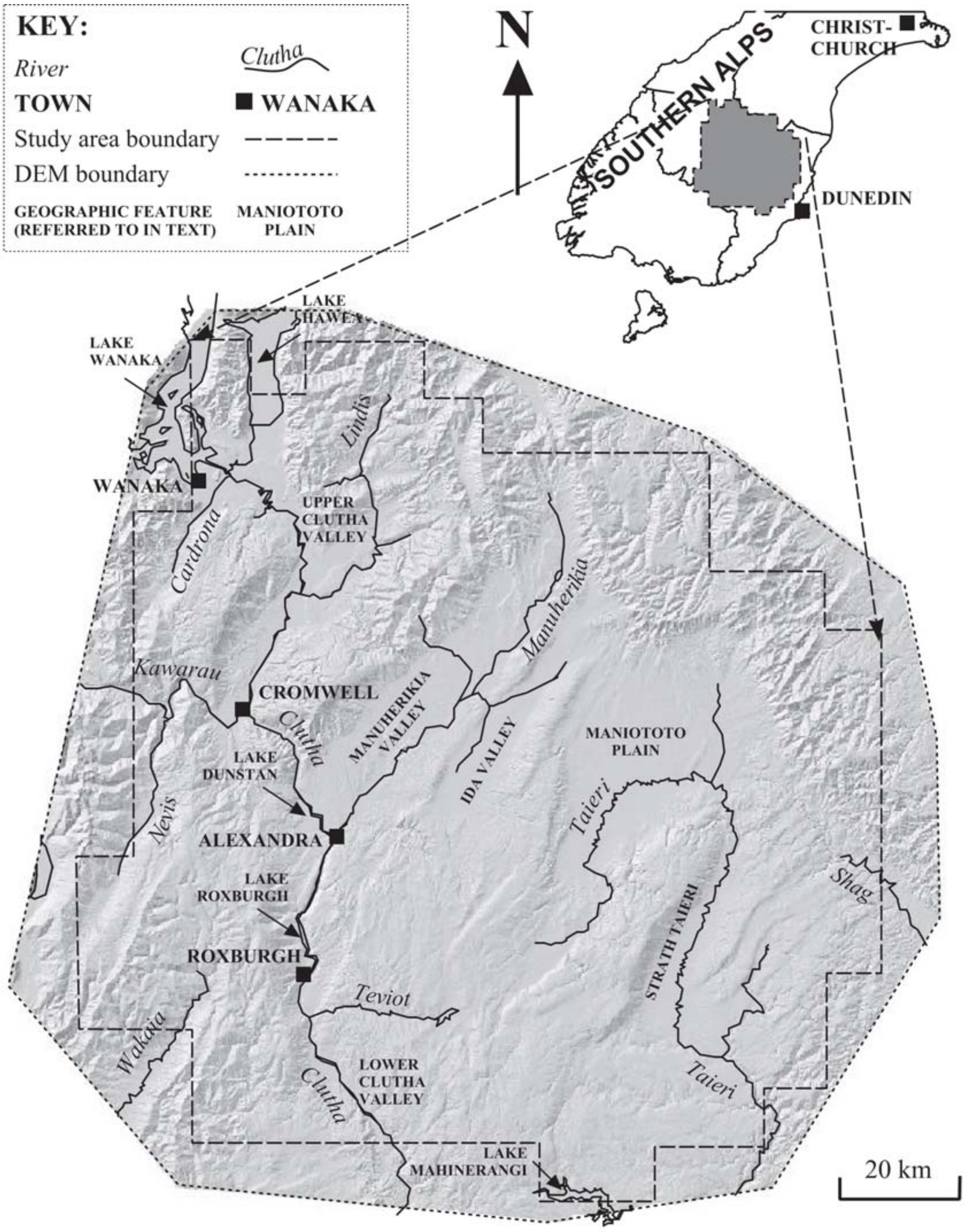

Figure 1A Digital elevation map of Central Otago, showing the major rivers, towns, and geographical areas mentioned in the text, in relation to the boundaries of the study area. The inset maps shows the position of the study area in South Island, New Zealand, in relation to population centres and the Main Divide of the Southern Alps.

region is a Cretaceous schist and greywacke peneplain, which has been uplifted and block-faulted. In the centre of the region, a series of sub-parallel northeast-trending flat-topped schist ranges rise to 2200 m, with broad intervening valleys drained by the Clutha and Taieri Rivers and their tributaries (McCraw 1965). Rising to similar elevations along the north-eastern margin of the region is a series of northwest-trending greywacke ranges, with extensive scree slopes on their steep south-western faces. The basin floors of Central Otago experience both the hottest summers and the coldest winters recorded in New Zealand. Severe winter frosts affect the basin floors as a consequence of temperature

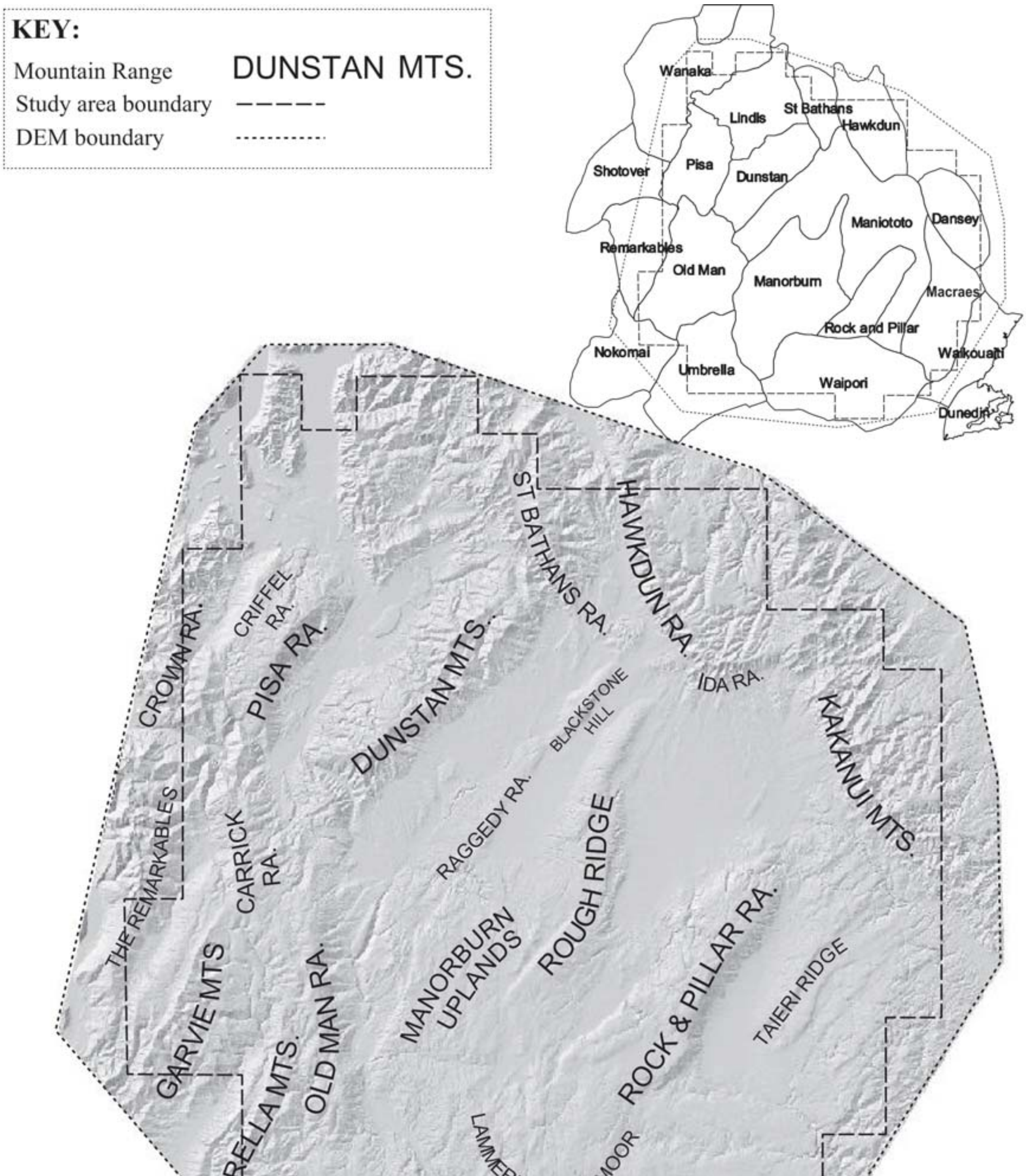

Figure 1B Digital elevation map of Central Otago, showing the major mountain ranges mentioned in the text, in relation to the boundaries of the study area. The inset shows the boundaries of ecological districts included in, and adajacent to, the study area.

inversions and extended periods of calm conditions. The range tops experience low temperatures all year round, and the higher ranges carry snow for much of winter and early spring (Meurk 1978; Mark & Dickinson 1997). Strong, desiccating föhn winds, and high irradiance due to clear skies are characteristic climatic features. Present vegetation patterns of the Central Otago region have been shown to be determined mainly by the steep gradients in rainfall and temperature that follow the altitudinal gradients (Mark 1965; Partridge et al. 1991; Wilson et al. 1989; Walker 1997). However, local variations in topography and aspect markedly influence soil moisture availability, and strongly determine the vegetation pattern at smaller scales (Walker et al. 1995).

5. Methods

5.1 METHODOLOGICAL FRAMEWORK

The framework of the study comprised six phases of data collection and analysis, which we outline below:

1. Classification and description of environmental domains

In the first phase, we assembled and classified environmental (climate and substrate) data for Central Otago to describe 18 environmental domains for the region (described more fully in Section 5.2).

2. Compilation of woody species database for Central Otago

The environmental domains provided the basis for the collation of a woody species database for Otago, in which we collected and compiled data on woody plant species occurrences across a representative range of environments (Section 5.3).

3. Classification and ordination of present-day woody vegetation

Using ordination and classification, we described the present woody vegetation in terms of vegetation gradients and woody plant associations, and its relationship with environmental and historical factors (Section 5.4).

4. Defining zones of pre-settlement woody vegetation, and assessing their likely composition

As a basis for understanding the origins of the present woody vegetation, we predicted the likely distribution of pre-settlement woody vegetation zones for the Central Otago region (Methods Section 5.5). We used generalised additive models in GRASP (Generalized Regression Analysis and Spatial Prediction, Lehmann et al. 2002) to predict the probability of occurrence of 74 native woody species on a 1 × 1 km grid across the region (Section 5.5.1). Twelve zones of similar pre-settlement woody vegetation were defined on the basis of the predicted ranges of 15 potential canopy species (Section 5.5.2), and described in terms of the main environmental factors that account for each zone, their relationship with environmental domains, and the present-day woody plant associations they contain. The likely woody species composition of the zones in pre-settlement times is considered in terms of the predictions of the models (Section 5.5.3) and the pollen and subfossil evidence (Section 5.5.4). Each pre-settlement zone was assigned to a broad vegetation structural class simplified from Atkinson (1985), and the loss of woody vegetation following human arrival was estimated (Section 5.5.5). Finally, the strengths and limitations of the different approaches used to assess pre-settlement vegetation composition are discussed (Section 5.5.6).

5. Potential distributions of exotic woody species

We examined the present distributions of 12 exotic woody species in relation to the environment, and used GRASP to determine their minimum potential ranges (Section 5.6). We used these models to comment on the implications for future trends in the exotic components of pre-settlement woody vegetation zones.

6. Pre-settlement woody vegetation zones in public conservation lands

Finally, we investigated the distribution of land presently administered by the Department of Conservation in relation to pre-settlement woody vegetation zones in Central Otago (Section 5.7).

5.2 CLASSIFICATION AND DESCRIPTION OF ENVIRONMENTAL DOMAINS

To describe the environmental pattern of the study area, we summarised environmental variation within Central Otago into 18 environmental domains, which represent areas of similar environmental character, defined on an objective basis. The environmental domains are areas of similar climate and soil defined by the classification of several different environmental surfaces contained in GIS. For the classification, climate factors were estimated for c. 320 000 points on a 250-m grid encompassing the area of interest, using thin-plate-spline spatial interpolation of data from 364 irregularly distributed New Zealand meteorological stations (Leathwick & Stephens 1998). Soil factors were derived from the New Zealand Land Resource Inventory (NZLRI: National Water and Soil Conservation Organisation 1979).

The climate factors selected for the domain classification were mean annual temperature, temperature seasonality, rainfall: potential evapotranspiration ratio, October vapour pressure deficit, annual precipitation deficit (i.e. potential evapotranspiration—precipitation), mean annual solar radiation and solar radiation seasonality (Appendix 1). These factors show strong, consistent relationships with tree species distributions in New Zealand (Leathwick & Whitehead 2001; Leathwick 2001). The other factors included in the domain classification were predominant slope or relief, and six soil factors (soil age since last major reset of soil formation, calcium, acid soluble phosphate, particle size, salinity and drainage).

The environmental domain classification was performed using ALOC (Belbin 1987, 1991), a non-hierarchical clustering strategy designed for very large datasets. The Gower metric, which automatically standardises each variable (Sneath & Sokal 1973), was used as a measure of environmental dissimilarity. We imported the resulting domain classification table (of c. 320 000 points) into GIS ArcView (Environmental Systems Research Institute 2000).

Our environmental domain classification uses the same methodology and many of the same environmental surfaces as the recent LENZ classification for all of New Zealand (Leathwick et al. 2002a). However, ours is an independently derived domain classification, that is intended to be appropriate for this particular study and region, which covers the arid, continental extreme of the range of New Zealand environments. The resolution of the grid, the number of groups, and the classification variables were chosen to suit this particular study.

5.3 COMPILATION OF A WOODY SPECIES DATABASE FOR CENTRAL OTAGO

A database of woody species distributions in Central Otago was compiled (Appendix 2). The final database comprises 5419 grid-referenced locations within a subjectively selected area of 15 500 km^2 (155, 10 × 10 km grid squares) which includes part or all of 18 Ecological Districts. Three categories of sources were used:

1. *Base dataset* (presence/absence): 2632 grid-referenced plot records of species presence/absence were collated from published and unpublished botanical surveys (e.g. Protected Natural Areas surveys; hereafter PNA surveys). Most of these plots had the dimensions 10 × 20 m (exceptions are noted; Appendix 2). The compiled data were mapped to assess the adequacy of their coverage of the 18 environmental domains.
2. *Supplementary survey dataset* (presence/absence): We carried out supplementary field surveys in the summers of 1999/2000 and 2000/2001. These surveys added 869 presence/absence plot (10 × 20 m) records to the database, which ensured that the full range of environmental domains was covered by plots, and that plots covered the full spatial extent of each domain. A further 1097 grid-referenced point records of single native woody plants were also added to the database from these surveys. Base and supplementary survey datasets were used to describe current woody vegetation gradients and types.
3. *Supplementary dataset* (presence only): 821 records were drawn from herbaria collections (OTA and CHR) and from other published and unpublished sources (including DOC tenure review resource reports and land inventory records, and personal records of individuals). These presence data were used in addition to the base and supplementary data in generating generalised additive models for individual plant species.

We accepted the species identifications of each source, but updated nomenclature where appropriate. Because *Pinus* spp. were not well distinguished at species level in the source data, we amalgamated their records and treated the genus as a single entity (cf. Leathwick 2001). Prior to compiling the database, records for each species were plotted against rainfall and temperature estimates, and records outlying from the normal distribution were excluded. No herbaceous species were included in the database or in the data analyses that follow.

5.4 CLASSIFICATION AND ORDINATION OF PRESENT-DAY WOODY VEGETATION

For classification and ordination we used the base and supplementary (i.e. presence/absence) datasets. We removed all rare species records (i.e. those 59 native and 31 exotic species for which we had < 13 records: Appendix 3), and all plots that contained only those rare species, leaving a dataset of 125 (107 native and 18 exotic) woody plant species within 3389 presence/absence plots.

Cluster analysis (using the flexible sorting strategy, and the Jaccard measure of dissimilarity in species presence) was used to identify present-day woody plant associations on the basis of the joint presence of species in the 3389 presence/absence plots. We describe these as associations, since quantitative data (i.e. relative abundance, stature, density of woody plants) were not consistently measured in the data sources, and were therefore not included in the database or considered in the analyses.

A Detrended Correspondence Analysis (DCA) ordination was used to arrange the plots along the major gradients of vegetation composition. Simple regressions of climate, soil and vegetation composition (i.e. native and exotic richness and native proportion) on the principal ordination axes were used to interpret these gradients (i.e. to identify the environmental drivers of the major regional trends in woody vegetation). Plots comprising a single woody species after the exclusion of rare species were also eliminated from the DCA ordination analysis for computational reasons, leaving 2901 presence/absence plots.

5.5 DEFINING ZONES OF PRE-SETTLEMENT WOODY VEGETATION, AND ASSESSING THEIR LIKELY COMPOSITION

5.5.1 Model fitting

We use generalised additive models in GRASP (Generalized Regression Analysis and Spatial Prediction, Lehmann et al. 2002) to predict the probability of occurrence of native woody species on a 1 × 1 km grid across the region. Models were fitted for each of 74 native species for which we had > 40 records (i.e. all very common, common and less common species, Appendix 3); models built on fewer than 40 records proved less robust in exploratory analyses. We subjectively defined three categories of species within the 74 most common native species. Fifteen species were categorised as potential canopy dominants in the pre-settlement vegetation on the basis of their stature and environmental tolerances. A further 12 species were categorised as shade-tolerant non-canopy species (i.e. forest understorey species) and the remaining 49 species as non-canopy, shade-intolerant species.

A binomial generalised additive model (GAM: Hastie & Tibshirani 1990) was fitted for each species. The procedure allows the shapes of the species responses to environment to be determined from the data, rather than using fixed parametric terms. Our models are based on a small set of environmental factors and predict vegetation at the relatively coarse scale of 1 × 1 km. They do not account for the influence of aspect, slope, topographic complexity, and other microtopographic factors. Slope and aspect are unreliable predictors because they are strongly confounded with the degree of human disturbance in the landscape (fire-protected sites generally occur on steep, shady slopes in Central Otago) while topographic factors operate at finer scales than we examine here; these factors were not included in the models.

Prior to model fitting, we examined correlations between the remaining environmental variables. Five 'temperature' factors, which were primarily determined by elevation (mean annual temperature, temperature seasonality, rainfall:potential evapotranspiration ratio, October vapour pressure deficit, and annual precipitation deficit), and two 'solar radiation' factors (mean annual solar radiation and solar radiation seasonality) were strongly correlated (i.e. non-independent). Therefore, each model was able to contain six soil variables but only two independent climate variables: i.e. one of the five 'temperature' factor, and one of the two 'solar radiation' factors. For each species, we fitted models using each of the possible combinations of eight independent variables, and selected that returning the lowest residual deviance as the final model.

All records of a species in the entire dataset of 5419 records were used to build the GAM for that species. A stepwise procedure was used to fit each of the GAMs. First, an initial model was fitted containing a set of independent variables. Then, the significance of dropping each variable in turn was tested using the scaled change in deviance, which is distributed approximately as for an F-statistic (Venables & Ripley 1999). Testing proceeded until no fitted terms could be removed, or previously removed terms added, at $P < 0.01$.

For each species, the final model (Appendix 4) was used to predict a probability of occurrence *(P)* onto a 1 × 1 km grid of 15 319 points, for which environmental data had been estimated. We recognise that the number of records of a woody species in Central Otago today may be unrelated to pre-settlement density, and that it probably largely reflects the response of that species to fire and disturbance. We therefore standardised the predicted a probability of occurrence *(P)* to a percentage of the maximum predicted *P* for that species (the percentage likelihood of a species occurring P_s). The standardised predictions (P_s) therefore represent the predicted pattern of distribution of each species, rather than their abundance relative to other species.

5.5.2 Classification of pre-settlement woody vegetation zones

Zones of pre-settlement woody vegetation were defined on the basis of the predicted distributions of the 15 most common, potential canopy-dominant species from the generalised additive models only. To define the zones, the matrix of 15 × 15 319 P_s values was classified using cluster analysis (flexible sorting strategy, Canberra distance measure, $\beta = -0.25$; Clifford & Stephenson

1975). Following inspection of the classification dendrogram, clustering was terminated at the arbitrary level of 12 principal clusters (zones), and each of the 15 319 grid points was assigned to one of these zones. We imported the classification table into GIS ArcView in order to summarise the environmental characteristics of each biogeographic zone, and to examine their relationships with environmental domains.

5.5.3 Predicted composition from the models

We summarised the predicted vegetation composition for each pre-settlement woody vegetation zone, based on the generalised additive models, by calculating the average (raw or adjusted) P_s value for each of the 74 native woody species. P_s values for the 49 shade-intolerant species were adjusted for the likely effects of competition with taller species prior to calculating the average value. In this adjustment, we reduced the P_s value for each shade-intolerant species by a proportion equivalent to the maximum P_s value for any one of the 15 potential canopy species at that point. To examine the present distribution of less common native species (i.e. those that were recorded < 40 times, and therefore not included in the predictive models) we tabulated the sum of records for each species in the database within each pre-settlement woody vegetation zone. We performed a cluster analysis classification on the plot by species table of less common native and exotic species (hereafter referred to as the 'rare species classification') which categorised them into eight groups of ecologically similar rare species.

5.5.4 Evidence from charcoal, subfossil wood and pollen

In order to evaluate the modelled predictions of the potential species composition of each zone, we assembled available evidence of pre-settlement species composition from charcoals, subfossil wood remains, and pollen. Subfossil wood, charcoal, buried podzols and forest dimples indicating pre-settlement forests in eastern South Island were mapped by Molloy et al. (1963). More recently, Wardle (2001a) documented the distribution of charcoals in the Upper Clutha district of Central Otago, and the Landcare Research radiocarbon database holds further records. Four Central Otago pollen sites (Idaburn Valley: 420 m, McGlone & Moar 1998; Clarks Junction: 520 m, McGlone 2001; Earnscleugh Cave: 540 m, Clark et al. 1996; Kawarau Gorge: 800 m, McGlone et al. 1995) are most relevant to estimates of lowland and montane vegetation composition (Table 12). Interpretations of data from Pomahaka Road and Teviot Swamp (875 m and 980 m, respectively) have not been published (M. McGlone and J. Wilmshurst, pers. comm.). Several pollen cores from high-elevation sites have been described from the southern Garvie Mountains (1400 m, McGlone et al. 1995), and from the Old Man Range (McGlone et al. 1995, 1997).

5.5.5 Structural classes and loss of woody vegetation since human settlement

On the basis of modelled predictions of the 15 potential canopy species, the actual present distributions of woody life-forms, and charcoal and pollen evidence, we tentatively assigned each pre-settlement woody zone to a broad vegetation structural class simplified from Atkinson (1985). To estimate the loss of woody vegetation following human arrival, we made preliminary assumptions on the proportions of woody and non-woody vegetation types in each pre-settlement woody vegetation zone. These are that each of three lowland pre-settlement woody vegetation zones comprised 25% tall or low forest, 25% shrubland, and 50% herbaceous non-forest vegetation. Since tall shrubs are common in these zones today, these proportions probably over-estimate the pre-settlement extent of lowland non-forest vegetation. Within the six forest zones (IV, V, VI, VII, XI, XII) and the two shrubland zones (VIII, IX), we assumed that 5% of the total land area would have been covered by herbaceous non-forest vegetation, bare rock, or bare soil. We calculated the probable proportions of deforestation in each of these 11 pre-settlement woody vegetation zones since human arrival, using the GIS surfaces for Indigenous Forest and Scrub from the national New Zealand Land Cover Database (LCDB1; Ministry for the Environment 2000). The alpine tussock shrubland zone was excluded from our estimates of change in woody vegetation cover, since we judged that there was too little evidence of the type of pre-settlement vegetation cover to make underlying assumptions.

5.5.6 Strengths and limitations of the approaches

Past reconstructions of pre-settlement vegetation in Central Otago, as elsewhere in New Zealand, have been largely qualitative in nature (e.g. McGlone 2001). However, recently developed statistical tools for the interpolation of point climate data and the analysis of spatial patterns have extended our ability to objectively predict the likely biological character of regions in the absence of human activity (Leathwick 2001). In this study, we applied these tools to predict potential distributions of woody species, and derived a landscape-scale spatial framework of twelve pre-settlement woody vegetation zones, which we used as a basis to assess and describe the likely pattern of pre-settlement woody vegetation in Central Otago. The likely pre-settlement vegetation composition of each of the twelve pre-settlement woody vegetation zones was assessed using both the predictions of generalised additive models, and published interpretations of subfossil wood, charcoal and pollen data. These different approaches contribute different insights into the potential pre-settlement vegetation of Central Otago and their combination provides a more comprehensive estimate of the pre-settlement vegetation composition than either approach alone. However, both tend to provide conservative estimates of pre-settlement woody vegetation extent and composition, particularly in lowland zones and those of the upper slopes and range tops, where deforestation has been most complete.

Like any other classification, the framework of twelve pre-settlement woody vegetation zones imposes relatively arbitrary boundaries on continuous biotic and environmental variation. Our twelve zones are based on the species-environment relationships of the 15 presently most common potential canopy trees and shrubs that remain in Central Otago. Since the present-day distributions of this subset of former canopy species are likely to reflect their pre-settlement distributions to some extent, the zones represent an aspect of the pre-settlement biotic pattern, and therefore offer a more appropriate framework for understanding the former woody vegetation patterns in Central Otago than a classification based purely on environmental factors.

Predictions from the generalised additive models of the potential composition of the zones were evaluated with considerable caution. There is no reason to expect that climate change since the arrival of humans has been ecologically significant (Hall & McGlone 2001). However, predicted distributions for fire- and/or grazing-intolerant canopy species and subcanopy shrubs will be skewed towards mid-elevation sites, where sheltered and probably atypical refugia occur today. Conversely, more fire- and grazing tolerant indigenous species (particularly *Sophora microphylla*, which persists in rock tors at low elevations, and *Kunzea ericoides* and *Leptospermum scoparium*, which are often present in seral communities and regenerate readily following fire) will be over-predicted in disturbed areas, relative to more disturbance-sensitive species that have been eliminated. The species richness of the pre-settlement vegetation will tend to be under-estimated by the predictive models, since an unknown number of canopy and understorey species may have become locally extinct or too rare to be modelled. Furthermore, predictions for slow-dispersing trees that had not occupied all potentially suitable environments in Central Otago since the last glaciation (e.g. *Nothofagus* spp.) are likely be inaccurate, because the generalised additive models predict potential rather than realised ranges of woody species. Finally, the generalised additive models predict composition at a coarse scale (1 × 1 km), and do not account for the local influences of aspect, slope, topographic complexity and other micro-environmental factors, or for competitive interactions among canopy tree species in pre-settlement communities.

Subfossil remains indicate where the predicted composition of the pre-settlement woody vegetation zones, based on current distributions, are compromised by the elimination of species from parts of their former ranges, or by the recent rise to dominance of more disturbance-tolerant trees. However, both charcoal and pollen evidence have limitations, and contain biases that demand experienced and informed interpretation. Not all Central Otago environments have been well searched for sites of charcoal and pollen preservation, and less charcoal evidence tends to be preserved in Central Otago's schist-derived soils than in the greywacke soils in Canterbury, where they are more frequently buried by debris avalanching following fires (Wardle 2001). Therefore, the subfossil charcoal/wood and pollen records are far from complete. Moreover, charcoal and wood preservation is biased in favour of larger species and more durable woods, and varies according to combustion conditions, so that identifications may be probable rather than definitive (Wardle 2001; G.M. Rogers unpubl. data). The pollen record is more generalised, and ambiguous, than *in situ* charcoal evidence. Pollens that are preserved are dominated by wind-pollinated species, which may represent only a small fraction of the source vegetation; in particular, *Nothofagus* and emergent podocarps may be over-represented. Contamination with pollen from distant rather than local sources may be difficult to quantify. Finally, many insect- and bird-pollinated species that were potentially important in Central Otago (e.g. *Sophora*, *Kunzea*, *Griselinia*, *Hoheria* and *Plagianthus*) are poor pollen contributors, and may be under-represented in pollen sites.

5.6 POTENTIAL DISTRIBUTIONS OF EXOTIC WOODY SPECIES

Using methods identical to those for native species, we used GAMs of species' presence on environment to predict the probability of occurrence (P_s) of the 12 most frequent exotic woody species (i.e. all those that occurred > 40 times), at 15 319 points on the 1 × 1 km grid, using the entire dataset of 5419 records. For each exotic species, we calculated the average P_s for each environmental domain and each pre-settlement woody vegetation zone. Inadequate taxonomic distinctions in the database forced us to group all *Pinus* spp. into a single category. For each uncommon, local and rare exotic species, we summed the number of plot records within each pre-settlement woody vegetation zone.

5.7 PUBLIC CONSERVATION LANDS IN ZONES OF PRE-SETTLEMENT VEGETATION

We used ArcView to overlay the areas of land administered by the Department of Conservation (as of February 2002) on the regional zones of pre-settlement woody vegetation, and on environmental domains. We calculated the area and proportion of each pre-settlement woody vegetation zone and each environmental domain represented in public conservation lands.

6. Results

6.1 ENVIRONMENTAL DOMAINS

Following inspection, clustering of the environmental domains classification was terminated at the level of 18 groups. In this section, we briefly describe the spatial distribution of the environmental domains in the region, and give their average elevation ± 1 SD. The environmental domains are mapped (Fig. 2A) and the distribution of sample plots is shown in relation to them (Fig. 2B). Their areal extent and average environmental characteristics of environmental domains are shown in Table 1. In Table 2 we summarise the present extent of Indigenous Forest and Scrub categories from the LCDB1 (Ministry for the Environment 2000) and present-day woody plant associations within each environmental domain (as defined in Section 6.2.2).

Environmental Domain 1 (Clutha Basin, mean elevation 330 m) encompasses gently sloping basin floors from Alexandra to the shores of Lakes Wanaka and Hawea.

Environmental Domain 2 (Alexandra Basin rim, mean elevation 450 m) comprises the hillslopes around the semiarid Alexandra Basin. It extends south along the Clutha Valley to Roxburgh, as well as north-east up the Manuherikia and Ida valleys, including the Raggedy Range and the lower flanks of Rough Ridge, and the Knobby and Old Man ranges.

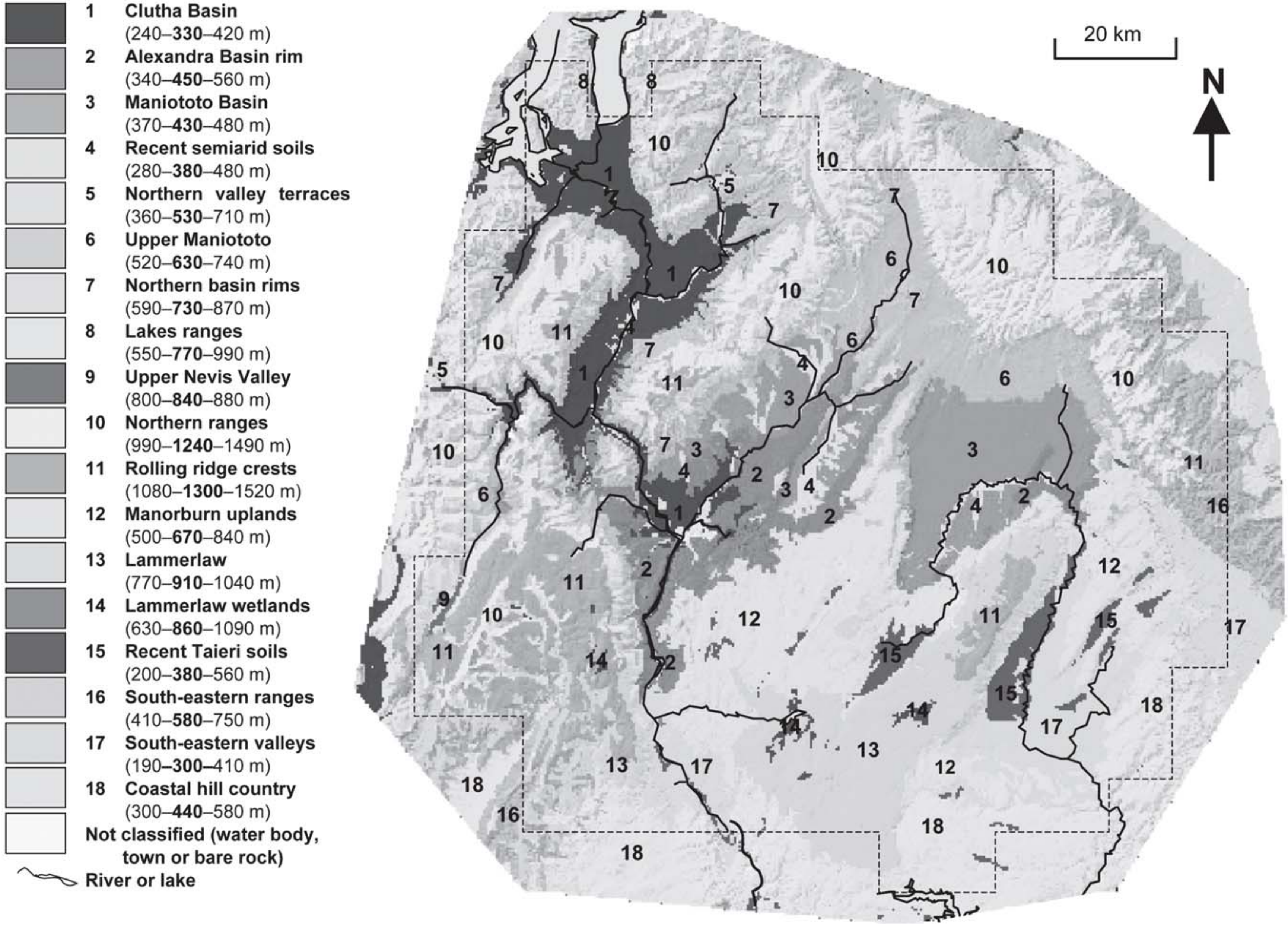

Figure 2A Environmental domains of Central Otago (dashed line indicates study area boundaries).

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