Mapping Hurunui forest community distribution, using computer models

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Claire L. Newell and John R. Leathwick

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Cover: Hurunui River 'mainland island' area, Canterbury Conservancy, South Island, New Zealand. July 1998. *Photo: Ian McFadden, Information Resource Centre, DOC.*

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Claire L. Newell[1] and John R. Leathwick[2]

[1] Landcare Research, PO Box 69, Lincoln 8152, New Zealand
newellc@landcareresearch.co.nz
[2] Landcare Research, Hamilton. Current address: NIWA, PO Box 11-115, Hamilton, New Zealand

ABSTRACT

Data from permanent forest plots were used to map the spatial distribution of forest vegetation in the North Hurunui catchment, situated within the Hurunui Mainland Island, North Canterbury, New Zealand. In a nested classification, 9 vegetation subcommunities were identified within 5 broad communities. The relationship between each community and the environment was quantified using classification tree analysis. These equations were used to map the distribution of each community in the North Hurunui catchment. The process was repeated to map subcommunities. The relationship between *Griselinia littoralis* (an important food species for native fauna) and the environment was quantified using logistic regression and used to generate a map of *Griselinia* abundance. Community, subcommunity, and *Griselinia* distribution was related to temperature and rainfall. The accuracy of mapped community and subcommunity distribution and *Griselinia* abundance was tested using a permanent-forest-plot dataset from the adjacent South Hurunui catchment. The maps predicted the proportion of coarse-scale vegetation groups, i.e. communities, more accurately in the South Hurunui catchment than the finer-scale subcommunities, or the single species *Griselinia*. These discrepancies may relate to shortcomings of the environmental data used, the absence of site-scale non-environmental factors in the vegetation–environment equations, and underlying differences in the past and present environment between the North and South Hurunui catchments. Adequate quantitative plot data and a sound ecological understanding of vegetation patterns and processes must underpin any computer-generated vegetation map. We recommend additional sampling be undertaken in the North Hurunui catchment for subcommunities that are currently under-represented by permanent plots.

Keywords: Hurunui, mainland island, Canterbury, New Zealand, vegetation distribution, computer-generated maps, classification, vegetation–environment relationships, permanent plots, forest, GIS database, validation

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1. Introduction

Accurately defining the spatial distribution of species and species groups is fundamental to the management of any conservation area. Vegetation maps provide important baseline information on the spatial distribution of species and vegetation communities. Used in conjunction with digital environmental information vegetation maps are essential for managing issues related to biodiversity conservation. Such issues include the distribution and long-term sustainability of vegetation communities with high conservation values, the presence and survival of rare plants and animals, the reintroduction of rare species, the impact and spatial distribution of introduced plants and animals, and their interaction with rare native plants and animals. For example, for the management of rare mohūa / yellowhead populations, it is important to know the distribution of specific beech forest communities to be able to target poison and / or trapping of predators during mast seeding years in beech forest. Similarly, understanding the distribution of specific vegetation communities that may contain rare plant species, such as *Pittosporum patulum*, would help target future field surveys for this species and pest control operations.

Traditional methods of describing the spatial distribution of vegetation communities were based on aerial photography and interpolation of information from point-based plot data or knowledge from other catchments. Boundaries between vegetation units were subjectively identified using coarse-scale differences in the composition, colour, and texture of the overstorey vegetation and differences in broad geomorphic units that were distinguishable by stereoscope. Differences could be accurately defined between major vegetation groups, separating, for example, shrublands, alpine grasslands, and forests. However, the ability to distinguish between individual communities within a major vegetation group is often more difficult because of subtle compositional and structural differences between communities. This is particularly problematic in New Zealand forests dominated by *Nothofagus* species, where individual communities are difficult to differentiate by aerial photography and where all communities within an entire conservation area may be dominated by one or two canopy species. This is a major issue for much of the eastern South Island and some North Island areas. The Hurunui Mainland Island, in North Canterbury, is one example where forest canopies are dominated by a limited number of *Nothofagus* species with typically very subtle differences in canopy composition between communities.

The spatial distribution of vegetation is, at least in part, controlled by environmental processes, which influence the composition, structure, and functioning of vegetation communities and hence their geographic distribution (Whittaker 1975). Understanding how specific environmental processes relate to vegetation distribution goes hand in hand with the development of vegetation maps for an area. Developments in computer technology and statistical techniques have enabled us to quantify the relationship between vegetation and the environment and express this information spatially in the form of vegetation maps in a geographic information system (GIS). These techniques can be used to map both the distribution of vegetation communities and individual species and will be particularly important for mapping the distribution of rare species. These maps can be refined as additional information comes to hand. For example, quantitative information on nesting sites of mohūa could be added to existing data used to quantify the distribution of this rare and endangered bird.

2. Background

The Department of Conservation (DOC) manages the headwaters of the north and south branches of the Hurunui River as a 'mainland island' management unit. Intensive management of the Hurunui Mainland Island for the purposes of conserving threatened wildlife and other conservation values requires a sound understanding of the broad patterns of vegetation across the area. Knowledge of plant communities, their composition, distribution, and relationship with the environment will influence management actions directed at wildlife or plant conservation, as well as pest and weed control. An important focus of the Hurunui Mainland Island programme is to provide effective and efficient methods for minimising the adverse impact of introduced browsing animals on vegetation composition, structure, and community function. There is a strong focus on the management of rare flora and fauna. Detailed maps defining the distribution of vegetation communities and rare plant species are an important prerequisite for the management of this area. Newell & Burrows (2000) recommended that such maps be derived by modelling community and species distribution rather than by interpretation of aerial photography, with models based on quantified relationships between community composition and specific environmental variables.

Vegetation maps based on aerial photography are of limited use to the day-to-day management of the Hurunui Mainland Island. The forests of this management area are dominated by one to three *Nothofagus* species. Canopy composition varies little between some communities and therefore community distribution cannot be easily interpreted using aerial photography. Compositional differences between communities occur in the understorey strata and these cannot be detected from aerial photographs (Newell & Burrows 2000). However, such differences can be detected by understanding how specific environmental processes influence the distribution of individual communities. These vegetation–environment relationships can be used to map community distribution and when used in combination with quantitative information on other biota, such as pest distribution and abundance, and home range size of rare birds, provide a powerful, quantitative tool for managing the Hurunui Mainland Island. For example, to determine the appropriate level for controlling populations of the introduced brushtail possum, managers could model distribution at several different population levels to determine how variation in possum population density affects mistletoe distribution. Visual representations of these scenarios would also help identify which areas of the mainland island need greater pest control.

3. Objectives

- To classify data from permanent forest plots in the North Hurunui catchment into vegetation communities for management purposes.
- To describe methods and produce a computer-generated map showing the distribution of forest vegetation communities in the North Hurunui catchment. Vegetation community distribution will be derived from equations that quantify the relationship between species composition and characteristic environmental conditions.
- To map the distribution of a rare or significant species based on species abundance and its relationship with the environment.
- To test the ability to use quantitative vegetation–environment relationships derived in the North Hurunui catchment to accurately predict the distribution of forest vegetation communities and a single species in the adjacent South Hurunui catchment.
- To assess the accuracy of predicting vegetation communities and a single species and determine whether coarse- and / or fine-scale compositional information can be mapped accurately.
- To discuss the benefits and limitations of computer-generated vegetation maps.
- To provide recommendations on the future development of computer-generated vegetation maps.

4. Methods

4.1 STUDY AREA

The Hurunui Mainland Island is situated immediately east of the Main Divide in Lake Sumner Forest Park. One of the significant features of this mainland island is that it provides habitat for a range of rare bird and plant species. The North Branch and South Branch of the Hurunui River are the two major catchments in this conservation unit and they flow west to east with the North Hurunui draining into Lake Sumner (520 m; see Fig. 3). There is also a west–east rainfall gradient, ranging from approximately 4000 mm to 1200 mm per year (Jane 1985). Both valleys have similar mountainous terrain, with highest peaks reaching 1716 m and 1815 m, respectively, in the North and South Hurunui catchments. The floor of each valley is about 650 m in the east rising to 800 m at the western-head. The area is underlain with interbedded greywacke and argillite (Suggate et al. 1978) and is classified as environmental units P1, P2 of the Central Mountains Environment and R1 of the Southern Alps Environment by the recent *Land Environments of New Zealand* classification (Leathwick et al. 2003). The two valleys are forested and are dominated by mountain, red and silver beech (*Nothofagus solandri* var. *cliffortioides*, *N. fusca*, and *N. menziesii*) (Burrows et al. 1976; Jane 1985; Newell & Burrows 2000).

4.2 DATA COLLECTION

Over the summers of 1999 and 2000 DOC staff remeasured 101 of the existing permanently marked forest plots (20 × 20 m; 400 m^2) in the North Branch of the Hurunui River valley (Appendix 1). These plots were part of a larger set established by the former New Zealand Forest Service in 1975 (see Burrows et al. 1976; Newell & Burrows 2000). The plots are systematically spaced along randomly located lines which follow a compass bearing from a point on the valley floor to the nearest subalpine grassland or ridge top (Burrows et al. 1976). The composition of vascular plant species present in each plot was quantified using the standard reconnaissance plot procedure (see Allen 1992 for method details). Each plot is categorised into six standardised height classes (< 0.30 m tall, 0.30–2.0 m, 2.0–5.0 m, 5.0–12 m, 12–25 m, > 25 m) and the composition of each height class is quantified by estimating the foliage cover of each vascular species within the height class. Foliage cover is recorded as one of six cover classes (cover class 1 = < 1% foliage cover within a height class, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%). Plant species nomenclature followed Webb et al. (1988), Brownsey & Smith-Dodsworth (1989), Parsons et al. (1995), Cameron (1999), and Edgar & Connor (2000).

The physical characteristics of each plot (altitude, slope, and aspect) were also estimated in the field. Plot position was geo-referenced using a global positioning system for all but three plots. Vegetation structural characteristics (tree diameters, sapling and seedling counts; see Allen (1993) for method details) were also recorded at each plot but these data were not used in the present study.

4.3 NESTED FOREST COMMUNITY CLASSIFICATION

The first step in generating a vegetation map is to identify which vegetation groups will be mapped. These vegetation groups represent the management units for the conservation area. The characteristics of a vegetation group, the composition of the flora and fauna, regeneration patterns, stand structure, and environmental conditions define the group and its relevance to management issues in the conservation area.

In this study we quantified the vegetation groups present in the North Hurunui catchment using a classification procedure that categorises plots into groups with similar composition. We used a nested classification with vegetation groups classified at two different levels within the classification to enable us to determine whether vegetation groups can be accurately mapped at more than one level of compositional detail.

The classification was based on plant species composition information from each of the 101 North Hurunui permanent forest plots and was run in the package PC-ORD (McCune & Mefford 1999) using default settings. The procedure involved three steps. Firstly, species composition was quantified by calculating the total cover for each species in a plot as the sum of the foliage cover-class scores across all tiers. Species abundance was standardised by plot with the total cover of each species divided by the sum of total cover values for all species in the plot (Noy-Meir et al. 1975; van Tongeren 1995). This standardisation gives equal weight to the compositional information from each plot (Noy-Meir et al. 1975) and takes species rank-order into account. Rank-order is important in forests where most compositional differences between vegetation groups occur in the understorey tiers. This applies to *Nothofagus*-dominated forests of the North Hurunui and many other eastern South Island areas where forests have only a limited number of canopy species and there are only subtle changes in their relative abundance between different vegetation groups. The second step used Sørenson's distance measure (Bray & Curtis 1957) to develop a similarity matrix based on standardised species abundance where the composition of each plot was compared with every other plot to determine which plots were compositionally similar to each other. In the final step plots were grouped in a nested classification using the Unweighted Pair-Group Method using arithmetic Averages (UPGMA) clustering method, which groups plots by their average compositional similarity (Sneath & Sokal 1973). The degree of compositional similarity changes at different levels in the classification. At the coarsest level of compositional similarity the 101 plots divided into two large groups. With subsequent subdivisions within the classification, the compositional similarity within each group increased and the number of plots in each group decreased. We recognised groups at two different levels of compositional similarity. 'Communities' represented ecologically meaningful groups of plots that had a coarse level of compositional similarity. These subdivided into 'subcommunities' where distinct subgroups with greater compositional similarity within a community existed. Subcommunities could be recognised in the field by an observer.

The composition of each community and subcommunity was summarised using RECSUM in PC-RECCE (Hall 1992). For each group we calculated the percentage frequency of plots that each species occurred in, the mean cover class of each species, and mean species richness representing the average number of species per plot. Communities and subcommunities were named using the most frequent species in the respective group and frequent species that distinguished specific groups from each other.

4.4 MAPPING VEGETATION DISTRIBUTION

We used 98 of the 101 plots to develop a computer-generated map of the communities and subcommunities identified in the nested UPGMA classification. The three plots without an accurate spatial location were not used. The distribution of a single species was also mapped. *Griselinia littoralis* was selected because of its significance in the North Hurunui catchment as a food species for rare birds (O'Donnell & Dilks 1994) and its high palatability to introduced deer (Stewart et al. 1987). The presence of *G. littoralis* in more than half the plots used in this study was also another consideration. Other significant, highly palatable species occurred in only a limited number of plots and therefore did not have sufficient information for accurate mapping.

Plot locations were imported into the GIS ArcView 3.2, where environmental values, known to be correlated with New Zealand's forest pattern (see

Leathwick (1998, 2002) for detailed information), were extracted by overlay onto the following raster environmental layers:

- Aspect (°)
- Mean average temperature of the warmest month (°C)
- Mean annual minimum temperature (°C)
- Mean monthly ratio of rainfall to potential evaporation
- October vapour pressure deficit (kPa)
- Slope (°)

Although estimates of solar radiation have been shown to correlate with variation in forest pattern at national scales (Leathwick 2002), they were not used in this analysis because of their minimal variation over the geographic range of the study area. All environmental layers were stored at a spatial resolution of 100 m.

We used a technique called 'classification tree analysis' to quantify the relationship between the above environmental variables and the UPGMA vegetation classification and this was run in S-Plus (Anon. 1998). Two classification tree analyses were performed to quantify, firstly, the relationship between vegetation communities and the environment, and secondly, the relationship between vegetation subcommunities and the environment. The results of each set of analyses were input into the ArcView Spatial Analyst's 'map calculator' to produce a map of communities and a map of subcommunities in the North Hurunui catchment.

We chose classification tree analysis, as it has been shown to have greater predictive accuracy than other statistical techniques for generating computerised vegetation maps because of its ability to identify and estimate complex relationships between response and predictor variables (see Michaelson et al. 1994; Vayssières et al. 2000; Franklin 2002). Classification trees (Breiman et al. 1984) belong to a family of algorithmic methods that generate decision trees from a set of learning cases. With this method the data are successively subdivided into increasingly homogeneous subsets based on values of predictor variables, in our case environmental variables. Subdivisions occur at a particular value of the predictor variable. At the first subdivision, all possible splits are considered for all predictor variables; these are ranked and the best possible split is chosen. The analysis then evaluates all possible splits in each subset and the process is repeated at subsequent levels until further splitting becomes impossible (Vayssières et al. 2000). An advantage of classification tree analysis is the ability to capture non-linear relationships and relationships between response and predictor variables that are conditional on the values of other predictors (Michaelson et al. 1994). For example, a classification tree may split the data based on rainfall and then find that the next division on one side of the original split relates to humidity, whereas the subdivision of data in the other half of the original split relates strongly to soil pH. The analysis devises a series of rules applied to the predictor variables that classify observations according to their membership in different levels of a factor response variable; the level of correct classification giving a measure of the discriminatory power of the predictor variables. For example, if the first rule for the classification tree analysis of vegetation communities is 'mean annual minimum temperatures < –9.0ºC', a community with temperatures less than –9.0°C will be split off from other communities predominantly not meeting this environmental condition. Once redundant splits have been eliminated (i.e. in which both sides of the rule led to the same outcome), the equations derived from the classification tree can be used to quantify the distribution of each community on a vegetation map.

The single-species *Griselinia littoralis* map used *Griselinia*-cover-class values summed across all tiers within a plot, with a maximum value of 11 per plot. We chose to use cover-class values to produce the single-species map rather than stem density or basal area, as species with high conservation values are mostly herbaceous or understorey species that are not captured adequately by other standard vegetation measures recorded on 20 × 20 m plots (e.g. tree diameter information, sapling and seedling counts). The use of *Griselinia*-cover-class values rather than presence / absence per plot enabled us to estimate variation in the abundance of this species across the North Hurunui catchment. The relationship between *G. littoralis* abundance and the environment was analysed using logistic regression with the summed cover class values treated as a binary denominator. Initially we fitted a generalised additive model (Hastie & Tibshirani 1990) using all six environmental variables listed above. Generalised additive models have the advantage over conventional regression models in their ability to model both linear and complex relationships with environmental parameters (Bio et al. 1998; Leathwick 1998). Backwards elimination of variables left only the average temperature of the warmest month, the ratio of rainfall to potential evaporation (PET), and October vapour pressure deficit as significant terms. Inspection of the relationships fitted in this regression revealed generally linear relationships, so to simplify prediction in ArcView, a generalised linear model (McCullagh & Nelder 1989) was fitted using a quadratic term for summer temperatures, and linear terms for rain / PET and October vapour pressure deficit. Inspection of the distribution of residuals from this model indicated that treatment of the data as a pseudo-binary variable was a satisfactory choice with regard to model specification.

4.5 MAP VALIDATION AND PREDICTION IN THE SOUTH HURUNUI

Where a computer-generated vegetation map has been derived from a set of quantitative relationships between vegetation communities and the environment it should be possible to use those equations to predict the distribution of vegetation in an adjacent catchment with similar environmental parameters. If the results are reliable this would reduce the costs of collecting baseline data, freeing up money for more-focused management work. In this study we predicted vegetation distribution in the South Hurunui catchment, immediately to the south of the North Hurunui catchment, using the quantitative equations that defined the relationship of North Hurunui vegetation communities and subcommunities with the environment.

The North and South Hurunui catchments adjoin north–south, and run west–east across a broadly similar longitudinal range (see Fig. 3 on page 19). The underlying geology, climate, and topography are generally similar in both catchments, with a decreasing rainfall gradient running west–east. However, the South Hurunui catchment is offset slightly to the east of the North Hurunui and most likely has a lower rainfall than the latter catchment (C. Woolmore, DOC, pers. comm.). A recent regional classification of forest data, which included the North and South Hurunui catchments and adjacent catchments east of the Main Divide, showed that the North and South Hurunui catchments have a similar range of forest vegetation communities and subcommunities present, although the abundance of individual groups varies between the two catchments (Newell & Burrows 2000). A number of subcommunities found in the South Hurunui are absent from the North Hurunui catchment, possibly reflecting environmental differences between the two catchments (Newell & Burrows 2000). Such differences are likely to reduce the ability to validate our computer-generated maps. We attempted to minimise any environmental differences associated with the west–east rainfall gradient by only using the section of the South Hurunui catchment that fell within the same longitudinal range as our North Hurunui study area.

It is important to determine the accuracy of any computer-generated vegetation map. Field checking provides one of the most rigorous validation methods where the modelled vegetation unit(s) is compared with the actual vegetation (Congalton 1991) at randomly chosen sites across the study area. This method is expensive in a remote area such as the North Hurunui catchment and was beyond the financial constraints of the present study. Another approach is to randomly select half the plot data to generate computer maps and use the remaining plot data to validate the maps. However, for our study, quantitative relationships between vegetation and the environment based on 45 plots would not have provided the level of accuracy to reliably map vegetation distribution, particularly at the subcommunity level where the number of plots within a group might be low. An alternative approach is to use an existing dataset from an adjacent area with similar environmental conditions to validate the maps. We chose the latter validation method and used data from the 1986 remeasurement of 89 permanent forest plots (20 × 20 m) located in the South Hurunui catchment (see Appendix 1). The data were collected using the methods described for the North Hurunui data used in this study.

To test the accuracy of the two predictive vegetation maps we compared the predicted vegetation classification assignment of each permanent plot, based on the predicted South Hurunui community and subcommunity maps, with the actual UPGMA classification assignment of each plot, which was derived from the species composition of each permanent plot. To assess the ability to predict single-species distributions we used the logistic regression equation that defined the relationship of *Griselinia littoralis* abundance in the North Hurunui catchment to predict the distribution and abundance of *G. littoralis* in the South Hurunui catchment and compared predicted abundance of this species at a plot with observed abundance on each permanent plot.

The first step in the validation was to identify where each South Hurunui plot fitted into the nested North Hurunui UPGMA classification. At the community level, we calculated the compositional distance between each South Hurunui plot and the average composition of each North Hurunui community. Compositional distance was calculated using a similarity matrix based on

Sørenson's distance measure (Bray & Curtis 1957) with species abundance standardised by plot following the procedures used to generate the North Hurunui UPGMA classification. The maximum compositional distance defining plot assignment at the community level in the UPGMA classification was used to assign South Hurunui plots to a North Hurunui community. Each South Hurunui plot was tentatively assigned to a community by identifying the community with the smallest compositional distance to the respective South Hurunui plot. The assignment to this community was accepted if the distance between the community and the South Hurunui plot was less than the maximum compositional distance used to define communities in the UPGMA classification. Where the distance exceeded the maximum, plots were considered to be compositionally different to any North Hurunui community and were not assigned. The same procedure was used to assign South Hurunui plots to North Hurunui subcommunities, with compositional distance calculated between each South Hurunui plot and the average composition of each subcommunity. Maximum compositional distance defining plot assignment at the subcommunity level in the UPGMA classification was used to determine to which subcommunity, if any, a South Hurunui plot should be assigned.

In the second validation step the equations used to produce the computer-generated vegetation maps for the North Hurunui catchment were run to produce predictive maps of community and subcommunity distribution in the South Hurunui catchment. The predicted classification assignments were extracted for each permanent plot location and these were compared with actual UPGMA assignments of each plot identified by calculating compositional similarity with the nested North Hurunui UPGMA classification.

The equation used to map *Griselinia littoralis* distribution in the North Hurunui catchment was run to predict *G. littoralis* distribution and abundance in the South Hurunui catchment. Predicted values were compared with actual recorded values for each South Hurunui plot and differences were assessed using the Wilcoxon's rank-sum test. The similarity of observed and predicted *G. littoralis* abundance values were examined using Spearman's correlation analysis. These analyses were performed in SAS, version 8.2 (SAS Institute Inc. 2001).

5. Results

5.1 NESTED FOREST COMMUNITY CLASSIFICATION

The nested UPGMA classification recognised five communities (Table 1).

Silver beech (*Nothofagus menziesii*) dominates the canopy of subcommunities in one community (Silver Beech forest). This species also co-dominates with red beech (*N. fusca*) in Red Beech–Silver Beech forest, and with red and mountain beech (*N. solandri* var. *cliffortioides*) in Red Beech–Silver Beech–Mountain Beech forest. Mountain beech dominates the fourth community (Mountain Beech forest). The remaining community, Seral forest, is represented by only two plots, which precluded us quantifying its relationship with the environment and mapping its distribution. Four of the five communities subdivided into more than one subcommunity, with a total of nine subcommunities recognised within the five communities (Table 1). The composition of each community and subcommunity is described in Section 5.3.

5.2 USING QUANTITATIVE VEGETATION–ENVIRONMENT RELATIONSHIPS

Twelve terminal nodes were identified in the classification tree analysis that quantified the relationship between the environment and North Hurunui communities identified using the UPGMA classification (Fig. 1). The initial split in the classification tree related to mean annual minimum temperatures, separating plots according to whether temperatures were mostly greater or less than 8.95°C, written as 'Nz.anntmin<-89.5' and 'Nz.anntmin>-89.5' in Fig. 1. Sites

TABLE 1. THE FIVE COMMUNITIES AND NINE SUBCOMMUNITIES IN THE NORTH HURUNUI CATCHMENT, IDENTIFIED BY THE NESTED UPGMA CLASSIFICATION.

COMMUNITY	SUBCOMMUNITY*	N*	SPECIES RICHNESS* MEAN	SPECIES RICHNESS* SD
1. Silver Beech forests	1.1 Silver beech / *Polystichum vestitum–Coprosma depressa* forest	7	27.00	4.73
	1.2 Silver beech / *Olearia lacunosa* forest	4	21.00	4.24
2. Red Beech–Silver Beech forests	2.1 Red beech–Silver beech / *Myrsine divaricata–Coprosma ciliata* forest	25	25.80	5.73
	2.2 Red beech–Silver beech / *Pseudopanax crassifolius* forest	9	23.44	11.56
3. Red Beech–Silver Beech–Mountain Beech forests	3.1 Red beech–Silver beech–Mountain beech forest	31	15.00	8.24
4. Mountain Beech forests	4.1 Mountain beech–Silver beech forest	14	11.43	6.50
	4.2 Mountain beech forest	4	5.50	3.70
	4.3 Mountain beech / *Phyllocladus alpinus* forest	5	20.40	5.94
5. Seral forests	5.1 Seral forest	2	26.50	10.61

* Number (N) of the permanent forest plots (20 × 20 m) and species richness are shown by subcommunity.

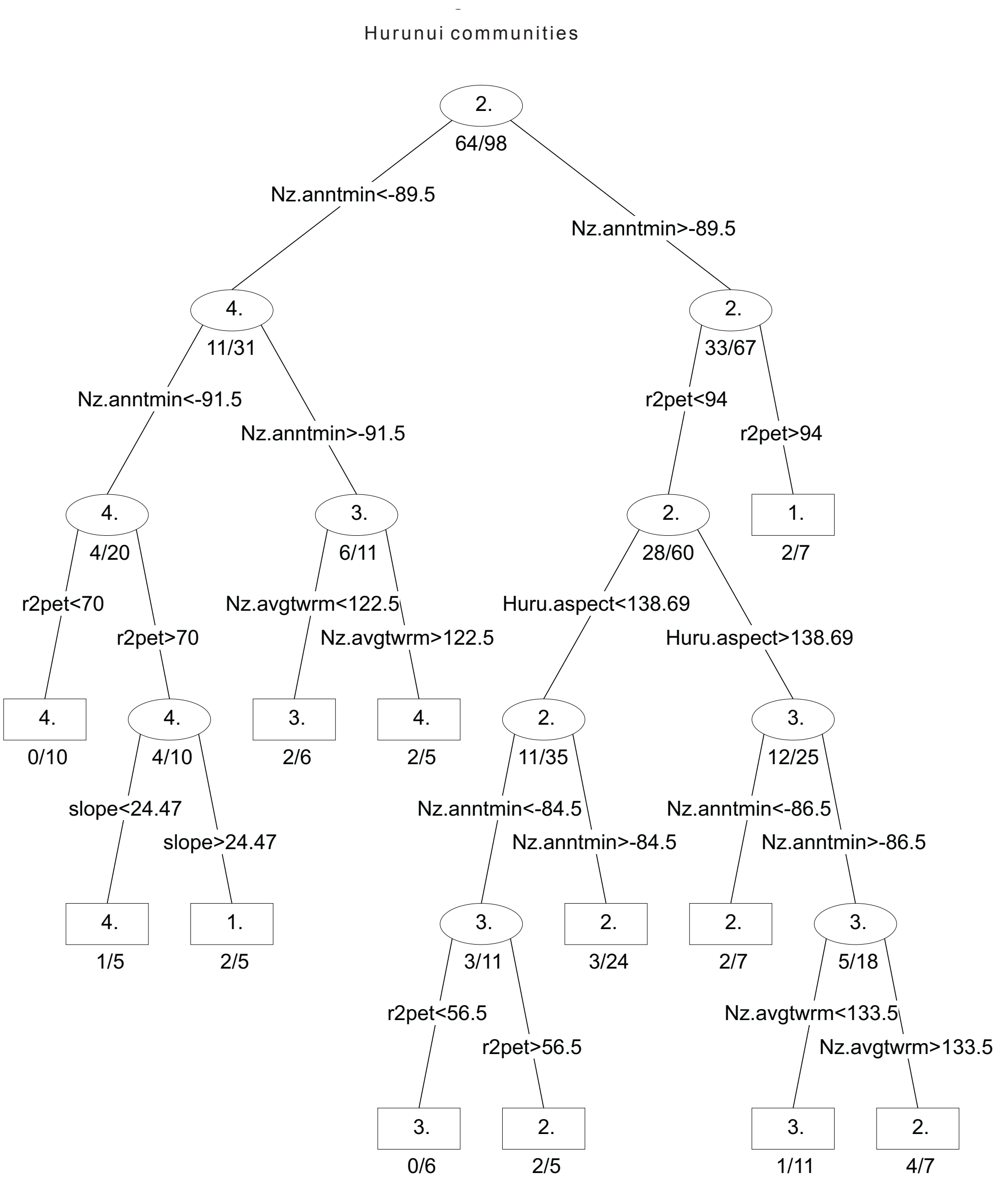
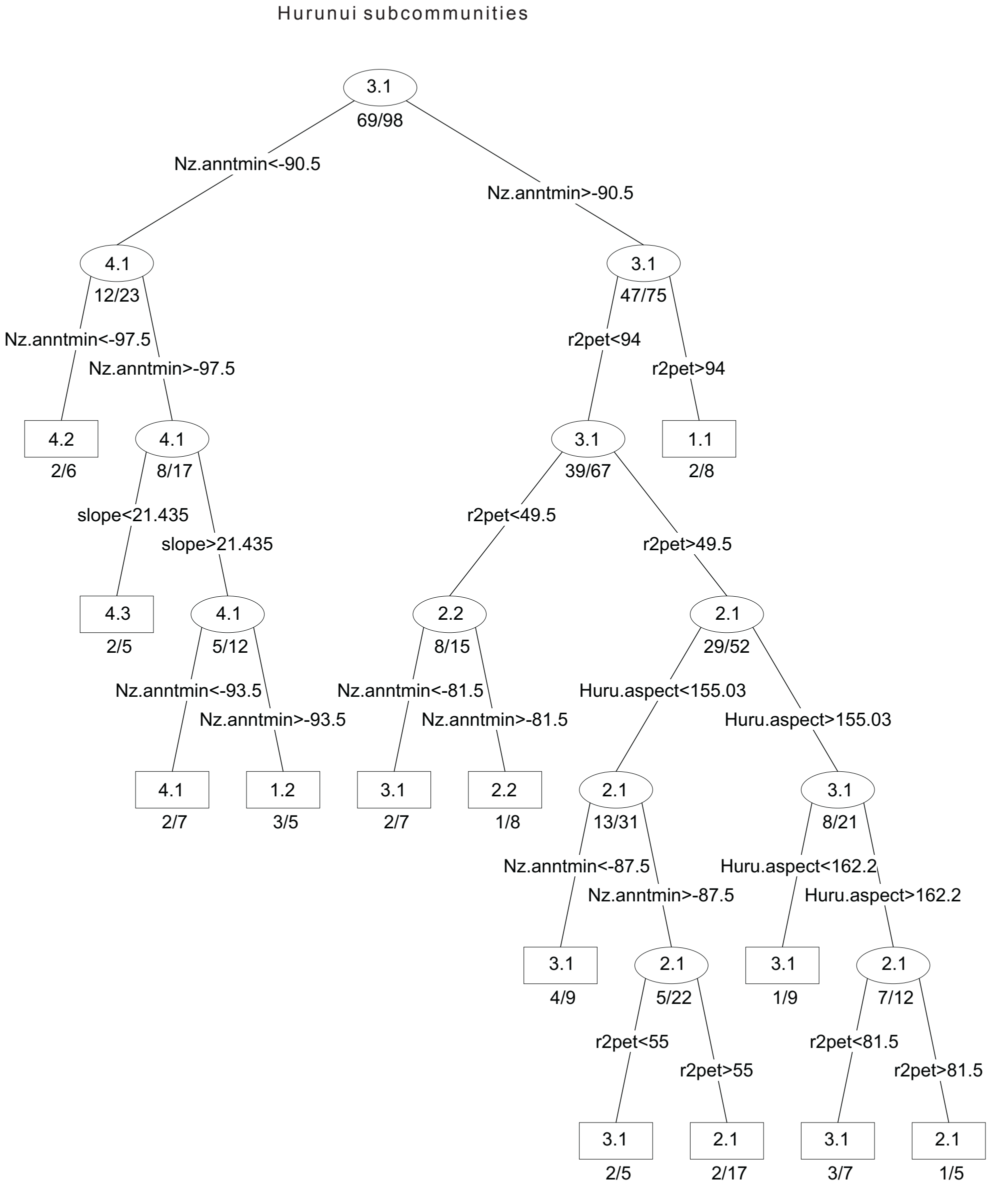


Figure 1. Classification tree analysis for North Hurunui communities. Abbreviations used for variables are as follows: aspect = aspect (°), Nz.anntmin = Mean annual minimum temperature (°C), Nz.avgtwrm = Mean average temperature of the warmest month (°C), r2pet = Mean monthly ratio of rainfall to potential evaporation, slope = slope (°). The ellipses represent internal nodes and the rectangles represent terminal nodes of the tree. The numbers inside ellipses and rectangles represent the community split off (see Table 1 for full community names). Beneath each ellipse or rectangle is the number of observations misclassified out of the total observations made at that node.

with temperatures less than 8.95°C mostly fell within Mountain Beech forests (community 4; shown by '4' written inside the ellipse below the initial split in Fig. 1). Lower splits in the classification tree were mostly predicted by differences in the mean monthly ratio of rainfall to potential evaporation (r2pet) and mean average temperature of the warmest month (Nz.avgtwrm). Slope and aspect were each used only once. The overall misclassification rate for this classification tree is 21.4%, which means that the analysis will accurately predict the distribution of vegetation communities, based on the environmental information supplied, approximately 80% of the time. This is a high level of accuracy considering the inherent noise in vegetation data. The equations derived from the classification tree were used to generate the map of vegetation community distribution in the North Hurunui catchment (shown later in Fig. 4).

The classification tree analysis of subcommunities also identified 12 terminal nodes (Fig. 2), with minimum temperatures and rainfall again used more

Figure 2. Classification tree analysis for North Hurunui subcommunities. See Fig. 1 for list of abbreviations for environmental variables and explanation of the ellipses and rectangles. The numbers inside ellipses and rectangles represent the subcommunity split off (see Table 1 for full subcommunity names).



frequently to define splits than slope and aspect. Mean average temperature of the warmest month was not used to define splits in contrast to the community classification tree analysis (Figs 1, and 2). The initial split in the subcommunity analysis also related to mean annual minimum temperatures, separating plots according to whether temperatures were mostly greater or less than 9.5°C (Nz.anntmin> 90.5 in Fig. 2). Sites with temperatures less than 9.5°C were mostly subcommunities within Mountain Beech forests (Community 4). The overall misclassification rate for this tree is 28%, indicating that the analysis will accurately predict the distribution of subcommunities approximately 70% of the time. The higher misclassification rate for the subcommunity tree probably relates to local factors, such as disturbance, that were not included in the model. Equations derived from the classification tree of subcommunities were used to generate a map of subcommunity distribution in the North Hurunui catchment (shown in Fig. 5, below).

5.3 PLANT COMMUNITY COMPOSITION, NORTH HURUNUI CATCHMENT

Plant community composition and mapped distribution in the North Hurunui catchment.

1. Silver Beech forests

Silver Beech forests account for 11% of the permanent plots in the North Hurunui catchment and the computer-generated map shows their distribution at high altitudes in the wetter, western half of the North Hurunui catchment (Fig. 4). The nested UPGMA classification identified two distinct subcommunities within this community.

1.1 Silver beech / *Polystichum vestitum–Coprosma depressa* forest

Silver beech dominates the canopy (Table 2, see page 23) (mean top height 18.9 m, standard deviation [hereafter SD] 4.1 m; Table 3, see page 24) and mid-storeys while mountain beech has limited abundance in the canopy. Prickly shield fern (*Polystichum vestitum*) and creeping *Coprosma depressa* dominate the forest floor. The diverse range of shrub species and low-cover forest floor species contribute to the high species richness, with the average of 27 species per 400-m^2 plot making this subcommunity the most species-rich subcommunity of all nine recognised in the study (Table 1). High rainfall also may contribute to high species richness. The computer-generated maps show the distribution of this subcommunity in the wet, western head of the North Hurunui catchment as well as some high-altitude sites further east (Fig. 5). The altitudinal distribution of the permanent plots indicates that this subcommunity occurs at mid-altitudes (962 m mean altitude, SD 96 m; Table 3) whereas the computer-generated map based on the classification tree equations suggests a higher-altitude distribution.

1.2 Silver beech / *Olearia lacunosa* forest

Silver beech dominates the canopy of this stunted forest (mean top height 16.0 m, SD 8.0 m; Table 3). *Olearia lacunosa* is the major species in the small tree and shrub storeys and *Dracophyllum traversii* has patchy abundance (Table 2). The forest floor is densely covered with *Coprosma depressa*. This subcommunity is restricted to a narrow, high-altitude band (1082 m mean altitude, SD 40.1 m; Table 3) that has been mapped across the entire North Hurunui catchment (Fig. 5).

2. Red Beech–Silver Beech forests

Red Beech–Silver Beech forests account for 34% of the permanent plots. The computer-generated map shows their wide distribution across the study area at low- and mid-altitudes (Fig. 4). Two subcommunities were recognised in this community.

2.1 Red beech–Silver beech / *Myrsine divaricata–Coprosma ciliata* forest

Red and silver beech dominate the tall canopy (mean top height 25.4 m, SD 5.2 m) and mid-storeys of this subcommunity (Tables 2, and 3). There is a diverse range of small-leaved species in the small-tree and shrub tiers with *Myrsine divaricata* and *Coprosma ciliata* most abundant. The diversity in

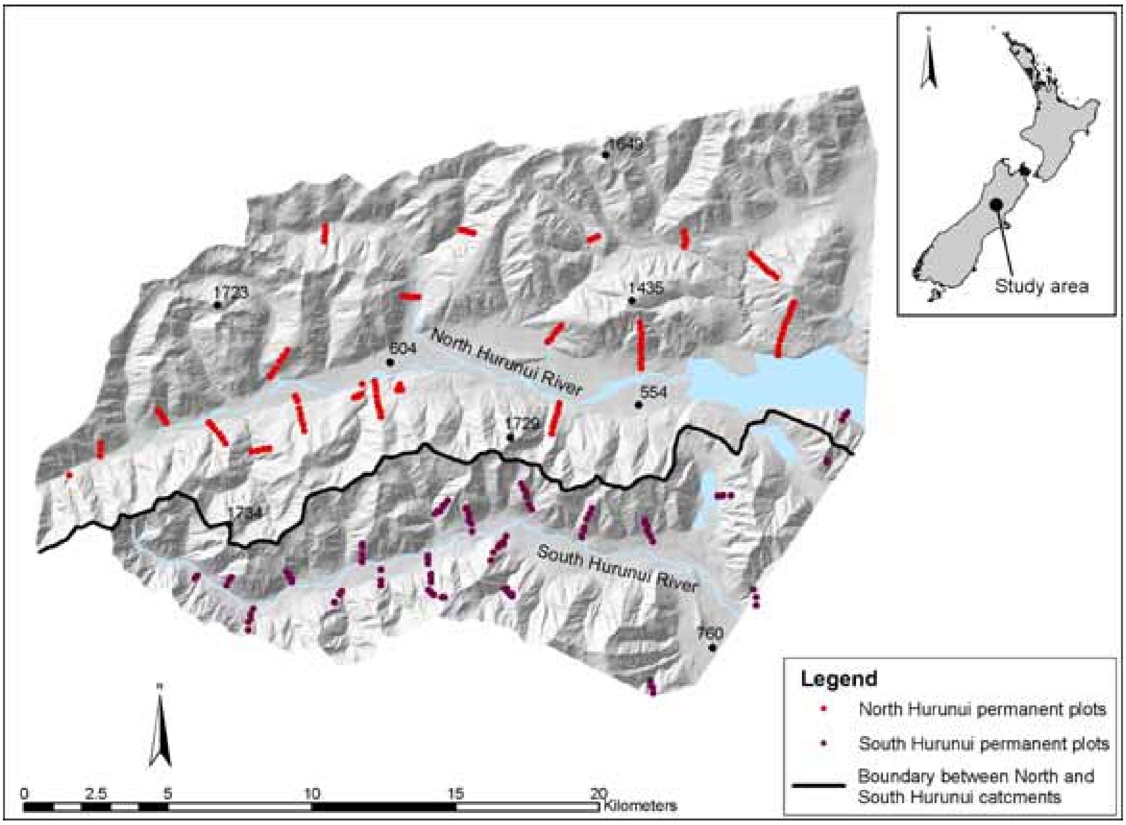


Figure 3. Digital elevation model showing location of permanent forest plots (20 × 20 m) in the North (red dots) and South (pink dots) Hurunui River catchments. Lake Sumner (520 m a.s.l.) is on the right side of the map. The black line represents the boundary between the North and South Hurunui catchments. Spot heights are shown in metres.

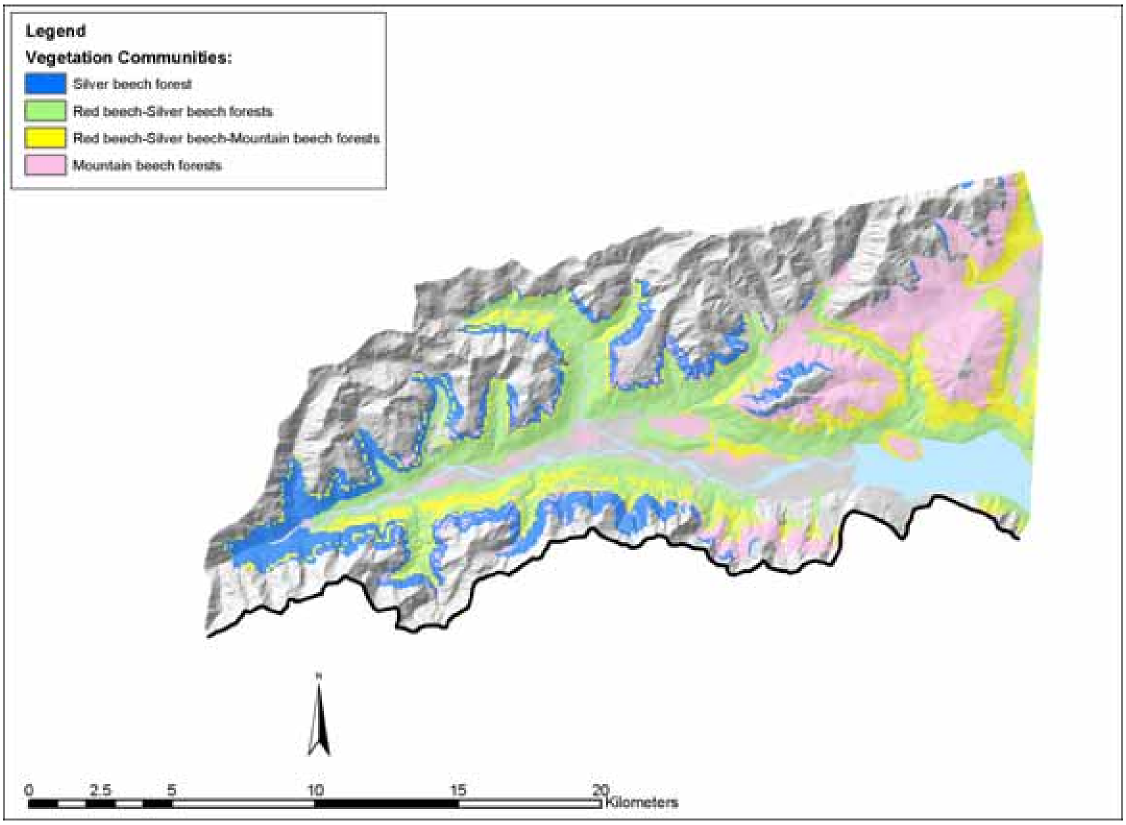


Figure 4. Computer-generated map showing the distribution of forest communities in the North Hurunui catchment. The distribution is derived from equations defining the relationship between each community and the environment using classification tree analysis. Plots were assigned to communities using the UPGMA classification.

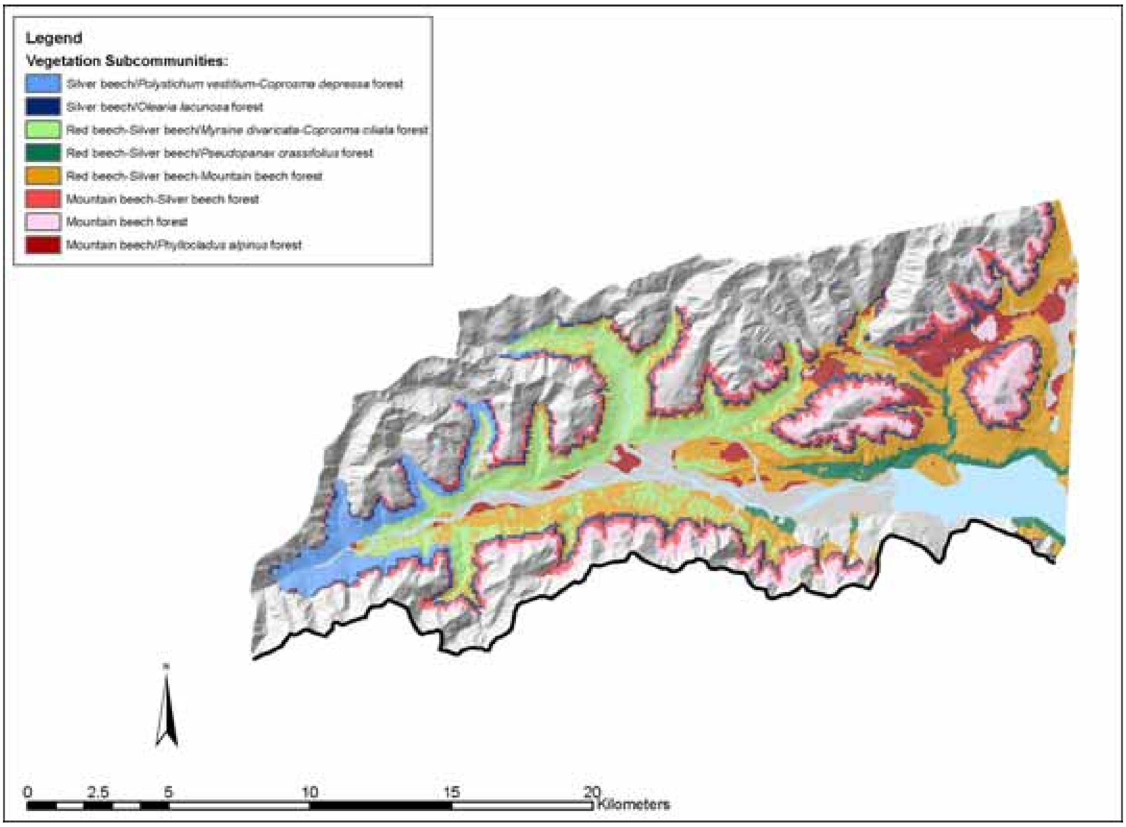


Figure 5. Computer-generated map showing the distribution of forest subcommunities in the North Hurunui catchment. The distribution is derived from equations defining the relationship between each subcommunity and the environment using classification tree analysis. Plots were assigned to subcommunities using the UPGMA classification.

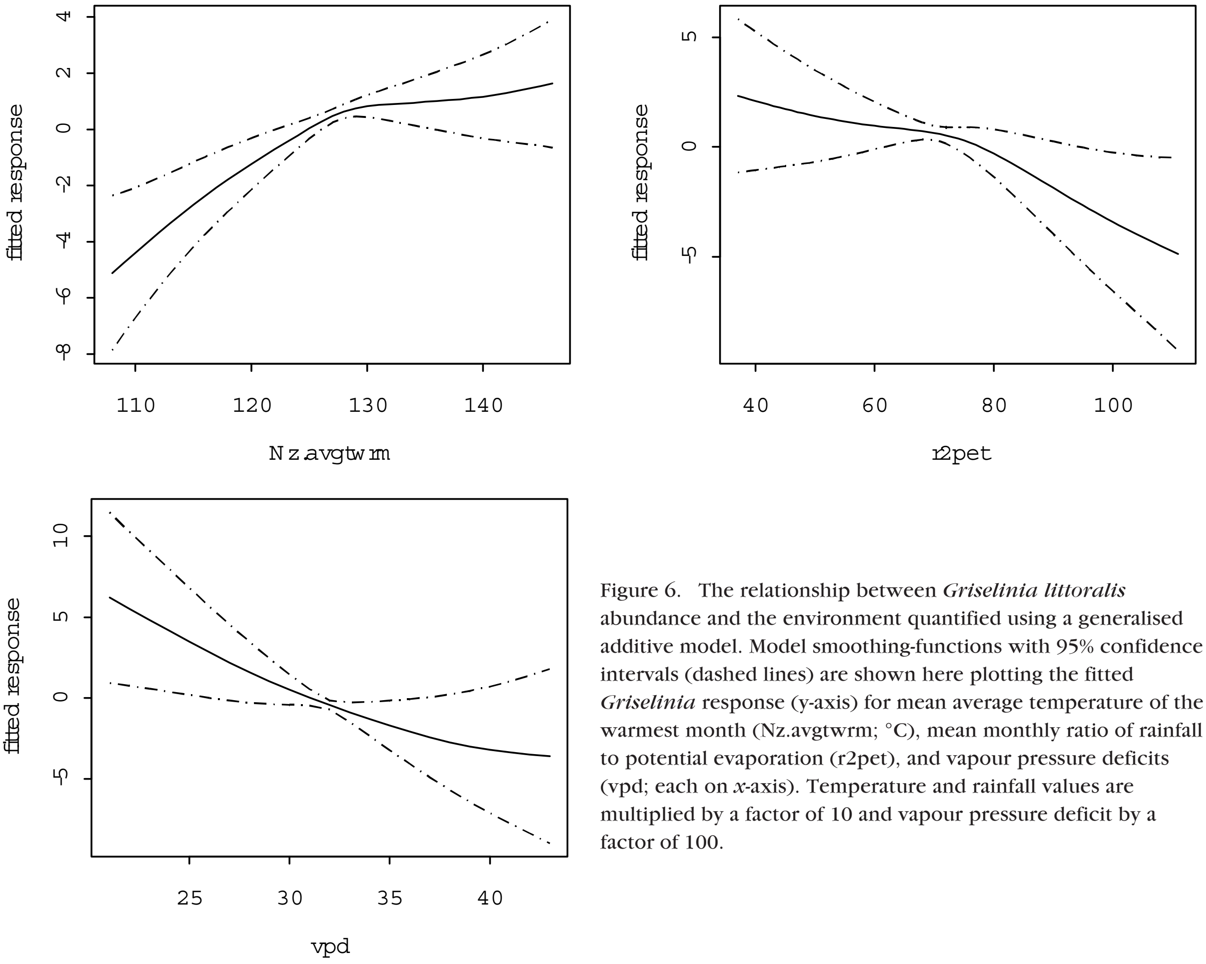


Figure 6. The relationship between *Griselinia littoralis* abundance and the environment quantified using a generalised additive model. Model smoothing-functions with 95% confidence intervals (dashed lines) are shown here plotting the fitted *Griselinia* response (y-axis) for mean average temperature of the warmest month (Nz.avgtwrm; °C), mean monthly ratio of rainfall to potential evaporation (r2pet), and vapour pressure deficits (vpd; each on *x*-axis). Temperature and rainfall values are multiplied by a factor of 10 and vapour pressure deficit by a factor of 100.

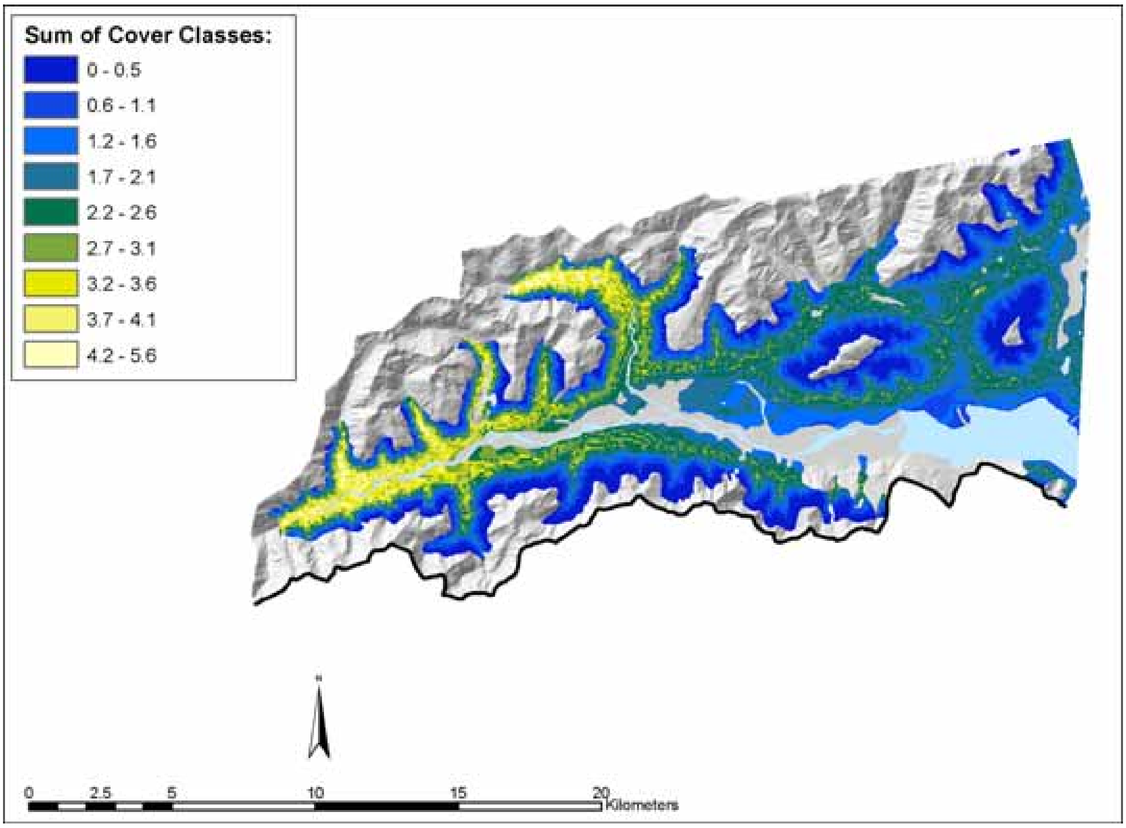


Figure 7. Mapped distribution of *Griselinia littoralis* in the North Hurunui catchment, based on the relationship between plot-based environment information and *G. littoralis* abundance data, and quantified using logistic regression.

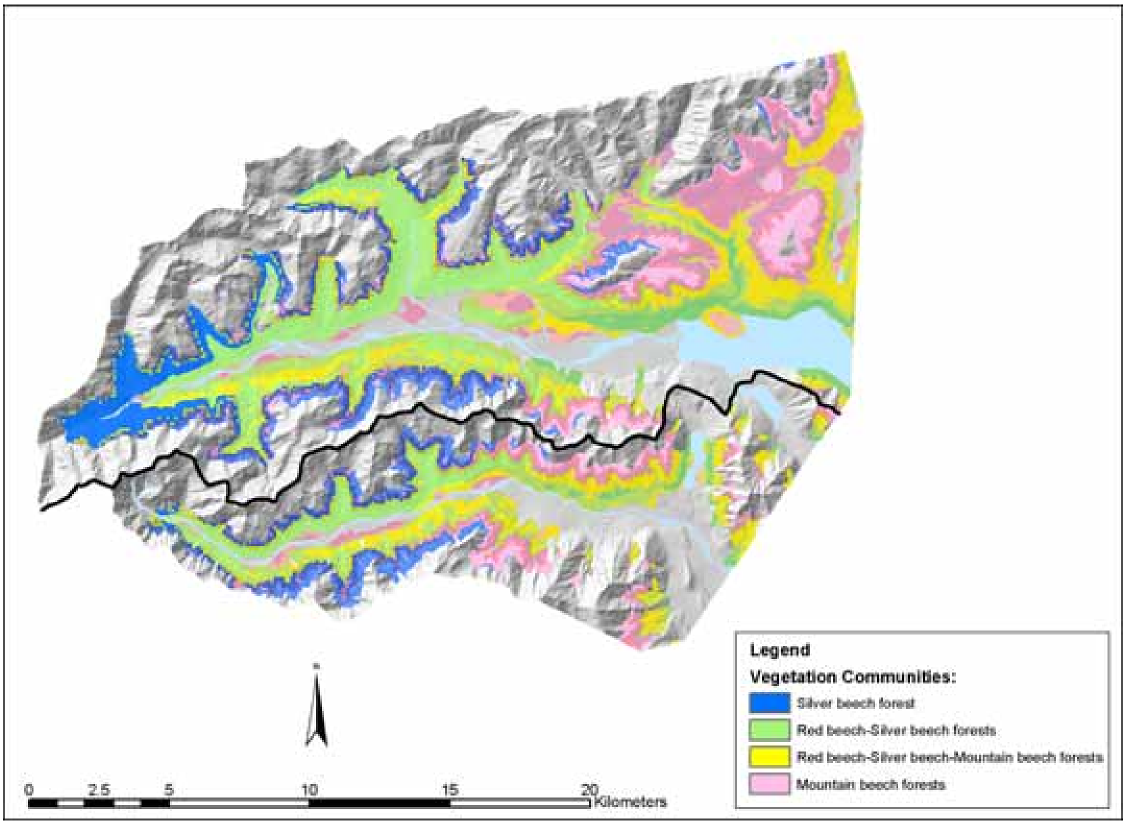


Figure 8. Predicted distribution of forest communities in the South Hurunui catchment derived by mapping the quantitative vegetation–environment relationships of each North Hurunui community, shown here above the black catchment boundary line.

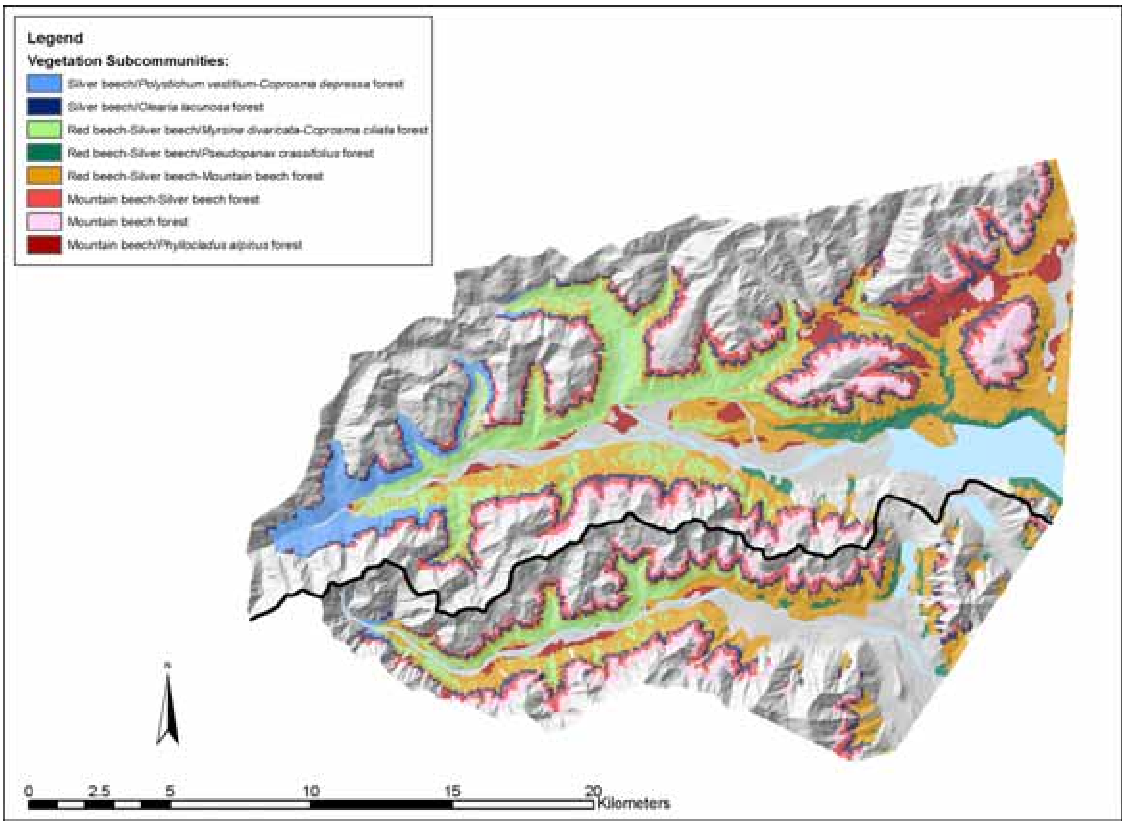


Figure 9. Predicted distribution of forest subcommunities in the South Hurunui catchment derived by mapping the quantitative vegetation–environment relationships of each North Hurunui subcommunity, shown here above the black catchment boundary line.

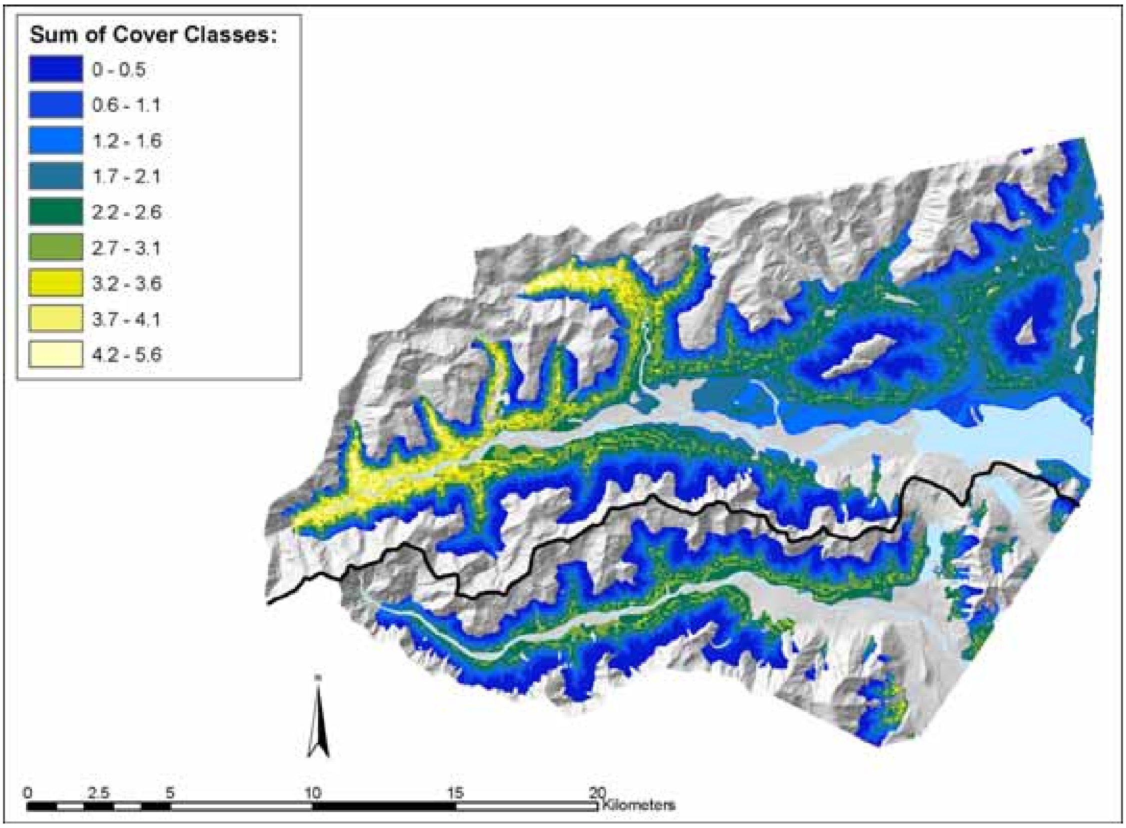


Figure 10. Predicted distribution and abundance of *Griselinia littoralis* in the South Hurunui catchment (mapped below the black catchment boundary line) derived from the logistic regression equation defining the relationship between *G. littoralis* abundance and the environment in the North Hurunui catchment.

TABLE 2. MEAN COVER CLASS (C*) FOR THE PLOTS THAT A SPECIES OCCURS IN AND PERCENTAGE FREQUENCY (%) OF EACH SPECIES PER SUBCOMMUNITY.

COMMUNITY	1				2				3		4					
SUBCOMMUNITY	1.1		1.2		2.1		2.2		3.1		4.1		4.2		4.3	
SPECIES	C*	%	C*	%	C*	%	C*	%	C*	%	C*	%	C*	%	C*	%
Archeria traversii	3	57														
Asplenium flaccidum	1	71	1	50	1	68			1	71					1	60
Astelia fragrans			1	50												
Astelia nervosa	1	71														
Blechnum penna-marina							2	56								
Blechnum fluviatile							2	56								
Carpodetus serratus							2	56								
Chiloglottis cornuta															1	60
Coprosma ciliata	1	86	2	50	3	68										
Coprosma colensoi	1	71	1	75	1	88										
Coprosma depressa	3	86	2	100	1	64									2	60
Coprosma foetidissima	2	86	2	100	2	88	1	67							1	60
Coprosma linariifolia			2	50												
Coprosma microcarpa							2	56								
Coprosma pseudocuneata	4	100	3	75	1	80			1	52	2	64			3	80
Coprosma rhamnoides					2	76	2	100								
Coprosma species 't'			2	75			2	67								
Corybas trilobus					1	88	1	67	1	52						
Dracophyllum traversii			3	50												
Gaultheria antipoda															1	60
Grammitis billardieri	1	71	1	75	1	100	1	100	1	87	1	71	1	75	1	60
Grammitis magellanica	1	57														
Griselinia littoralis	1	100	2	100	2	100	2	78	2	74	1	50			1	60
Hebe canterburiensis			2	50												
Hoheria glabrata	3	57														
Hymenophyllum flabellatum															2	60
Hymenophyllum multifidum	1	71														
Hymenophyllum villosum	1	100	1	100	1	84	1	56	1	71	1	64			1	80
Luzula congesta	1	57														
Myrsine divaricata	2	71			2	72					2	67			2	80
Nertera villosa	1	71			1	84	2	56								
Nothofagus fusca					4	100	4	100	3	100						
Nothofagus menziesii	4	100	4	100	3	96	3	100	3	100	3	100	2	50		
Nothofagus solandri var. *cliffortioides*	3	57							3	100	4	100	4	100	4	100
Olearia lacunosa	2	57	3	75												
Phyllocladus alpinus															3	100
Polystichum vestitum	3	86	1	100	2	88	2	56			1	64				
Pseudopanax colensoi	1	57														
Pseudopanax crassifolius							1	89								
Raukaua simplex			1	75	1	84										
Uncinia filiformis	1	100	2	100												
Uncinia uncinata	2	57					2	67								

* Cover class 1 = < 1% foliage cover, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%. Only species frequently occurring within a subcommunity (≥ 50% frequency) are shown. Subcommunities are grouped by their respective community and are listed by their group number.

See Table 1 for full group names in the nested classification. Information is not provided for the Seral forests subcommunity (5.1) because of insufficient plot representation.

TABLE 3. MEAN VALUES FOR MEAN TOP HEIGHT (MTH), ALTITUDE, SLOPE, AND FOREST-FLOOR GROUND COVER (VEG. = VEGETATION) FOR EACH SUBCOMMUNITY, SUMMARISED FROM THE PERMANENT PLOT DATA.

SUBCOMMUNITY*	MTH (m)	ALTITUDE (m)	SLOPE (°)	VEG. (%)	MOSS (%)	LITTER (%)	SOIL (%)	ROCK (%)
1.1	19	962	29	11	49	40	0	1
1.2	16	1082	30	51	38	34	0	0
2.1	25	720	23	27	42	39	0	2
2.2	24	664	17	42	22	40	1	1
3.1	23	807	25	24	39	44	1	1
4.1	20	1061	25	41	39	34	1	3
4.2	19	1183	26	36	28	44	0	3
4.3	12	1008	19	41	61	25	0	0
5.1	10	830	9	90	35	10	1	0

* Subcommunities are listed by their numeric abbreviation, see Table 1 for full subcommunity names and communities in the nested classification.

these tiers and those on the forest floor contribute to the high species richness of this subcommunity, with richness second only to the Silver beech / *Polystichum vestitum–Coprosma depressa* forest (subcommunity 1.1; Table 1). Red beech–Silver beech / *Myrsine divaricata–Coprosma ciliata* forest accounts for 28% of permanent plots in the North Hurunui catchment. This subcommunity is one of the two low-elevation subcommunities present (720 m mean altitude, SD 174.7 m; Table 3) and occurs in the centre of North Hurunui catchment at mid- and low-altitudes on the northern side of the river (Fig. 5).

2.2 Red beech–Silver beech / *Pseudopanax crassifolius* forest

The canopy and mid-storeys of this tall (mean top height 24.4 m, SD 6.1 m; Table 3) subcommunity are dominated by red beech with silver beech less abundant (Table 2). The diverse range of low-cover species in the lower tiers contributes to the high mean species richness of this subcommunity (Table 1). The plot data indicate that Red beech–Silver beech / *Pseudopanax crassifolius* forest occurs on shallower slopes, at lower altitudes, on average, than other subcommunities identified in this study (mean slope 17.3°, SD 9.4°; mean altitude 664.0 m, SD 120.5 m; Table 3). This matches the distribution derived from the computer-generated map, which shows Red beech–Silver beech / *Pseudopanax crassifolius* forest restricted to lower-slopes in the drier, eastern end of the North Hurunui catchment (Fig. 5).

3. Red Beech–Silver Beech–Mountain Beech forests

Red Beech–Silver Beech–Mountain Beech forests represent 31% of permanent plots in the North Hurunui catchment but contain only one subcommunity (Table 1). The computer-generated distribution derived from the subcommunity-level classification tree analysis shows a wider distribution across a broader range of slope positions and altitudes than the distribution derived from the community-level classification tree analysis (Figs 4, and 5). This probably reflects a weaker ability to discriminate subcommunity distribution with the environmental data used in the subcommunity analysis. See Section 6 for further discussion of this topic.

3.1 Red beech–Silver beech–Mountain beech forest

Red, silver and mountain beech co-dominate the tall canopy and mid-storeys of this subcommunity with *Griselinia littoralis* dominating the open storeys below (Table 2). This subcommunity accounts for the largest proportion of North Hurunui permanent plots and is one of three low-altitude subcommunities (mean altitude 806.9 m, SD 133.5 m; Table 3). This subcommunity occurs across a similar range of altitudes and slope angles to Red beech–Silver beech / *Myrsine divaricata–Coprosma ciliata* forest (subcommunity 2.1), but the two are distinguished by aspect, composition and species richness. The computer-generated maps indicate that both occur in the central portion of the study area. However, Red beech–Silver beech–Mountain Beech forest mostly occurs on drier, broadly north-facing slopes on the true right of the North Hurunui catchment, whereas Red beech–Silver beech / *Myrsine divaricata–Coprosma ciliata* forest occurs on broadly south-facing slopes on the true left of the North Hurunui catchment (Fig. 5). Much lower species richness (mean 15.00 per 400 m^2, SD 8.24; Table 1) and the presence of mountain beech in the canopy of Red beech–Silver beech–Mountain Beech forest suggest that this subcommunity inhabits dryer and / or less fertile sites than Red beech–Silver beech / *Myrsine divaricata–Coprosma ciliata* forest (mean 25.80 species per 400 m^2, SD 5.73). This is shown on the computer-generated map by the presence of Red beech–Silver beech–Mountain beech forest in the dryer, eastern half of the catchment, where Red beech–Silver beech / *Myrsine divaricata–Coprosma ciliata* forest has very limited presence (Fig. 5).

4. Mountain Beech forests

This community accounts for 23% of the permanent plots and dominates the upper slopes in the drier eastern-half of the study area, as well as some upper slopes and river flats in the western-half of the valley (Fig. 4). Three subcommunities were recognised in the nested UPGMA classification.

4.1 Mountain beech–Silver beech forest

Mountain and silver beech co-dominate the canopy and mid-storeys of this subcommunity. There is a limited range of low-cover understorey and forest floor species, with woody *Coprosma pseudocuneata*, and *Myrsine divaricata*, and ferns *Grammitis billardieri*, *Hymenophyllum villosum*, and *Polystichum vestitum* present in most plots (Table 2). Species richness is low in comparison to most other subcommunities (mean 11.43 species per 400 m^2, SD 6.50; Table 1). This subcommunity has a subalpine distribution (mean altitude 1061 m, SD 125.8; Table 3) throughout the catchment, typically occurring down-slope from Mountain beech forest (4.2; Fig. 5).

4.2 Mountain beech forest

This subcommunity has simple structure and composition with mountain beech predominant throughout all tiers from the canopy to the forest floor. *Grammitis billardieri* is the only other species consistently present (Table 2). This subcommunity has on average less than half the number of species of any other subcommunity identified in the study (5.50 mean species richness per 400 m^2, SD 3.70; Table 1), reflecting its subalpine position (mean altitude 1183 m, SD 72.3 m) and location in areas with lower rainfall. Mountain beech forest occurs at tree line in the drier, eastern-half of the study area and north-facing slopes on the true-right of the catchment (Fig. 5).

4.3 Mountain beech / *Phyllocladus alpinus* forest

Mountain beech dominates the canopy and mid-storeys of this stunted subcommunity type (mean top height 12.1 m, SD 5.7 m; Tables 2, and 3) with *Phyllocladus alpinus* also present in the small-tree and shrub tiers. The shrubs *Coprosma pseudocuneata*, *Gaultheria antipoda*, *Griselinia littoralis*, and *Myrsine divaricata* are consistently present. The forest floor is mossy and inhabited by *Asplenium flaccidum*, *Chiloglottis cornuta*, *Coprosma depressa*, *Grammitis billardieri*, *Hymenophyllum flabellatum* and *H. villosum*. This subcommunity has much higher species richness than other Mountain beech forests subcommunities (mean 20.40 species per 400 m^2, SD 5.94, Table 1), possibly reflecting its location on shallower-sloping, lower-altitudinal (mean altitude 1008 m, SD 200.7 m; Table 3) river terraces and lower slopes (Fig. 5).

5. Seral forests

With only two plots classified in this community there was insufficient information to map its distribution or provide a detailed account of species composition. In brief, the dense, stunted Seral forests are dominated by broadleaf (*Griselinia littoralis*), *Hoheria glabrata*, and mountain beech with dense prickly shield fern (*Polystichum vestitum*) on the ground.

5.4 MAPPED DISTRIBUTION OF *Griselinia littoralis,* NORTH HURUNUI CATCHMENT

The relationship between *Griselinia littoralis* and the environment, derived from the logistic regression, indicated that *G. littoralis* abundance is greatest on sites with average summer temperatures of 13°C, high rainfall, and low-to-moderate vapour pressure deficits (Fig. 6). The computer-generated map of *G. littoralis* distribution derived from this relationship showed wide distribution throughout the North Hurunui catchment (Fig. 7). Abundance is highest on mid and lower slopes in the wetter, western end of the North Hurunui catchment, reflecting the relationship with rainfall and temperature.

5.5 MAP VALIDATION, SOUTH HURUNUI CATCHMENT

5.5.1 Communities

Compositional distance was used to fit the South Hurunui permanent plots to the nested North Hurunui UPGMA classification. Thirty-nine (44%) of the plots were not assigned to a North Hurunui community suggesting that there is only partial compositional overlap between these two catchments at the community level. South Hurunui plots were assigned to four of the five North Hurunui communities (including Seral forests), with none assigned to the Red Beech–Silver Beech forests (Community 2.; Table 4).

TABLE 4. COMPARISON OF ACTUAL AND PREDICTED CLASSIFICATION ASSIGNMENT OF THE 89 SOUTH HURUNUI PERMANENT PLOTS TO NORTH HURUNUI COMMUNITIES.*

COMMUNITY	ACTUAL CLASSIFICTN ASSIGNMENT	PREDICTED CLASSIFICTN ASSIGNMENT	PLOTS WHERE PREDICTED MATCHED ACTUAL ASSIGNMENT	ACTUAL ASSIGNMENT OF PLOTS INCORRECTLY CLASSIFIED IN THE PREDICTIVE CLASSIFICTN
1. Silver Beech forests	5	12	1	33% in 4 58% unassign.
2. Red Beech–Silver Beech forests	0	40	0	40% in 3 25% in 4 13% in 5
3. Red Beech–Silver Beech–Mountain Beech forests	21	20	5	55% unassign.
4. Mountain Beech forests	16	17	2	82% unassign.
5. Seral forests	8	Not quantified	N / A	
Unassigned SH plots	39 (44%)			

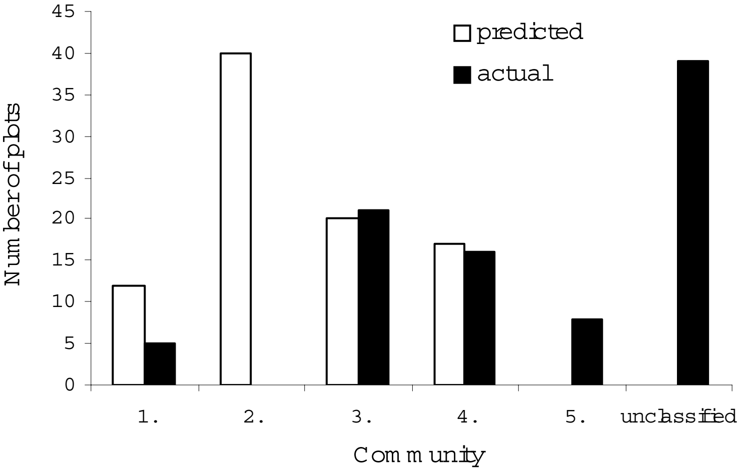
* The actual classification was assigned using compositional distance to the UPGMA classification of the North Hurunui plots and the predicted classification was derived by mapping the quantitative vegetation–environment relationship of each North Hurunui community to determine which community each South Hurunui permanent plot was mapped as. ‘Unassigned SH plots’ (also unassign.) represent South Hurunui plots that were not compositionally similar to any North Hurunui community. Also see Figs 4, 8, and 11.

In contrast, the predicted classification assignment, derived by mapping the quantitative vegetation–environment relationship of each community, assigned all 89 South Hurunui plots to all four mapped North Hurunui communities (omitting Seral forests, which was not mapped). There were discrepancies between the actual and predicted classification. Forty (45%) of the 89 South Hurunui plots were assigned to Red Beech–Silver Beech forests by the predictive classification (Figs 4, 8, and 11) whereas none were assigned to this community by the actual classification. Similarly, twice as many plots were assigned by the predicted classification to Silver Beech forests (Community 1) than were actually assigned using compositional distance to the UPGMA classification. However, there were a similar proportion of plots assigned to Red Beech–Silver Beech–Mountain Beech forests (Community 3) and the Mountain Beech forests (Community 4) by the predicted and actual UPGMA classifications. For individual plots, there was a low match between the predicted and actual classification assignment. Red Beech–Silver Beech–Mountain Beech forests (Community 3) had the best match with five of 20 plots predicted to occur in this community actually assigned using compositional distance.

5.5.2 Subcommunities

At the subcommunity level only 17% of South Hurunui plots were not assigned to a North Hurunui subcommunity identified in the UPGMA classification (Table 5) by their compositional distance. This compares with 44% unassigned at the community level. This suggests that it is possible to quantify greater compositional overlap between the two catchments when the plots are categorised in groups with fine-scale compositional similarity. The actual classification assigned South Hurunui plots to four of the eight mapped North

Figure 11. Graph showing the proportion of South Hurunui plots assigned by the actual and predicted classification to each North Hurunui community. 'Unclassified' represents plots that were not compositionally similar to any North Hurunui community. See Table 4 for further breakdown and Table 1 for full community names.



Hurunui subcommunities. This contrasted with the predicted classification which assigned all 89 plots to seven of the eight subcommunities (except Silver beech / *Polystichum vestitum-Coprosma depressa* forest (1.1); Figs 5, 9, and 12; Table 5). The predictive classification assigned 36 (40%) of plots to the Red beech-Silver beech-Mountain beech forest (3.1) with a further 18% in the Red beech-Silver beech / *Myrsine divaricata-Coprosma ciliata* forest (2.1) whereas the actual classification assigned the majority (70%) of plots to the Mountain beech forest (4.2).

5.5.3 *Griselinia littoralis*

The predicted distribution of *G littoralis* in the South Hurunui catchment was much wider than was actually observed by the permanent plot data (Fig. 10) with *G. littoralis* predicted to occur in 86 (97%) of the 89 plots but was only observed on 27 plots. For each plot observed values were significantly different from predicted values (Wilcoxon's rank-sum test; Z = 7.9681, $P \leq 0.01$). Predicted abundance was higher than observed on 76 of the 89 plots, and lower than observed on 11 plots. Across all plots there was low correlation between actual and predicted *Griselinia* abundance ($r_s = 0.256$, $P \leq 0.02$), suggesting that the abundance was not uniformly over-predicted by the predictive model.

Figure 12. Graph showing the proportion of South Hurunui plots assigned by the actual and predicted classification to each North Hurunui subcommunity. 'Unclassified' represents plots that were not compositionally similar to any North Hurunui subcommunity. See Table 5 for further breakdown and Table 1 for full subcommunity names.

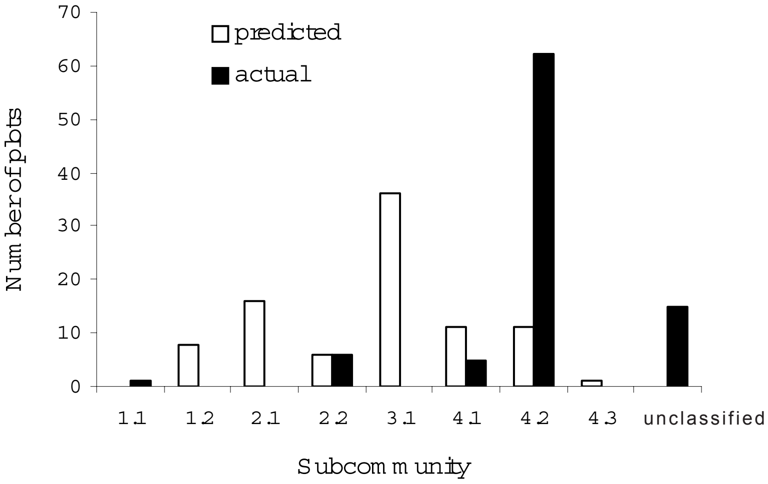


TABLE 5. COMPARISON OF ACTUAL AND PREDICTED CLASSIFICATION ASSIGNMENT OF THE 89 SOUTH HURUNUI PERMANENT PLOTS TO NORTH HURUNUI SUBCOMMUNITIES.

SUBCOMMUNITY*	ACTUAL CLASSIFICTN ASSIGNMENT†	PREDICTED CLASSIFICTN ASSIGNMENT†	PLOTS WHERE PREDICTED MATCHED ACTUAL ASSIGNMENT	ACTUAL ASSIGNMENT OF PLOTS INCORRECTLY CLASSIFIED IN THE PREDICTIVE CLASSIFICTN
1.1	1	0	0	
1.2	0	8	0	100% in 4.2
2.1	0	16	0	50% in 4.2 25% unassign.
2.2	6	6	0	50% in 4.2
3.1	0	36	0	58% in 4.2 19% unassign.
4.1	5	11	0	91% in 4.2
4.2	62	11	11	
4.3	0	1	0	100% in 4.2
5.1	0	Not quantified	N / A	
Unassigned SH plots†	15 (17%)			

* See Table 1 for full subcommunity names.

† See Table 4 for further explanation of actual and predicted classification and ‘Unassigned SH‘ plots. Also see Figs 5, 9, and 12.

6. Discussion

6.1 BENEFITS OF COMPUTER-GENERATED VEGETATION MAPS

One of the strongest points in favour of computer-generated vegetation maps is that they are based on quantitative data on the presence or abundance of all species within a vegetation group and its relationship with specific environmental variables. This is potentially a major step forward from vegetation maps derived from aerial photography where vegetation boundaries were based on the qualitative interpretation of canopy species distribution and often-crude environmental information. Such advancements are critical for many conservation areas in New Zealand, particularly eastern South Island forests where much of the compositional variation occurs below the canopy and where management of species with conservation significance necessitates an accurate understanding of species distribution and abundance. However, high-quality plot data and quantitative environmental information must underpin the generation of any computer-derived vegetation map.

Maps based on quantitative vegetation–environment relationships provide rigour, repeatability and flexibility to vegetation mapping. Relationships between vegetation and predictor variables are often complex. However, computer models have the ability to synthesise these complex relationships (Michaelson et al. 1994) and express them spatially in a GIS. Furthermore, because repeatable methods of quantifying vegetation–environment relationships have been used, a computer-generated vegetation map can easily be recreated and refined as additional environmental information comes to hand. The potential distribution of vegetation, relating to the potential change in a specific environment variable, can also be mapped by manipulating environmental parameters in the vegetation–environment equations. This will enable managers to consider the possible effects of changing environmental conditions on vegetation distribution in the management of a conservation area: for example, manipulating temperature and rainfall to understand how climate change might affect the distribution of rare species and / or significant communities.

6.2 LIMITATIONS OF COMPUTER-GENERATED VEGETATION MAPS

6.2.1 Environmental data

The quality of a computer-generated vegetation map relates directly to the quality of the data used to quantify the vegetation–environment relationships. Most of the environmental variables used in this study had large-scale variation across the study area. We determined that climatic variables did influence the distribution of communities and subcommunities across the North Hurunui catchment, following larger-scale relationships quantified for general trends across New Zealand (see Leathwick 1998, 2002; Leathwick & Whitehead 2001). In the North Hurunui, the suite of climatic variables defining vegetation–environment distribution was similar for both levels of the nested vegetation classification. However, at the scale of our study, other environmental variables that vary with finer resolution might help refine the boundaries between vegetation units. Our study included aspect and slope, which vary at a fine scale, although they generally did not add to the vegetation–environment relationships. Other fine-scale variables may correspond more closely with processes that influence vegetation distribution. Examples include topographic position, soil moisture, site water characteristics, soil characteristics, past geomorphic processes, and disturbance history, although their significance may vary from catchment to catchment. Environmental variables with fine-scale variation may also help differentiate the boundaries of two vegetation groups with very similar environmental conditions. However, increases in mapping-boundary accuracy may not offset the additional time and money required to quantify some of these fine-scale variables. There is also a fine balance between using variables that have large- and fine-scale variation. The inclusion of too many fine-scale variables in the analyses quantifying vegetation–environment relationships may reduce any ability to identify the general habitat requirements of a vegetation group.

6.2.2 Vegetation plot data

The quality and quantity of vegetation plot data underpin the reliability of any computer-generated vegetation map. In this study we were fortunate to use data from two of the most ‘data-rich’ catchments in the South Island. However, number of plots did still restrict the accuracy of our maps. Not all groups in the classification were represented by enough plots to reliably quantify their distribution once the North Hurunui dataset of 101 forest plots were categorised into communities and then subcommunities. Plot representation per vegetation group was obviously higher at the community level, although still inadequate for one community that was represented by less than 15 plots (Table 1). Subcommunities represent a more meaningful unit for conservation management, and only two of the nine included more than 15 plots. Additional plot sampling should be undertaken with a target of a minimum of 15 plots per subcommunity.

Plot location may also influence the accuracy of defining vegetation–environment relationships. If plots are not well-distributed across their habitat range it may be difficult to accurately define the habitat and habitat boundaries of a vegetation group. This is particularly true where a vegetation group occurs across a wide environmental range. In some instances the number of plots in a vegetation group may not be sufficient to adequately define the group's habitat requirements. This is generally a greater problem when a vegetation group is represented by a limited number of plots. These problems can be identified through field checking and the solution generally involves undertaking additional fieldwork to supplement the current information used in analyses.

Some studies have suggested that satellite imagery can increase map accuracy (Ferrier et al. 2002). Satellite imagery provides quantitative spectral information at a fine resolution across the whole study area rather than just at specific points, providing useful information to help differentiate between vegetation groups and define their boundaries. One of the main benefits of satellite imagery is that it can help identify local variation in vegetation, such as a change in vegetation due to a landslide, which cannot be accounted for by the environmental variables used in the classification tree analyses. However, satellite imagery should not replace a classification based on plot data, as the spectral information is mostly based on canopy species. This is particularly true for evergreen forests, where winter imagery cannot pick up differences in understorey composition. This is highly relevant for the New Zealand situation where most native forests have evergreen canopies.

6.2.3 Rare species

Attempts to define the distribution of rare species and species with conservation significance often suffer from inadequate plot representation and therefore insufficient data to reliably quantify relationships with the environment. This is particularly problematic as these species are often the taxa that we want to map. The North Hurunui was no exception, with only one rare species and / or food-source species for rare birds (*Griselinia littoralis*) present in more than a small number of plots. Under-representation is likely to be a problem in most datasets unless the rare species in question has a high frequency in a catchment. In most cases it will be necessary to undertake additional fieldwork to obtain enough data to quantify the distribution of rare or significant species.

In this report we mapped the distribution and abundance of species using cover abundance scores where cover was estimated as one score for the entire plot. For woody species, basal area or stem density measurements would provide a more rigorous assessment of species abundance because the value for each plot would represent an average, or some other combined value, of all stems per plot for the species in question.

6.3 OTHER FACTORS DRIVING VEGETATION DISTRIBUTION

A recent study of red beech and silver beech forests at Maruia suggests that environmental factors may have only a minor role in defining the presence of species and a community at a site (Allen et al. 2003). This site classification study has shown that < 25% of plot-level variation in forest structure, regeneration, and individual tree growth was predicted by environmental information (e.g. slope shape, site protection, soil chemistry) whereas > 85% of the variation related to within-site characteristics such as canopy height, basal area, and stem density (Allen et al. 2003). Similar results have been documented by a study of Austrian forests (Monserud & Sterba 1996). This suggests that it is important to understand the role of small-scale site factors on community distribution before any modifications are made to the equations defining the distribution of vegetation.

6.4 PREDICTING VEGETATION DISTRIBUTION IN ANOTHER CATCHMENT

Our study suggests that the distribution of vegetation groups with coarse-scale compositional similarity was easier to predict than groups with finer-scale compositional similarity or individual species. In the South Hurunui catchment, the match between the proportion of plots assigned by the actual and predictive classification was greater at the community-level than at the subcommunity-level. At the single-species level, there was also little match between the predicted and actual abundance of *Griselinia littoralis*. However, the match between the predicted and actual classification assignment of each plot was low at both the community and subcommunity level suggesting that the vegetation–environment equations used to predict vegetation distribution were not able to accurately map the boundaries of individual communities or subcommunites.

There are several reasons why there may be difficulties in accurately predicting vegetation distribution. It is possible that key environmental variables were missed from the suite of environmental variables used to create the vegetation–environment relationships. However, the low misclassification rates for each North Hurunui classification tree analysis suggests that this is not true. Additional environmental variables with fine-scale variation may have been required to accurately delineate the habitat boundaries of vegetation units. The closer match between the predicted and actual classification at the community level suggests that we did not have the fine-scale variables to define subcommunity boundaries. Alternatively, the resolution of environmental data used in this study may not have been fine enough to reliably represent local-scale variation in the South Hurunui. In particular, the steep rainfall gradient across the two Hurunui catchments may not have been modelled accurately at the scale required in this study. In addition, environmental differences between the two catchments may also have been greater than expected. These differences may be large scale, such as greater than anticipated differences in climate, or small scale but overriding or obscuring the relationship between specific vegetation units and environmental variables quantified by our analyses. Small-scale or localised differences in microclimate, geology, landform processes, and disturbance history (e.g. wind damage, insect attack, fire) might also subtly alter the habitat requirements and / or boundaries of a vegetation group between the catchment where the equations were derived and the catchment where vegetation distribution is being predicted.

It is possible that environmental parameters alone do not adequately explain vegetation distribution in the two Hurunui catchments. The impact of historical processes, such as glaciation (Wardle 1963), may differ between the two catchments with the distribution of at least some vegetation groups relating to past processes rather than current environmental conditions (see Ferrier et al. 2002). Topographic barriers may also prevent species evenly occupying geographic space (see Wardle 1980) and, therefore, reduce the predictability of species and vegetation groups. In addition, the findings of Allen et al. (2003) suggest that subcommunity distribution may be driven by site-scale processes, such as competition, that occur within a stand.

We believe that the resolution of the rainfall surface was too coarse to reliably quantify the steep east–west rainfall gradient and other local-scale variation in the Hurunui catchments. The low misclassification rates for the North Hurunui community classification tree suggests that the resolution was sufficient to model coarse-scale patterns. A slightly higher misclassification rate for the subcommunity classification tree may relate to the limitations of the rainfall data used or other fine-scale variation that was not quantified. Indeed, we believe that the over-prediction of silver-beech-dominated forest and under prediction of mountain-beech-dominated forest in the South Hurunui catchment most likely relates to inadequacies of the rainfall data. Silver beech typically dominates wetter areas of the South Island whereas mountain beech dominates drier areas of this region (Wardle 1984; Ogden et al. 1996) including the South Hurunui catchment (Jane 1985). Our results suggest that the rainfall surfaces used did not adequately model local-scale rainfall differences between the North and South Hurunui catchments, and possibly within the South Hurunui catchment. The inclusion of more-reliable fine-scale rainfall data in the vegetation–environment equations should improve the ability to predict mountain beech distribution in the South Hurunui catchment.

Inaccurate rainfall information may also partly account for the over-prediction of red-beech-dominated forests in the South Hurunui catchment. The red beech forests previously described for this catchment loosely fit our North Hurunui classification. A subcommunity resembling Red beech–Silver beech forest (2.2) was described on lowland river terraces in the head of the South Hurunui (Jane 1985). In addition, a mountain beech forest with occasional large red beech emergents, found on slopes (Jane 1985), probably fits in the Red Beech–Silver Beech–Mountain Beech forests (Community 3), but was most likely included in the group of unassigned plots in the subcommunity actual classification. The over-prediction of red beech may also relate to less fertile soil conditions in the South Hurunui catchment relative to the similar sites in the North Hurunui catchment. Red beech typically occurs on more fertile soils than mountain or silver beech (Ogden et al. 1996). In the South Hurunui catchment silver or mountain beech occurred on sites that red beech was predicted to occur on. Dispersal barriers may also limit red beech presence in the South Hurunui catchment. High red beech presence in the North Hurunui catchment may indicate a dispersal link with nearby West Coast forests where red beech can be a major canopy species (Wardle 1984). This species is present near the head of the Taramakau River valley (Wardle & Hayward 1970), immediately west of the North and South Hurunui catchments. The Harper Pass (962 m), which separates the North Hurunui catchment from the Taramakau, is perhaps low enough to allow red beech migration from the west. In contrast, the 1767 m and 1815 m peaks at the head of the South Hurunui catchment would create a topographic barrier to red beech migration from the west. The low pass (676 m) between the North and South Hurunui catchments, near Lake Mason, may have been a possible route for red beech migration from the North Hurunui catchment.

Large-scale *Nothofagus* patterns in New Zealand are considered only partially related to the physical environment, with a range of factors such as limited seed dispersal and mycorrhizal associations also important (e.g. Baylis 1980; Wardle 1984; McGlone et al. 1996). A study of widespread New Zealand tree species found that each of the four *Nothofagus* species had a weaker relationship with the environment than the 11 other tree species included in the study (Leathwick 1998). These factors point to possible inherent difficulties with using environmental factors alone to accurately map local-scale *Nothofagus*-dominated communities. These limitations have been highlighted at the local scale by Allen et al. (2003) who suggest that local-scale variation in silver and red beech forests is mostly driven by small-scale within-site processes rather than environmental parameters.

This study highlights the difficulties of using equations defining vegetation–environment relationships from one catchment to predict vegetation distribution in another catchment. To predict vegetation distribution with any accuracy, it is important to take account of the complexities of the species in question as well as the interplay of current and historical processes, and local differences in present-day large- and small-scale environmental and other site processes. It will be imperative to carefully assess the merits before attempting to predict the vegetation in another catchment. A first step will be to understand the degree of overlap between the two catchments and to understand which vegetation groups might be more difficult to predict. This step must be based on a sound understanding of both catchments as well as the ecology and stand dynamics of the vegetation in question. A second step will be to consider the consequences for management if the predictability is poor, keeping in mind that any deficiencies in the vegetation–environment relationships may be compounded when used to predict the distribution of vegetation of another catchment.

6.5 VALIDATION OF NORTH HURUNUI VEGETATION MAP

We also used the South Hurunui catchment to test the accuracy of the vegetation maps created for the North Hurunui catchment. Although validation provides rigour and a quantitative assessment of accuracy, there are many reasons why a validation based on data from an adjacent, environmentally similar catchment is not a fair method of assessment. These issues are outlined in Section 6.4 and apply as much to validation as the previous section. Ideally, validation should be undertaken in the catchment that the vegetation map was generated in, using an independent dataset. However, in most cases other datasets will not be available to undertake this approach. An alternative approach would be to undertake extensive field checking to validate the maps.

6.6 POTENTIAL APPLICATIONS

A GIS database with maps of vegetation community and species distribution and layers of environmental information is an important and powerful tool for modern-day management of a conservation area. Such a database could provide a cost-effective, dynamic approach to planning and prioritising management issues and help direct management in the short, medium, and long term. For example, management options for forest remnants in a fragmented landscape could consider the impact of future rural development on the long-term survival of native forest birds by modelling the removal of specific forest fragments in the landscape in the GIS. Similarly, the effect of forest restoration on bird survival could also be examined by adding new forest patches to the fragmented landscape model. A GIS database would greatly aid pest management of a conservation area. For example, to manage the spread of rodents through native beech forest, different control operation intensities could be modelled to identify the appropriate level of control or to determine what level of control could be achieved for a specific level of funding. Such a database could also be used to identify the most effective trapping layout for reducing rodent numbers quickly and cost effectively. This would consider terrain, access, and vegetation community distribution. The GIS database provides a helpful tool to understand the temporal spread of organisms across the landscape. For example, in the Harper–Avoca catchments of Canterbury, data from permanent grassland plots collected from seven summers between 1955 and 2000 could be used to model the invasion of *Hieracium* species over the last four decades across these two catchments (C. Newell and A. Rose unpubl. data). Management options can also be readdressed as additional information comes to hand. For example, seasonal information on the palatability of native species could be added to a pest management model to refine which areas should be targeted for pest control. Complex issues can be quantified and synthesised in a spatial context in a GIS database, with the ability to readjust predictor environmental parameters to determine the outcome based on a range of possible scenarios or hypothesised changes of a particular parameter. For example, long-term management of alpine vegetation considering the potential impact of climate change could model different scenarios by varying different climatic parameters and rerunning the vegetation–environment equations to quantify vegetation distribution under each scenario. In all cases the information in the GIS database must be based on adequate quantitative plot data and a sound ecological understanding of the patterns and processes of the vegetation and other biota in the conservation area.

7. Recommendations

The authors recommend the following directions for future research in the development of generating computer-derived vegetation maps:

- Focus on understanding the basic management units (subcommunities) rather than rare species, which have greater problems with data under-representation.
- Quantify local-scale environmental variation, such as topographic position, soil moisture, and soil characteristics.
- Determine whether spectral information from satellite imagery can help define community and subcommunity boundaries.
- Develop finer-scale rainfall and temperate surfaces in the two Hurunui catchments and validate these in the field with climate stations throughout the two catchments.
- Determine the degree to which small-scale within-site characteristics and environmental parameters influence community and species distribution, following Allen et al. (2003).
- Ensure that all vegetation groups to be mapped are represented by at least 15 plots per group. For the North Hurunui, undertake additional sampling in subcommunities that are currently under-represented by permanent plots. The additional data should be collected using the same methods as used in this study, i.e. the standard Reconnaissance method on 20 × 20 m plots. Each plot would take 1–3 hours to sample.
- For North Hurunui communities and subcommunities refine the quantitative vegetation–environment relationships based on the above findings.
- Undertake additional sampling of rare species to work towards adequately quantifying vegetation–environment relationships of these species.

8. Executive summary

Project and Client

One of the main objectives of this study was to produce a computer-generated map of the distribution of forest vegetation in the North Hurunui catchment, one of the two major catchments in the Hurunui Mainland Island. A major benefit of this approach is that the vegetation map is based on quantitative vegetation plot data and quantitative relationships between vegetation and specific environmental variables. Additionally, maps can be modified to include new environmental information by rerunning the vegetation–environment equations. The maps can also be manipulated to examine the potential effect of a change in an environmental parameter. Used in conjunction with spatial information on other organisms, such as threatened species and introduced browsers, computer-generated vegetation maps potentially have wide application for managing threatened species and designing future management programmes. Landcare Research carried out this study for DOC in 2002 and 2003.

Objectives

- To classify data from permanent forest plots in the North Hurunui catchment into vegetation communities for management purposes.
- To describe methods and produce a computer-generated map showing the distribution of forest vegetation communities in the North Hurunui catchment. Vegetation community distribution will be derived from equations that quantify the relationship between species composition and characteristic environmental conditions.
- To map the distribution of a rare or significant species based on species abundance and its relationship with the environment.
- To test the ability to use quantitative vegetation–environment relationships derived in the North Hurunui catchment to accurately predict the distribution of forest vegetation communities and a single species in the adjacent South Hurunui catchment.
- To assess the accuracy of predicting vegetation communities and a single species and determine whether coarse- and / or fine-scale compositional information can be mapped accurately.
- To discuss the benefits and limitations of computer-generated vegetation maps.
- To provide recommendations on the future development of computer-generated vegetation maps.

Methods and results

A two-step procedure was used to map the distribution of forest vegetation in the North Hurunui catchment. Data from permanent plots were grouped at two different levels in a nested classification with nine vegetation subcommunities identified within five communities. We used ‘classification tree analysis’ to quantify the relationship between vegetation and environmental parameters with two classification tree analyses performed to quantify, firstly, the relationship between vegetation communities and the environment and, secondly, between vegetation subcommunities and the environment. Climatic variables, in particular temperature and rainfall, were important for defining the distribution of individual communities and subcommunities. The misclassification rates for the two analyses were low indicating that the distribution of vegetation communities and subcommunities, respectively, could be predicted approximately 80% and 70% of the time. The equations derived from each set of analyses were used to map the distribution of each community and subcommunity across the North Hurunui catchment. We also mapped the distribution of a single species, *Griselinia littoralis*—an important food species for rare birds in the North and South Hurunui catchment. The relationship between *G. littoralis* and the environment was quantified using logistic regression with variation in *G. litoralis* abundance relating to temperature, rainfall, and vapour pressure deficits.

The ability to predict community, subcommunity, and *G. littoralis* distribution in a nearby catchment was tested using a permanent-forest-plot dataset from the adjacent South Hurunui catchment. Plots from this dataset were assigned to the North Hurunui classification by their compositional similarity to individual communities and subcommunities. Forty-four percent of the South Hurunui plots were not assigned to a community in the North Hurunui classification suggesting only partial compositional overlap between the two catchments at the community level. However, there is greater compositional overlap at the subcommunity level with only 17% of the South Hurunui plots not assigned to a subcommunity in the North Hurunui classification. There was greater match in the proportion of plots assigned by the actual classification and the predicted classification at the community-level than the subcommunity level. The match between predicted and actual abundance of *G. littoralis* was limited. The proportion of silver-beech-dominated plots was over predicted in the South Hurunui catchment whereas the proportion of mountain-beech-dominated plots was under predicted, suggesting that South Hurunui rainfall levels were lower than those quantified by the rainfall surfaces. Red-beech-dominated forest distribution and *G. littoralis* abundance and distribution were also lower in the South Hurunui catchment than predicted.

These discrepancies may in part relate to shortcomings of the environmental data used, the absence of site-scale non-environmental factors in the vegetation–environment equations, and underlying differences in the past and present environment between the North and South Hurunui catchments. Adequate quantitative plot data and a sound ecological understanding of vegetation patterns and processes must underpin any computer-generated vegetation map. Accordingly, we recommend additional sampling be undertaken in the North Hurunui catchment for subcommunities that are currently under-represented by permanent plots. In addition, further research is required to determine the degree to which small-scale site processes versus environmental factors may influence subcommunity distribution.

Conclusions

Temperature and rainfall were important environmental variables for defining the distribution of communities and subcommunities in the North Hurunui catchment. *Griselinia* distribution also related to climate. Equations defining the relationships of North Hurunui groups with the environment could not accurately predict vegetation distribution in the adjacent South Hurunui catchment, although the full range of North Hurunui communities and subcommunities were present in the South Hurunui catchment. In the South Hurunui, the match between predicted and actual classification assignment of each plot was higher for communities than subcommunities or *Griselinia littoralis* suggesting that groups with coarse-scale vegetation compositional similarity are easier to predict than single species or groups with finer-scale compositional similarity. Discrepancies between the actual assignment of South Hurunui plots to the North Hurunui classification and the assignment predicted by the vegetation–environment equations may in part relate to shortcomings of the rainfall surface used in this study. The resolution of this surface was most likely too coarse to reliably interpolate local-scale variation in rain within and between the two Hurunui catchments. Furthermore, it seems likely that *Nothofagus* distribution relates in part to non-environmental site factors, such as stem density and basal area. The test of the North Hurunui maps using the South Hurunui catchment highlights the difficulties of predicting vegetation at the local scale, where special characteristics of the dominant species and inaccuracies in the scale at which major environmental data have been interpolated reduce the ability to predict vegetation distribution in an adjacent catchment with a reasonably similar environment. Predictability may be further reduced by the interplay of current and historical processes, as well as local differences in present-day large- and small-scale environmental and other site processes

Recommendations

An adequate quantitative plot database and a sound ecological understanding of the patterns and processes of the vegetation in the conservation area must underpin any computer-generated model. We recommend that local-scale environmental variation is quantified and used to refine vegetation–environment relationships. Future work should focus on subcommunities rather than individual rare species, which have greater problems with data under-representation. Additional sampling should be undertaken in the North Hurunui catchment for subcommunities that are currently under-represented by permanent plots. In addition, further research is required to determine the degree to which small-scale site processes versus environmental factors may influence community distribution.

9. Acknowledgements

The North and South Hurunui data are archived in the National Vegetation Survey Databank, managed by Landcare Research, at Lincoln. Staff of the Canterbury Conservancy of the Department of Conservation collected the North Hurunui vegetation data used in this report and the South Hurunui data were collected by the former New Zealand Forest Service. Thanks to Chris Woolmore, DOC, for helping initiate this study and to Craig Briggs and Kirsty Cullen, Landcare Research, for producing the vegetation maps. Thanks to Rob Allen, Christine Bezar, Larry Burrows, Duane Peltzer, Susan Walker, and an anonymous reviewer for reviewing earlier drafts of the manuscript. Funding was provided by the Department of Conservation, Investigation no. 3357.

10. References

Allen, R.B. 1992: RECCE an inventory method for describing New Zealand vegetation. *FRI Bulletin 176.* Forest Research Institute, Christchurch, New Zealand.

Allen, R.B. 1993: A permanent plot method for monitoring changes in indigenous forests. Manaaki Whenua–Landcare Research, Christchurch, New Zealand.

Allen, R.B.; R.B.; Burrows, L.E.; Peltzer, D.A.; Wiser, S.K. 2003: Ecological site classification of a red-silver beech forest. Landcare Research Contract Report LC0203 / 161 for the Ministry of Agriculture and Forestry. (unpublished) 34 p.

Anon. 1998: S-Plus 4.5 Guide to statistics. MathSoft Inc., Seattle, Washington.

Baylis, G.T.S. 1980: Mycorrhizas and the spread of beech. *New Zealand Journal of Ecology 3*: 151–153.

Bio, A.M.F.; Alkemade, R.; Barendregt, A. 1998: Determining alternative models for vegetation response analysis: a non-parametric approach. *Journal of Vegetation Science 9*: 5–10.

Bray, J.R.; Curtis, J.T. 1957: An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs 27*: 325–349.

Breiman, L.; Friedman, J.H.; Olsen, R.A.; Stone, C.J. 1984: Classification and regression trees. The Wadsworth statistics / probability series, Chapman & Hall, New York.

Brownsey, P.J.; Smith-Dodsworth, J.C. 1989: New Zealand ferns and allied plants. David Bateman, Auckland, New Zealand.

Burrows, L.E.; Cuddihy, M.J.; Moore, E.D.; Reynolds, R.N. 1976: The forest, scrublands, and animals of the upper Hurunui. New Zealand Forest Service, Protection Forestry Report 144. 32 p.

Cameron, E.K. 1999: New names, combinations or comments from the journals. *Newsletter, New Zealand Botanical Society 56*: 18–24.

Congalton, R.G. 1991: A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sensing of Environment 37*: 35–46.

Edgar, E.; Connor, H.E. 2000: Flora of New Zealand. Volume V. The grasses. Manaaki Whenua Press, Lincoln, New Zealand.

Ferrier, S.; Drielsma, M.; Manion, G.; Watson, G. 2002: Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II Community-level modelling. *Biodiversity and Conservation 11*: 2309–2002.

Franklin, J. 2002: Enhancing a regional vegetation map with predictive models of dominant plant species in chaparral. *Applied Vegetation Science 5*: 135–146.

Hall, G.M.J. 1992: PC-RECCE. Vegetation inventory data analysis. *Forest Research Institute Bulletin 177.* Forest Research Institute, Christchurch, New Zealand.

Hastie, T.; Tibshirani, R.J. 1990: Generalised additive models. Chapman and Hall, London.

Jane, G.T. 1985: Hurunui Survey 1976–1977. New Zealand Forest Service Technical Report, Canterbury Conservancy Survey Report No. 3 (unpublished).

Leathwick, J.R. 1998: Are New Zealand's *Nothofagus* species in equilibrium with their environment? *Journal of Vegetation Science 9*: 719–732.

Leathwick, J.R. 2002: New Zealand's potential forest pattern as predicted from current species-environment relationships. *New Zealand Journal of Botany 39*: 447–464.

Leathwick, J.R.; Whitehead, D. 2001: Soil and atmospheric water deficits and the distribution of New Zealand's indigenous tree species. *Functional Ecology 15*: 233–242.

Leathwick, J.; Wilson G.; Rutledge, D.; Wardle, P.; Morgan, F.; Johnston, K.; McLeod, M.; Kirkpatrick R. 2003: Land environments of New Zealand. Nga Taiao o Aotearoa. David Bateman, New Zealand.

McCullagh, P.; Nelder, J.A. 1989: Generalised linear models. 2nd ed. Chapman and Hall, London.

McCune, B.; Mefford, M.J. 1999: *PC-ORD.* Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Oregon, USA.

McGlone, M.S.; Mildenhall, D.C.; Pole, M. S. 1996: History and paleoecology of New Zealand *Nothofagus* forests. Pp. 83–130 in Veblen, T.T; Hill, R.S.; Read, J. (Eds): The ecology and biogeography of *Nothofagus* forests. Yale University Press, New Haven and London.

Michaelson, J.; Schimel, D.S.; Friedl, M.A.; Davis F.; Dudayah, R.C. 1994: Regression tree analysis of satellite and terrain data to guide vegetation sampling and surveys. *Journal of Vegetation Science 5*: 673–686.

Monserud, R.A.; Sterba, H. 1996: A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. *Forest Ecology and Management 80*: 57–80.

Newell, C.L.; Burrows, L.E. 2000: Vegetation communities of the Hurunui Mainland Island and implications for management. Landcare Research Contract Report LC9900 / 75 for the Department of Conservation. (unpublished) 30 p.

Noy-Meir, I.D.; Walker, D.; Williams, W.T. 1975: Data transformation in ecological ordination. II On the meaning of data standardization. *Journal of Ecology 63*: 779–800.

O'Donnell, C.F.J.; Dilks, P.J. 1994: Foods and foraging of forest birds in temperate rainforest, South Westland. *New Zealand Journal of Ecology 18*: 87–107.

Ogden, J.; Stewart, G.H.; Allen, R.B. 1996: Ecology of New Zealand *Nothofagus* forests. Pp. 25–82 in Veblen, T.T.; Hill, R.S.; Read, J. (Eds): The ecology and biogeography of *Nothofagus* forests. Yale University Press, New Haven and London.

Parsons, M.J.; Douglass, P.; Macmillian, B.H. 1995: Current names for wild gymnosperm, dicotyledons and monocotyledons (except grasses) in New Zealand as used in herbarium CHR. Landcare Research, Lincoln, New Zealand.

SAS Institute Inc. 2001: SAS Version 8.2. SAS Institute Inc, Cary, North Carolina, USA.

Sneath, P.H.A.; Sokal, R.R. 1973: Numerical taxonomy. W.H. Freeman, San Fransisco.

Stewart, G.H.; Wardle, J.A.; Burrows, L.E. 1987: Forest understorey changes after reduction in deer numbers, northern Fiordland, New Zealand. *New Zealand Journal of Ecology 10*: 35–42.

Suggate, R.P.; Stevens, G.R.; Te Punga, M.T. 1978: The geology of New Zealand. New Zealand Geological Survey, DSIR, Wellington, New Zealand.

van Tongeren, O.F.R. 1995: Cluster analysis. Pp. 172–212 in Jongman, R.H.; ter Braak, C.J.F.; van Tongeren, O.F.R. (Eds): Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.

Vayssières, M.P.; Plant, R.E.; Allen-Diaz, B.H. 2000: Classification trees: An alternative non-parametric approach for predicting species distributions. *Journal of Vegetation Science 11*: 679–694.

Wardle, J. 1984: The New Zealand beeches. Ecology, utilisation and management. New Zealand Forest Service, Wellington, New Zealand

Wardle, J.; Hayward, J. 1970: The forests and scrublands of the Taramakau and the effects of browsing by deer and chamois. *Proceedings of the New Zealand Ecological Society 17*: 80–91.

Wardle, P. 1963: Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. *New Zealand Journal of Botany 1*: 3–17

Wardle, P. 1980: Ecology and distribution of silver beech (*Nothofagus menziesii*) in the Paringa district, South Westland, New Zealand. *New Zealand Journal of Ecology 3*: 23–36.

Webb, C.J.; Sykes, W.R., Garnock-Jones, P.J. 1988: Flora of New Zealand. Volume IV. Botany Division, D.S.I.R., Christchurch, New Zealand.

Whittaker, R.H. 1975: Communities and ecosystems. 2nd ed. Macmillan, London.

Appendix 1

DATASETS FOR THE PLOTS USED

Datasets for the permanently marked 20 × 20 m plots used in this study.

North Hurunui catchment. Filenames: HURUNU99.REC, HURU99D.REC. Measured in 1999 and 2000 and part of a larger set of plots established in 1975.

South Hurunui catchment. Filename: HURSTH86.REC. Measured in 1986 and part of a larger set of plots established in 1977.

Data collection methods follow Allen (1992, 1993) for both datasets. These datasets are archived in the National Vegetation Survey Databank, managed by Landcare Research, at Lincoln. See wensite nvs.landcareresearch.co.nz for further information.