Mapping vegetation spatial patterns from modeled water, temperature and solar radiation gradients

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Abstract

Maps of current and potential vegetation spatial patterns can be used to assess land cover changes, and aid in ecosystem management and restoration. The vegetation spatial patterns of subalpine forest species are largely controlled by variation in temperature, water and solar radiation resources. These fundamental resources were quantified across a 1100-km² landscape using biophysical models, a digital elevation model (DEM), and weather station data. Field data of species abundances were used to define species–habitat relationships and calibrate maximum likelihood classifications of the biophysical gradients. For comparison, a standard land cover classification of Landsat Thematic Mapper satellite imagery had an overall accuracy 68.3%. Using the biophysical gradients alone gave a similar 67.4% accuracy. The highest accuracy classification (83.2%) used both biophysical and spectral data. The biophysical resources were also used to map the presence or absence of four herb and shrub species that cannot be sensed remotely. These predictions ranged from 60% to 79% accurate. Maps of relative abundance were less accurate, from 61% to 63.2%. This low result may be due to historical and stochastic events, or simply a small data set. The spatial pattern of species and communities that are controlled by resources can be predicted using general biophysical models. The species–habitat relationships can also be used to improve remote sensing products.

Keywords: spatial pattern prediction; species distribution; land cover change; subalpine

1. Introduction

There is a growing need to predict vegetation spatial patterns for assessing land cover change, for planning restorations, and for implementing sustainable management. Changes in land cover due to human influence could be estimated by comparing current patterns with landscape scale predictions of natural species distributions (Davis and Goetz, 1990; Iverson et al., 1997). This kind of landscape scale model could identify restoration sites for rare species (Wiser et al., 1998). These predicted sites could be expanded to extirpated species if the model was general enough to be calibrated on one landscape and applied to a different one. This ability to predict the landscape pattern of individual plant species could also be used to identify existing or potential wildlife habitat (Dettmers and Bart, 1999). In addition, efficient mapping of herbs, shrubs, and habitats across landscapes would help bring about the mandate of

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ecosystem management (CCFM, 1998). These needs have led this study to the development of a landscape scale model that employs general physical processes in order to predict species spatial patterns.

One approach to understanding and predicting vegetation patterns is to relate species abundance to environmental descriptors. However, application of this approach is limited to because the gradients are locally defined. For example, in high relief areas, species distributions have been correlated to elevation, topographic indices and aspect in ordination studies (Whittaker, 1973; La Roi and Hnatiuk, 1980; Peet, 1981), and in vegetation prediction studies (Brzeziecki et al., 1993; Bolstad et al., 1998). These studies cannot be applied to different areas because elevation and aspect do not affect plants directly, but are correlated to climate processes (Whittaker et al., 1968; Zobel et al., 1976; Wentworth, 1981). These climate processes will change from one landscape to the next. For example, the same elevation at two different latitudes will have different temperatures and radiation levels, in effect, different levels of the resources affecting plant physiology. Topographic indices are similarly limited because they are categorical, so a moisture ranking of 4 is probably not twice as wet as a ranking of 2 (e.g. Allen and Peet, 1990). These relative, rather than absolute, gradients make it difficult to apply the models for large-scale mapping or compare between research protocols.

The correlation or association of species to each other has been used map the shrub and herbaceous layers that cannot be remotely sense through a forest canopy (Lillesand and Kiefer, 1994). For example, communities have been mapped using the association between tree species and understory species (He et al., 1998). Inaccuracies can occur when the underlying assumption of similar niche widths is invalid because different species have wider or narrower niches than others (Gleason, 1926).

Another approach to mapping vegetation communities depends on their relationship to ecosystem and gap dynamics models that incorporate biological feedback into models of resource availability. These models tend to be complex and data intensive (Shugart and West, 1977; Running and Gower, 1991; Botkin et al., 1972). Part of the intricacy of these models is the local definition of biotic and abiotic feedback systems and relationships. The detail required prohibits the models from being applied to landscapes where these relationships are not well understood. The costs, complexity and limited predictive ability associated with these models also prevent their widespread application in the management and conservation communities (Korzukhin et al., 1996).

It may be possible to improve vegetation maps with simpler, more general biophysical models. Successful predictions of communities with this method include: local dune communities using hydrological parameters (Noest, 1994), California chapparal using climate parameters and regional north temperate forests using climate parameters (Lenihan, 1993; Monserud and Tchebakova, 1996). These studies relied on biophysical process models that defined species–habitat relationships which were comparable and transferable to other scales or sites, unlike environmental descriptors. These biophysical process models have no biological feedback and parameterization required only simple measurements (e.g. Tchebakova et al., 1994; Ostendorf and Reynolds, 1998), thus avoiding the complexity of ecosystem models. The three biophysical resources that are fundamental to physiological function are temperature, water and solar radiation (Jarvis and Leverenz, 1983; Stephenson, 1990; Larcher, 1995). These resources have been identified as controlling much of the spatial pattern in subalpine forests at the landscape scale (Whittaker and Neiring, 1965; Busing et al., 1993; Wentworth, 1981). In addition, these resources have large variance within subalpine landscapes, and that variability can be captured with simple, mechanistic models.

There are many other factors affecting vegetation patterns. Stochastic, dispersal and historical processes also affect species distribution (McCune and Allen, 1985; Ricklefs, 1987). Therefore, our predictions do not attempt to explain all spatial variability. For example, landscape scale patterns may depend on climatic variability, but those same climate models cannot be used to predict variability within a stand.

In this study, we combined the general nature of process models with the precision and predictive power of empirical models (Levins, 1966; Korzukhin et al., 1996). The purpose was to test the ability of general species–habitat relationships to map the spa-
tial pattern of vegetation across a mountainous landscape. Our objectives were to (1) understand the relationships between moisture input, temperature and solar radiation with the current species distribution; (2) map the spatial pattern of the tree, shrub and herbaceous species using a maximum-likelihood classifier to characterize species–habitat relationships. (3) The effectiveness of the predictions were tested by comparing the accuracy of the maps to similar maps made from remotely sensed observations of the land cover, or to a null model when direct observations were not possible. This study was completed in the Kananaskis River and Spray River watershed in the southeastern Canadian Rockies. This area provides an ideal test site because subalpine vegetation is well known to have strong relationships to physical gradients, (Whittaker, 1973; La Roi and Hnatiuk, 1980; Peet, 1981).

2. Methods

2.1. Study area geology and climate

The Kananaskis River and Spray Reservoir watersheds are located in the front ranges of the Southern Canadian Rockies (Fig. 1). The watersheds occupy 1184 km² of high relief mountains, with the outflow from the valley at 1350 m a.s.l., and the mountain peaks between 2400 and 3000 m a.s.l. The structure of the front ranges is defined by a series of thrust faults that resulted in parallel ridges of older (Paleozoic) limestone over younger (Cretaceous) sandstone and shale. Erosional processes on these bedrock layers formed valleys in the softer sandstone and shale, leaving the more resistant limestone as ridges (McMechan, 1988).

Climate in the Kananaskis river watershed is a transition between the Continental climate and the Cordilleran climate. The average precipitation regime has a winter maximum (22.3 mm) and a summer maximum (102.6 mm), with minima in late winter and again in autumn (Janz and Storr, 1977). The annual temperature profile follows a typical pattern for this latitude, with the lowest average monthly temperatures in January (−6 °C), and the highest in July (14 °C) (Kananaskis Field Stations, 1410 m a.s.l.).

The climate also changes spatially with elevation (Storr and Ferguson, 1972). The average annual precipitation increases linearly from 474.5 mm at 1400 m to 1110.5 mm at 2400 m, based on an 8-year study of a sub-basin in the watershed. Data from the same study showed that the average of the July maximum daily temperature decreases from 21.9 °C at 1400 m to 14.2 °C at 2400 m (Janz and Storr, 1977).

Large-scale climate processes drive the large sized and high intensity fires which drive population dynamics of the subalpine forest (Johnson and Larsen, 1991). The stand-replacing fires burned independent of forest type or elevation, therefore, the same disturbance rate occurs throughout the study area. Human disturbances have had little impact on most of the study area (Johnson and Fryer, 1987). Logging occurred in limited parts of the Kananaskis valley from 1886 to 1947. This disturbance effectively ended when the leases were burned by a large fire in 1936. The logging did not significantly impact species composition. Development in the study area is restricted to recreational facilities, hydroelectric dams and associated reservoirs.

2.2. Subalpine species

The subalpine forest is primarily coniferous and ranges in elevation from 1350 to around 2350 m. Lodgepole pine (Pinus contorta Dougl. ex Loud. var. latifolia Engelm.), white spruce (Picea glauca (Moench)Voss), white spruce/Engleman spruce hybrids (Picea engelmanni × P. glauca) and trembling aspen (Populus tremuloides Michx.) are the predominant trees in the lower subalpine. Engelman spruce (P. engelmanni Parry ex. Engelm.), and subalpine fir (Abies lasiocarpa (Hook.)Nutt.), with some subalpine larch (Larix lyallii Parl.) at tree-line, are predominant in the upper subalpine. The most common understory shrubs are soapberry (Shepherdia canadensis (L.) Nutt.), prickly rose (Rosa acicularis Lindl.) and willow (Salix sp.). Common herbaceous plants are asters and erigerons (Compositae), strawberry (Fragaria virginianum Duchesne), twinflower (Linnaea borealis L.), heart-leaved arnica (Arnica cordifolia Hook.), and bearberry (Arctostaphylos uva-ursi L.). Common mosses include feather moss (Pleurozium schreberi (Brid.) Mitt.), and common lichen include Peltigera aphthosa (L.) Wild. and Cladonia species.
Steep gully walls were too small to be included in this study, but are often occupied by dwarf adult trees of *Populus balsamifera* (L.), *P. contorta* or *Pinus flexilis* (James).

2.3. Input data

Species abundances were measured at 58 stands from 1993 to 1995, to calibrate and test the model.
predictions. Selection criteria for the forest stands was: (1) as wide a range of species and habitats as possible, (2) only stands greater than 3 ha, (3) visual homogeneity in height, diameter, and species composition, (4) lack of standing water, (5) absence of human disturbance (i.e. no cut stumps and a minimum of 30 m from trails or roads).

In each stand, vegetation was sampled along a transect with 15 points which were 15 or 30 m apart. This transect encompassed about nine pixels on the TM image. Canopy trees, saplings and shrubs were sampled with the point centered quarter method (Cottam et al., 1953). Canopy trees (> 7 cm diameter at base) were sampled for frequency, density and diameter at base (DB). A tree is defined as a species that could grow to the height of the canopy in the study area. Saplings (trees < 7 cm diameter at base and >1 m tall) and shrubs (non-trees >1 m tall) were measured for their density. At each point, herbs (non-tree species <1 m tall) were sampled for their presence in two 25 x 25 cm quadrats. Seedlings (tree species <1 m tall) were also sampled for frequency in two 1 x 1 m quadrats. Importance values were calculated as: the average of relative frequency, relative density and relative basal area for canopy trees; relative densities of understorey sapling trees and shrubs; and absolute frequencies for herbs and tree seedling (Greig-Smith, 1983). Voucher specimens were stored in the herbarium at the Kananaskis Field Stations.

The location of each site was measured with a global positioning system that was differentially corrected for an accuracy within 5 m. The stands were on-screen digitised by their location on a 30-m resolution (or 30 x 30 m pixel size) Thematic Mapper 4 satellite image. The image was taken on August 8, 1984, with a sun elevation of 49.3° and azimuth 138°. This scene was used because of previous classification success and knowledge of no large disturbance in the intervening period (Franklin et al., 1994). The image was geocorrected to the Universal Trans-Mercator grid using a previously corrected 25 m digital elevation model (DEM). The DEM was part of the Alberta (provincial) Base Mapping Digital Terrain Data System. Independent ground control points confirmed an error of less than 1 pixel.

The non-forested land cover classes were bare rock, alpine, lake, or stream. The training and testing pixels characterizing these classes were identified by visual interpretation of Thematic Mapper images and air photos. A minimum of 100 pixels per class was sampled.

2.4. Resource model description

The models of moisture input, temperature and solar radiation are designed to characterise resource variables as they are controlled by the terrain and climate. The equations were simple so they have easily measured input terms and intuitively understandable behaviour. The modeled resources were independent of species specific interactions with the environment, so that definitions of species tolerances did not depend on a priori knowledge of species distributions.

2.4.1. Moisture input (m)

The water input to plants was determined by climatological scale processes of precipitation and hillslope scale processes of drainage (Beven and Kirkby, 1979). This relationship was formalized by multiplying the annual precipitation (Eq. (2)) by the wetness index (Eq. (3)) so that the moisture input (Eq. (1)) was determined by:

\[ m_i = wp \]  \hspace{1cm} (1)

where \( m_i \) was the moisture input (m³ per meter contour length per year), \( w \) was the wetness index, and \( p \) was the precipitation. The moisture input was a physically based index which was correlated to the actual moisture available to the plants.

The moisture input was calculated on an annual basis because the known relationship between precipitation and elevation in the study area was for an average year, and other climate data were not available across the elevation range in the study area.

Precipitation (m/year) was calculated from:

\[ p = -415.9 + 0.636E \]  \hspace{1cm} (2)

where \( E \) was the elevation (m) from the DEM. This relationship was empirically determined for a sub-basin of the Kananaskis (Storr and Ferguson, 1972). The 8-year study used eleven precipitation gauges at elevations ranging from 1780 to 2285 m.
The local hillslope processes distribute the precipitation (Eq. (2)). The wetness was the amount of water draining into a point, divided by the rate water would be flowing through that point. For example, when two sites have the same catchment area, the steeper one will be drier. The model of hillslope wetness was computed as:

\[ w = \ln\left(\frac{A}{\tan B}\right) \]  

where \( B \) was the slope angle in the site and \( A \), the catchment area (\( m^2/m \)), was the size of the area that collects the water that flows through 1 m of contour length (Beven and Kirkby, 1979). This model of hillslope processes has been shown to be effective, despite its simplicity and the assumption of uniform ground water loss (Beven et al., 1984; Wolock et al., 1989). More detailed models that include soil texture and variation in the water flux within the drainage area (e.g. O’Loughlin, 1986) were not used because the required data was not available.

The catchment area values for the wetness model (Eq. (3)) were based on an accumulation algorithm where the water from each pixel on the DEM flows into the lowest elevation pixel of its eight neighbouring pixels (Jenson and Domingue, 1988; PCI, 1996). The first step was to use this accumulation algorithm to determine the upslope area of each pixel by calculating how many pixels drained into each pixel. This was done by tracing the flow of water upslope from the pixel in question, until the point where the pixels in the path are no longer the lowest in a neighbourhood and water ceases to flow into them. The second step was to calculate the median of a 3×3 pixel neighbourhood. This step was necessary to smooth out some of the high variance in accumulation that is a consequence of all of the flow from a pixel going into a single neighbouring pixel (Tarboton, 1997). In the third step, the value one was added to the median, so that each site had at least its own climate water flux as input. In other words, the minimum upslope area was one pixel. The last step was to convert from pixels to meters, by multiplying the number of pixels by the area of a pixel (900 m²), and then dividing the product by 30 m, the length of a pixel edge. The result was the area drained per meter contour length for a site; assuming that water flows out of a pixel edge.

The angle of the slope (\( B \)) was calculated as the angle of the plane formed by the vector connecting the left and right neighbour pixels, and the vector connecting the upper and lower neighbours of the pixel in question (PCI, 1996).

2.4.2. Temperature

The mean July maximum temperature in degrees Celsius (\( T_\)J) changed with elevation in meters (\( E \)) such that:

\[ T_J = 32.7 - 0.00771E \]  

This linear regression relationship was determined over an 8-year period for a sub-basin of the Kananaskis watershed. The study used seven weather stations located from 1370 to 2285 m a.s.l. (Janz and Storr, 1977). This study also found that the highest temperatures occurred in July, therefore this represents the optimal growing month.

2.4.3. Solar radiation

The incoming shortwave radiation for an average July day was calculated using the DEM and Nikolov and Zeller’s (1992) algorithm for estimating solar radiation received by mountain slopes. The month of July was used for consistency with the temperature variable. The cloudiness estimate used long-term averages of July relative humidity from the nearby Banff weather station. The incoming radiation varies with elevation, aspect and slope angle, which changed considerably within the study area, as well as with latitude and date (Nikolov and Zeller, 1992). The horizon was set at 15° to compensate for the mountain shadows on the predominantly N–S valley. The solar incidence angle and solar altitude angle were calculated for each daylight hour of an average July day, then averaged across the hours. The incoming solar radiation was subsequently calculated for an average July day.

2.5. Gradient analyses

Canonical correspondence analyses (CCA) were run using standard topographical descriptors (elevation, slope tangent and cosine of aspect), and with the modeled resources to compare the two methods of defining habitats. CCA is considered the best general
purpose direct ordination method because it assumes a unimodal frequency distribution and is relatively robust against curvilinear distortion (Fasham, 1977; Gauch et al., 1977). To reduce distortions caused by species which were absent in a large number of sites (see Swan, 1970), species present in <60% of the stands were deleted from the analysis. When ordinations were run with species present in <10% to 60% of the stands, the patterns of species and stand distribution along the ordination axes were consistent. However, when species presence was above or below these thresholds, the pattern changed markedly.

2.6. Classification of biophysical and spectral data

Two-thirds of the pixels that were sampled in the field were assigned to classes (defined below), and used to train a maximum-likelihood classifier (PCI, 1996). This classifier used the distributions of the training data on the resource gradients or on the spectral bands to assign the rest of the pixels in the study area to the classes. Three classifications were performed and compared to determine differences in class discrimination. These classifications were bases on the resource variables, spectral variables of TM bands 3,4,5 (Nelson et al., 1984; Horler and Ahern, 1986) and the combination of all six variables.

2.6.1. Class definitions

The forest cover vegetation classes were defined using measured abundances so that the accuracy of the map was maximized. If a canopy tree species had an importance value of >16% then that species was included in the class name (e.g. the name lodgepole pine was applied to stands that had only lodgepole pine with a >16% importance value). The resulting tree classes were: lodgepole pine, trembling aspen, lodgepole pine and Engelman/white spruce, and sub-alpine fir and Engelman/white spruce. The non-forested classes of rock, alpine, deep water and shallow water largely occupied the remainder of the landscape. There are roads and small developments in the watersheds, but these represent less than 5% of the area.

Five herb and shrub species were used to test the predictive ability of the resource gradients beyond what can be mapped by remote sensing. The species were chosen for their frequency in the stands. The high frequency of a species represents a large enough sample to derive signatures for the classification. From among the common species, a subset was chosen that represented a variety of growth habits. Specifically, prickly rose is a large shrub, bearberry is a small shrub, Arnica is flowering herb, P. apthosa is a lichen, and feather moss.

Herb and shrub individual species classes were defined in terms of presence/absence and in terms of abundance classes. Low abundance was 7% to 38%. Medium abundance was 38% to 69%. High abundance was importance greater than 69%. Absence was defined as an importance value less than 7% and presence was importance greater than 7%. Importance values less than 7% were assumed to be due more to historical, dispersal, or stochastic factors than physiological tolerances. The higher class thresholds were based on adequate sample size to define signatures.

2.6.2. Accuracy assessment

The one-third of pixels with known classes, but not used to train the classifier, were compared to the output in order to test the accuracy of the map. The overall accuracy was expressed as a percent of the test pixels successfully assigned to the correct class. The Kappa statistic (KHAT) is a statistical method of assessing accuracy that takes into account the chance of random agreement (Congalton and Green, 1999). We used the KHAT and corresponding 95% confidence intervals as a null model to ensure that the predictions were significantly better than a random classification.

3. Results

3.1. Resource model behaviour

The distributions of stands showed the modelled resources were independent. Linear regressions of each pair-wise relationship between resources had \( r^2 \) values less than 0.035. Despite the co-dependence on the terrain, each resource variable represented a different aspect of the vegetation habitat.

3.1.1. Moisture input

The moisture input distribution among stands reflected the interplay of the local and landscape
climate processes (Fig. 2a). Within lower elevations, the gentle bases of long hillslopes had more moisture than the steep, short sites. However, the same relationship was not found at high elevations, possibly because most hillslopes are short, and therefore had small catchment areas. The slopes at high elevations had as much moisture input as gentle slopes at low elevation because of the higher amounts of precipitation (Fig. 2a). The driest sites occurred on some of the flat slopes because they were on the ridges and

Fig. 2. Relationships between the three modeled resource gradients and three common environmental descriptors. (a) Moisture response to slope angle for two elevation classes. Only two classes were used here to illustrate the different relationships that occurred. (b) Temperature correspondence to changing elevation. (c) Temperature correspondence to slope angle. (d) Solar radiation response to slope angle. (e) Solar radiation response to aspect. (f) Lack of radiation correspondence to elevation.
therefore had very small catchment areas. These sites were no sites with less than 6 m$^3$/m$^2$ moisture input sampled at high elevations because ridges were generally not forested. The moisture input did not respond to aspect because the drying associated with south facing slopes was not incorporated into the model.

### 3.1.2. Temperature

Unlike the moisture input, July temperature only varied with landscape processes. As expected from Eq. (4), the July temperature was directly correlated with elevation (Fig. 2b). The scatter around the correlation was due to averaging the temperature values among the pixels of a stand. There was a spurious pattern of temperature with slope angle where the warmest temperatures rarely occur on steep sites (Fig. 2c). This pattern occurred because steep slopes were less likely to occur where temperatures were warmest within the watershed. Hillslopes tended to be gentler at lower elevations compared to higher elevations because of erosional and depositional processes. Temperature did not vary with aspect because the warming affect associated with south facing slopes was not incorporated into the model (Dymond, 1998).

### 3.1.3. Solar radiation

In contrast to temperature, the effects of slope angle and slope aspect outweighed the elevational affect on incoming solar radiation. The variation in the radiation increased as slope angle increased because steep, north facing slopes are more shadowed and steep, south facing slopes intercept more beam radiation (Fig. 2d). Radiation generally decreased from south to north facing slopes as the amount of time and exposure to direct beam radiation decreased (Fig. 2e). As elevation increased, there is less atmosphere to absorb solar radiation, so more should reach

![Fig. 3. Canonical correspondence analysis of common species and modeled July temperature, moisture input and solar radiation.](image)

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Accuracy assessment for three land cover maps with different types of data being classified</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>KHAT$^*$</td>
</tr>
<tr>
<td>Spectral classification</td>
<td>0.61</td>
</tr>
<tr>
<td>Resource variable classification</td>
<td>0.60</td>
</tr>
<tr>
<td>Combination classification</td>
<td>0.79</td>
</tr>
</tbody>
</table>

$^*$KHAT accuracies are significantly different when their confidence intervals do not overlap.
Fig. 4. Land cover classifications from three types of input data. (a) Classification of TM spectral data. (b) Predicted land cover using July temperature, moisture input, and solar radiation. (c) Classification of modeled resources and TM spectral data.
3.2. Gradient analysis

Using these modeled resource in a direct ordination explained slightly more variation in the vegetation abundance than the traditional topographic descriptors. The CCA using temperature, moisture input and radiation explained 17.2% of the species variance with the first axis and 5.7% with the second axis. Using the slope angle, aspect and elevation explained 16.3% variance with the first axis and 3.8% with the second axis.

The species–habitat relationships for canopy trees can be described from the CCA results (Fig. 3). Lodgepole pine and Aspen stands occupied higher temperature habitats. Aspen stands tended to be found in areas with higher moisture input and solar radiation, whereas pine habitat included the range of moisture and solar radiation conditions. Spruce and fir stands occupied lower temperature habitats, with fir concentrated in lower moisture and solar radiation habitats, and spruce in higher moisture and higher solar radiation conditions. Pine and spruce occur together in habitats with relatively moderate temperatures.

3.3. Land cover maps

The spectral classification of land cover had low accuracy at mapping vegetation pattern (Table 1). A large percentage of the forest was mapped to pure lodgepole pine forests (61.9% accuracy) and the small area in pine/spruce (18%) and spruce/fir forests (12% accuracy) (Fig. 4a). While lodgepole pine was abundant in the watersheds, it did not dominate the landscape to such a degree. The most accurate classes were the broad land cover classes of deep water (97.3%), alpine (91.5%), and rock (81.6%).

Using the modeled resources produced a similarly accurate representation of the spatial pattern on the landscape (Table 1). Trembling aspen occupied the warmer and higher radiation sites with 83.3% accuracy (Fig. 4b). Lodgepole pine occupied the warm and lower radiation sites with 61.9% accuracy, but was confused with the pine/spruce class. The pine/spruce class was mapped to cooler sites, but the accuracy was low at 21.2%. Since this class represented the transition class, it was not surprising that 44% of the pine/spruce sites were predicted as lodgepole pine or
spruce/fir. Forests of spruce and subalpine fir occupied the coolest and wettest areas with 68% accuracy. There was some confusion between spruce/fir stands and pine/spruce or alpine. The rock and alpine landcover types were otherwise accurately mapped (78.8% and 79.2%). Deep water areas were successfully mapped 90.2%, and were only confused with shallow water. The shallow water class was poorly mapped (39.3%).

Combining the spectral with modeled resources had the highest accuracy at representing the forest cover pattern (Table 1). The KHAT accuracy was significantly better than using the spectral data alone or the resource gradients alone (Fig. 4c). The combination of spectral and resource variables improved the distribution of the lodgepole pine and spruce/subalpine fir compared to either the spectral or the resource variable classification. The aspen and pine/spruce mapping was poor, at 52% and 36.4%, largely because of confusion with lodgepole pine. The combination of variables also produced a more accurate map of spruce/fir, rock, deep water, shallow water and alpine (80%, 96.8%, 98.2%, 63.7%, 94.2% accuracy). The most significant change from using spectral data alone was the assignment of areas to pine/spruce or spruce/fir rather than pine. The most significant change from using resource data alone was the assignment of areas to spruce/fir rather than alpine.

### 3.4. Herb and shrub predicted maps

In addition to forest cover types, understorey species with narrow niches defined by temperature, solar radiation and moisture input were accurately predicted from the resource variables. For example, sites with high abundance of prickly rose were clumped where July temperatures were highest, and radiation levels were high and moderate (Fig. 5a). The resulting prickly rose presence/absence classification

<table>
<thead>
<tr>
<th>Species</th>
<th>KHAT</th>
<th>95% Confidence interval for KHAT</th>
<th>Percent accuracy (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prickly rose</td>
<td>0.57</td>
<td>0.13</td>
<td>78.7</td>
</tr>
<tr>
<td>Bearberry</td>
<td>0.46</td>
<td>0.14</td>
<td>71.3</td>
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<td>Peltigera</td>
<td>0.28</td>
<td>0.17</td>
<td>61.7</td>
</tr>
<tr>
<td>Feather moss</td>
<td>0.30</td>
<td>0.18</td>
<td>60.3</td>
</tr>
<tr>
<td>Arnica</td>
<td>0.15</td>
<td>0.17</td>
<td>62.3</td>
</tr>
</tbody>
</table>

*When the KHAT confidence interval does not overlap with zero, then the map was significantly more accurate than a random map.
of the forested part of the landscape was 78.7% accurate (Fig. 5b). Prickly rose was predicted to be present at lower elevations on flat and south facing slopes, where sites tended to have relatively high July temperatures and high levels of solar radiation.

The species presence/absence pattern could not be predicted for species without a relationship to the modeled resource variables. *A. cordifolia* clearly had variation in abundance, but there was no obvious pattern with the modeled gradients (Fig. 6a). The presence/absence maximum likelihood classification of *A. cordifolia* was 62.3% accurate (Fig. 6b). However, this was not significantly better than a null model (Table 2). The accuracy of presence/absence classifications for a variety of understorey species ranged from 60% to 79% (Table 2). Four of the five classifications...
predicted significantly more of the spatial pattern than a null model (Table 2). The predictions were successful across the range of growth forms.

The spatial pattern of relative abundance was also predictable for some species. For example, the relative abundance classification of prickly rose had 63.2% overall accuracy (Fig. 7). In this prediction, the highest abundance of prickly rose occurred where the temperatures were warmest and the solar radiation was highest. Prickly rose was predicted at lower abundance in some of the cooler areas where radiation levels were high, such as on south facing slopes. As with presence/absence, herb and shrub abundance predictions were statistically better than the null model, except for *A. cordifolia* (Table 3). The decrease in accuracy from presence/absence to relative abundance was greater for some species than others. For example, feather moss accuracy dropped 24.3%, whereas bearberry dropped less than 1%. Part of the drop in accuracy was due to the limited amount of ground truth data that was divided among three classes (absent/low/medium) for bearberry and four classes (absent/low/medium/high) for *Peltigera*, instead of just presence or absence.

4. Discussion

Biophysical variables can explain as much, or more variation in subalpine species composition than traditional environmental descriptors. Elevation, slope, and aspect are correlated to subalpine vegetation (e.g., Whittaker et al., 1968; Allen and Peet, 1990), but by using some simple process models we can move beyond descriptions into testing hypotheses about what controls species patterns and predicting those patterns. Since the incorporation of additional descriptors has helped explain vegetation variation in the past (e.g., Zobel et al., 1976; Busing et al., 1993; McAuliffe, 1994), adding models of soil nutrient flow, soil development, or evapotranspiration may further the success of using process models. This success will be limited to the variation in the species spatial patterns that is controlled by deterministic relationships (McCune and Allen, 1985; Ricklefs, 1987).

Simple, mechanistic models of temperature, solar radiation and moisture can be used to improve vegetation maps in mountainous areas. The most accurate map of subalpine land cover used the combination of spectral and resource variable data. This result supports the improvement in classifications achieved using environmental descriptors (Franklin, 1992; Franklin et al., 1994). The resource models combined hillslope processes that predict local communities (e.g., Ostendorf and Reynolds, 1998) and regional climate processes that predict subcontinental and global vegetation patterns (e.g., Woodward and Williams, 1987; Tchebakova et al., 1994; Monserud and Tchebakova, 1996). Improving the accuracy of the predictions would require more sophisticated environmental models. For example, incorporating the shading effect of the surrounding mountains on solar radiation may improve mapping on north facing slopes.

Furthermore, using resource variables as one of the input data sets can reduce the dependence of mapping processes on spectral data. For example, areas of cloud, shadow or saturation could be separately mapped using resource variables. The resulting classification could be merged with a spectral and resource variable classification of the surrounding area.

The herb and shrub classifications showed that species which have clumped distributions with respect to the modeled resources were accurately predicted to be present or absent (accuracy greater than 60% and KHAT significantly better than random). The relative abundance of some species was also accurately predicted. This approach to predicting individual species is uncommon (Iverson and Prasad, 1998; Wiser et al., 1998). However, there is a growing conservation, restoration and ecosystem management need to understand and predict individual species and species richness variation across landscapes (Hill and Keddy, Table 3

<table>
<thead>
<tr>
<th>Species</th>
<th>KHAT</th>
<th>95% Confidence interval for KHAT</th>
<th>Percent accuracy (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prickly rose</td>
<td>0.46</td>
<td>0.12</td>
<td>63.2</td>
</tr>
<tr>
<td>Bearberry</td>
<td>0.40</td>
<td>0.13</td>
<td>61.0</td>
</tr>
<tr>
<td>Peltigera</td>
<td>0.35</td>
<td>0.15</td>
<td>61.0</td>
</tr>
<tr>
<td>Feather moss</td>
<td>0.18</td>
<td>0.12</td>
<td>36.0</td>
</tr>
<tr>
<td>Arnica</td>
<td>0.11</td>
<td>0.14</td>
<td>39.5</td>
</tr>
</tbody>
</table>

* When the KHAT confidence interval does not overlap with zero, then the map was significantly more accurate than a random map.
Improving the predictive ability for more species will probably require including more environmental processes, such as the effect of canopy density on understory radiation, since not all species respond to the same variables (Hill and Keddy, 1992). Species that do not have clumped distributions with respect to temperature, radiation and moisture input may have distributions predictable by other habitat variables that can be modeled. The prediction of relative abundances would likely be improved with more ground truth data. Having more data can produce more reliable signatures for the classification, and better results (Congalton and Green, 1999).

Applying biophysical-based predictions to other types of vegetation requires knowledge about the resources controlling the species abundances. Gradient analyses and other studies in a particular area can help determine which biophysical gradients are most likely to successfully predict species distributions (e.g. Host et al., 1987; Davis and Goetz, 1990). These studies will also help determine the scale at which successful predictions may be possible. For the Kananaskis and Spray watersheds, a combination of local and landscape scale processes predicted the landscape scale vegetation pattern.

5. Conclusion

The first purpose of this study was to test the ability of general species–habitat relationships to map the spatial pattern of vegetation across a mountainous landscape. The use of simple biophysical models improved the maps of the Kananaskis and Spray watersheds in three ways. First, the accuracy of the land cover was improved by combining the resource variables with spectral data. Second, the presence and absence of sub-canopy shrub and herb species can be accurately mapped using the resource variables. Third, ecological or management sensitive areas, due to rare or exotic species can be mapped based on the resource variables.

The second purpose of this study was to provide ecological tools to people mapping large areas. The incorporation of topographical information is an established tool to improve remote sensing products (e.g. Franklin et al., 1994). Replacing the standard topographical measurements with biophysical models will provide more ecologically based information to the mapping process. This is especially important when the study area spans sub-continents or continents and the relationship between species and topography changes.

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