Andrew, M.E., Nelson, T.A., Wulder, M.A., Hobart, G.W., Coops, N.C. and Farmer, C.J.Q. (2013) Ecosystem classifications based on summer and winter conditions. Environmental Monitoring and Assessment, 185 (4). pp. 3057-3079.

Ecosystem classifications based on summer and winter conditions

Margaret E. Andrew[1^], Trisalyn A. Nelson[2], Michael A. Wulder[1], George W. Hobart[1], Nicholas C. Coops[3], Carson J. Q. Farmer[4]

Author Affiliations:

[1]Canadian Forest Service (Pacific Forestry Centre), Natural Resources Canada, 506 West Burnside Road, Victoria, British Columbia, V8Z 1M5, Canada

[2]Spatial Pattern Analysis and Research (SPAR) Laboratory, Department of Geography, University of Victoria, PO Box 3060, Victoria, British Columbia, V8W 3R4, Canada

[3]Department of Forest Resource Management, 2424 Main Mall, University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada

[4]National Centre for Geocomputation, National University of Ireland, Maynooth, Maynooth, Co. Kildare, Ireland

^Corresponding author:
Margaret Andrew
Canadian Forest Service, Pacific Forestry Centre
506 West Burnside Rd., Victoria, BC V8Z 1M5;
Phone: 250-298-2428; Fax: 250-363-0775; Email: margaret.andrew@nrcan-rncan.gc.ca

Pre-print of published version.

Reference:
Andrew, M.E., T.A. Nelson, M.A. Wulder, G.W. Hobart, N.C. Coops, and C.J.Q. Farmer (in press). Ecosystem classifications based on summer and winter conditions. Environmental Monitoring and Assessment. **doi:**10.1007/s10661-012-2773-z.

DOI.
http://dx.doi.org/10.1007/s10661-012-2773-z

Keywords: Classification agreement; ecological regionalization; environmental domain classification; fraction of absorbed photosynthetically active radiation (fPAR); map comparison; snow water equivalent (SWE)

Abstract. Ecosystem classifications map an area into relatively homogenous units for environmental research, monitoring and management. However, their effectiveness is rarely tested. Here, three classifications are 1) defined and characterized for Canada along summertime productivity (MODIS fraction of absorbed photosynthetically active radiation) and wintertime snow conditions (SSM/I snow water equivalent), independently and in combination, and 2) comparatively evaluated to determine the ability of each classification to represent the spatial and environmental patterns of alternative schemes, including the Canadian ecozone framework.

All classifications depicted similar patterns across Canada, but detailed class distributions differed. Class spatial characteristics varied with environmental conditions within classifications, but were comparable between classifications. There was moderate correspondence between classifications. The strongest association was between productivity classes and ecozones. The classification along both productivity and snow balanced these two sets of variables, yielding intermediate levels of association in all pairwise comparisons. Despite relatively low spatial agreement between classifications, they successfully captured patterns of the environmental conditions underlying alternate schemes (e.g., snow classes explained variation in productivity, and vice versa).

The performance of ecosystem classifications and the relevance of their input variables depend on the environmental patterns and processes used for applications and evaluation. Productivity or snow regimes, as constructed here, may be desirable when summarizing patterns controlled by summer- or winter-time conditions, respectively, or of climate change responses. General-purpose ecosystem classifications should include both sets of drivers. Classifications should be carefully, quantitatively, and comparatively evaluated relative to a particular application prior to their implementation as monitoring and assessment frameworks.

1. Introduction

Natural systems are complex and variable over time and space, and at a range of scales. To better understand our surroundings, scientists and resource managers have developed a variety of ecosystem classifications. Also known as ecological regionalizations, these products are simplified conceptualizations of an area that classify a land base into regions characterized by similar environmental conditions (e.g., Bailey et al. 1985; Loveland and Merchant 2004), ecological processes (e.g., McMahon et al. 2004), and distinct biotic communities (e.g., Olson et al. 2001). Because conditions of interest are assumed to be relatively homogenous within component regions, classifications can provide frameworks for generalization, stratification, and to inform expectations of what is natural or appropriate for a site (e.g., Omernik 1987).

Regions help to organize, study, manage, and present monitoring and research results for large, diverse areas. For instance, a large nation such as Canada is not likely to be well characterized by average conditions (e.g., mean air pollution levels, mean forest volume), but conditions may be adequately represented by summary values from a system of homogenous, ecologically defined regions. In addition to experiencing similar conditions, sites within a region are expected to respond similarly to stressors (Bailey et al. 1985). Ecosystem classifications can, therefore, be used to pair pristine and degraded sites (or control and experimental sites), and to generalize and scale up observations from a limited data sample. Indeed, ecosystem classifications are often used as the areal units for national and international reporting requirements (e.g., Commission for Environmental Cooperation 1997; Government of Canada 1996; Petit et al. 2001). Ecosystem classifications are useful stratification tools because, if classes are characterized by internal homogeneity and between-class distinctness, a sample encompassing all classes is expected to include most of the variability of an area (McMahon et al. 2004). Management applications of ecosystem classifications include setting forestry (Banner et al. 1996; Beauchesne et al. 1996) and fire management recommendations (McRae 1996), monitoring water quality (Barton and Metzeling 2004; Wells et al. 2002) and genetically modified organisms (Graef et al. 2005), and defining representative protected area networks (Convention on Biological Diversity 2004; Olson and Dinerstein 1998; Parks Canada 1997).

Consequently, a number of ecosystem classifications have been developed, ranging from ecoregions, typically expert-based delineations of regional patterns (e.g., Ecological Stratification Working Group 1995; Wiken et al. 1996), to quantitative environmental domain classifications (environmental cluster analyses) of particular variables or combinations thereof, which may relax requirements of spatial contiguity (e.g., Host et al. 1996; Mackey et al. 2008). Ecosystem classifications are generally created along input variables of climate, topography, geology, and/or soils (e.g., Host et al. 1996; Kirkpatrick and Brown 1994; Leathwick et al. 2003; Mackey et al. 2008; Trakhtenbrot and Kadmon 2006). Remotely sensed indices of vegetation and ecosystem function have also been used (Fernández et al. 2010; Mackey et al. 2008), but are surprisingly less common. Earth observation data have strong traditions of providing spatially-extensive, physically-based estimates of a variety of environmental variables from sensors with optimized spatial, spectral, and temporal characteristics. For example, optical sensors provide a wealth of information about vegetation pattern, condition, and vegetation-mediated processes; information in the microwave portion of the spectrum indicates meteorological and hydrological parameters. The combination of these two types of information may provide an integrated picture of ecosystem distributions and functioning at regional to global scales.

To be useful, ecosystem classifications must not only effectively partition within- and between-class variability (often achieved with statistical clustering algorithms), they must also capture patterns of variability that are meaningful to biota and ecological processes. Thus, the specific environmental variables along which ecosystem classifications are defined are of paramount importance, with different choices of variables leading to diverse results (Bailey et al. 1985). For example, a variety of ecoregion frameworks have been developed for North America, emphasizing different gradients (e.g., Bailey 1995; Omernik 1987). Although the region cores are broadly similar, ambiguities of where to delineate region boundaries cause them to differ in their specifics (Bailey 2004; Omernik 2004). The capacity for discrepancies between ecosystem classifications can be much more marked than questions of boundary placement. Because alternative input variables may be largely unrelated, the resultant classifications may bear little to no resemblance to each other. Both spatial patterns and scales of variation may differ with input variables, resulting in classifications that differ in class placement, pattern, and effective spatial resolution.

It is likely that no optimal, singular ecosystem classification exists. Rather, the choice of classification product and its defining variables should depend upon the planning area extent (Barton and Metzeling 2004) and the application at hand (Loveland and Merchant 2004; Wells et al. 2002). For example, productivity, which is predominantly a result of growing-season (i.e., summertime) processes, is an important control of biodiversity (Evans et al. 2005; Hawkins et al. 2003); regions derived from productivity metrics, which are supported by the availability of remotely sensed measures of vegetation productivity (Kerr and Ostrovsky 2003), may thus provide useful areal units for representing the variation and status of biodiversity. In contrast, wintertime conditions such as snow depth can have direct impacts on plant and animal phenology, water balance, and habitat quality (Dussault et al. 2005; Madsen et al. 2007; Walker et al. 1993). Consequently, regions based on snow conditions, which may be estimated via passive microwave remote sensing (Tait 1998), may also be useful and capture different ecological processes and limiting factors than those based on productivity. Generality may be increased by including both summer and winter conditions in a single ecosystem classification, avoiding idiosyncrasies that may arise from each alone. However, productivity- and snow-based classifications need not be markedly different. Snow cover and, in particular, timing of snow events are suspected to drive local and regional productivity patterns (Kimball et al. 2000; 2004; Lafleur and Humphreys 2007; but see Litaor et al. 2008), which may lead to consistent patterns whether a classification is trained with productivity, snow, or both.

How then should an ecosystem classification be selected for a particular application? Classifications are predominantly evaluated and compared with accuracy (or agreement) statistics computed from entries in a confusion matrix (Congalton 1991). However, this strategy is less than ideal in many circumstances, and alternative or supplemental measures should be considered. Products depicting markedly different spatial patterns may nevertheless yield similar accuracy measures. For example, existing global land cover products each have accuracies approaching 70%, yet agreement between products is relatively low (Fritz and See 2008; Giri et al. 2005; Herold et al. 2008; Jung et al. 2006; Kaptué Tchuenté et al. 2011). Moreover, particular applications will be less influenced by overall accuracy than by the sensitivity of a product to the patterns of interest. These may be particular land cover classes, in which case thematic resolution, class-based accuracies, and the nature of class confusions will be most relevant (Fritz and See 2008; Jung et al. 2006). Or the mapped classes may simply be indirect proxies of the patterns of interest. For example, in biodiversity conservation applications, species composition is assumed to vary with land cover (Andrew et al. 2011; Mac Nally et al. 2002); likewise, carbon models use land cover to parameterize differences in physiology, leaf traits, architecture, albedo, etc. (Jung et al. 2006; Moody et al. 2007). In these cases, an evaluation of land cover classifications at capturing those patterns is a more direct assessment of applicability than are class accuracies, and is a clear departure from the confusion matrix framework. Another shortcoming of comparisons using confusion matrices is that they require pairing of classes from potentially distinct thematic legends (Foody 2006), usually by aggregating classes until comparable, coarse categories are reached, with subsequent loss of information (Herold et al. 2008; Jung et al. 2006; Kaptué Tchuenté et al. 2011), although one-to-many class mappings with agreement weighting schemes have also been investigated (Fritz and See 2008). Such approaches are feasible for comparing land cover classifications, which ultimately have similar objectives and, at some level, similar legends. Yet class pairings may never be possible for classifications of distinct ecosystem functions. Map comparison techniques that are independent of classification schemes exist (e.g., Foody 2006) and merit more widespread use.

The goals of this research are to 1) define and characterize ecosystem classifications along summertime productivity, wintertime snow conditions, and the combination of the two; and 2) determine how well these classifications correspond, both geographically as well as along the underlying productivity and snow gradients, and how this correspondence varies with environmental conditions. As such, we synthesize, extend, and evaluate the frameworks of

Coops et al. (2009) and Farmer et al. (2010), who have generated ecosystem classifications of Canada along productivity axes and of the Canadian prairies along snow conditions, respectively.

2. Methods

2.1. Study area and datasets

Canada encompasses nearly 10 million km^2 in area, spanning a range of physical and environmental conditions. Northern areas can be snow covered for more than half of the year, with all other areas of the country typically experiencing snow cover for some period of time during the winter months. Considered nationally, the average length of the snow season is 4.2 ± 1.0 months. Adaptive strategies are required by both plants and animals to cope with the variability of resources across seasons. This study used remotely sensed datasets of vegetation productivity (fPAR; fraction of absorbed photosynthetically active radiation; refer to Table 1 for a list of abbreviations used in the text) and snow water equivalent (SWE) for Canada south of 75^{o}N. This extent includes 96% of Canada's land area (see Fig. 1), including all of the Canadian boreal forest. It was necessary to exclude arctic islands north of 75^{o}N due to limited satellite coverage for the fPAR dataset.

2.1.1. Dynamic habitat index

The dynamic habitat index (DHI) is a tripartite, spatially explicit, productivity-based set of metrics that has been developed to inform on biodiversity and natural resource monitoring and management in Canada (Duro et al. 2007). The DHI uses monthly fPAR estimates as recorded by the MODIS sensor (MODerate-resolution Imaging Spectrometer) at 1 km spatial resolution (Myneni et al. 2002). Annual productivity characteristics are summarized with the minimum annual fPAR, integrated fPAR, and fPAR seasonality (represented by the coefficient of variation of fPAR estimates) for each pixel (Coops et al. 2008). These three annual DHI components were produced for years 2000-2005 and temporally averaged. Elevation (shuttle radar topography mission; Rabus et al. 2003) is often considered in conjunction with the DHI, as it has strong influences on abiotic and biotic patterns and processes (Coops et al. 2008; Duro et al. 2007). Seasonality, integrated annual productivity, and elevation are mapped for Canada in Fig. 1a. For ecosystem classifications, the DHI components and elevation were aggregated to the 25 km resolution of the snow data (below) by pixel averaging.

2.1.2. Snow water equivalent

Daily SWE measurements were estimated from Special Sensor Microwave/Imager (SSM/I) passive microwave brightness temperatures at 37 and 19 GHz with vertical polarization and a spatial resolution of 25 km. (For a discussion of estimating snow cover with passive microwave radiometry and a more thorough description of this dataset and its processing, see Farmer et al. 2010.) Annual metrics summarizing SWE amount and timing were computed with the spline-fitting approach of Farmer et al. (2010), yielding 10 independent variables for each pixel: 1) maximum SWE, 2) range of SWE, 3) time of minimum SWE, 4) time of maximum SWE, 5) total SWE, 6) start of SWE accumulation, 7) start of melt, 8) end of melt, 9) accumulation rate, and 10) melt rate. SWE metrics were computed for years 1999-2006 and temporally averaged. All SWE processing was performed in R (R Core Development Team 2008).

2.1.3. Ecozones

The ecozone stratification of Canada (Ecological Stratification Working Group 1995) was used for comparative purposes. Ecozones are "higher order ecosystems" that are the coarsest product of an expert-based hierarchical ecosystem classification. Ecozones delineate large areas expressing similar geology, topography, soil, vegetation, climate, wildlife, hydrology, and land use. Ecozones are widely used reporting units for science and have a strong lineage in management of natural resources in Canada (Government of Canada 1996). To facilitate comparisons, ecozones were rasterized to 25 km spatial resolution (Fig. 1f).

2.2. Ecosystem classifications

Three ecosystem classifications were produced (this study's workflow is diagrammed in Fig. 2), using each dataset independently and in combination (henceforth: DHI, SWE, and SWE + DHI classifications), with the TwoStep multivariate classification algorithm (Zhang et al. 1997) in SPSS (SPSS Inc. 2008). This algorithm generates a large number of initial pre-clusters along a feature-cluster tree, which are then hierarchically agglomerated into the final classes. The log-likelihood distance measure was used to determine both pixel- and cluster-dissimilarities, which are used to generate the feature-cluster tree and to aggregate pre-clusters into classes, respectively. The thematic resolution (i.e., number of classes) of a classification can have a strong effect upon its resulting patterns (Castilla et al. 2009; Huang et al. 2006) and applications (e.g., Pharo and Beattie 2001; Pressey and Logan 1994). For each classification, we generated 14 (DHI) or 15 (SWE, SWE + DHI) classes. This thematic resolution was chosen to match the categorical detail of Canada's ecozone stratification and thereby avoid confounding comparisons between our classifications and ecozones with differences in resolution. Classes were not required to be spatially contiguous. All classifications were initially assessed with MANOVA, ANOVA and Tukey's pairwise comparisons along the input variables, confirming that, within a classification, all classes were unique from all others.

Coops et al. (2009) has previously constructed an environmental domain classification for Canada using the DHI framework. We used this pre-existing DHI classification in our comparisons, although it has several slight differences from the two new classifications produced in this study: 1) it included the University of Maryland land cover product (Hansen et al. 2000), in addition to the three DHI components and elevation, as input variables; and 2) it was produced at the finer 1 km resolution of the DHI data. Consequently, it was resampled to the most common non-null class within each 25 km SWE pixel for the present analyses.

Many of the SWE metrics were highly correlated, which can lead to instability in clustering algorithm performance. Multicollinearity was removed by classifying along SWE principal components (PCs) computed from the covariance matrix of SWE variables normalized by mean and mean absolute deviation (MAD). MAD is the mean of the absolute value of the residuals from the variable mean and tends to give outliers less prominence than normalizing by the standard deviation, which is computed from squared residuals. Principal components analyses (PCA) were performed in ENVI (ITT Visual Information Solutions 2009). The top three PCs (Fig. 1b) contained 86% of the SWE variation. PC1 (53.1% of variation) was highly inversely correlated with maximum, total, and range of SWE and the melt and accumulation rates, and is therefore a representation of the amount of snow present in a pixel. In contrast, PC2 (20.6%) and PC3 (12.3%) represented snow timing; PC2, which was strongly correlated to the time of maximum SWE and the end of the melt season, responded to late-snow-season timing; PC3 was dominated by the time of the start of snow accumulation (inverse correlation). These three PCs were normalized by their means and MADs, in order to weight each equally in the classification, and input into TwoStep.

The SWE + DHI classification followed the same process as the SWE classification. A combined SWE + DHI PCA was performed on normalized SWE, DHI, and elevation variables (but not land cover). The first 4 PCs, containing 84% of the combined variation, were normalized and used in the classifier. PC1 (47.0% of variation) represented shared variation between snow and productivity, and was correlated to most SWE metrics, particularly those representing amount rather than timing, and the three DHI components, but not elevation. PC2 (17.8%) was composed primarily of SWE variables, representing variation in SWE, especially timing and rates, that is independent of productivity. PC3 (11.0%) and PC4 (7.7%) were both correlated with elevation and with the time of the onset of the snow season; PC4 also included a signal from minimum annual productivity.

Ecosystems from each classification were described geographically with maps and environmentally with class summary statistics (mean and standard deviation) computed along the input DHI and SWE variables, as well as land cover (Hansen et al. 2000).

2.3. Analyses

Ideally, ecosystem classifications should be evaluated against independent datasets to determine if the resultant classes successfully describe variation in the environmental patterns and processes of interest. However, we are constrained by a lack of spatially explicit environmental variables that are national in scope for Canada. Furthermore, a classification's performance will depend upon whether it includes the variables most relevant to the specific pattern they are evaluated against, and would thus vary between distinct evaluation datasets. In the absence of a representative sample of response datasets, we have chosen to assess variation in spatial pattern between classes generated from different input variables, and to comparatively evaluate the classifications against each other as well as against the alternative inputs. These comparisons will reveal the degree to which classifications capture patterns of independent environmental gradients and the level of agreement between alternative ecosystem classifications.

2.3.1. Patch characteristics

It is important to understand the effect of ecosystem classification on landscape pattern as such patterns may be used to infer ecological processes, influencing conclusions and recommendations. Further, the size, shape, and spatial autocorrelation of class patches are expected to vary with the geographic structure of the input variables. To characterize spatial patterns, each classification was converted to vector format, with individual polygons delineating contiguous areas of the same class. These polygons, henceforth referred to as patches, were used to compute spatial pattern metrics, including the number of patches, mean and standard deviation of patch area, the proportion of single-pixel patches (singletons), the mean and standard deviation of patch shape, and the degree of class dispersion at both the patch and pixel levels. These metrics, along with their variability, represent independent and frequently important components of landscape pattern (Cushman et al. 2008). Patch shape was measured with the ratio of the patch perimeter to the perimeter of a maximally compact patch of the same area (Patton 1975), adjusted for the square patches of raster data (McGarigal and Marks 1995), and is a measure of patch shape complexity or edginess. It has a minimum value of 1 for square patches, and increases for elongated or convoluted patches. Dispersion was estimated with the mean nearest neighbour distance per class, standardized by the expected value under a random distribution of the same number of points in the same area. The mean nearest neighbour ratio approaches 1 for classes distributed randomly, is <1 for clustered classes, and >1 if classes are over-dispersed. Mean nearest neighbour ratios were calculated both for individual pixels and using patch centroid locations. The prevalence of singleton patches also provides an indication of the spatial cohesion of a class. Spatial pattern metrics were calculated in ArcMap (ESRI 2008) and Statistica (StatSoft Inc. 2008).

Spatial pattern metrics were compared between classifications with ANOVAs and Tukey's pairwise comparisons. Within a classification, the dependence of patch characteristics on class characteristics was determined with the correlation between the mean and standard deviation of patch metrics and the mean and standard deviation of the input environmental variables (either DHI, SWE, or both), with classes as the analysis units.

2.3.2. Spatial correspondence

Geographic correspondence was determined with pixel-wise contingency tables between pairs of classifications (DHI, SWE, SWE + DHI, ecozones). These were compared graphically and summarized by the % average mutual information (%AMI) reviewed by Foody (2006) and Pearson's χ^2 statistic. Both of these measures are based on the cell and marginal probabilities of a contingency table, and do not require pairing classes between classifications. The %AMI estimates the amount of information in a classification that is shared with an alternate product. The χ^2 statistic was used as an index of the relative strength of region associations between two classifications. Larger χ^2 values are associated with stronger relationships between categorical variables (i.e., observed cross-tabulated frequencies deviate more from those expected under random distributions). We did not evaluate the significance of the χ^2 as, with such large sample sizes, statistical significance would be trivial.

2.3.3. Environmental correspondence

Space is only one set of axes along which an area can be considered. Classifications that strongly disagree on a per-pixel basis may nevertheless successfully explain environmental variation in the variables along which their counterparts were defined. Correspondence in environmental space, or the ability of a given classification to represent variation in the alternative dataset, was assessed with reciprocal analyses of similarity (ANOSIM; Clarke 1993). ANOSIM tests if a response variable or set of variables is more similar within than between classes. By definition, pixels clustered by a set of variables will be more similar within than between clusters along those variables. This analysis tested whether that also holds true along a different set of variables. If DHI and SWE variables lead to the identification of similar classifications, ANOSIMs of DHI components on SWE clusters and of SWE variables on DHI clusters will tend to be significant. These analyses were performed only for the DHI and SWE clusters, since there were no independent evaluation variables available for the SWE + DHI clusters.

ANOSIM determines the ranks of the pairwise distances (Euclidean distance of normalized variables in this study) between all pixels. The test statistic, ANOSIM R, is the difference between mean within- and between-class distance ranks, standardized by the number of comparisons, and is tested by permutation. We performed four sets of ANOSIMs for each classification, varying the set of pixel pairs considered to be within- or between- classes. The first, $\text{ANOSIM}_{\text{GO}}$ (grand, overall), used all possible pairwise combinations, resulting in a single R statistic. In recognition that this value may be optimistic due to large underlying differences between highly divergent regions (e.g., SWE classes that are very distinct in snow conditions may also be very distinct in productivity conditions as a result of a spurious correlation driven by unmeasured variables), we performed a second test, $\text{ANOSIM}_{\text{GA}}$ (grand, adjacent), which considered only between-class comparisons for classes that are adjacent along an environmental axis used to define the regions. This was performed separately considering adjacency along each DHI (3 components + elevation) and SWE (3 PCs) axis. These ANOSIMs also result in a single R statistic each. The last 2 ANOSIMs were performed for individual classes, yielding an ANOSIM R for each class. Both of these tests, $\text{ANOSIM}_{\text{CO}}$ (class-wise, overall) and

$ANOSIM_{CA}$ (class-wise, adjacent) used only pixels in the focal class to compute within-class distances. For between-class distances, $ANOSIM_{CO}$ took a random sample of distances; $ANOSIM_{CA}$ took a random sample of distances between any two pixels in the environmental neighbourhood (along a given productivity or snow axis) surrounding the focal class. All ANOSIMs were performed in R, using functions in the add-on package vegan (Oksanen et al. 2008) and coded by the authors.

The ability of SWE classes to represent the DHI components, and vice versa, was assessed with $ANOSIM_{GO}$ and $ANOSIM_{GA}$ R values. The dependence of classification performance on environmental conditions was determined by correlating $ANOSIM_{CO}$ and $ANOSIM_{CA}$ Rs with the region mean and standard deviation of the variables used to define the regions, as well as the number of pixels assigned to each class.

3. Results

3.1. Class characteristics

3.1.1. Descriptions of ecosystem classifications

The four ecosystem classifications (SWE, DHI, SWE + DHI, ecozones) present different pictures of Canada's landmass, but all share some commonalities (Fig. 1c-f). For instance, each classification illustrates elongated arcing bands, trending from the Yukon south-east around Hudson Bay and back north-east, paralleling the distribution of boreal forest. This gradient is also evident in both the input DHI and SWE components (Fig. 1a, b). All classifications successfully delineate the Canadian Prairies (ecozone 10), although this is assigned to (essentially) a single class by the DHI classification and ecozones, but divided into two by those including SWE variables. Classifications along DHI are most effective at delineating mountainous regions in the west and the Mixedwood Plain ecozone (ecozone 8) of southern Ontario and Quebec.

The ecosystem classifications also create fairly intuitive groupings along the main environmental gradients considered (Fig. 3). The DHI classes are described in greater detail in Coops et al. (2009), so here we will focus on the new SWE and SWE + DHI ecosystem classifications.

3.1.1.1. SWE classes.

SWE classes 2, 4, and 7 are maritime regions, with classes 4 and 7 in low elevation coastal areas. Class 7 has the highest productivity of the SWE classes. Class 2 is located primarily in mountainous areas with a maritime climate influence, and has the highest mean elevation of the SWE classes and high forest cover. There are three additional montane SWE classes, which overlap with arctic tundra ecosystems (3, 6, 12). These classes have low forest cover, late snowmelt, high seasonality, and low productivity. Class 12 in northwest Canada, in particular, receives a large amount of snowfall, which is surpassed only by class 14, spanning the wetlands of the Hudson Plain and northern boreal forest. Two arctic classes remain that do not also include alpine ecosystems (5, 13). Class 13 exhibits the most limiting conditions in Canada: the lowest productivities, latest snowmelts, and, consequently, the lowest forest cover. The remaining SWE classes can be divided into boreal forest (8, 9, 10, 15) and prairie/sparse forest (1, 10, 11) ecosystems. The boreal forest classes form a gradient from south to north: class 9 contains the productive mixedwood and southern boreal forests receiving relatively low snow; class 8 in the central boreal and montane forests has very high forest cover, moderate snow, and is relatively productive; and classes 10 and 15 in the northern boreal forest are substantially snowier, with moderate positions on the remaining environmental axes. For the prairie and sparse forest classes, class 1 is differentiated by lower amounts of snow, higher productivity, and higher forest cover. Class 10, which does not have a prairie component, has a correspondingly greater forest cover, but later snowmelt and, thus, higher seasonality.

3.1.1.2. SWE + DHI classes

Montane regions are delineated more clearly by the SWE + DHI classification, as noted above from visual inspection of the class maps, with less overlap between mountainous classes and maritime and arctic classes. The highest elevations in western Canada are found in SWE + DHI class 8. Lower elevation montane ecosystems are divided between the shorter mountains of northwest Canada (4) and the heavily forested, lower elevation systems in mountainous regions (9). The arctic ecosystems of the SWE + DHI classification are classes 1, 2, 5, and 7. Classes 1 and 7 occur along the arctic-boreal ecotone. Class 1 is the snowiest in Canada, with moderately late snowmelt and low forest cover. This grades into class 2, nearing Hudson Bay, which has slightly less snow, higher productivity, and greater forest cover. Classes 5 and 7 are the least productive and most seasonal, with the latest snowmelt and lowest forest cover. A number of SWE + DHI classes capture the forest ecosystems of Canada (6, 10, 12, 13, 14). Classes 10 and 14 are highly productive maritime and mixedwood forests, respectively, though both include extensive areas of the southern boreal forest as well. Class 10 receives the least snow in Canada. Like class 10, class 13 encompasses both maritime and southern boreal forests, and has similar snow characteristics, but is characterized by lower forest cover and, hence, lower productivity. Classes 6 and 12 span the boreal forests. Class 12 has higher forest cover and slightly less snow. As in the SWE classification, there are two prairie classes which also include areas of sparse forest (3, 11). Again, these are largely differentiated by the amount of snow. Finally, class 15 contains forested ecosystems along the coasts and southern border.

3.1.2. Class spatial patterns

Each classification had highly variable spatial pattern metrics, precluding significant differences (Fig. 4a, b). All three classifications produced a large proportion of single-pixel patches (>55% of patches, but only ~10% of the total area; Fig. 4c), with the DHI classification having a significantly greater proportion of singletons (67% of patches) than those including SWE (Pearson $\chi^2 = 45.76$, $p < 0.00001$). The spatial distributions of classes for all products were significantly clustered at both patch and pixel levels (mean nearest neighbour ratios < 1; Fig. 4d, e), but the degree of class dispersion was relatively similar between classifications. SWE class patches were more dispersed than SWE + DHI class patches (Fig. 4d), but no other comparisons were significant. To test if these patterns were skewed by singleton patches, which may numerically dominate an inventory of patches despite contributing only negligible area, we repeated analyses with singletons excluded. The conclusions were unchanged (results not shown).

Within classifications, patch characteristics were strongly correlated with the environmental conditions of the class, particularly for classes constructed with SWE variables (Fig. 5). For the DHI classification, the number of patches per class declined with the variability of minimum annual fPAR and the variability of patch shape was greatest in classes with homogenous elevations. SWE class patches were larger and more irregularly shaped, but with greater variation in size and shape, in classes with more snow; and more irregularly shaped, with a smaller proportion of singletons in classes with late snow seasons. SWE + DHI classes were more likely to be singletons in classes with lower seasonality as well as greater variability in productivity, and snow amount and timing, which were those classes with less snow overall. All other SWE + DHI patch characteristics (size, shape, and their variability) were positively related to the amount of snow and negatively related to productivity. Class dispersion was also correlated with environmental characteristics, but, in contrast to patch metrics, tended to be more closely related to productivity than to snow (Fig. 6). For both classifications including productivity, more productive classes were more clustered (i.e., had lower nearest neighbour distances), at both the patch and pixel levels. Of the SWE variables, only snow timing was related to class clustering. Clustering of SWE classes increased with variability in late snow season timing. Clustering of SWE + DHI classes decreased as melt was delayed.

3.2. Class agreement

Although there was no clear one-to-one pixel-level correspondence between the classifications, all exhibited a fair degree of spatial correspondence (Fig. 7). Both %AMI and χ^2 values yielded the same ranking of pair-wise map agreement. Agreement was lowest between the SWE results and both the DHI and ecozone classifications, highest between the DHI classes and the ecozones, and intermediate for all comparisons with the SWE + DHI classification.

Grand ANOSIMs found that both SWE classes significantly explained patterns in productivity and DHI classes significantly explained patterns of SWE, regardless of whether classes were compared against all others or against only their environmental neighbours ($p < 0.005$ for all tests; Fig. 8). $ANOSIM_{GO}$ R was 0.3904 for both of the reciprocal tests. For comparison, $ANOSIM_{GO}$ $R = 0.85$ and $R = 0.81$ when evaluating SWE clusters on SWE variables and DHI clusters on DHI variables, respectively. (Note that the maximum, $R = 1$, will only be reached when classes are not only distinct, but distant from each other in environmental space.) Between class uniqueness, and thus $ANOSIM_{GA}$ R, declined when considering only adjacent classes along all DHI axes and along the first SWE PC (Fig. 8).

Most individual DHI and SWE classes were also significant when evaluated against their counterpart SWE or DHI variables with $ANOSIM_{CO}$ and $ANOSIM_{CA}$ (data not shown). DHI class performance relative to SWE variables was unrelated to the regional productivity characteristics (results not shown). The only significant correlation was between $ANOSIM_{CA}$ R when adjacency was considered along fPAR seasonality and class mean seasonality ($r = 0.54$, $p < 0.05$). That is, at high seasonalities, DHI classes were more likely to have different snow characteristics than their neighbours in seasonality. In contrast, the ability of SWE classes to represent variation in productivity was strongly related to the snow conditions of each class (Fig. 9). In particular, overall performance ($ANOSIM_{CO}$) was greatest in the snowiest classes and performance when comparing classes only to their neighbours ($ANOSIM_{CA}$) in terms of amount of snow (PC1) improved with increasing within-class variability in snow timing (both beginning and end of snow season) and was best for classes containing fewer pixels.

4. Discussion

Variation in the spatial patterns portrayed by each of the classifications (Fig. 1) is linked to the input variables. The two classifications including DHI most successfully captured topographic differences because they explicitly considered elevation. (Note also the limited scatter of SWE class centroids along elevation in Fig. 3h.) The DHI classification is also the only one that distinguished the Mixedwood Plain (ecozone 8). The forests in this region likely differ from the coniferous forests to the north in their productivity and, especially, the seasonality of productivity, due to the substantial presence of deciduous trees. Differences in forest type are also apparent in the land cover product included in the DHI classification, but not the other two. The sensitivity to topography, seasonality, and land cover seems to make the DHI product better able to capture smaller, more complex regions (such as the mountainous regions and the

Mixedwood Plain). Both classifications including DHI also seem slightly more effective at spanning the tree cover gradient (Fig. 3g-i). However, the SWE data may also contain signals of land cover as land cover influences both the physical process of snow accumulation as well as the microwave response viewed by the sensor (Derksen et al. 2005; Foster et al. 2005). The two classifications including SWE split the Prairies into two parts, distinguishing areas in the rain shadow of the Rocky Mountains because SWE is a precipitation variable.

Surprisingly, differences arising from input variables did not translate into differences in the geometric characteristics of class patches (Fig. 4). We expected productivity-based class patches to be smaller than those derived from snow cover. Variation in the latter largely arises from broad-scale circulation patterns, particularly at the coarse 25 km spatial resolution of the SWE data. In contrast, variation in productivity will stem from broad-scale climate, but also from a variety of finer-scaled drivers, including vegetation type, soils, and disturbance. Despite these expectations, patches of productivity-based classes were not significantly smaller than those derived from SWE, although productivity did produce the largest proportion of single-pixel patches. Most likely, the large, coherent DHI classes are a function of the coarse grain of the classification inputs. There is substantial fine-grained variation in the DHI classification at its original 1 km scale. For example, when contiguous pixels of the same class from the 1 km classification results are aggregated into patches, 61% of the patches (19% of the area) are isolated pixels; only 0.07% of patches have an area equal to or greater than the 625 km^2 SWE pixels (and see figures in Coops et al. 2009). Yet this detailed variation does not influence the *dominant* productivity regime within a 25 km pixel, which, as shown in Fig. 1c, remains constant over broad extents.

The spatial resolution of the variables used to define a classification may be as important as the variables themselves. Both the size and configuration of aggregation units affect observed spatial patterns, as well as the results of statistical analyses (the modifiable areal unit problem, MAUP: Dark and Bram 2007; Dungan et al. 2002; Fotheringham and Wong 1991; Jelinski and Wu 1996). MAUP effects are a byproduct of classification, which may be reduced when defining classes by minimizing variance, but also of the size of the input units that are grouped into classes (e.g., pixels in this study). Twenty-five kilometers may be too coarse for a productivity classification, particularly if one is interested in detailed patterning due to finer-scaled drivers (which, in the case of slope, aspect, and elevation, are relevant to snow characteristics as well). At coarser spatial resolutions, classes generally contain more azonal areas, or those that do not exhibit the prevailing class characteristics. Reportedly, up to 15% of each ecozone is azonal (Wiken 1996) as it is unavoidable for atypical areas to be incorporated into large, spatially contiguous regions such as ecozones. This number is even higher for the DHI classes, when the 25 km and 1 km resolutions are compared. Overall, one-third of all 1 km pixels differed from the dominant class of their 25 km pixel. At the level of individual DHI classes, 40 ± 14% of each is azonal, ranging from 15-20% in the arctic (classes 9 and 13) and prairie classes (class 8) to 50-60% in heterogeneous mountainous (class 4) and coastal (class 7) classes. (Note that it is possible for more than half of a class to be azonal when assessed at finer scales as the dominant class has only to receive more pixels than any other single class rather than a majority of 1 km pixels). Graef et al. (2005) also report ecoregions to be highly heterogeneous at the pixel level.

In addition to sharing similar patch characteristics, all classifications shared moderate pixel-wise class associations. However, because each classification divided Canada in different ways and along different environmental characteristics, classes from a particular scheme tended to be subdivided among several dominant classes from alternate schemes (Fig. 7). For example, many of the boreal ecozones (e.g., ecozones 4, 5, 6, 9, 11, 15), were split among several productivity or snow classes due to differences in the generalized distributions of these classes. All of the quantitative productivity and snow classifications exhibit strong north-south gradients, with elongated bands of class occurrence (Fig. 1). These distribution patterns are likely related to prevailing atmospheric circulation patterns controlling snow cover and, indirectly, vegetation productivity. For example, Derksen et al. (1998) demonstrated that the orientation of snow regions was closely related to the direction of atmospheric airflow during the observation period. In contrast, ecozones subdivide this pattern longitudinally into more compact regions, perhaps in response to input variables displaying east-west as well as north-south structure (e.g., geology, soils, wildlife).

Class associations also highlight similarities in the environmental patterns and physical processes underlying each product. The strongest association was observed between productivity classes and ecozones, suggesting that ecozones are most representative of growing season processes, and may be less adequate at describing winter conditions. Additionally, this level of agreement highlights that the many variables incorporated into ecozone delineation (geology, topography, soil, vegetation, climate, wildlife, hydrology, and land use) are well proxied by productivity, elevation, and land cover alone. This is not surprising as productivity is an integrated vegetation response to many of the factors informing ecozone placement, including geology, soils, and climate.

Generality is an important feature of ecosystem classifications. Incorporating a variety of independent environmental variables into a classification is encouraged and believed to increase the generality and reduce the artificiality of the result (Bailey et al. 1978). The intermediate degree of association between the SWE + DHI classification and the other three products implies that including both productivity and snow metrics as input variables does yield a compromise between the two sets and may produce a more general environmental classification. Nevertheless, the classifications along DHI and SWE alone were found to be somewhat general, at least with respect to evaluations along snow and productivity conditions, respectively (Fig. 8). The ability of productivity classes to represent variation in snow space, and vice versa, indicates that these variables are related across Canada and that frameworks based on summertime productivity may be somewhat meaningful for monitoring winter processes, and vice versa. The robustness of this relationship is shown by its continued significance in the more stringent test for differences using only nearest neighbours, although class distinctness is weaker when restricting comparisons to environmental neighbourhoods. The exception is that ANOSIM Rs increased when defining neighbourhoods along the two snow PCs representing timing. However, this is unlikely to be meaningful. These PCs contain only 21% and 12% of the SWE variation, respectively. Therefore, considering them in isolation may obscure more important gradients; i.e., classes may be neighbours in snow timing, but quite distinct in terms of snow amount, which is a more information-rich (53% of SWE variation) and potentially more important variable. Although class correspondence suggests that productivity and snow are related, the strength and even direction of the snow-productivity relationship is not likely to be constant throughout Canada. For example, individual SWE classes were much more strongly representative of productivity in the snowiest classes and in those with the most variable snow timing. This suggests that snow may have the greatest effect on productivity in areas where snow is a dominant feature, but that other limiting factors occur elsewhere. The nature of the snow/productivity relationship over broad scales is the subject of ongoing research.

Ecosystem classifications are rarely quantitatively compared, so it is unclear if the levels of geographic and environmental correspondence observed between productivity regimes, snow classes, and ecozones are typical. However, several comparative evaluations against independent datasets do exist. Research evaluating the relevance of ecoregions for monitoring and management appears to be most active in freshwater ecology (e.g., Cheruvelil et al. 2008; the special issue of the *Journal of the North American Benthological Society* synthesized in Hawkins et al. 2000), although tests of classifications against community types and composition (Andrew et al. 2011; Oliver et al. 2004; Trakhtenbrot and Kadmon 2006; Wright et al. 1998), physiography (Thompson et al. 2004), forest productivity (Carmean 1996), and forest ecotypic variation (Parker et al. 1996) have also been conducted. These studies generally find that ecosystem classifications capture patterns of environmental conditions, community structure, and local adaptation successfully, albeit weakly (Hawkins et al. 2000, but see Carmean 1996). Much of the success of spatially discrete classifications can be attributed to spatial autocorrelation of the response variables, rather than relevance of the classification specifically (Andrew et al. 2011; Hawkins and Vinson 2000; Pyne et al. 2007; Van Sickle and Hughes 2000). In the present study, the correspondence between productivity and snow classes is certainly due in part to shared spatial structuring of these two characteristics and the extent that this is the case should be the subject of future work. Alternatively, environmental conditions, species, and communities are often patchily and widely distributed, hampering the utility of compact, spatially contiguous regions (Hawkins and Vinson 2000; Jenerette et al. 2002; McCormick et al. 2000; Van Sickle and Hughes 2000; Wright et al. 1998).

Neither productivity nor snow conditions are often included in ecosystem classifications. Yet regions defined by these variables are potentially very important frameworks, particularly for monitoring and reporting responses to climate change. Both snow (Brown 2000; Brown and Braaten 1998; Räisänen 2008) and productivity (Goetz et al. 2005; Myneni et al. 1997; Zhou et al. 2001) are key response variables to climate change. Yet these and other responses show regional variation (e.g., Angert et al. 2005; Baker and Weisberg 1997; Bunn and Goetz 2006; Räisänen 2008), depending upon current climate, changing precipitation, or the land cover present. Ecosystem classifications based on climate-sensitive variables may capture these patterns of regional variation, allowing scientists and managers to make sense of and effectively communicate abiotic and biotic responses to climate change. We encourage more widespread use of productivity and snow in classification frameworks, and their application to environmental monitoring and management.

5. Conclusions

Ecosystem classifications are valuable generalizations of spatial variability that may facilitate environmental monitoring, management, and study; however, they should be carefully considered prior to use. A variety of ecosystem classifications constructed upon a diversity of environmental variables exists, and each may provide widely different generalizations of an area. Successful application will depend on whether an appropriate classification was selected. Classifications driven by remotely sensed productivity or snow, such as those described here, may be ideal when the environmental patterns or processes of interest are highly seasonal. Since productivity and snow are both sensitive to variations in climate conditions, such classifications may be especially valuable for monitoring climate change and its biotic and abiotic responses.

We found productivity- and snow-based classes to be only moderately spatially associated and, when evaluated reciprocally, to be only half as successful at describing continuous variation in each other's input variables as in their own. Furthermore, the ability of snow classes to represent productivity varied with snow conditions. Thus, although snow and productivity are related across Canada, this correlation is imperfect and variable over space and environmental conditions, and classes derived from summer (winter) conditions may not adequately represent winter- (summer-) controlled patterns and processes. When constant regions are required for monitoring a variety of variables, an ecosystem classification incorporating both summer and winter conditions should be used. The existing and widely used ecozone framework was found to be most associated with summer patterns, calling its generality into question. In contrast, the combined snow and productivity classification had intermediate levels of association with the individual season schemes as well as the ecozones, suggesting that it may be the most general of those stratifications produced and evaluated here.

Acknowledgements
This research was facilitated through support of "BioSpace: Biodiversity monitoring with Earth Observation data" through the Government Related Initiatives Program (GRIP) of the Canadian Space Agency.

References

Andrew, M. E., Wulder, M. A., & Coops, N. C. (2011). How do butterflies define ecosystems? A comparison of ecological regionalization schemes. *Biological Conservation, 144,* 1409-1418.

Angert, A., Biraud, S., Bonfils, C., Henning, C. C., Buermann, W., Pinzon, J., et al. (2005). Drier summers cancel out the CO_2 uptake enhancement induced by warmer springs. *Proceedings of the National Academy of Sciences of the United States of America, 102,* 10823-10827.

Bailey, R. G. (1995). *Description of the ecoregions of the United States*, 2nd edition. US Department of Agriculture, Forest Service, Miscellaneous Publication 1391.

Bailey, R. G. (2004). Identifying ecoregion boundaries. *Environmental Management*, *34*, S14-S26.

Bailey, R. G., Pfister, R. D., & Henderson, J. A. (1978). Nature of land and resource classification - review. *Journal of Forestry*, *76*, 650-655.

Bailey, R. G., Zoltai, S. C., & Wiken, E. B. (1985). Ecological regionalization in Canada and the United States. *Geoforum*, *16*, 265-275.

Baker, W. L., & Weisberg, P. J. (1997). Using GIS to model tree population parameters in the Rocky Mountain National Park forest-tundra ecotone. *Journal of Biogeography*, *24*, 513-526.

Banner, A., Meidinger, D. V., Lea, E. C., Maxwell, R. E., & Von Sacken, B. C. (1996). Ecosystem mapping methods for British Columbia. *Environmental Monitoring and Assessment, 39,* 97-117.

Barton, J. L. & Metzeling, L. (2004). The development of biological objectives for streams in a single catchment: a case study on the Catchment of Western Port Bay, Victoria, Australia. *Environmental Monitoring and Assessment, 95,* 239-256.
Beauchesne, P., Ducruc, J. P., & Gerardin, V. (1996). Ecological mapping: a framework for delimiting forest management units. *Environmental Monitoring and Assessment, 39,* 173-186.

Brown, R. D. (2000). Northern hemisphere snow cover variability and change, 1915-97. *Journal of Climate*, *13*, 2339-2355.

Brown, R. D., & Braaten, R. O. (1998). Spatial and temporal variability of Canadian monthly snow depths, 1946-1995. *Atmosphere-Ocean*, *36*, 37-54.

Bunn, A. G., & Goetz, S. J. (2006). Trends in satellite-observed circumpolar photosynthetic activity from 1982 to 2003: the influence of seasonality, cover type, and vegetation density. *Earth Interactions*, *10*, 12.

Carmean, W. H. (1996). Forest site-quality estimation using forest ecosystem classification in northwestern Ontario. *Environmental Monitoring and Assessment, 39,* 493-508.

Castilla, G., Larkin, K., Linke, J., & Hay, G. J. (2009). The impact of thematic resolution on the patch-mosaic model of natural landscapes. *Landscape Ecology*, *24*, 15-23.

Cheruvelil, K. S., Soranno, P. A., Bremigan, M. T., Wagner, T., & Martin, S. L. (2008). Grouping lakes for water quality assessment and monitoring: the roles of regionalization and spatial scale. *Environmental Management*, *41*, 425-440.

Clarke, K. R. (1993). Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*, 117-143.

Commission for Environmental Cooperation. (1997). *Ecological Regions of North America: Toward a Common Perspective*. Montreal: Commission for Environmental Cooperation.

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

Convention on Biological Diversity. (2004). *Decisions adopted by the Conference of the Parties to the Convention on Biological Diversity at its Seventh Meeting*. Montreal: Convention on Biological Diversity.

Coops, N. C., Wulder, M. A., Duro, D. C., Han, T., & Berry, S. (2008). The development of a Canadian dynamic habitat index using multi-temporal satellite estimates of canopy light absorbance. *Ecological Indicators*, *8*, 754-766.

Coops, N. C., Wulder, M. A., & Iwanicka, D. (2009). An environmental domain classification of Canada using earth observation data for biodiversity assessment. *Ecological Informatics*, *4*, 8-22.

Cushman, S. A., McGarigal, K., & Neel, M. C. (2008). Parsimony in landscape metrics: strength, universality, and consistency. *Ecological Indicators*, *8*, 691-703.

Dark, S. J., & Bram, D. (2007). The modifiable areal unit problem (MAUP) in physical geography. *Progress in Physical Geography*, *31*, 471-479.

Derksen, C., Wulder, M., Ledrew, E., & Goodison, B. (1998). Associations between spatially autocorrelated patterns of SSM/I-derived prairie snow cover and atmospheric circulation. *Hydrological Processes*, *12*, 2307-2316.

Derksen, C., Walker, A., & Goodison, B. (2005). Evaluation of passive microwave snow water equivalent retrievals across the boreal forest/tundra transition of western Canada. *Remote Sensing of Environment*, *96*, 315-327.

Dungan, J. L., Perry, J. N., Dale, M. R. T., Legendre, P., Citron-Pousty, S., Fortin, M. J., et al. (2002). A balanced view of scale in spatial statistical analysis. *Ecography*, *25*, 626-640.

Duro, D., Coops, N. C., Wulder, M. A., & Han, T. (2007). Development of a large area biodiversity monitoring system driven by remote sensing. *Progress in Physical Geography*, *31*, 235-260.

Dussault, C., Ouellet, J. P., Courtois, R., Huot, J., Breton, L., & Jolicoeur, H. (2005). Linking moose habitat selection to limiting factors. *Ecography*, *28*, 619-628.

Ecological Stratification Working Group. (1995). *A National Ecological Framework for Canada*. Ottaway/Hull: Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch.

ESRI. (2008). *ArcMap, version 9.3*. Redlands, CA: ESRI.

Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, *80*, 1-25.

Farmer, C. J. Q., Nelson, T. A., Wulder, M. A., & Derksen, C. (2010). Identification of snow cover regimes through spatial and temporal clustering of satellite microwave brightness temperatures. *Remote Sensing of Environment*, *114*, 199-210.

Fernández, N., Paruelo, J. M., & Delibes, M. (2010). Ecosystem functioning of protected and altered Mediterranean environments: a remote sensing classification in Doñana, Spain. *Remote Sensing of Environment*, *114*, 211-220.

Foody, G. M. (2006). What is the difference between two maps? A remote senser's view. *Journal of Geographical Systems*, *8*, 119-130.

Foster, J. L., Sun, C. J., Walker, J. P., Kelly, R., Chang, A., Dong, J. R., & Powell, H. (2005). Quantifying the uncertainty in passive microwave snow water equivalent observations. *Remote Sensing of Environment*, *94*, 187-203.

Fotheringham, A. S., & Wong, D. W. S. (1991). The modifiable areal unit problem in multivariate statistical analysis. *Environment and Planning A*, *23*, 1025-1044.

Fritz, S., & See, L. (2008). Identifying and quantifying uncertainty and spatial disagreement in the comparison of global land cover for different applications. *Global Change Biology*, *14*, 1057-1075.

Giri, C., Zhu, Z. L., & Reed, B. (2005). A comparative analysis of the Global Land Cover 2000 and MODIS land cover data sets. *Remote Sensing of Environment*, *94*, 123-132.

Goetz, S. J., Bunn, A. G., Fiske, G. J., & Houghton, R. A. (2005). Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 13521-13525.

Government of Canada. (1996). *The State of Canada's Environment*. Ottawa: Government of Canada.

Graef, F., Schmidt, G., Schröder, W., & Stachow, U. (2005). Determining ecoregions for environmental and GMO monitoring networks. *Environmental Monitoring and Assessment, 108,* 189-203.

Hansen, M. C., Defries, R. S., Townshend, J. R. G., & Sohlberg, R. (2000). Global land cover classification at 1km spatial resolution using a classification tree approach. *International Journal of Remote Sensing*, *21*, 1331-1364.

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J. F., Kaufman, D. M., et al. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, *84*, 3105-3117.

Hawkins, C. P., & Vinson, M. R. (2000). Weak correspondence between landscape classifications and stream invertebrate assemblages: implications for bioassessment. *Journal of the North American Benthological Society*, *19*, 501-517.

Hawkins, C. P., Norris, R. H., Gerritsen, J., Hughes, R. M., Jackson, S. K., Johnson, R. K., & Stevenson, R. J. (2000). Evaluation of the use of landscape classifications for the prediction of freshwater biota: synthesis and recommendations. *Journal of the North American Benthological Society*, *19*, 541-556.

Herold, M., Mayaux, P., Woodcock, C. E., Baccini, A., & Schmullius, C. (2008). Some challenges in global land cover mapping: an assessment of agreement and accuracy in existing 1 km datasets. *Remote Sensing of Environment*, *112*, 2538-2556.

Host, G. E., Polzer, P. L., Mladenoff, D. J., White, M. A., & Crow, T. R. (1996). A quantitative approach to developing regional ecosystem classifications. *Ecological Applications*, *6*, 608-618.

Huang, C., Geiger, E. L., & Kupfer, J. A. (2006). Sensitivity of landscape metrics to classification scheme. *International Journal of Remote Sensing*, *27*, 2927-2948.

ITT Visual Information Solutions. (2009). *ENVI, version 4.7*. Boulder, CO: ITT Visual Information Solutions.

Jelinski, D. E., & Wu, J. G. (1996). The modifiable areal unit problem and implications for landscape ecology. *Landscape Ecology*, *11*, 129-140.

Jenerette, G. D., Lee, J., Waller, D. W., & Carlson, R. E. (2002). Multivariate analysis of the ecoregion delineation for aquatic systems. *Environmental Management*, *29*, 67-75.

Jung, M., Henkel, K., Herold, M., & Churkina, G. (2006). Exploiting synergies of global land cover products for carbon cycle modeling. *Remote Sensing of Environment*, *101*, 534-553.

Kaptué-Tchuenté, A. T., Roujean, J. L., & De Jong, S. M. (2011). Comparison and relative auality assessment of the GLC2000, GLOBCOVER, MODIS and ECOCLIMAP land cover data sets at the African continental scale. *International Journal of Applied Earth Observation and Geoinformation*, *13*, 207-219.

Kerr, J. T., & Ostrovsky, M. (2003). From space to species: ecological applications for remote sensing. *Trends in Ecology and Evolution*, *18*, 299-305.

Kimball, J. S., Keyser, A. R., Running, S. W., & Saatchi, S. S. (2000). Regional assessment of boreal forest productivity using an ecological process model and remote sensing parameter maps. *Tree Physiology*, *20*, 761-775.

Kimball, J. S., McDonald, K. C., Running, S. W., & Frolking, S. E. (2004). Satellite radar remote sensing of seasonal growing seasons for boreal and subalpine evergreen forests. *Remote Sensing of Environment*, *90*, 243-258.

Kirkpatrick, J. B., & Brown, M. J. (1994). A comparison of direct and environmental domain approaches to planning reservation of forest higher-plant communities and species in Tasmania. *Conservation Biology*, *8*, 217-224.

Lafleur, P. M., & Humphreys, E. R. (2007). Spring warming and carbon dioxide exchange over low arctic tundra in central Canada. *Global Change Biology*, *14*, 740-756.

Leathwick, J. R., Overton, J. M., & Mcleod, M. (2003). An environmental domain classification of New Zealand and its use as a tool for biodiversity management. *Conservation Biology*, *17*, 1612-1623.

Litaor, M. I., Williams, M., & Seastedt, T. R. (2008). Topographic controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. *Journal of Geophysical Research-Biogeosciences*, *113,* G02008, doi:10.1029/2007JG000419.

Loveland, T. R., & Merchant, J. M. (2004). Ecoregions and ecoregionalization: geographical and ecological perspectives. *Environmental Management*, *34*, S1-S13.

Mac Nally, R., Bennett, A. F., Brown, G. W., Lumsden, L. F., Yen, A., Hinkley, S., et al. (2002). How well do ecosystem-based planning units represent different components of biodiversity? *Ecological Applications*, *12*, 900-912.

Mackey, B. G., Berry, S. L., & Brown, T. (2008). Reconciling approaches to biogeographical regionalization: a systematic and generic framework examined with a case study of the Australian continent. *Journal of Biogeography*, *35*, 213-229.

Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F., et al. (2007). Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biology*, *30*, 1363-1372.

McCormick, F. H., Peck, D. V., & Larsen, D. P. (2000). Comparison of geographic classification schemes for Mid-Atlantic stream fish assemblages. *Journal of the North American Benthological Society*, *19*, 385-404.

McGarigal, K., & Marks, B. J. (1995). *FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure*. General Technical Report PNW-GTR-351. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

McMahon, G., Wiken, E. B., & Gauthier, D. A. (2004). Toward a scientifically rigorous basis for developing mapped ecological regions. *Environmental Management*, *34*, S111-S124.

McRae, D. J. (1996). Use of forest ecosystem classification systems in fire management. *Environmental Monitoring and Assessment, 39,* 559-570.

Moody, E. G., King, M. D., Schaaf, C. B., Hall, D. K., & Platnick, S. (2007). Northern hemisphere five-year average (2000-2004) spectral albedos of surfaces in the presence of snow: statistics computed from Terra MODIS land products. *Remote Sensing of Environment*, *111*, 337-345.

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., & Nemani, R. R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, *386*, 698-702.

Myneni, R. B., Hoffman, S., Knyazikhin, Y., Privette, J. L., Glassy, J., Tian, Y., et al. (2002). Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. *Remote Sensing of Environment*, *83*, 214-231.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., et al. (2008). *The vegan Package*. http://vegan.r-forge.r-project.org/

Oliver, I., Holmes, A., Dangerfield, J. M., Gillings, M., Pik, A. J., Britton, D. R., et al. (2004). Land systems as surrogates for biodiversity in conservation planning. *Ecological Applications*, *14*, 485-503.

Olson, D. M., & Dinerstein, E. (1998). The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology*, *12*, 502-515.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., et al. (2001). Terrestrial ecoregions of the worlds: a new map of life on Earth. *Bioscience*, *51*, 933-938.

Omernik, J. M. (1987). Ecoregions of the conterminous United States. *Annals of the Association of American Geographers*, *77*, 118-125.

Omernik, J. M. (2004). Perspectives on the nature and definition of ecological regions. *Environmental Management*, *34*, S27-S38.

Parks Canada (1997). *National Parks System Plan*. Ottawa: Parks Canada.

Parker, W. H., Van Niejenhuis, A., & Ward, J. (1996). Genecological variation corresponding to forest ecosystem classification vegetation and soil types for jack pine and black spruce from northwestern Ontario. *Environmental Monitoring and Assessment, 39,* 589-599.

Patton, D. R. (1975). A diversity index for quantifying habitat "edge". *Wildlife Society Bulletin*, *3*, 171-173.

Petit, S., Firbank, R., Wyatt, B., & Howard, D. (2001). MIRABEL: Models for integrated review and assessment of biodiversity in European landscapes. *Ambio*, *30*, 81-88.

Pharo, E. J., & Beattie, A. J. (2001). Management forest types as a surrogate for vascular plant, bryophyte and lichen diversity. *Australian Journal of Botany*, *49*, 23-30.

Pressey, R. L., & Logan, V. S. (1994). Level of geographical subdivision and its effects on assessments of reserve coverage - a review of regional studies. *Conservation Biology*, *8*, 1037-1046.

Pyne, M. I., Rader, R. B., & Christensen, W. F. (2007). Predicting local biological characteristics in streams: a comparison of landscape classifications. *Freshwater Biology*, *52*, 1302-1321.

R Core Development Team. (2008). *R, version 2.8.1*. R Core Development Team, http://www.r-project.org.

Rabus, B., Eineder, M., Roth, A., & Bamler, R. (2003). The Shuttle Radar Topography Mission - a new class of digital elevation models acquired by spaceborne radar. *ISPRS Journal of Photogrammetry and Remote Sensing*, *57*, 241-262.

Räisänen, J. (2008). Warmer climate: less or more snow? *Climate Dynamics*, *30*, 307-319.

SPSS Inc. (2008). *SPSS, version 17.0*. Chicago, IL: SPSS Inc.

StatSoft Inc. (2008). *STATISTICA, version 8.0*. Tulsa, OK: StatSoft Inc..

Tait, A. B. (1998). Estimation of snow water equivalent using passive microwave radiation data. *Remote Sensing of Environment*, *64*, 286-291.

Thompson, R. S., Shafer, S. L., Anderson, K. H., Strickland, L. E., Pelltier, R. T., Bartlein, P. J., & Kerwin, M. W. (2004). Topographic, bioclimatic, and vegetation characteristics of three ecoregion classification systems in North America: comparisons along continent-wide transects. *Environmental Management*, *34*, S125-S148.

Trakhtenbrot, A., & Kadmon, R. (2006). Effectiveness of environmental cluster analysis in representing regional species diversity. *Conservation Biology*, *20*, 1087-1098.

Van Sickle, J., & Hughes, R. M. (2000). Classification strengths of ecoregions, catchments, and geographic clusters for aquatic vertebrates in Oregon. *Journal of the North American Benthological Society*, *19*, 370-384.

Walker, D. A., Halfpenny, J. C., Walker, M. D., & Wessman, C. A. (1993). Long-term studies of snow-vegetation interactions. *Bioscience*, *43*, 287-301.

Wells, F., Metzeling, L., & Newall, P. (2002). Macroinvertebrate regionalisation for use in the management of aquatic ecosystems in Victoria, Australia. *Environmental Monitoring and Assessment, 74,* 271-294.

Wiken, E. B., Gauthier, D., Marshall, I., Lawton, K., & Hirvonen, H. (1996). *A Perspective on Canada's Ecosystems: An Overview of the Terrestrial and Marine Ecozones*. Occasional paper no. 14. Canadian Council on Ecological Areas, Ottawa, Ontario.

Wright, R. G., Murray, M. P., & Merrill, T. (1998). Ecoregions as a level of ecological analysis. *Biological Conservation*, *86*, 207-213.

Zhang, T., Ramakrishnan, R., & Livny, M. (1997). BIRCH: A new data clustering algorithm and its applications. *Data Mining and Knowledge Discovery*, *1*, 141-182.

Zhou, L. M., Tucker, C. J., Kaufmann, R. K., Slayback, D., Shabanov, N. V., & Myneni, R. B. (2001). Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research-Atmospheres*, *106*, 20069-20083.

Table 1. Definitions of abbreviations used in the text.

acronym	**definition**
AMI	Average Mutual Information
ANOSIM	ANalysis Of SIMilarity
GO	Grand, Overall
GA	Grand, Adjacent
CO	Class-wise, Overall
CA	Class-wise, Adjacent
DHI	Dynamic Habitat Index
fPAR	fraction of absorbed Photosynthetically Active Radiation
MAD	Mean Absolute Deviance
MAUP	Modifiable Areal Unit Problem
MODIS	MODerate-resolution Imaging Spectrometer
NN	Nearest Neighbour
PC	Principal Component
SSM/I	Special Sensor Microwave/Imager
SWE	Snow Water Equivalent

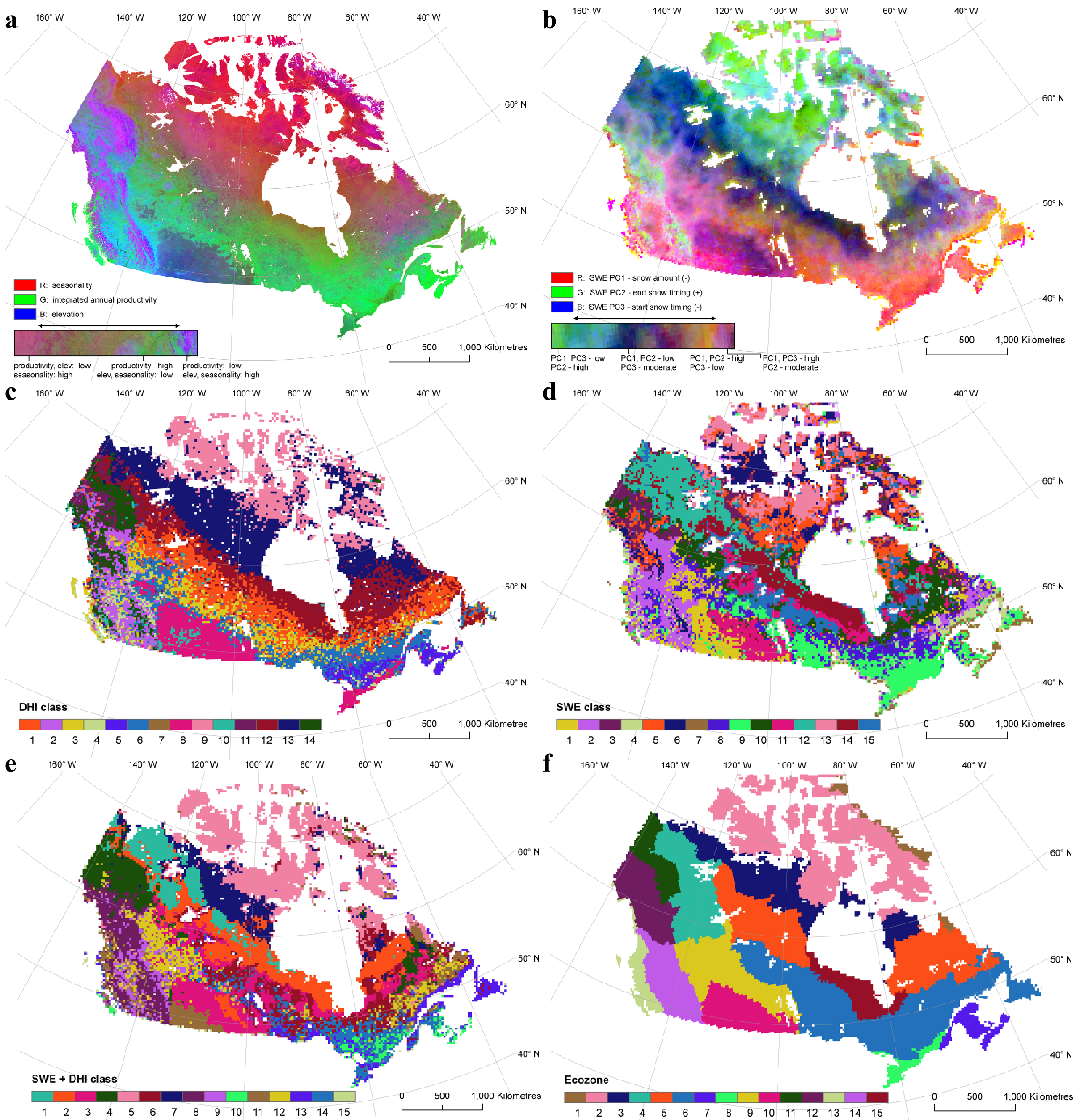

Figure 1. False color composite images of a) productivity metrics (DHI = dynamic habitat index) and b) SWE (snow water equivalent) principal components, with an annotated gradient to assist interpretation of the color mixing. The ecosystem classifications derived from c) productivity, d) snow, e) productivity and snow, and f) the ecozones are also mapped. Ecozone numbers in panel f correspond to: 1. Arctic Cordillera, 2. Northern Arctic, 3. Southern Arctic, 4. Taiga Plain, 5. Taiga Shield, 6. Boreal Shield, 7. Atlantic Maritime, 8. Mixedwood Plain, 9. Boreal Plain, 10. Prairie, 11. Taiga Cordillera, 12. Boreal Cordillera, 13. Pacific Maritime, 14. Montane Cordillera, and 15. Hudson Plain. All maps are in the Lambert Conformal Conic projection.

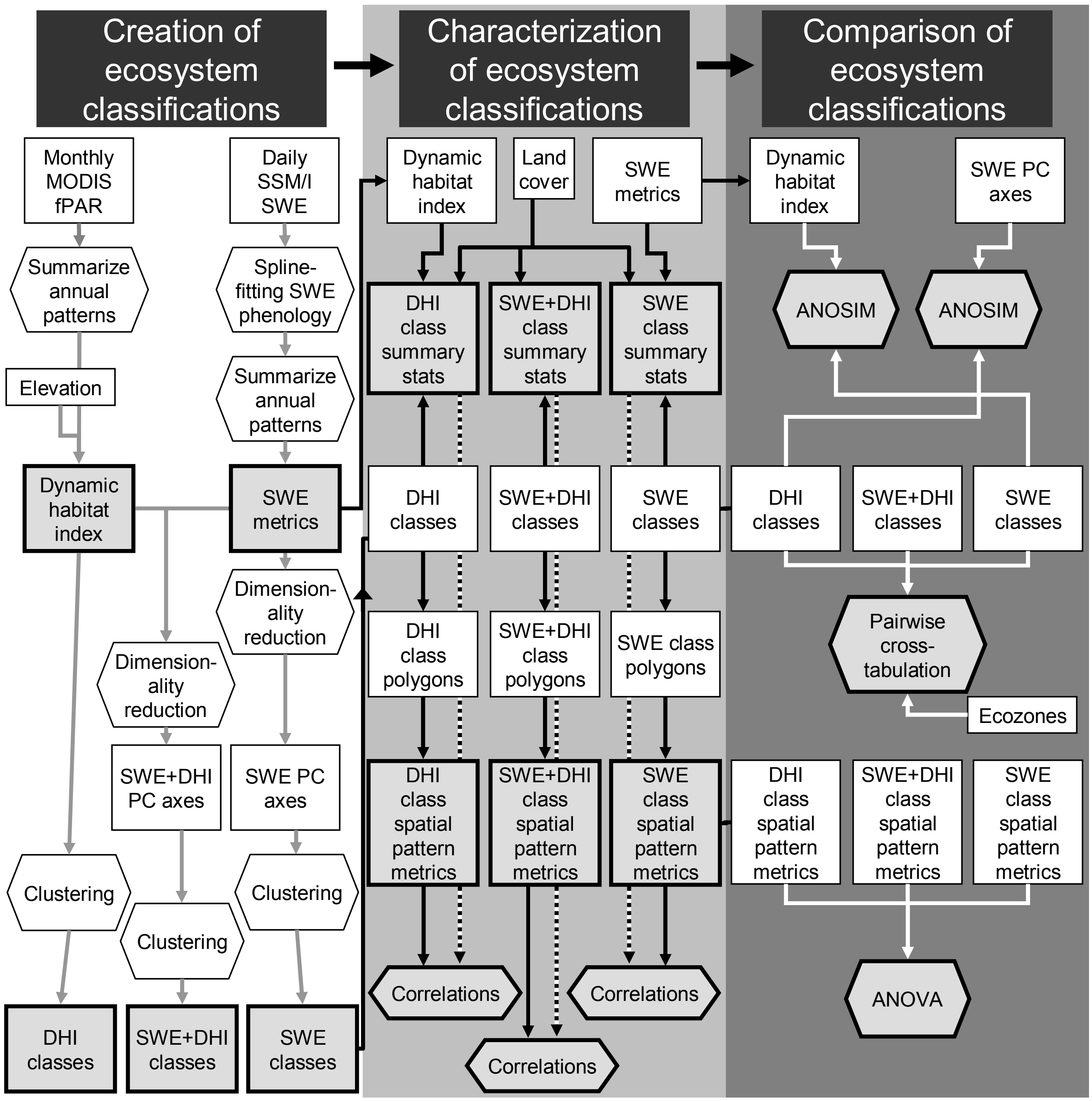

Figure 2. Flowchart diagramming the creation, characterization, and comparison of ecosystem classifications based on summer and/or winter conditions. See Table 1 for a list of abbreviations.

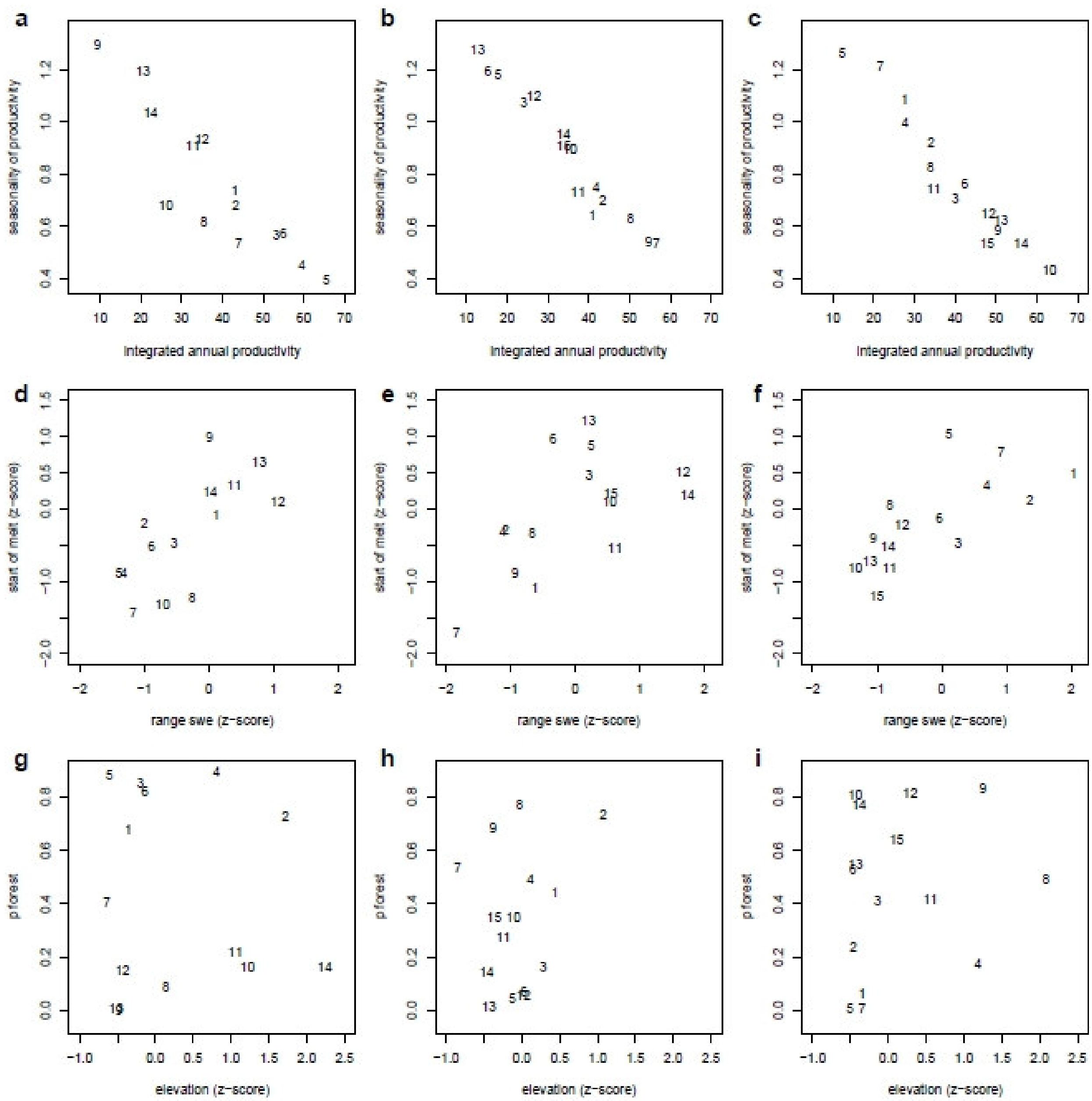

Figure 3. Average characteristics of the ecosystems classified along productivity (a, d, g), snow conditions (b, e, h), and both (c, f, i). Scatterplots illustrate patch centroids along productivity axes (a-c), snow gradients (d-f), and elevation and land cover (g-i). Class numbers correspond to those mapped in Fig. 1.

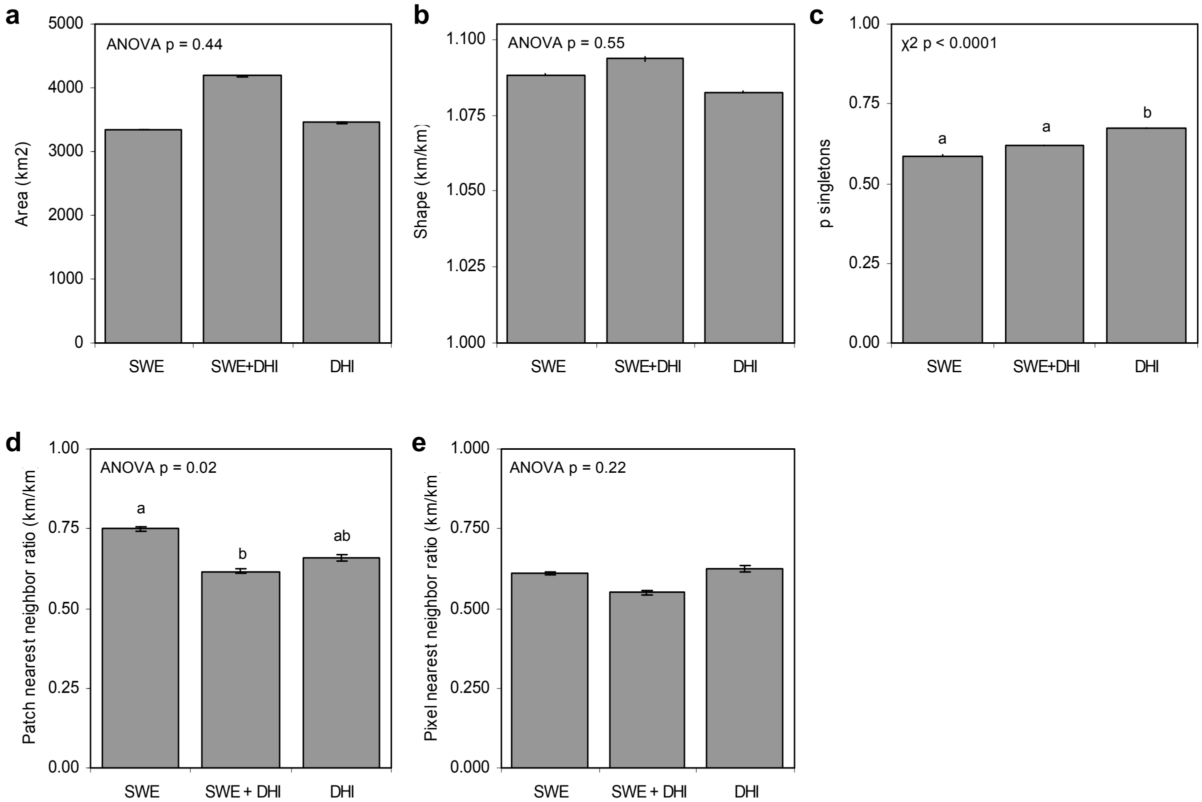

Figure 4. Patch characteristics of contiguous blocks of the same class from each classification: a) patch area (km^2), b) patch shape index (km/km), c) the proportion of single pixel patches, and the mean nearest neighbour distance relative to a random distribution (km/km) for both d) patches, and e) pixels within each class. Plots are of means with standard error bars. Analysis of variance significance levels are indicated in the plot and, where significant differences exist, significantly different pairs ($p < 0.05$) are indicated by the letter above the bar.

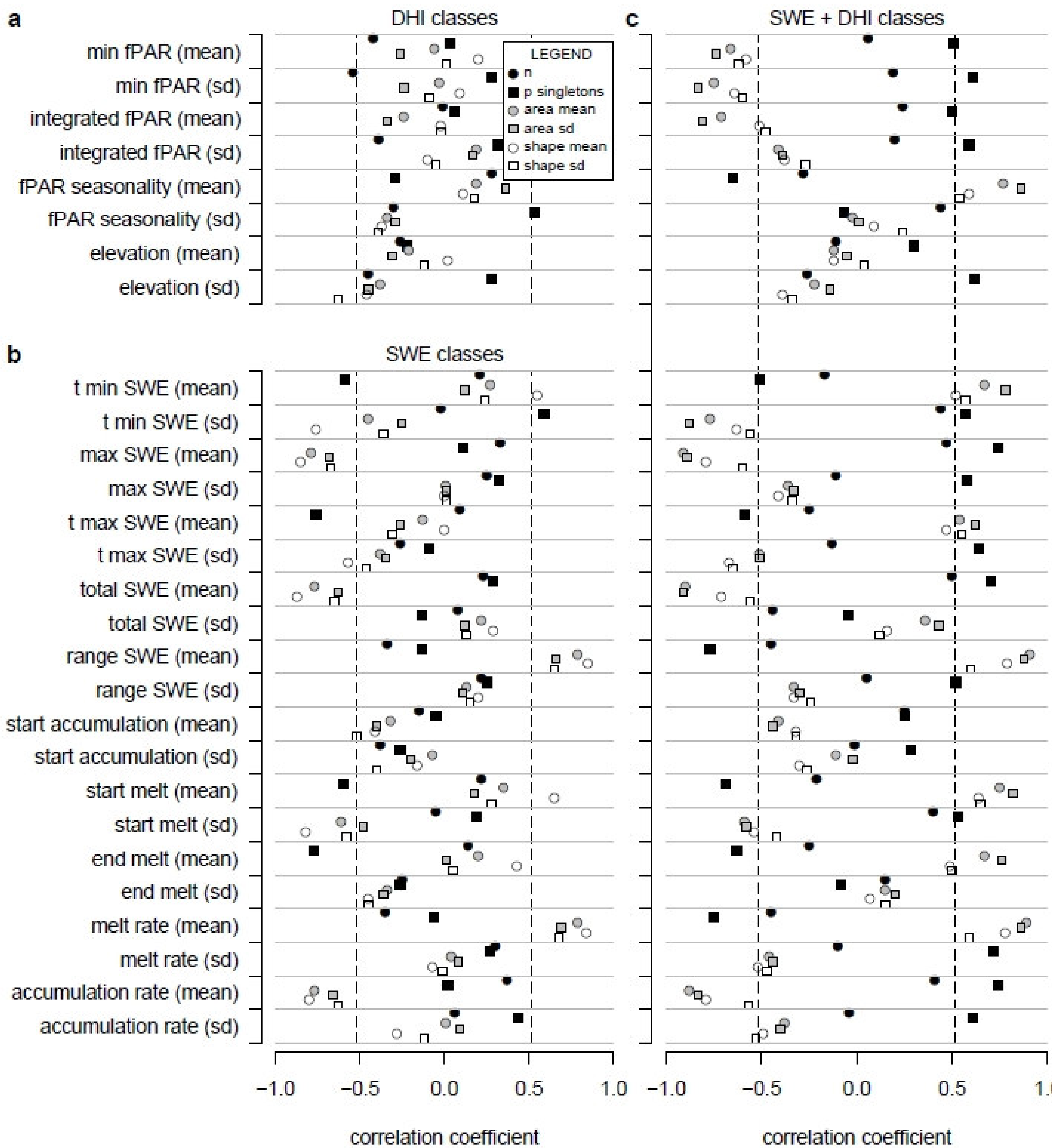

Figure 5. Correlations between patch metrics (n patches, proportion of single-pixel patches and mean and standard deviation of patch size and shape) for each class and the characteristics of that class (mean and standard deviation of input variables). Correlation coefficients that fall outside of the dashed lines are significant. Note that the max SWE, total SWE, and accumulation rate metrics are scaled inversely to the processes they describe.

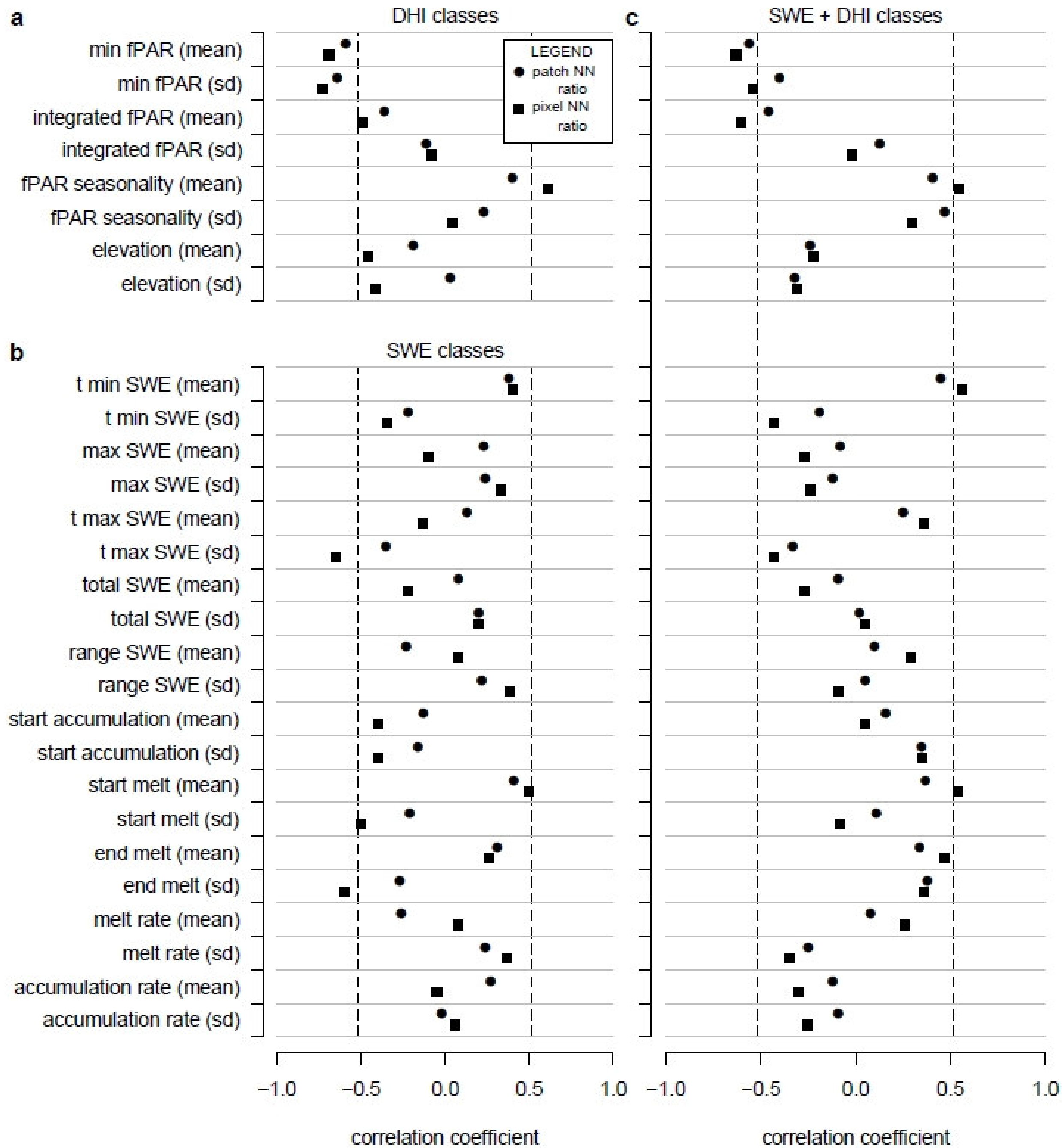

Figure 6. Correlations between dispersion metrics (NN ratio: mean nearest neighbour distances standardized by expected values given the sample size, calculated for both patches and individual pixels) for each class and the characteristics of that class (mean and standard deviation of input variables). Correlation coefficients that fall outside of the dashed lines are significant. Note that the max SWE, total SWE, and accumulation rate metrics are scaled inversely to the processes they describe.

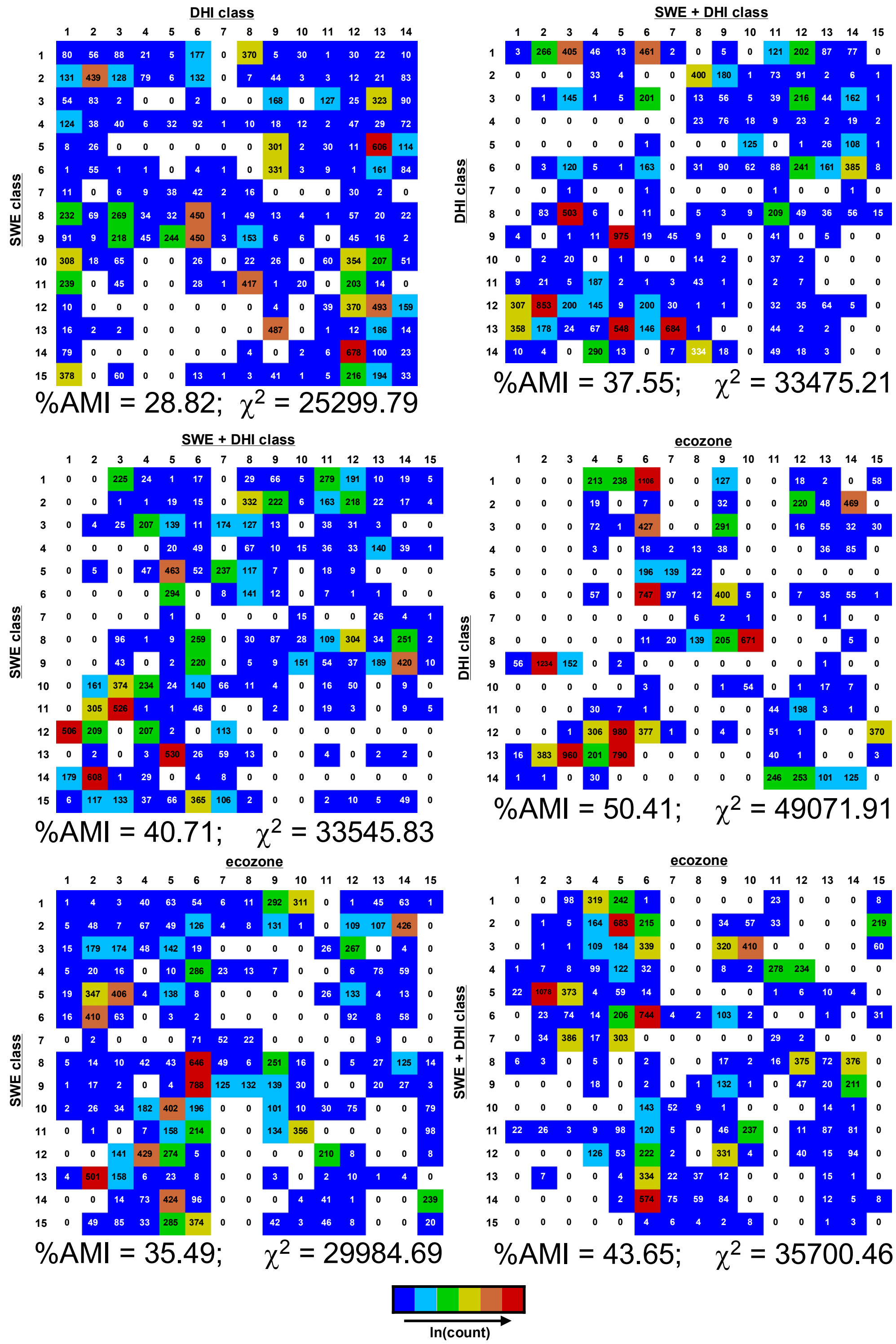

Figure 7. Contingency tables of pixel-wise class associations between classification pairs. DHI (dynamic habitat index) refers to the productivity metrics and SWE (snow water equivalent) to the set of snow metrics. These tables are presented graphically, with the entries color-coded by count, in order to facilitate intercomparison. The % average mutual information (%AMI) and Pearson's χ^2 statistics for each contingency table are also presented.

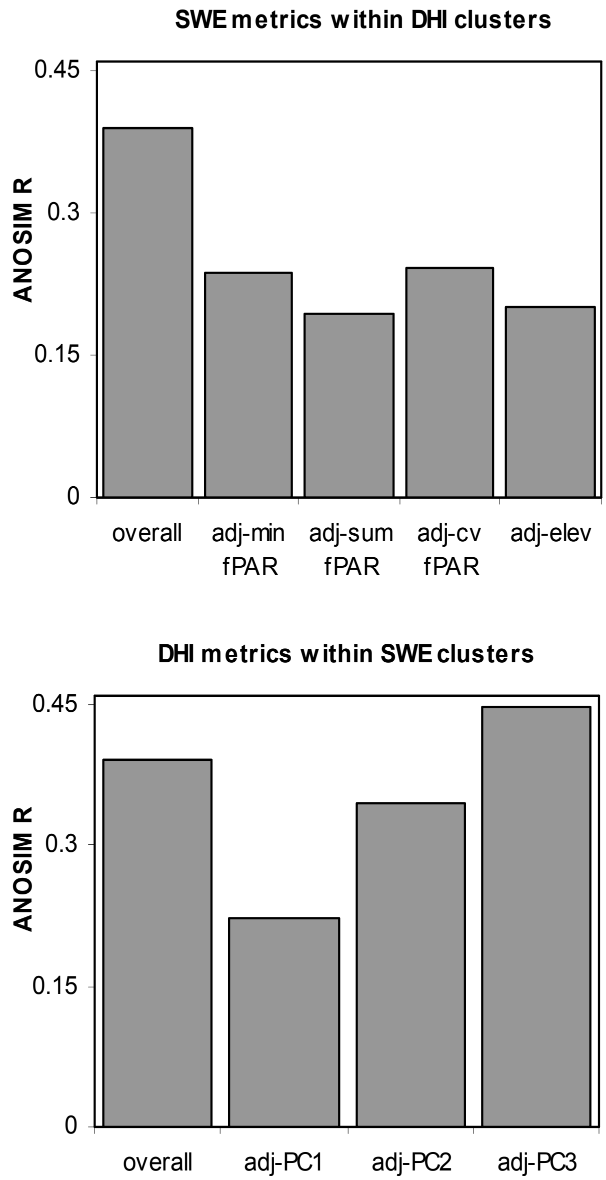

Figure 8. Results of $ANOSIM_{GO}$ (overall) and $ANOSIM_{GA}$ (adjacent) analyses testing if productivity-based clusters effectively explain variation in snow characteristics (top) and if snow-based clusters successfully describe patterns of productivity (bottom). Productivity and snow are abbreviated with DHI (dynamic habitat index) and SWE (snow water equivalent), respectively. The adjacent ANOSIMs compare only between classes that are nearest neighbours in the specified axis.

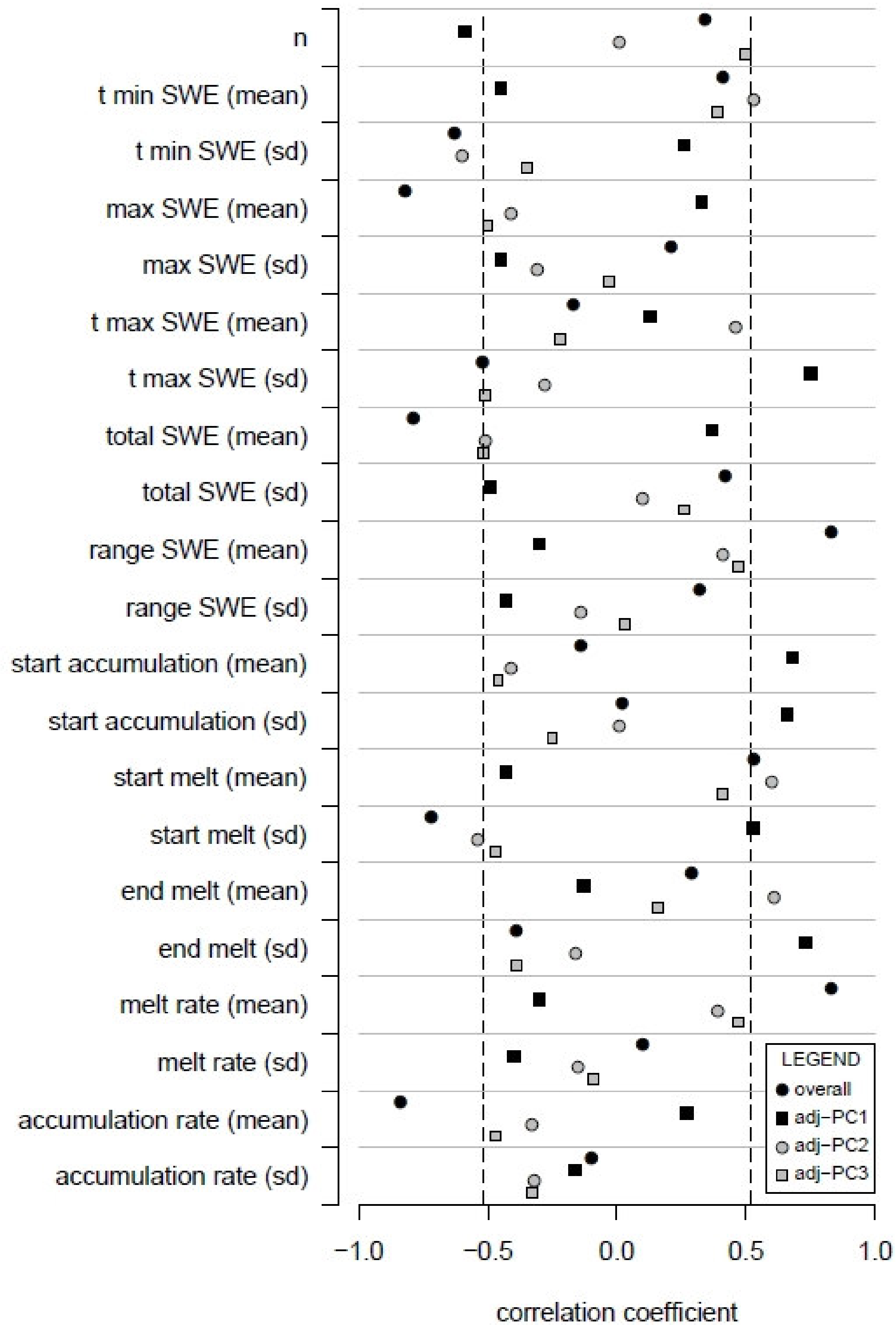

Figure 9. Correlations between individual class ANOSIM Rs when evaluating clusters derived from SWE metrics against DHI variables and the characteristics of that class (number of pixels in the class, mean and standard deviation of input SWE variables). Correlation coefficients that fall outside of the dashed lines are significant. Note that the max SWE, total SWE, and accumulation rate metrics are scaled inversely to the processes they describe.