**How do butterflies define ecosystems? A comparison of ecological regionalization schemes**

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**Abstract.** Ecological regionalizations, such as ecoregions or environmental clusters, are often used as coarse filters for conservation. To be effective biodiversity surrogates, regionalizations should contain distinct species assemblages. This condition is not frequently evaluated and regionalizations are rarely assessed comparatively. We used a national dataset of Canadian butterfly collections to evaluate four regionalizations (ecoregions, land cover and productivity regime classifications, and a spatial grid) at two thematic resolutions using analysis of similarity (ANOSIM) and species indicator values. Overall, the spatially constrained schemes (ecoregions and grids) best captured patterns of butterfly community composition and species affinities, indicating that butterfly communities are strongly structured by space at the continent scale. In contrast, when comparing regions only within spatial or environmental neighbourhoods (i.e., comparing between regions that are adjacent along geographic or environmental gradients), all regionalizations performed similarly. Adjacency in environmental space is thus as important as physical adjacency at determining community dissimilarity. Productivity regimes and land cover will be useful biodiversity surrogates when considered in conjunction with space or within a spatially constrained area. This finding was confirmed with two ecoregional case studies (of the Algonquin-Lake Nipissing and Thompson-Okanagan Plateau ecoregions), which also revealed that the relative performance of regionalizations depends upon the context of the study area. We conclude that including species data can improve the efficiency of environmental surrogates for systematic conservation planning.

## 1. Introduction

Concern over the status and maintenance of biodiversity and ecological processes has sparked broad interest in systematic conservation planning. Protected areas remain a major component of conservation. Systematic conservation planning identifies the optimal, most efficient locations of reserves (Margules and Pressey, 2000). The currency of many biodiversity planning efforts is species richness, with the goal of maximizing the number of species in protected areas. However, such efforts are necessarily data-starved and biodiversity proxies must be used (Margules et al., 2002).

Environmental surrogates, derived from readily available spatial datasets (e.g., satellite data, soil maps, vegetation communities, climate data) are often used to represent biodiversity and may be the only data available for conservation planning. The planning region is first partitioned into homogenous units, known variously as ecoregions (Bailey et al., 1985; Olson et al., 2001); environmental clusters (Trakhtenbrot and Kadmon, 2005) or domains (Kirkpatrick and Brown, 1994; Leathwick et al., 2003; Mackey et al., 2008); and land types (Reyers et al., 2002), facets (Wessels et al., 1999), classes (Lombard et al., 2003), or systems (Oliver et al., 2004). These are expected to correspond to different habitats containing different species assemblages (Oliver et al., 2004). A representative reserve network, i.e., one that contains all habitat types and is expected to contain a large part of the region's species diversity because of the implied complementarity between habitats, is then defined.

Environmental surrogates often unsuccessfully represent regional biodiversity (Araújo et al., 2001; Bonn and Gaston, 2005; but see Trakhtenbrot and Kadmon, 2006), especially for species of conservation concern (Kintsch and Urban, 2002; Lombard et al., 2003). One problem of environmental surrogates stems from the thematic resolution (the number of types) provided

(Pharo and Beattie, 2001; Pressey and Logan, 1994). A representative network from a very fine ecological regionalization (one with many types) will contain many species, but will require a vast protected area to include all types (Reyers et al., 2002). High overlap in species composition between types will reduce the efficiency of environmental surrogates (Fox and Beckley, 2005). In contrast, a very coarse regionalization may not have excessive area costs, but may not include many species due to internal heterogeneity (Reyers et al., 2002).

Similarly, the choice of regionalization matters. Partitioning physical and environmental space along different axes will identify different types with different boundaries. Species affinities may differ between the resulting types due to differential sensitivities to the variables involved. Surprisingly, then, ecological regionalizations have rarely been evaluated with respect to each other (but see Butler, 2009; Reyers et al., 2002; Ward et al., 1999). Our goal is to comparatively evaluate two thematic resolutions of four regionalizations (productivity regimes, land cover classification, ecoregions, and a spatial grid) relative to a primary biodiversity butterfly dataset to answer the questions: 1) How well do ecological regionalizations represent butterfly communities? 2) Which regionalizations and 3) resolutions are optimal? 4) What does this tell us about butterfly community structuring? The primary focus is determining the relative performance of the regionalization schemes. The butterfly dataset, one of the few national-level primary biodiversity datasets available for Canada, provides a convenient basis for independent evaluation of the regionalizations, thus, conclusions about butterfly community structure are an added benefit, but secondary outcome of this research.

## 2. Methods

### 2.1. Ecological regionalizations

The regionalizations tested were created from different environmental variables, intended to capture different ecological processes, and represent philosophically different approaches to regionalization.

### 2.1.1. Ecoregions

Ecoregions are discrete regions sharing similar geology, topography, soil, vegetation, climate, wildlife, hydrology, and land use. Because ecoregion definition is expert-based, variables are not weighted consistently. Ecoregions form a nested hierarchy; in Canada there are ecozones at the highest level, regional ecoregions, and local ecodistricts (Ecological Stratification Working Group, 1995), all of which are considered to be "higher order ecosystems". Ecoregions have been adopted as the logical units for conservation, either for representation goals (Olson and Dinerstein, 1998) or to bound planning areas (Groves et al., 2000).

However, ecoregions may sacrifice environmental homogeneity for spatial contiguity. Sites expected to manifest similar biota and ecological processes should they experience the same abiotic conditions are classified together (Bailey et al., 1985). In general, up to 15% of an ecoregion may be dissimilar, or azonal (Wiken et al., 1996). Tests of ecoregions are few, but those performed support their relevance to community composition (van Rensburg et al., 2004; Williams, 1996; Williams et al., 1999; but see McDonald et al., 2005).

### 2.1.2. Land cover

Vegetation and land cover maps are important determinants of species distributions and community structuring (Kerr and Ostrovsky, 2003) and are commonly used as coarse filter surrogates (GAP Analysis: Scott et al., 1993; The Nature Conservancy: Groves et al., 2000). But vegetation classes do not necessarily host different species (Mac Nally et al., 2002) and, as

for any proxy, their utility as a biodiversity surrogate should be tested (e.g., Pharo and Beattie, 2001).

Land cover data for Canada were derived from the GLC 2000-NCA land cover map of North and Central America (Latifovic et al., 2004). This product maps 28 land cover classes (25 in Canada) at 1 km resolution from SPOT4/VEGETATION satellite data. Classes were aggregated to the 17-class IGBP (International Geosphere-Biosphere Programme) legend (Loveland et al., 2000), with 13 occurring in Canada, to test the implications of decreased thematic resolution.

2.1.3. Dynamic Habitat Index clusters

Environmental domain classifications have been proposed as improvements to ecoregions as they are automated, objective, and remove the spatial contiguity requirement (Belbin, 1993, 1995; Mackey et al., 1988, 2008). Environmental domains are also quantitatively interpretable and intercomparable along their input environmental variables. Environmental domains are often created from climate, topography, geology, and soil axes (Host et al., 1996; Kirkpatrick and Brown, 1994; Leathwick et al., 2003; Mackey et al., 2008; Trakhtenbrot and Kadmon, 2005, 2006), but can be generated from remotely-sensed vegetation indexes (Mackey et al., 2008) or species data (Fox and Beckley, 2005; Ward et al., 1999). The few evaluations of environmental domains demonstrate that they are successful surrogates of biodiversity (Trakhtenbrot and Kadmon, 2005, 2006; but see Kirkpatrick and Brown, 1994).

An environmental domain classification of Canada was constructed from a productivity-based dynamic habitat index (DHI) at 1 km resolution (Coops et al., 2008, 2009a). The DHI contains three axes derived from monthly MODIS (MODerate-resolution Imaging Spectrometer) fPAR (fraction of absorbed photosynthetically active radiation) estimates: summed, minimum, and coefficient of variation of monthly fPAR, representing integrated, minimum, and seasonality of annual productivity (Coops et al., 2008). Annual DHI components were created for 2000 through 2005 and averaged. The three DHI components and elevation (shuttle radar topography mission; Rabus et al., 2003) were used in the two-step multivariate classification algorithm in SPSS (Coops et al., 2009a) which 1) groups the data into an initial set of clusters that are 2) combined with an agglomerative hierarchical method. Canada's land base was classified into 100 clusters, which were grouped into 14 higher order environmental domains. Both thematic resolutions were evaluated.

2.1.4. Spatial grid

The above regionalizations differ largely in their treatment of space. Ecoregions are discrete spatial entities, with a consequent loss of internal consistency. Land cover and environmental domain classifications emphasize internal homogeneity achieved through spatial dispersion. Yet space is a major component of ecological patterns and processes. Most environmental variables are spatially autocorrelated, as are species distributions, due to both a spatially structured environment and dispersal limitation. Contiguous locations are thus likely to be similar (Nekola and White, 1999). Spatial structure should be taken advantage of, rather than considered a nuisance (Legendre, 1993), and the spatial coherence of ecoregions may be not a limitation but a strength.

To assess the role of space on the performance of regionalizations relative to butterfly communities and their structuring, a final regionalization was created based entirely on space. Regions were square grid cells in the Albers equal-area projection for North America. Analyses focused on the two spatial resolutions – 300 km and 1000 km – that yielded thematic resolutions most comparable to the other regionalizations, but grid resolutions between 100 km and 1000

km, with a step of 100 km, were also tested to determine the optimal resolution to describe butterfly communities.

*2.2. Response dataset*

2.2.1. Butterfly data

The Canadian Biodiversity Information Facility's (http://www.cbif.gc.ca/) dataset of georeferenced butterfly specimens and observations, containing nearly 200 000 records, 300 species (Layberry et al., 1998) and more than 10 000 sites, was used. Sampling resolution is as high as 1 km$^2$ in southern Canada and along major roads (median: 101 km$^2$). We excluded points containing fewer than three species to avoid bias from incomplete sampling (n=5076). Table 1 lists the numbers of classes of each regionalization containing sufficient points ($\geq$2) and species ($\geq$3).

2.2.2. Butterfly data evaluation

Specimen records are known to contain biases due to spatially variable sampling effort (Moerman and Estabrook, 2006; Schulman et al., 2007) and skill (Ahrends et al., 2010). Moreover, they are often collected over long time periods, and may thus contain confounding signals of temporal turnover. The butterfly dataset used here has highly variable sampling density and contains records from 1860 to the present (although 75% of the records used in this study were collected after 1960). We evaluated the potential for spatial sampling biases and temporal turnover to confound our analyses with partial canonical correspondence analyses (pCCA; Borcard et al., 1992; ter Braak, 1986), testing the degree to which the variation in butterfly community composition explained by each regionalization is also shared by covariate proxies of sampling effort. The covariates tested were the distance to a road or to a highway, calculated from the 2010 Road Network file (Statistics Canada, 2010), sample density, estimated as the area of a Thiessen polygon surrounding each sample point (e.g., Schulman et al., 2007), and the decade in which each specimen was observed. Sample points were the analysis units for pCCAs conditional on spatial covariates (distances to road and highway, sample density). However, because ~40% of the sample points were sampled in multiple decades, it was necessary to pool points into region-decade aggregates for the temporal pCCAs to avoid creating singleton records when separating points and decades.

*2.3. Analyses*

The ability of each regionalization to capture butterfly patterns was assessed in two ways. Analysis of similarity (ANOSIM) is a community-level analysis testing the degree to which community composition differs between regions. Indicator values are species-based, testing the strength of individual species' affinities to the defined regions. An additional community analysis, canonical correspondence analysis (CCA; ter Braak, 1986), was also tested, but yielded identical conclusions as the other analyses and, thus, will not be presented.

2.3.1. ANOSIM

Analysis of similarity (Clarke, 1993) is a nonparametric test of whether points are more similar within than between regions. Pairwise dissimilarities were calculated with Jaccard's distance, the proportion of unshared species between sites, and rank ordered. The test statistic, ANOSIM R (range: [-1, 1]), is the difference between mean within-region and between-region ranks, standardized by the number of pairwise comparisons. A significant ANOSIM R, tested by permutation, indicates that the regionalization captures patterns of butterfly communities. Four ANOSIMs were performed for each regionalization:

1. Grand, overall (ANOSIM$_{GO}$) – This analysis used all possible pairwise within- and between-region dissimilarities to generate a single ANOSIM R. Labels (within or between) were permuted 1000 times to test significance.
2. Grand, adjacent (ANOSIM$_{GA}$) – This ANOSIM used all within-region dissimilarities, but between-region dissimilarites were only considered for regions adjacent in the environmental space in which they were constructed. For ecoregions and the spatial grid, spatial adjacency was considered (including diagonals). Productivity regimes were ranked along each of the four DHI axes, adjacency was identified, and ANOSIMs were performed separately for each ordering. Land cover classes were considered adjacent if they were aggregated together in a broader classification scheme. (A land cover category had no neighbours if the same class definition existed at both thematic resolutions.) Labels were permuted 1000 times for significance testing.
3. Per-region, overall (ANOSIM$_{RO}$) – This analysis calculated an ANOSIM R for each region to determine its potential contribution to national biodiversity conservation. Within-region dissimilarities were tested against 1000 random samples of dissimilarities of the same size.
4. Per-region, adjacent (ANOSIM$_{RA}$) – As in ANOSIM$_{RO}$, however the population of dissimilarities against which within-region dissimilarities was tested was restricted to the focal region plus those adjacent to it. This analysis tests if a region is redundant with those most similar to it.

The relative performance of each regionalization was determined from the ANOSIM$_{GO}$ and ANOSIM$_{GA}$ Rs and the proportion of regions identified by ANOSIM$_{RO}$ and ANOSIM$_{RA}$ as containing significantly unique communities. For the DHI clusters, the relationship between environmental similarity and community similarity was tested by regressing ANOSIM$_{RO}$ and ANOSIM$_{RA}$ Rs against the environmental distance (Euclidean distance between cluster centroids in DHI space) from the focal region to its nearest neighbour. Finally, ANOSIM analyses were performed for all 10 resolutions (100 to 1000 km) of the spatial grid.

2.3.2. Indicator values

Indicator values (Dufrêne and Legendre, 1997) were developed to determine indicator species with which sites could be rapidly identified to community type, but can also evaluate the relative performance of environmental classifications. Indicator values are first calculated for all species-region combinations as the product of specificity, the proportion of sites containing species $i$ that belong to region $j$ ($n_{ij}/n_{i\cdot}$), and fidelity, the proportion of sites in region $j$ that contain species $i$ ($n_{ij}/n_{\cdot j}$), multiplied by 100. Species indicator values (range: (0, 100]) are the maximum indicator value for each species over all regions. Regionalizations can be compared with the sum of all species indicator values (Dufrêne and Legendre, 1997). The number of significant (tested with 250 permutations) indicator species was also determined for each regionalization.

2.3.3. Regional-scale analyses

All of the above analyses were performed at the national level. However, land cover is more typically used as a biodiversity surrogate for regional conservation planning. Land cover classifications over large extents are necessarily highly generalized. A representative selection of a small number of general classes nationally may be extremely biased. Achieving their representation within each ecoregion may more fully represent regional variants and, thus, overall biodiversity. All analyses were therefore repeated with DHI and land cover classifications for two well-sampled ecoregions (Fig. 1): the Algonquin-Lake Nipissing

ecoregion (n=387) and the Thompson-Okanagan Plateau (n=168). The Algonquin-Lake Nipissing ecoregion is in southern Ontario in the Boreal Shield ecozone. It experiences warm summers and cold winters, is dominated by mixedwood forest, and has little variability in soils (Ecological Stratification Working Group, 1995). The Thompson-Okanagan Plateau, in southern British Columbia and the Montane Cordillera ecozone, is located at higher elevation, contains greater topographic complexity, and has a diversity of land cover, wildlife communities, and soils, related to elevation gradients. The climate is warm with mild winters (Ecological Stratification Working Group, 1995).

   All analyses were performed in R (R Core Development Team, http://www.r-project.org). Functions in the add-on package vegan (Oksanen et al., 2008) were used for pCCA analyses, to calculate Jaccard's distances, and to perform $ANOSIM_{GO}$ analyses. All other analyses were coded in R by the authors.

## 3. Results

### 3.1. Butterfly data evaluation

   The spatial and temporal covariates all explained significant variation in butterfly community composition ($p<0.005$), indicating that butterfly community composition differs due to temporal turnover; sample density and proximity to roads, either actually, as a result of road disturbance, or apparently, as a result of sampling differences that covary with site accessibility. However, the proportion of variation explained was consistently low (distance to road: 0.4%, distance to highway: 0.6%, sample density: 0.3%, decade: 0.4-2.1%), and one to two orders of magnitude lower than that explained by the ecological regionalizations. (Note that the higher explanatory power of decade relative to the spatial covariates is due to the greater aggregation of data points for these tests.) Moreover, there was very little shared variation between the ecological regionalizations and the covariates (not shown). On average, 95% of the explanatory power of the regionalizations was uncontaminated by the confounding effects tested. These tests demonstrate that the results of our regionalization analyses are not likely to be confounded by biases in the butterfly dataset. The effects of spatial sampling biases and temporal turnover on recorded community composition, while present, are weak and largely unshared with the effects of the regionalizations.

### 3.2. ANOSIM

   All ecological regionalizations over all resolutions captured highly significant patterns ($p<0.001$) of butterfly community composition, whether considering all between-region comparisons ($ANOSIM_{GO}$) or only comparisons between adjacent regions ($ANOSIM_{GA}$). However, $ANOSIM_{GO}$ R varied considerably between regionalizations (Fig. 2a). Ecoregions and geographic grid cells were the most successful at depicting environmental differences relevant to butterfly communities. Restricting comparisons to neighbourhoods ($ANOSIM_{GA}$) reduced the performance of all regionalizations (Fig. 2a) except for the 100 cluster DHI regionalization with adjacency along seasonality (Fig. 2b). $ANOSIM_{GA}$ R values were less variable. Within a regionalization, $ANOSIM_{GO}$ and $ANOSIM_{GA}$ R values decreased with degrading thematic resolution, except for adjacent $ANOSIM_{GA}$ tests for grid cells and ecoregions (Fig. 2a).

   Similar results were obtained for the proportion of significant regions in each regionalization ($ANOSIM_{RO}$ and $ANOSIM_{RA}$; Fig. 2c). Grid cells and ecoregions had the greatest proportion of regions with unique butterfly communities; the number that was significant was reduced when considering only adjacent regions ($ANOSIM_{RA}$; anomalous results from the 13 class land cover classification are due to classes with no neighbours), but increased

with degrading thematic resolution (Fig. 2c). $ANOSIM_{RO}$ and $ANOSIM_{RA}$ R values are mapped for ecoregions and ecozones in Figure 3.

Per-region $ANOSIM_{RO}$ and especially $ANOSIM_{RA}$ R values were related to the distance to the nearest neighbour in DHI space (Table 2). Relationships were strongest with minimum and integrated annual productivity and at the fine thematic resolution (Table 2).

Overall $ANOSIM_{GO}$ R declined with coarsening spatial (and thematic) resolution of the geographic grid (Fig. 4). In contrast, adjacent $ANOSIM_{GA}$ R was more variable, but peaked at a grid resolution of 400 km.

*3.3. Indicator values*

Summed indicator values were highest for the grid cell and ecoregion schemes (Fig. 5). Changing thematic resolution had little effect. The number of significant indicator species was relatively consistent across regionalizations and was more strongly affected by thematic resolution (Fig. 5). More coarse thematic resolutions had more indicator species, but species indicator values for all regionalizations were generally low (not shown).

*3.4. Regional-scale analyses*

For the Algonquin-Lake Nipissing ecoregion, both the environmental domain and land cover classifications captured significant patterns of butterfly community composition (Table 3). Both performed similarly, as seen by their inconsistent rankings by the different analyses. Land cover received higher R values from both $ANOSIM_{GO}$ and $ANOSIM_{GA}$ and was favored by indicator values while $ANOSIM_{RO}$ and $ANOSIM_{RA}$ found a higher proportion of significant productivity regimes. Unexpectedly, when evaluating the DHI clusters, butterfly communities were more dissimilar from their neighbours in productivity space than from all clusters within the ecoregion.

Butterfly communities of the Thompson-Okanagan Plateau were structured more strongly by productivity regimes than land cover (Table 3) when evaluated with ANOSIMs. Indicator values were also greater for the DHI classification, but were not significant, presumably because of the large number of classes (39) and small number of samples (168). Adjacent ANOSIMs revealed communities in this ecoregion to be most strongly structured along minimum and integrated annual productivity. There was not significant structuring along elevation, however, more classes were significantly different from their elevational neighbours than from neighbours along any other DHI axis or in general, indicating that there is an important effect of elevation.

**4. Discussion**

*4.1. Structuring of butterfly communities by space and productivity*

The ecoregion/ecozone system was consistently the most relevant ecological regionalization to butterfly communities. Component regions contained more distinct species assemblages and corresponded more strongly to species affinities than did either remotely-sensed productivity regimes or land cover classes. The environmental variables along which ecoregions are delineated may be more important to butterfly species distributions and community composition than are productivity and land cover. However, this seems unlikely. Both productivity (Bailey et al., 2004; Hawkins and Porter, 2003a, 2003b; Luck, 2007) and land cover (Kerr et al., 2001) are important drivers of butterfly diversity. Reported correlations between butterfly diversity and habitat diversity (Kerr et al., 2001) and productivity heterogeneity (Seto et al., 2004) imply that there should be marked partitioning of butterfly communities along these gradients.

Alternatively, ecoregions may more fully characterize the ecosystems experienced by butterflies because they incorporate more environmental variables. Indeed, authors have argued that "more is better" when constructing biodiversity surrogates (Bonn and Gaston, 2005; Lombard et al., 2003; Mackey et al., 2008; Reyers et al., 2002; Sarkar et al., 2005). Individual surrogates may be idiosyncratic; the amalgamation of multiple surrogates may produce a more coherent picture, more effectively representing biodiversity.

However, the most important factor underlying regionalization performance appears to be space. The geographic grid cell "regions" performed nearly as well as ecoregions in all evaluations. Both of these schemes define spatially contiguous regions. In contrast, the environmental domain and land cover classifications, which do not incorporate space into their regionalization algorithms and result in patchy, dispersed types, performed similarly poorly (agreeing with the findings of Butler, 2009). Since space is an important influence on biological communities, it should be considered in conjunction with environmental proxies during conservation planning (Oliver et al., 2004). Space may be especially relevant for butterflies. Butterflies typically disperse only meters to a few kilometers per generation (Baguette and Schtickzelle, 2006; Fric and Konvicka, 2007; Thomas et al., 1992), although larger, gradual range shifts have been observed in response to climate change (Hickling et al., 2006; Parmesan et al., 1999).

The above discussion focuses on the distinctiveness of regions nationally. However, when considering only dissimilarity in an immediate spatial or environmental neighbourhood, all regionalizations were roughly equivalent at representing butterfly communities. Butterfly communities in nearby localities are as similar to each other as those in "nearby" productivity regimes or in land cover classes of the same functional type. This reinforces the conclusion that productivity regimes and land cover are important to butterflies, but perform poorly as regionalizations because of the spatial dispersion of each class, resulting in heterogeneous species composition at a continental scale. Indeed, the environmental domain classification is the most successful at representing butterfly communities that are unique from their nearest neighbours in seasonality, performing better than many of the overall $ANOSIM_{GO}$ comparisons. Seasonality might therefore be especially important to butterflies, as has been demonstrated for birds (Coops et al., 2009b). Alternatively, since all else is not held equal when ordering along a productivity axis, high $ANOSIM_{GA}$ values may indicate a *lack* of importance of seasonality. Clusters adjacent in seasonality may be quite distant along more meaningful variables, resulting in strongly dissimilar butterfly communities. The unimportance of seasonality relative to other productivity variables is also suggested by the absence of a significant relationship between $ANOSIM_{RO}$ and $ANOSIM_{RA}$ R values and the distance to the nearest neighbour along seasonality (Table 2).

Adjacent region results and ecoregional case studies suggest that environmental domain and land cover classifications will be useful biodiversity surrogates when spatially stratified (Oliver et al., 2004), such as for ecoregional conservation planning. Both schemes captured significant differences in butterfly community composition for both the Algonquin-Lake Nipissing and Thompson-Okanagan Plateau ecoregions. This is notable since these classifications were defined over much broader extents (national for productivity regimes, continental for land cover), yet are still capable of characterizing relevant variation at the regional level. For the Thompson-Okanagan Plateau, these regionalizations captured species affinities better at the ecoregional than the national level, as shown by higher indicator values.

Finally, the ecoregional cases show that regionalization performance depends upon the study area and the specific environmental conditions present.

*4.2. Advantages of quantitative environmental domain classifications*

The environmental domain approach provides more than an ecological regionalization. Instead, it is coupled with the physically meaningful variables used to derive the regions, which can be further used to interpret the classes and guide their application. The uniqueness of a productivity regime's butterfly community was strongly related to the difference from its nearest productivity neighbour. This environmental distance can be used to prioritize the order of reserve establishment or to infer region uniqueness in the absence of biodiversity data (Belbin, 1995; Woinarski et al., 1996). In contrast, class dissimilarity can only be determined qualitatively for land cover classes, and perhaps not at all for ecoregions.

*4.3. Thematic resolution*

The tradeoff between within-region homogeneity and between-region heterogeneity is apparent in the effects of thematic resolution. Although coarse regions are more likely to be distinct from both neighbouring and distant regions, increased internal variability reduces their ability to represent community patterns. The only exceptions were ecoregions and grid cells, which performed better in the adjacent region comparisons at the coarser resolution. The boundaries of these coarse regions may represent major biotic transition zones (McDonald et al., 2005).

Thematic resolution is inseparable from spatial resolution for ecoregions and grid cells. Because regions are spatially coherent, the size of each region (spatial resolution) determines how many are possible (thematic resolution). (For the other two schemes, spatial resolution remains fixed at 1 km, but the areal extent of each region depends upon thematic resolution.) Our tests of grid cells show that the scale of variation for butterfly community composition is ~400 km. Below this resolution, communities are not sufficiently distinct from those in neighbouring cells; above it, increased within-cell heterogeneity causes important detail to be lost. Ecoregions (mean [SD] $\sqrt{area}$ = 240 km [270]) may be too fine to represent butterfly communities efficiently. The proportion of ecoregions that are significantly distinct from their neighbours (40%) is substantially lower than that for 400 km grid cells (56%).

*4.4. Environmental surrogate redundancy and conservation efficiency*

The major shortcoming of environmental surrogates is an inefficiency at conserving biodiversity (Fox and Beckley, 2005; Reyers et al., 2002). Heterogeneity within types prevents the actual conservation of all species, especially rare and threatened species, and overlap between types increases the land cost relative to species based conservation planning. This can be overcome by incorporating both environmental surrogates and available species data in conservation planning (Ferrier, 2002; Ferrier et al., 2002, 2007; Kirkpatrick and Brown, 1994; Leathwick et al., 2010; Lombard et al., 2003; Reyers et al., 2002). If the relative conservation value of each region is known, inefficient, constant conservation targets (e.g., 10% of each region) can be avoided. Instead, the proportion of each region to be conserved can be tailored to its conservation need (Bonn and Gaston, 2005). Highly variable regions may require extra protection. Regions that are redundant with their neighbours need not be separately represented, reducing the area needed for conservation (Wessels et al., 1999). For example, the results of the per-region ANOSIM analyses from this study, presented graphically in Figure 3 for the ecoregion regionalization, clearly indicate region redundancies and can be used to set conservation priorities. All regions with significantly unique communities, especially in the more stringent test against their neighbours, should be represented in a preserve network. In

contrast, those regions that do not differ from their spatial or environmental neighborhood need only be included if adjacent regions are not represented. Region selection at this stage can be optimized by the regional ANOSIM R value or by the level of dissimilarity in community composition between regions in the neighborhood of interest and those already prioritized for conservation. This strategy should be applicable at both national and regional planning levels.

## 5. Conclusions

All four regionalizations (ecoregions, productivity regimes, land cover, and spatial grid cells) represent patterns of butterfly community composition and, therefore, may be useful biodiversity surrogates. Spatially constrained regionalizations (ecoregions and grid cells) best captured unique butterfly assemblages when evaluated over all of Canada, indicating that an optimal conservation network should be well distributed spatially, with reserves separated by no more than 400 km. However, comparisons of neighbouring assemblages in geographic and environmental space revealed comparable performance of productivity regimes and land cover classes relative to the spatial regions, highlighting that environmental and physical distance have similar effects. Environmental domain and land cover classifications thus possess considerable value as conservation proxies, especially when used in conjunction with a spatial stratification, such as the existing ecoregion framework. At the ecoregional level, the relative performance of different ecological regionalizations will depend upon the major gradients present in each ecoregion. Environmental domains have the added benefit of enhanced interpretability and information content from the environmental variables along which the classification was generated, which can further inform conservation planning. A reserve network might thus be optimized by iteratively selecting sites most environmentally distinct from those already protected. The environmental dissimilarity measures inherent in the productivity regime classification and the butterfly community dissimilarity measures generated by this study can be used to increase the efficiency of environmental biodiversity surrogates. However, the patterns illustrated here may be specific to butterflies, and should be corroborated against other taxa before specific targets are established.

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**Table 1**.  Number of classes in each regionalization scheme containing two or more butterfly sample points, each sampling more than three species.

| | Thematic Resolution | |
|---|---|---|
| **Regionalization** | **high** | **low** |
| Ecoregions | 129 | 14 |
| Land cover | 25 | 13 |
| Productivity regimes | 96 | 14 |
| Grid cells | 106 | 19 |

**Table 2.**  Results of regression analyses between per-region ANOSIM R, when evaluated against all other regions ($ANOSIM_{RO}$) or against neighbours in productivity space ($ANOSIM_{RA}$), and the distance from that region to its nearest productivity neighbour along the four productivity axes. Significance is indicated with • ($p < 0.1$), * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

| n clusters | variable | Overall ($ANOSIM_{RO}$) | | | Adjacent ($ANOSIM_{RA}$) | | |
|---|---|---|---|---|---|---|---|
| | | **Coef** | **$R^2$** | | **Coef** | **$R^2$** | |
| 100 | All DHI axes | 0.020 | 0.012 | | - | - | |
| | minimum productivity | 0.003 | 0.000 | | 0.098 | 0.218 | *** |
| | integrated productivity | 0.151 | 0.106 | ** | 0.179 | 0.174 | *** |
| | seasonality | 4.590 | 0.024 | | 1.291 | 0.002 | |
| | elevation | -0.219 | 0.003 | | 0.808 | 0.034 | • |
| 14 | All DHI axes | 0.026 | 0.238 | • | - | - | |
| | minimum productivity | 0.028 | 0.253 | • | 0.041 | 0.193 | |
| | integrated productivity | 0.001 | 0.001 | | 0.055 | 0.313 | * |
| | seasonality | 3.011 | 0.172 | | 4.064 | 0.139 | |
| | elevation | -0.257 | 0.103 | | 0.546 | 0.178 | |

**Table 3.** Evaluation of the dynamic habitat index (DHI) productivity regime and land cover classification regionalizations by analysis of similarity (ANOSIM) and species indicator values for two case study ecoregions.

| | DHI clusters[a] | | Land cover[a] | |
|---|---|---|---|---|
| **Algonquin – Lake Nipissing** | | | | |
| ANOSIM | | | | |
| R | | | | |
| overall (ANOSIM$_{GO}$) | 0.0128 | | 0.0705 | *** |
| adjacent[b] (ANOSIM$_{GA}$) | 0.0042 | | 0.1033 | *** |
| | 0.0350 | *** | | |
| | 0.0193 | * | | |
| | 0.0124 | | | |
| p significant | | | | |
| overall (ANOSIM$_{GO}$) | 24% | - | 9% | - |
| adjacent[b] (ANOSIM$_{GA}$) | 20% | - | 0% | - |
| | 24% | - | | |
| | 24% | - | | |
| | 8% | - | | |
| Indicator values | | | | |
| sum indicator value | 760 | * | 824 | ** |
| n indicator species | 21 | - | 21 | - |
| **Thompson – Okanagan Plateau** | | | | |
| ANOSIM | | | | |
| R | | | | |
| overall (ANOSIM$_{GO}$) | 0.0536 | • | 0.0170 | |
| adjacent[b] (ANOSIM$_{GA}$) | 0.0574 | * | 0.0026 | |
| | 0.0516 | * | | |
| | 0.0431 | • | | |
| | 0.0389 | | | |
| p significant | | | | |
| overall (ANOSIM$_{GO}$) | 24% | - | 0% | - |
| adjacent[b] (ANOSIM$_{GA}$) | 21% | - | 0% | - |
| | 21% | - | | |
| | 30% | - | | |
| | 33% | - | | |
| Indicator values | | | | |
| sum indicator value | 1431 | | 1093 | * |
| n indicator species | 22 | - | 22 | - |

[a] Significance is indicated with • ($p < 0.1$), * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$), and - (not tested).
[b] Adjacent ANOSIM results for the DHI clusters are listed in the following order: minimum annual productivity, integrated annual productivity, seasonality, and elevation.
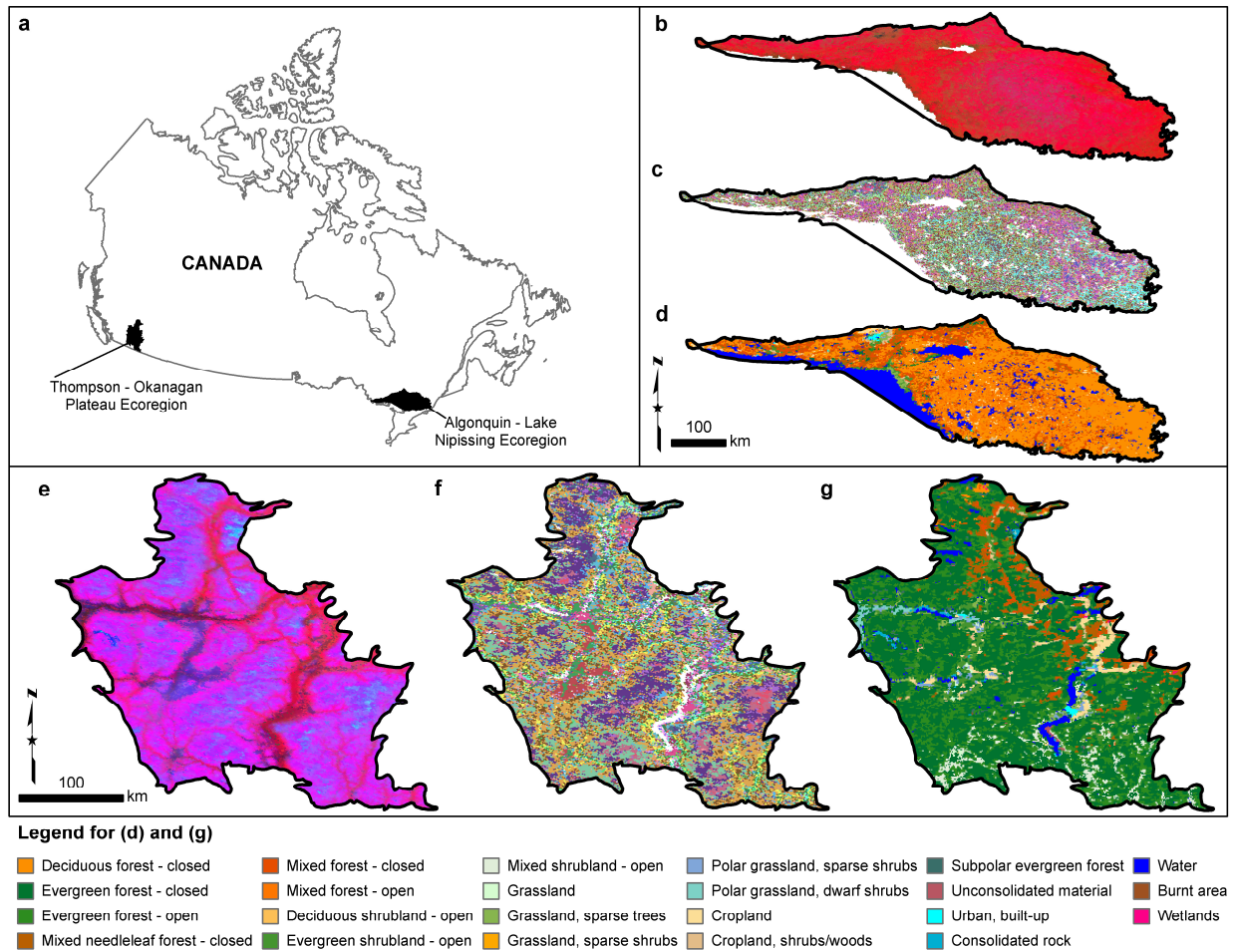
**Figure 1.** (a) Locator map showing the positions of the two case study ecoregions: the Algonquin-Lake Nipissing ecoregion (further illustrated in b-d) and the Thompson-Okanagan Plateau ecoregion (further illustrated in e-g). (b) and (e) plot false-color composites of three of the dynamic habitat index (DHI) components (integrated annual productivity in red, seasonality of productivity in green, and elevation in blue). (c) and (f) map the DHI productivity regimes present in each ecoregion. (d) and (g) provide the GLC 2000-NCA land cover maps for each ecoregion, the legend of which is given at the bottom.
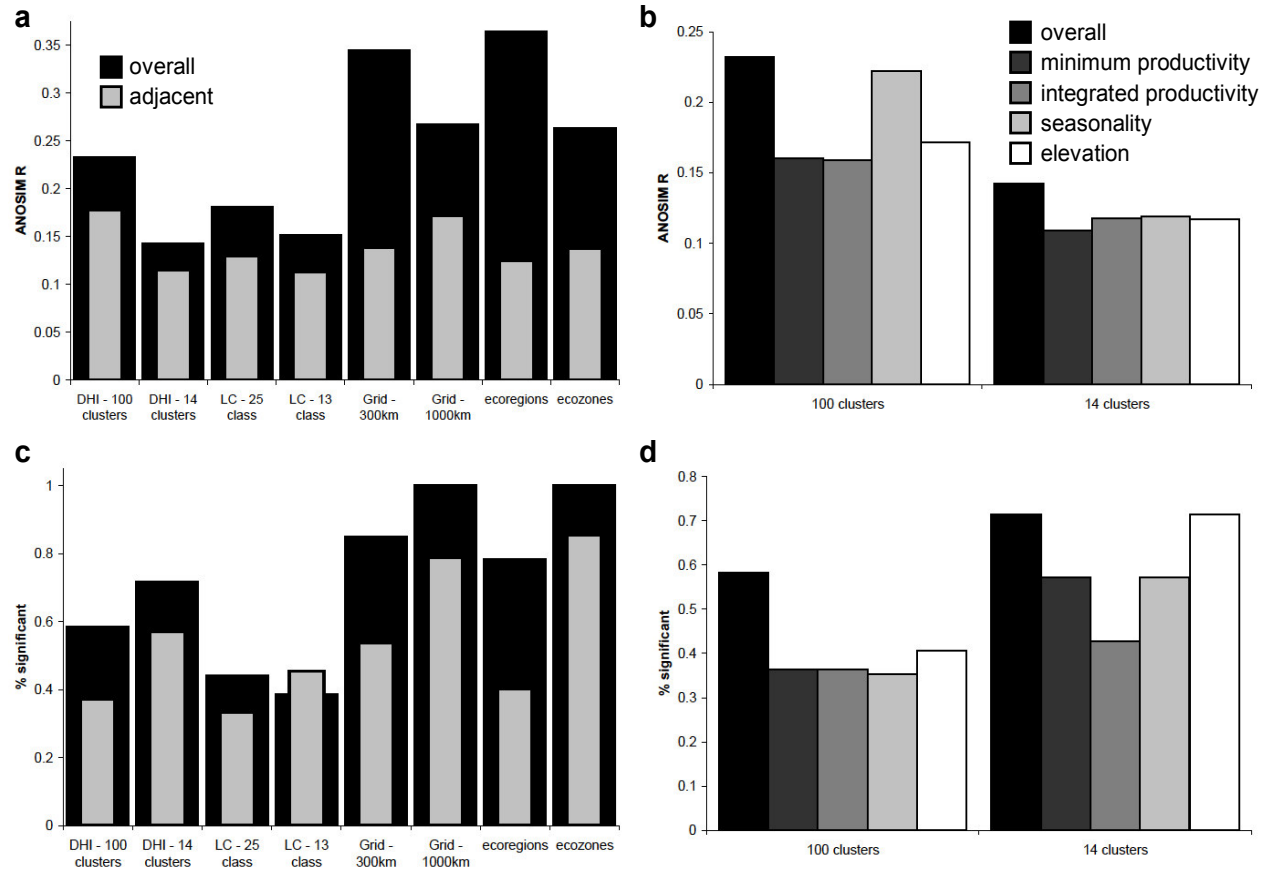
**Figure 2.** (a, b) $ANOSIM_{GO}$ and $ANOSIM_{GA}$ R statistics for each regionalization scheme at two thematic resolutions each for the grand, national level comparisons. (c, d) The proportion of regions found by $ANOSIM_{RO}$ and $ANOSIM_{RA}$ to contain unique butterfly assemblages for each regionalization scheme. In (a and c) evaluation against all pairwise between-region dissimilarities is shown in black ($ANOSIM_{GO}$ and $ANOSIM_{RO}$); against only dissimilarities between adjacent regions in grey ($ANOSIM_{GA}$ and $ANOSIM_{RA}$). (b, d) Adjacency for the dynamic habitat index (DHI) productivity regimes is broken up into each component axis. The average of these results is plotted in (a, c). LC = Land cover.
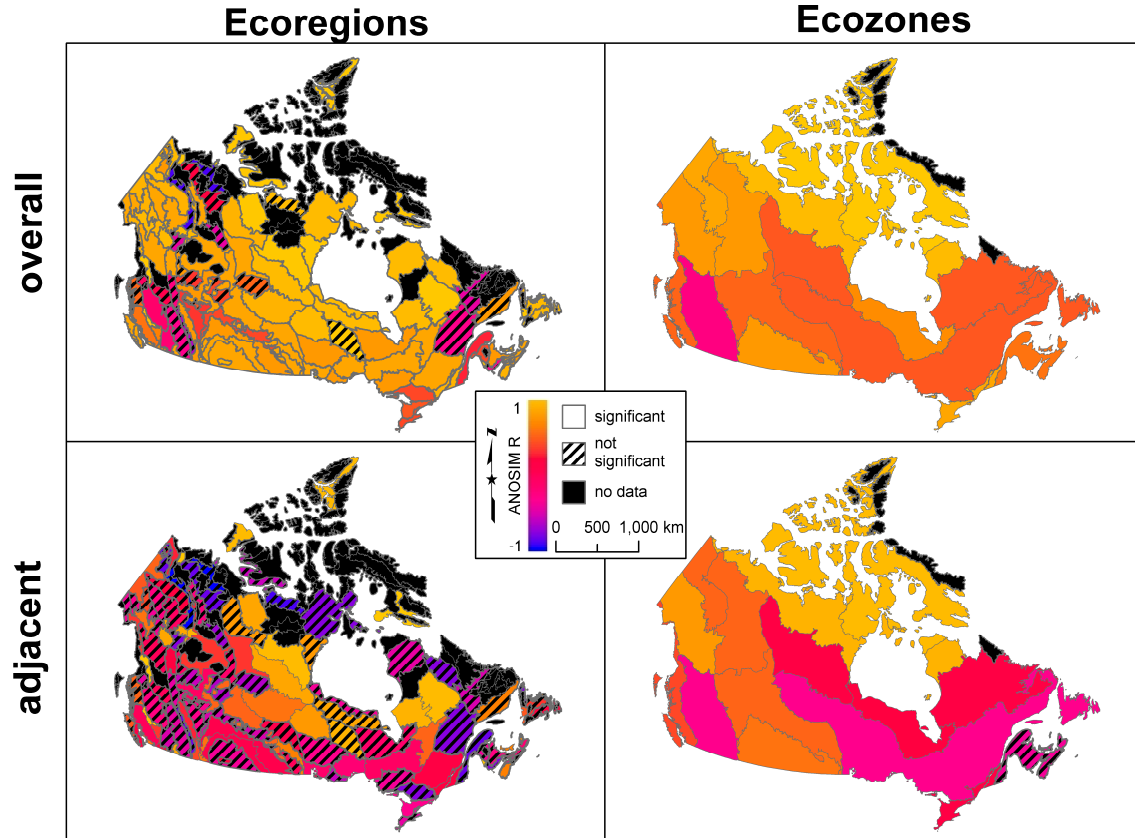
**Figure 3.** Map of butterfly assemblage uniqueness, as estimated by the ANOSIM R statistic, for Canadian ecoregions (left) and ecozones (right). Analyses presented in the top maps evaluated butterfly assemblages against those in all other ecoregions/ecozones ($ANOSIM_{RO}$). Maps on the bottom only considered assemblage dissimilarity between geographically adjacent ecoregions/ecozones ($ANOSIM_{RA}$). Regions with butterfly assemblages that are not significantly unique are cross-hatched.
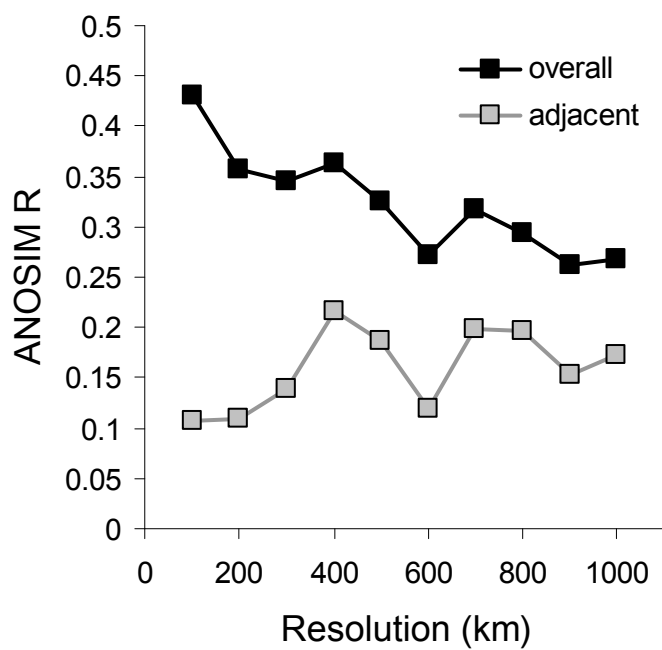
**Figure 4.** ANOSIM R statistics for butterfly communities within 10 resolutions of geographic grid cells, evaluated when comparing against all other cells within Canada (overall – $ANOSIM_{GO}$, black) and against neighbouring cells only (adjacent – $ANOSIM_{GA}$, grey).
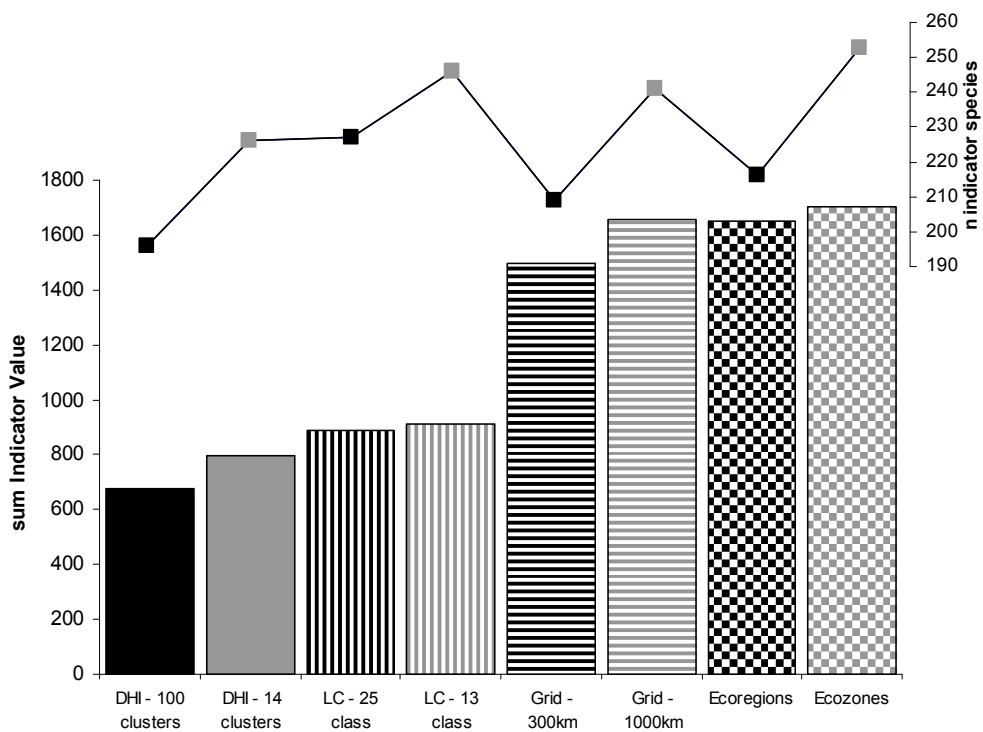


**Figure 5.** Summed species indicator values (bottom) and number of significant indicator species (top) identified for each regionalization scheme at two thematic resolutions each. LC = Land cover.