

The Influence of Analysis Design
on Systematic Conservation Planning

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Abstract

The field of systematic conservation planning has grown substantially in recent years as there are a broad range of applications to which systematic design is appropriate, and there is a growing recognition of the need to transparently and efficiently target conservation planning efforts. This study investigated four important aspects of the analysis design for systematically optimized conservation planning: the temporal stability of conservation features, the conservation target levels adopted, the choice of planning units, and the feature set chosen for planning. These are critical aspects of 'best-practices' for systematic conservation planning for all manner of spatially distributed features.

Analyses using Breeding Bird Survey data in the eastern USA showed that sets of counties selected to meet a range of present-day conservation targets provided coverage to 68 – 79 % of species in two potential future species distributions derived from climate change models. Changes in the geography of conservation priority from the present to each future were evident and compared to existing protected areas.

Point count data from the 2000-2005 Ontario Breeding Bird Atlas (OBBA) were used to explore effects of eight spatial classifications of potential utility for conservation planning on biogeographical patterns in species richness, Simpson's diversity, beta diversity, compositional nestedness and spatial variation in species composition. A hierarchical cluster analysis delimited a spatial classification scheme which reflected the biodiversity patterning in the OBBA data. This Avian classification approximated the existing boundaries of Bird Conservation Regions (BCR) 12 and 13. Significant diversity metric spatial patterns were found for all but the two coarsest classifications, when compared to randomized species assemblages.

The OBBA data were used to produce conservation priority surfaces for each spatial classification for the entire set of species and for a set of BCR priority species. The union of watersheds and ecodistricts produced the best agreement between conservation priority surfaces for the two species sets.

This research developed fundamental techniques for assessing spatial bias in conservation planning solutions, advancing the developing best practices for systematic conservation planning thereby aiding conservation planners in designing a framework for the efficient and practical conservation of biodiversity.

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Table of Contents	
Abstract	ii
Acknowledgements	iii
General Introduction	1
References Cited	7
Chapter 1	
Implications of Conservation Target Levels and Projected Climate- Induced Species Shifts For Systematic Conservation Planning	13
Introduction.....	13
Methods.....	16
Results.....	20
Discussion.....	21
References Cited	24
Tables.....	31
Figures.....	32
Chapter 2	
Effects of Spatial Classification Choice When Studying Avian Biogeography	36
Introduction.....	36
Methods.....	43
Results.....	57
Discussion.....	65
References Cited	72
Figures.....	80
Chapter 3	
Systematic Conservation Planning Using Different Species Sets, Targets and Spatial Classifications: A Case Study for Ontario	96
Introduction.....	96
Methods.....	103
Results.....	109
Discussion.....	116
References Cited	121
Figures.....	127
Conclusion	151
References Cited	158

List of Tables

Table 1: Summarized Species Occurrence Information (for 39 underrepresented species)...31

List of Figures

Chapter 1

Figure 1: Number of species meeting conservation targets under a present-day reserve design.....	32
Figure 2: Histogram of species incidence across the study area.....	33
Figure 3: County-centroids for the study region. Interpolated conservation priority values for the present-day, CCC and Hadley species distributions.....	34
Figure 4: Priority map for present-day species distributions, overlain with existing protected areas.....	35

Chapter 2

Figure 1: OBBA point counts included in these analyses, with Voronoi tessellation polygons included to show spatial tiling of points across the study region.....	80
Figure 2: Dendrogram representing a hierarchical partition of 50993 OBBA point counts....	81
Figure 3: Log-transformed Calinski index values.....	82
Figure 4: Spatial classification of avian biodiversity produced by merging neighbouring Voronoi polygons that share the same cluster.....	83
Figure 5: Inset showing the fine-scale detail of the Avian classification scheme.....	84
Figure 6: Boxplots of polygon areas for each classification scheme, showing the size distribution of polygons in each classification scheme.....	85
Figure 7: Boxplots of the polygon count values, the number of points assigned to each polygon in the classification scheme.....	86
Figure 8: Classification comparison of diversity metrics.....	87
Figure 9: Diversity metric summary showing mean and standard deviations for each classification.....	88
Figure 10: Tukey's Honestly Significant Difference comparisons show differences in mean metric values amongst all classifications, for each diversity metric.....	89
Figure 11: Avian classification scheme showing total polygon richness.....	90
Figure 12: Avian classification scheme showing mean point-level species richness.....	91
Figure 13: Avian classification scheme showing mean point-level beta diversity.....	92
Figure 14: Avian classification scheme showing mean point-level Simpson's diversity.....	93
Figure 15: Avian classification scheme showing nestedness temperature.....	94
Figure 16: Avian classification scheme showing the amount of variation in polygon species composition that can be explained using spatial components.....	95

Chapter 3

Figure 1: Dendrogram showing the hierarchical clustering of the 235 species in the OBBA dataset.....	127
Figure 2: Relationship between conservation target level and the associated total cost of reserve sets that meet those targets for the BCR priority species set.....	128
Figure 3: Point-weighted barplot-histogram of conservation priority values for the BCR species subset, for each classification scheme.....	129
Figure 4: Point-weighted difference between conservation priority values for the BCR species subset of species and for all species, for each classification scheme.....	130
Figure 5: Voro classification scheme showing the mean conservation priority for BCR ‘priority’ subset species.....	131
Figure 6: Voro classification scheme showing the mean difference between the conservation priority surface calculated for BCR ‘priority’ subset species, and the priority surface for all species.....	132
Figure 7: Voro classification scheme showing the point-level conservation priority for BCR ‘priority’ subset species.....	133
Figure 8: Voro classification scheme showing the difference between the conservation priority surface calculated for BCR ‘priority’ subset species, and the priority surface for all species.....	134
Figure 9: Avian classification scheme showing the conservation priority for BCR ‘priority’ subset species.....	135
Figure 10: Avian classification scheme showing the difference between the conservation priority surface calculated for BCR ‘priority’ subset species, and the priority surface for all species.....	136
Figure 11: Square classification scheme showing the conservation priority for BCR ‘priority’ subset species.....	137
Figure 12: Square classification scheme showing the difference between the conservation priority surface calculated for BCR ‘priority’ subset species, and the priority surface for all species.....	138
Figure 13: Hex classification scheme showing the conservation priority for BCR ‘priority’ subset species.....	139
Figure 14: Hex classification scheme showing the difference between the conservation priority surface calculated for BCR ‘priority’ subset species, and the priority surface for all species.....	140
Figure 15: Muni classification scheme showing the mean conservation priority for BCR ‘priority’ subset species.....	141
Figure 16: Muni classification scheme showing the mean difference between the conservation priority surface calculated for BCR ‘priority’ subset species, and the priority surface for all species.....	142
Figure 17: Basin classification scheme showing the point-level conservation priority for BCR ‘priority’ subset species.....	143

Figure 18: Basin classification scheme showing the difference between the conservation priority surface calculated for BCR 'priority' subset species, and the priority surface for all species.....	144
Figure 19: Ecod classification scheme showing the conservation priority for BCR 'priority' subset species.....	145
Figure 20: Avian classification scheme showing the difference between the conservation priority Ecod calculated for BCR 'priority' subset species, and the priority surface for all species.....	146
Figure 21: Ecobas classification scheme showing the conservation priority for BCR 'priority' subset species.....	147
Figure 22: Ecobas classification scheme showing the difference between the conservation priority surface calculated for BCR 'priority' subset species, and the priority surface for all species.....	148
Figure 23: Ebm classification scheme showing the conservation priority for BCR 'priority' subset species.....	149
Figure 24: Ebm classification scheme showing the difference between the conservation priority surface calculated for BCR 'priority' subset species, and the priority surface for all species.....	150

List of Appendices

Appendix A Biogeographic Mappings: 10 km² OBBA Sampling Square.....	162
Figure A.1: Results summary for total polygon richness.....	163
Figure A.2: Results summary for mean point-level species richness.....	164
Figure A.3: Results summary for mean point-level beta diversity.....	165
Figure A.4: Results summary for mean point-level Simpson's diversity.....	166
Figure A.5: Results summary for nestedness temperature.....	167
Figure A.6: Results summary for the amount of variation in polygon species composition that can be explained using spatial components.....	168
Appendix B Biogeographic Mappings: 10 km² Hexagon Classification.....	169
Figure B.1: Results summary for total polygon richness.....	170
Figure B.2: Results summary for mean point-level species richness.....	171
Figure B.3: Results summary for mean point-level beta diversity.....	172
Figure B.4: Results summary for mean point-level Simpson's diversity.....	173
Figure B.5: Results summary for nestedness temperature.....	174
Figure B.6: Results summary for the amount of variation in polygon species composition that can be explained using spatial components.....	175
Appendix C Biogeographic Mappings: Lower Tier Municipal Boundary.....	176
Figure C.1: Results summary for total polygon richness.....	177
Figure C.2: Results summary for mean point-level species richness.....	178
Figure C.3: Results summary for mean point-level beta diversity.....	179
Figure C.4: Results summary for mean point-level Simpson's diversity.....	180
Figure C.5: Results summary for nestedness temperature.....	181
Figure C.6: Results summary for the amount of variation in polygon species composition that can be explained using spatial components.....	182
Appendix D Biogeographic Mappings: Sub-Sub Basin Watershed Boundary.....	183
Figure D.1: Results summary for total polygon richness.....	184
Figure D.2: Results summary for mean point-level species richness.....	185
Figure D.3: Results summary for mean point-level beta diversity.....	186
Figure D.4: Results summary for mean point-level Simpson's diversity.....	187

Figure D.5: Results summary for nestedness temperature.....	188
Appendix E Biogeographic Mappings: Ecodistrict Classification.....	189
Figure E.1: Results summary for total polygon richness.....	190
Figure E.2: Results summary for mean point-level species richness.....	191
Figure E.3: Results summary for mean point-level beta diversity.....	192
Figure E.4: Results summary for mean point-level Simpson's diversity.....	193
Figure E.5: Results summary for nestedness temperature.....	194
Appendix E Biogeographic Mappings: Ecobas Classification.....	195
Figure 12.1: Results summary for total polygon richness.....	196
Figure 12.2: Results summary for mean point-level species richness.....	197
Figure 12.3: Results summary for mean point-level beta diversity.....	198
Figure 12.4: Results summary for mean point-level Simpson's diversity.....	199
Figure 12.5: Results summary for nestedness temperature.....	200
Figure 12.6: Results summary for the amount of variation in polygon species composition that can be explained using spatial components.....	201
Appendix G Biogeographic Mappings: Ebm Classification.....	202
Figure G.1: Results summary for total polygon richness.....	203
Figure G.2: Results summary for mean point-level species richness.....	204
Figure G.3: Results summary for mean point-level beta diversity.....	205
Figure G.4: Results summary for mean point-level Simpson's diversity.....	206
Figure G.5: Results summary for nestedness temperature.....	207
Figure G.6: Results summary for the amount of variation in polygon species composition that can be explained using spatial components.....	208
Appendix H Names For 235 Analyzed Species From the Ontario Breeding Bird Atlas Data For Bird Conservation Regions 12 and 13.....	209

General Introduction

Without an adequate understanding of natural pattern and process, the unintended consequences of human decisions can be great and far-reaching (Thuiller *et al.* 2004; Newton *et al.* 2009). The very real threats facing natural ecosystems demand a prompt and effective triage (Botrill *et al.* 2008), such that ongoing conservation efforts may be directed most efficiently and effectively, and human development is guided towards less disruptive designs over the long term.

Responsible stewardship requires conservation decisions be made in a timely fashion in the face of great uncertainty (Regan *et al.* 2002; Harwood and Stokes 2003), and poor planning decisions can bring tragic losses (Rabinowitz 1995; Grand *et al.* 2007). There is a resurging recognition that conservation efforts should be enacted from a holistic viewpoint rather than focussing on small endangered populations of single species (Kirkpatrick 1983; Ferrier *et al.* 2009). In the absence of a thorough understanding of the processes driving the development of natural patterns, conservation activities should strive to be at least representative of the present pattern of biodiversity, and to ensure that those patterns are maintained into the future.

Systematic conservation planning has emerged in response to the need for efficient and flexible solutions to multiple species representation problems. Systematic conservation planning is the process of identifying sets of areas which collectively meet specific targets of representation for a set of conservation features (Margules and Pressey 2000; Game and Grantham 2008). It has developed as the concepts of gap analysis (Rodrigues *et al.* 2004) and complementarity (Margules and Pressey 2000) have been incorporated into the design and establishment of conservation areas, resulting in algorithms for the systematic selection of conservation reserves to cover the most species in the most efficient manner (see Moilanen *et al.* 2009 for comprehensive review). These procedures identify areas that are irreplaceable, in that they contain the sole populations of regionally rare species, and areas that are efficient, in that they add a large variety of novel species to the conservation solution, for the least increase

in conserved area. However, this does not mean simply identifying ‘hotspots’ or species rich areas. Two hotspots may each contain the same set of species, so that protecting the second does not conserve any additional species, i.e. they are not complementary. Systematic conservation planning is intended to produce repeatable, defensible, efficient and representative conservation effort, and for this reason is increasingly part of the process of land-use planning and design (Knight *et al.* 2006; Sarkar *et al.* 2006).

Systematic approaches to conservation and land-use planning are increasingly prevalent, but the use of these tools is often opportunistic, implemented using a single temporal frame, under a single spatial classification scheme, for a fixed set of species and with a single conservation target (Stewart *et al.* 2003; Pryce *et al.* 2006; Green *et al.* 2009). The success of these conservation plans is contingent on the consistency of the data over time, the appropriateness of the planning units, the degree to which species are representative of overall biodiversity, and the long term viability of species populations in conserved areas (Moilanen *et al.* 2009).

Firstly, as conservation designs are the result of a particular dataset, there is an implicit assumption that the diversity patterns indicated in the data are accurate and enduring. The degree to which species distributions shift over time can confound efforts to fully represent natural assemblages within conservation reserves. Given the increasingly apparent potential impacts of climate-induced range-shifts across a wide range of taxa (e.g. Hughes 2000; Erasmus *et al.* 2002; Parmesan and Yohe 2003; Root *et al.* 2003; Thomas *et al.* 2004; Thuiller *et al.* 2005; Araújo and Rahbek 2006; Huntley *et al.* 2008; Lawler *et al.* 2009) conservation planners need to better consider temporal uncertainty when assessing the success of a conservation plan (Regan *et al.* 2009). If present-day species distributions are used to guide the establishment of conservation reserves, how effective will these reserves be in the future? Will presently important areas continue to provide coverage to species, or will many species shift out of these protected areas and into new regions? In short, it has become increasingly important to address the question: To what extent are conservation reserve designs influenced by climate-

driven shifts in species distribution over time? There is a potentially high ‘cost of waiting’ associated with planning for the present, then amending and refining once the future has arrived (Hannah *et al.* 2007). In many cases, when adequate predictive models exist, plans which include future scenarios as inputs may prove to be more robust over time (Game *et al.* 2008).

In Chapter 1 of this thesis, Breeding Bird Survey data from the eastern United States is used to assess the potential impacts of climate-driven shifts in species distributions, and what this may mean for systematic conservation design. Predicted bird species distributions for two potential future climate scenarios (calculated by Matthews *et al.* 2004) were compared to known present-day distributions to assess the impact of climate change on the future utility of conservation reserves.

Systematic conservation planning tools are used to produce solution sets of areas which taken together achieve specific conservation objectives (Margules and Pressey 2000; Moilanen *et al.* 2009). Each solution is the result of a heuristic which generates a low-cost configuration that meets the specified conservation targets. Using each planning unit scheme and its related species abundance matrix, systematic planning algorithms select sets of planning units to meet certain *a priori* conservation targets (Watts *et al.* 2009). At the most basic, the target is simply a single example of each species somewhere within the reserve set. This will include any irreplaceable planning units that contain the sole example of regionally restricted species, and some additional assortment of areas that contain sufficient examples of all other species. As targets increase, more and more units are selected, until the planning region saturates, and every planning unit becomes included in the reserve. Depending on the degree of overlap between species distributions, there may be many solutions to a given target.

Depending on the constraints on the problem (a factor of the conservation targets, the planning units, and the underlying species distributions) many configurations may be possible, alternately a consistent set of planning units may be required to achieve the targets. Looking at a single solution does not give a sense of which planning units are irreplaceable lynchpins, without which targets cannot be achieved, and which units are redundant, in that

they contribute towards overall targets but contain a species assemblage which can be found elsewhere (Pressey *et al.* 1997).

Rather than look at a single conservation solution, it is useful to summarize a large number of potential solutions into a single surface which shows an aggregate result. By summing the Boolean conservation solution sets of a wide range of targets, and including many different solutions to the same target, an average value can be calculated for each distribution (Wilhere *et al.* 2008); this describes the proportion of times a given planning unit is selected for conservation, or the conservation ‘priority’. High priority indicates a unit is selected repeatedly across all conservation targets, due to the presence of regionally restricted species. Lower priority units are included in a solution only at higher target values, adding redundant examples of species to the solution. Priority surfaces may be calculated for present day and projected future species distributions. By comparing the difference between present-day conservation priorities and potential future priorities, areas of expected change or stability can be detected; these latter areas containing persistently irreplaceable biodiversity should be considered critical components of conservation effort. Difference analysis explores the extent to which conservation planning needs to proactively identify future centers of biodiversity to ‘fill in the gaps’ in response to projected species distribution shifts (O’Hanley *et al.* 2007). Large magnitude changes in priority indicate extensive shifts of biodiversity, while agreement of priority values indicate that an area maintains a comparable composition of biodiversity. Conservation plans which incorporate temporal trends in their design will have greater chance of long term effectiveness than designs which focus solely on a snapshot in time.

The systematic planning process is also heavily influenced by the classification scheme selected to produce the planning unit surface, which defines the unique areas available for conservation. The way in which the area is subdivided affects the way we perceive and design for the extant biodiversity (Lewis *et al.* 2003; Warman *et al.* 2004a; Flather *et al.* 2009). When conservation planning is undertaken, some manner of spatial classification scheme is adopted, be it a raster grid, an ecological unit, or a municipal boundary (Schipper *et al.* 2007). The use

of these ‘planning units’ has a direct effect on the interpolation of survey data to a surface representing the planning region. Each classification scheme leads to a different aggregation of the data to produce species diversity or other conservation feature values in each planning unit. This may introduce a large bias in conservation priority, increasing priority as diverse points with very different species compositions are grouped together, and decreasing it as neighbouring points containing examples of rare species are assigned to different planning units. Neighbouring data points which share similar species may be bisected by planning unit boundaries. If biogeographic patterns are not well represented by the planning unit boundaries, then artificial aggregation and fragmentation may be introduced, occluding important patterns and hindering efficient and direct conservation efforts. Key questions include: How does the choice of spatial classification scheme bias our understanding of biogeographic patterns? What metrics best capture the spatial variation in bird species composition, and how does that vary across different spatial classification schemes? What underlying patterning is suggested by the data? And what difference does this all make when targeting conservation efforts?

In Chapter 2 of this thesis, the Ontario Breeding Bird Atlas (OBBA; Cadman *et al.* 2007) is used to explore a variety of classification schemes with respect to the underlying biogeographic patterns of bird species in Ontario. Classification schemes are defined in nine ways: (1) from the raw point data (using a Voronoi tessellation; Perry *et al.* 2002), (2) using a hierarchical spatial classification (clustering neighbouring polygons that share similar species composition; Gordon 1999), from equal-area schemes such as (3) the OBBA atlas sampling squares or (4) hexagon tilings, (5) a jurisdictional scheme of municipal districts, from ecological schemes such as (6) watersheds, (7) ecodistricts, or (8) the union of ecodistricts and watersheds, and finally (9) a socio-ecologic hybrid of the union of ecodistricts, watersheds and municipal districts. A bottom-up hierarchical classification of points by their species composition for this magnitude of data involves intensive computation and has rarely been implemented during planning efforts.

These nine different spatial classification schemes are compared using a number of

biodiversity metrics, species richness, beta diversity, Simpson's diversity, the disorder in species composition within planning units (using a nestedness metric), and the degree to which species composition can be explained using spatial variables (via an eigenanalysis of the spatial pattern of biodiversity). Each of these metrics has been used in a variety of applications to describe diversity patterns (Whittaker 1972; Legendre and Legendre 1998; Borcard and Legendre 2002; Borcard *et al.* 2004; Keylock 2005; Dray *et al.* 2006; Rodríguez-Gironés and Santamaría 2006), but are generally applied to a particular spatial classification scheme selected *a priori*. The current analysis explicitly considers the influence of a range of classification schemes by comparing changes in the mean and variance of each metric using a null model approach.

Sound systematic conservation planning should address the impacts of spatial classification and species set on the sensitivity of conservation solutions to varying degrees of conservation effort. The species set chosen for conservation may also play a large role in driving the pattern of the priority surface. If conservation effort focuses on a small subset of overall biodiversity, how will this change the computed conservation priority surface? If the distribution of subset species overlaps well with the overall species set, the set of selected planning units will provide equal coverage to the whole set, 'sweeping along' other species with the targeted set (Kiestler *et al.* 1996; White *et al.* 1999). However, previous work examining the sensitivity of systematic conservation planning solutions to changes in the distributional data used for analysis showed large differences in the sites selected for conservation (Underwood *et al.* 2010 found no higher than 50% overlap in site selection between three different forms of conservation feature distribution data), so the choice of inputs is not a trivial task. At the same time, others have shown that the sites selected to conserve bird diversity provide greater coverage to other taxa than a set of randomly selected sites (Warman *et al.* 2004b); this suggests that conservation effort focussed on bird species is a valid starting point. However, if the subset species are isolated or disjunct from the other species, then there will be substantial difference between the priority surface selected for the subset and the surface for all species, as additional areas need to be included to cover the remaining species.

In Chapter 3 of this thesis, the OBBA data is used along with the nine spatial classification schemes and a range of target values to calculate a series of conservation priority surfaces, for both a subset of Bird Conservation Region 'priority' bird species and the full suite of bird species. Contrasting these surfaces reveals the potential effects of planning unit choice and species set selection on the results of systematic conservation planning.

The opportunity to generate objective and explicit land-use designs may be confounded by a series of often implicit decisions when designing land-use strategies (Grand *et al.* 2007); a review of these effects will aid conservation efforts by documenting the influence of these decisions on potential conservation solutions. The grain and placement of planning units, the magnitude of conservation targets, the breadth of taxonomic diversity included in the data, and the confidence in the long-term fidelity of existing patterns of diversity all play important roles in determining the efficiency of a regional conservation plan. This research provides an opportunity to address these issues, by investigating the influence of planning unit classification and species set selection on systematic conservation planning. This thesis presents a series of analyses intended to document the existing patterns of avian biodiversity and indicate the extent to which these patterns can be relied upon over time and space; conservation and land-use stakeholders at local, regional, provincial and continental scales may benefit by explicitly incorporating this knowledge within a systematic planning strategy.

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Chapter 1

Implications of Conservation Target Levels and Projected Climate- Induced Species Shifts For Systematic Conservation Planning

Introduction

The recent collection of large-magnitude multi-species datasets across a broad extent allows for more systematic and comprehensive approaches to conservation planning. However, successful and efficient conservation planning may require more than detailed present-day species data. Understanding the potential impact of future changes in species distribution on the implementation and impact of conservation designs is important when optimizing conservation investment (Levitt 2005). Research into climate-driven species distributions predicts extensive changes in species richness (Currie 2001), abundance (Shoe *et al.* 2005), range (Walther *et al.* 2005 and Lawler *et al.* 2009), and thus regional extirpations and possible extinctions (Thomas *et al.* 2004, but see Thuiller *et al.* 2004), leading to a loss of diversity (Root *et al.* 2003; Parmesan and Yohe 2003; Araújo and Rahbek 2006). These broad, coarse-scale analyses have only recently begun to incorporate direct climatic effects on specific conservation designs. Erasmus *et al.* (2002) have shown the impact of climate on mammal distributions in South Africa. Araújo *et al.* (2004), Thuiller *et al.* (2005) and Hannah *et al.* (2002, 2005) demonstrated that climate change may result in loss of plant species from reserve networks in Europe and South Africa. Huntley *et al.* (2008) have shown similar results studying breeding bird populations in Europe. Midgley *et al.* (2002) have modelled potential distributional changes at the biome scale in response to climate shifts. Peterson *et al.* (2002) predict 'severe' turnover of local biological communities for 1,870 species of mammals, birds and butterflies in Mexico. To mitigate these effects, Hannah *et al.* (2007) explore options for incorporating climate change effects into the systematic selection of a minimum set reserve network. However, their use of a single conservation objective (a particular percentage target of the existing distribution of included species) does not reveal the sensitivity of reserve design algorithms to varying conservation targets. If the goal is, at a minimum, to represent all species within the conservation reserve set, will

climate change induce sufficient change in habitat to invalidate our conservation goals? As the degree of desired protection increases (above and beyond species presence within the reserve area), how well will selected areas meet these more demanding goals? How consistent are these potential range shifts over a set of potential climate futures? Can conservation regions be selected today, using existing knowledge of present day species distributions, which will remain important centers of biodiversity into the future? And how can this information best be conveyed to ensure widespread integration into land-use planning?

Conservation efforts are often costly in terms of time and resources, requiring large areas of land that are usually desired for other uses. The creation of additional conservation reserves involves a trade-off between the demands of human society and the needs of the ecosystem; see Naidoo *et al.* (2006) or Ferraro and Pattanayak (2006) for examples of modern approaches. The assessment of which lands are ecologically important today should be tempered and bolstered by predictions of how that importance may shift in response to natural and man-made change. Identifying inexpensive areas of land that are predicted to increase in importance over time may allow the creation of more robust designs (from an ecological perspective) at a fraction of the cost. At the same time, identifying regions of diminishing importance may allow for more informed assessment when it comes time to select one unit over another.

This chapter evaluates the impact of potential, climate-driven shifts in species distributions on the future success of a conservation reserve design based on present-day distributions. Bird occurrence data for 150 species are used to select a potential conservation reserve set, and the theoretical effectiveness of this reserve set is demonstrated using two predicted climate-driven future species distributions.

A variety of techniques have been established over the years to maximize the biotic diversity contained in a reserve network while minimizing the total cost of implementing and maintaining the reserve (see Csuti *et al.* 1997, Cabeza and Moilanen 2001 or Wilson *et al.* 2009 for review). A variety of site selection models have been specified for a range of conserva-

tion objectives, maximizing phylogenetic diversity (Faith 1992, Solow *et al.* 1993, Polasky *et al.* 2001, Rodrigues and Gaston 2002b), ecosystem representation (Schmidt 1996, Pressey *et al.* 1997, Snyder *et al.* 1999), and endangered species protection (Dobson *et al.* 1997, Ando *et al.* 1998, Arthur *et al.* 2004). Metrics such as irreplaceability (Ferrier *et al.* 2000) use known or estimated species distributions to efficiently select complementary conservation reserves to meet *a priori* conservation targets. This type of procedure has been used in recent years to explore conservation options (Margules and Pressey 2000, Warman *et al.* 2004, Rodrigues *et al.* 2004, Freemark *et al.* 2006, Turner and Wilcove 2006), but little has been done to examine the longer-term utility or viability of reserve designs. Implicit in the use of these methods is the assumption that reserves selected to protect present-day species distributions will remain important centers of species diversity in the future. The longer-term success of conservation effort hinges on the validity of this assumption.

This analysis is intended to further critical discussion regarding the identification and management of areas for longer-term conservation and protection, using species distributions today in comparison to those in the future. Spatial variation in conservation priority is presented using a technique equivalent to the averaged optimality metric (Wilhere *et al.* 2008) defined as the proportion of times a unit is selected for conservation across a range of conservation targets (from minimum to maximum degrees of conservation effort). This metric represents a unit's contribution to the reserve network, given its local species assemblage and the regional distribution of species, as a function of the degree of conservation effort available in a given planning region. A unit selected for conservation at low levels of conservation effort contains more unique species than a unit that is selected only at higher levels of conservation effort, i.e. adding only redundancy to the reserve network. Few conservation efforts are enacted wholesale; this metric provides a visualization of the trade-offs between low-effort, representational reserves and more intensive coverage of species distributions.

Priority surfaces may be calculated for present day and future species distributions. By comparing the difference between present-day conservation priorities and potential future

priorities, areas of expected change or stability can be detected; these latter areas containing persistently irreplaceable biodiversity should be considered critical components of long-term conservation action. It is also important to identify regions that consistently provide little or no unique biodiversity, drawing attention to areas that may benefit from actions other than protection, such as habitat improvement that increase the ecological benefit of presently species poor regions. Areas with present but dwindling importance over time may be best protected by more temporary measures that ensure adequate time for species to migrate to more suitable habitats. This triage process may help to guide conservation managers towards regions of long-term importance that may be occluded by existing present-day community patterns.

Methods

This analysis used three species incidence datasets generated by Matthews *et al.* (2004) documenting the present and potential future distribution of 150 bird species in the eastern United States. These data were previously used to evaluate the effect of distribution size on the extinction risk as a result of climate change (Schwartz *et al.* 2006). The first dataset contained species distributions aggregated from Breeding Bird Survey (BBS) data from 1981-1990, generalized to the county grain for the conterminous United States east of the 100th meridian.

The remaining two datasets comprised predicted future distributions. Matthews *et al.* (2004) produced the two future bird species distributions using two General Circulation Model climate scenarios, and future tree species distributions. Prasad and Iverson's (1999) work predicts tree cover change across the country, a key component in modelling many avian distributions (Huntley *et al.* 2006; Araújo *et al.* 2007). Matthews *et al.* (2004) used a regression tree approach to model species incidence functions using contemporary climate and tree species variables. The British Hadley Center for Climate Prediction and Research model (Hadley; Mitchell *et al.* 1995) and the Canadian Climate Center model (CCC; Boer *et al.* 2000, Kittel *et*

al. 2000) comprise climatic predictions for a set of eight temperature and precipitation variables assuming a doubling of current atmospheric CO₂ concentrations by 2070 to 2099. The Hadley scenario predicts greater precipitation increases across the continent, while the CCC scenario predicts greater temperature increases.

The 150 species included in this analysis were those for which the models explained more than 50% of the observed variation in present-day BBS incidence-by-county (ranging in total r² from 50.9 – 91.0%, with a mean value of 73.3%). Incidence was defined as the proportion of within-county BBS surveys in which the species occurs. Any species with an incidence > 0.05 was considered to occur within a given county, and all further analysis focused on the resulting Boolean occurrence data. The county-level occurrence information was assigned to the centroid of each county polygon, generating the 2121 ‘planning units’ used in this analysis.

The C-Plan software package (NSW-NPWS 1995 - 2002) was used to summarize these species distributions using the irreplaceability metric (Ferrier *et al.* 2000). This method quantifies the complementarity or unique contribution a unit makes towards pre-specified conservation targets; the species composition of a unit is weighted against the relative rarity of each species and the stringency of the targets. Units containing many highly regionally restricted species are assigned greater irreplaceability scores than units containing few or very common species. A value of 1, or completely irreplaceable, indicates that unless this unit is included in a conservation design, some aspect of the specified conservation targets cannot be met. Lower irreplaceability values indicate that the species set found within the unit can be found elsewhere, resulting in greater flexibility in the selection of the reserve network.

However, this metric depends on the particular conservation targets chosen for the analysis; at low targets, few units are necessary for the reserve network to meet its *a priori* species goals. At higher targets, proportionately more units are necessary, and units are more often selected to provide redundancy to the network. A range of 10 potential conservation targets were considered, ranging from 10 occurrences of each species within the reserve network (low

conservation effort, smaller total reserve area) to 100 occurrences (high conservation effort, equivalent to protecting every instance of the rarest species in the study).

Three reserve network sets were chosen by iteratively generating reserve network solutions to meet each of 10 conservation targets (10-100 units per species) for three bird species distributions (Present-day, Hadley and CCC). Processing each of the three datasets using the C-Plan software produced a set of minimum-set reserve network solutions (10 for each dataset), and three corresponding conservation priority maps for the study region. Minimum sets were chosen by ranking units by irreplaceability, then selecting one by one the most irreplaceable units, breaking tied scores by preferentially selecting units with greater total richness and smaller area. Each selected unit was then scored with regards to its conservation priority, the proportion of times over all solutions that unit is selected for conservation, a metric that has been referred to as average optimacy (c.f. Wilhere *et al.* 2008).

A high priority unit (priority approaching 1) contains regionally restricted species and was selected to meet even low levels of conservation (10 occurrences of each species within the reserve) while a low priority unit (priority approaching 0) was only rarely selected, at large magnitudes of conservation effort (targets approaching 100 occurrences of each species) and provides supplementary coverage to more widespread species; null values indicate that a unit does not contain irreplaceable biodiversity and was never required to meet any conservation target.

The efficacy of the present-day reserve network at conserving species in the future depends on how well it covers the Hadley and CCC future species distributions. Bird species are assumed to successfully disperse over time to track changes in climate; individual species' climatic envelopes are also assumed to remain constant over this time. For a reserve network, selected to meet a given conservation target in the present-day (e.g. 10 occurrences per species within the reserve), how many species meet these targets in the future distributions? An effective reserve network is one that maintains a high proportion of species at the conservation target levels for which it was designed.

For visualization purposes, a kriging interpolation was implemented (Bailey and Gatrell 1995, Jiguet *et al.* 2005; spherical semivariogram method) producing a smooth conservation priority surface across the study region for each dataset. This approach was more appropriate than using county polygons (from which the predicted-futures data is based), as this work was intended to be used as a illustrative guide to direct further monitoring and conservation effort, rather than as a reserve network design *per se*. Arbitrarily driving conservation effort to the county scale was not necessarily appropriate.

The potential effects of climate change on the impact of systematic conservation planning techniques were highlighted using two difference maps created by subtracting each future priority surface from that of the present-day surface. These maps highlight regions of increasing or decreasing conservation priority under climate change. The range of shifts in priority between the two climate scenarios was compared in terms of magnitude and geographic extent.

The correlations between shifts in priority and changes in species composition were also compared, using the Bray-Curtis distance metric (Legendre and Legendre 1998). Shifts in priority might be due to wholesale distribution shifts, or else driven by changes in the occurrence of a subset of regionally restricted species. The Bray-Curtis metric summarizes shifts in species composition in each county between the present day and future distributions, with greater magnitudes indicating greater dissimilarity. A significant correlation indicates that the sites with greatest change in priority also show the largest change in species composition.

Knowledge of the distribution of conservation priority within and outside of currently protected areas is of obvious benefit to conservation planning. Conservation efforts on private lands should be conducted using different methods than those on public and protected lands. The recent Commission for Environmental Cooperation's North American Environmental Atlas of Protected Areas (CEC 2008) was used to compare the average conservation priority within existing protected areas to that found outside established reserves.

Results

Present-day reserve designs failed to provide any future protection to 19 – 26% of the 150 analyzed species (Figure 1; 28 in Hadley, 38 in CCC, 27 in common, 39 in all; Table 1), 18 of which were extirpated from the CCC distribution. The CCC-based predictions showed these extirpated species moving northward and out of the study region, driven by shifts in Balsam Fir and Paper Birch (9 species), and temperature averages from January and July (9 species).

Of the remaining 21 species lacking coverage by the present-day reserve set, 61% had distribution models dominated by correlations with balsam fir and birch and 66% were impacted by climatic temperature variables (Matthews *et al.* 2004). The 39 “at risk” species had a significantly lower mean present-day incidence than species which met conservation targets (two-tailed unequal variance T-Test, $n_1 = 39$, $n_2 = 111$, $\alpha = 0.05$, $p = 0.000$; Levene’s test for Equality of Variance, $F = 70.311$, $p = 0.000$). Rare, restricted range species were more likely to be absent from future reserve designs. Both predicted future distributions showed reductions in mid-rarity species, and increases in the proportion of both common and rare species (Figure 2). This produces a bimodal range of species covered by reserve designs; rare species drive the selection process, and common species are swept along, but mid-rarity species are not necessarily covered.

The average priority values within the CEC protected area network were not significantly different ($p > 0.05$) than values seen outside the existing network when compared using a T-Test. Each scenario shows a similar range of variation in priority within and outside the protected areas. Areas within existing protected areas do show a higher mean priority (0.363) than those outside of protected areas (0.176), but the variance in the data precludes a significant result.

Correlation was low between shifts in conservation priority and changes in species composition, as measured by the Bray-Curtis distance metric. Pearson correlation coefficients of 0.106 (Present-CCC) and -0.025 (Hadley-CCC) ($\alpha = 0.05$, $p = 0.001$) indicated no

strong association between change in priority and wholesale change in species composition. Regions with high changes in conservation priority did not necessarily show great changes in species composition. This indicates that great shifts in priority may be caused by the movements of few rare species. Likewise regions with consistent priority still display changes in the species composition, albeit amongst species with similar degrees of rareness and distribution.

The Hadley-scenario displayed much greater temporal shifts in conservation priority (-0.991 to 0.885) than the CCC-scenario (-0.297 to 0.265), although both scenarios shared similar spatial distributions across the region (Figure 3). Substantially more variation in priority existed between the present-day and Hadley predictions (standard deviation 0.43) than between the present-day and CCC (standard deviation 0.13; Figure 4). The correlation (Spearman correlation, $\alpha = 0.05$, $p = 0.01$) between the present and Hadley priority values ($r = 0.10$) was substantially lower than that between present and CCC priority values ($r = 0.92$).

Despite differences in magnitude between the two futures, the spatial distribution of areas with no priority (those areas not selected for conservation in any scenario) was consistent between scenarios; large central and south-eastern portions of the study area contained no irreplaceable units. This result approximates the range of high-intensity agricultural land-use and extensive urban development in the study region. Areas with conservation priority tended to coincide between scenarios, albeit with significant variation in magnitude.

Discussion

These results suggest that present-day species distributions are necessary starting points for reserve design, but are not sufficient to ensure enduring protection to all species under climate change, in agreement with the results of others (Lemieux and Scott 2005; McClean *et al.* 2006). Existing protected areas are not sufficient to cover all existing or future areas with high conservation priority. In spite of the potential variation in conservation priority over time, many areas identified as important for conserving biodiversity using the present-day dis-

tribution remained important centers of conservation importance in the two potential future scenarios. Although the specific species composition varies, regions containing important or rare species today continue to do so under potential climate change. This suggests that geography and landcover may be limiting factors on the distribution of richness or endemism (Julliard *et al.* 2004; Lemoine *et al.* 2007), while climate may play a stronger role in determining the specific assortment of species found within a given location. Lemieux and Scott (2005) found shifts in biomes across a similar range to that seen in this analysis; based on global vegetation modeling, they calculated that 17 – 45% of Environment Canada National Wildlife Areas and Migratory Bird Sanctuaries could be expected to see a change in biome due to climate change.

Although the predicted future distributions used in this analysis were the best available for our study region, these results need to be used with caution in relation to guiding conservation action. In the future, it would be useful to expand the extent of the study to include all of North America as continuous, fine-scale tree species distributional data for other regions becomes available. The refinement of predictive datasets (discussed in Iverson and Prasad 2002 and further developed in Lawler *et al.* 2009) is an ongoing process, and revisions need to be incorporated as they become available (Heikkinen *et al.* 2006 detail many of the pitfalls encountered when modelling bioclimatic envelopes). However, the urgency of the conservation need demands we begin the process using data at hand.

Species with restricted present-day ranges will likely be under-represented in the future. Small disjunct populations of regionally restricted species (especially those existing at the edges of their present ranges) may find their unique niche-space vanish as climate shifts over the region. Special attention will be needed to identify these remnant populations, and to determine whether to act to preserve them (through remediation) or to shift focus to new areas (potentially beyond present planning regions) to track range changes. This assumes that populations are sufficiently capable of dispersing to newly appropriate areas, and very much depends on the suitability of the human-dominated landscape. Williams *et al.* (2005) present

potential techniques for tracking these dispersal requirements. Fuller *et al.* (2008) detail the potential confounding effects of climate change and human-induced disturbance on Stellar's Eider populations, where oil and gas developments tend to occur in areas where climate shifts are expected to introduce new habitat. This is an example where predictive modelling may be appropriately used to delimit important future biodiversity centers, and guide industrial development towards areas with lower future habitat potential.

Some under-represented species in the dataset show high associations with specific forest communities, particularly balsam and paper birch. Identifying these associations will allow us to proactively designate areas of future importance, preserving habitat with the potential to maintain populations that currently live elsewhere. Existing present-day reserves provide a nucleus of coverage; these can be modified in response to the changes in conservation priority expected over time, evident in both our findings and those of others (Parmesan 2006). The configuration of present-day reserves with respect to potential future reserves could encourage the effective dispersal of communities in response to changing environmental conditions. Without the explicit consideration of these potential avenues of dispersal, areas may become increasingly isolated by intensive land-use, preventing existing populations from dispersing to suitable habitat over time.

Conservation effort should be focussed on those regions with high future potential. Large human-dominated tracts of land, with little or no conservation value today, appear to have little potential in the future; without extensive remediation and management they are unlikely to develop into centers of biodiversity. Protecting high priority areas today will minimize ongoing species loss and give us time to identify the high priority areas of the future. In particular, present-day low priority regions with predicted increased future priority require monitoring and land-use planning to prevent erosion of their conservation potential. Hannah *et al.* (2007) have demonstrated an approach for incorporating climate change considerations into present-day network design in order to minimize the "cost of waiting". Solutions derived from present species distributions may require additional areas to cover future distributions.

Solutions which explicitly incorporate future distributions from the outset may produce adequate coverage to present and future distributions without requiring amendment and extension in later years. However, design methods which explicitly incorporate future predictions require careful consideration of how best to incorporate the predictive models, to ensure that more uncertain model outputs do not override existing information.

The emergence of new tools for financing, facilitating and implementing regional and landscape-scale conservation (such as external revolving loan funds; McBryde *et al.* 2005) hold significant potential to increase the pace and scope of adaptive land conservation in the face of climate change. A synthesis of present and future distributions (with acknowledgement of the uncertainty contained in these distributions) may fruitfully guide design considerations to produce robust conservation effort targeted in areas with expected stability. While this does not preclude monitoring efforts to maintain an accurate picture of the distribution of biodiversity, the flexibility of systematic conservation planning techniques makes it possible to explicitly include a range of future scenarios in the planning process.

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Table 1: Summarized species information (for 39 underrepresented species) Includes AOU code number and common name (Scientific names presented in Appendix H), and the number and proportion of units (N=2121) each species occurs in, for the present-day, Hadley and CCC distributions. Underrepresented species are those species that fail to meet any conservation targets in a future scenario (% Coverage = 0 for at least one scenario).

Species		Current		Hadley			CCC		
AOU #	Common Name	# units	% units	# units	% units	% coverage	# units	% units	% coverage
1900	American Bittern	242	11%	27	1%	0%	0	0%	0%
2210	American Coot	167	8%	12	1%	0%	0	0%	0%
770	Black Tern	194	9%	17	1%	0%	0	0%	0%
6620	Blackburnian Warbler	250	12%	18	1%	0%	0	0%	0%
6540	Black-throated Blue Warbler	232	11%	73	3%	0%	49	2%	0%
6670	Black-throated Green Warbler	433	20%	305	14%	100%	254	12%	0%
1400	Blue-winged Teal	365	17%	97	5%	0%	132	6%	0%
5100	Brewer's Blackbird	183	9%	5	0%	0%	0	0%	0%
7260	Brown Creeper	213	10%	137	6%	50%	96	5%	0%
5610	Clay-colored Sparrow	184	9%	3	0%	0%	0	0%	0%
6120	Cliff Swallow	903	43%	268	13%	100%	116	5%	0%
70	Common Loon	128	6%	8	0%	0%	0	0%	0%
5670	Dark-Eyed Slate-colored Junco	246	12%	51	2%	0%	27	1%	0%
5140	Evening Grosbeak	90	4%	7	0%	0%	0	0%	0%
6420	Golden-winged Warbler	288	14%	174	8%	100%	124	6%	0%
2881	Gray Partridge	194	9%	51	2%	0%	2	0%	0%
7590	Hermit Thrush	254	12%	138	7%	50%	96	5%	0%
4670	Least Flycatcher	397	19%	168	8%	100%	6	0%	0%
5830	Lincoln's Sparrow	71	3%	22	1%	0%	0	0%	0%
6570	Magnolia Warbler	197	9%	49	2%	0%	4	0%	0%
6790	Mourning Warbler	243	11%	21	1%	0%	0	0%	0%
6550	Myrtle Warbler	197	9%	22	1%	0%	0	0%	0%
6450	Nashville Warbler	206	10%	65	3%	0%	0	0%	0%
6750	Northern Waterthrush	208	10%	57	3%	0%	8	0%	0%
5170	Purple Finch	291	14%	111	5%	0%	69	3%	0%
7280	Red-breasted Nuthatch	230	11%	22	1%	0%	0	0%	0%
540	Ring-billed Gull	288	14%	87	4%	20%	1	0%	0%
3000	Ruffed Grouse	354	17%	174	8%	100%	123	6%	0%
7240	Sedge Wren	358	17%	132	6%	60%	70	3%	0%
2140	Sora	179	8%	6	0%	0%	0	0%	0%
7580	Swanson's Thrush	95	4%	22	1%	0%	0	0%	0%
5840	Swamp Sparrow	481	23%	183	9%	100%	27	1%	0%
7560	Veery	467	22%	216	10%	100%	148	7%	0%
5580	White-throated Sparrow	206	10%	22	1%	0%	0	0%	0%
2300	Wilson's Snipe	292	14%	42	2%	0%	0	0%	0%
7220	Winter Wren	220	10%	57	3%	0%	8	0%	0%
4020	Yellow-bellied Sapsucker	264	12%	65	3%	0%	0	0%	0%
4970	Yellow-headed Blackbird	242	11%	92	4%	0%	13	1%	0%
6410	Blue-winged Warbler	668	31%	336	16%	0%	244	12%	50%

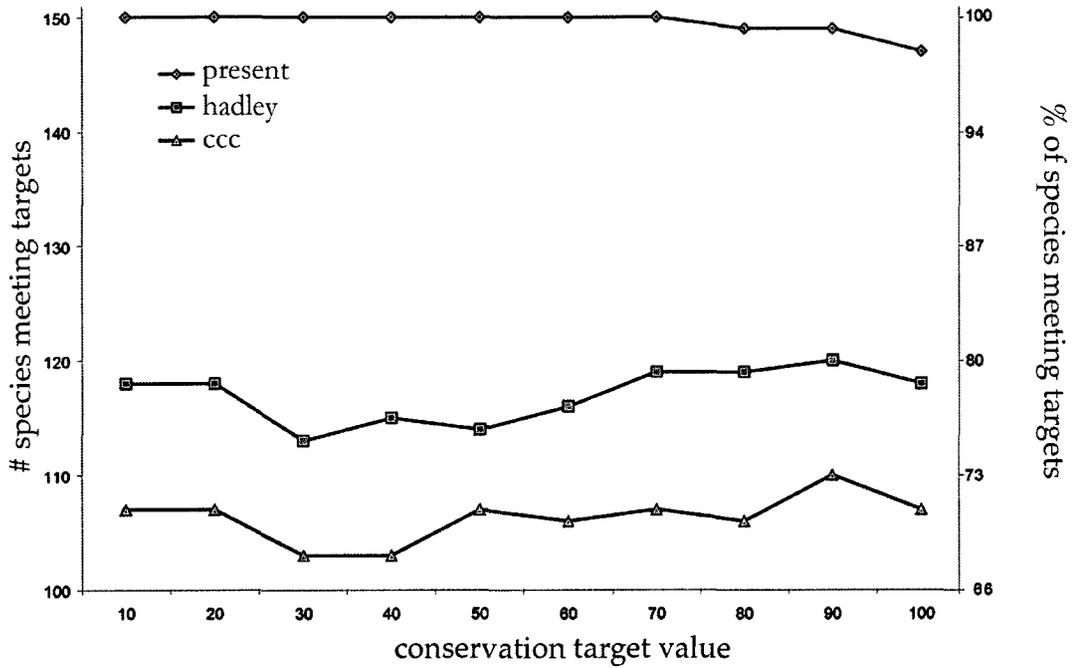


Figure 1: The number of species meeting conservation targets under a present-day reserve design, at varying levels of conservation effort. The present-day scenario (diamond points) contains some species that occur in less than 100 counties, and so cannot reach higher levels of conservation. The Hadley (square points) and CCC (triangular points) show consistent patterns of future species coverage across all levels of targets. Low present-day targets select only hotspots of biodiversity, and so translate into fairly good coverage in the future at this level. Mid-range targets are most affected by shifts in species distribution (especially in the Hadley scenario), as the sites selected to meet these targets do not necessarily remain hotspots over time.

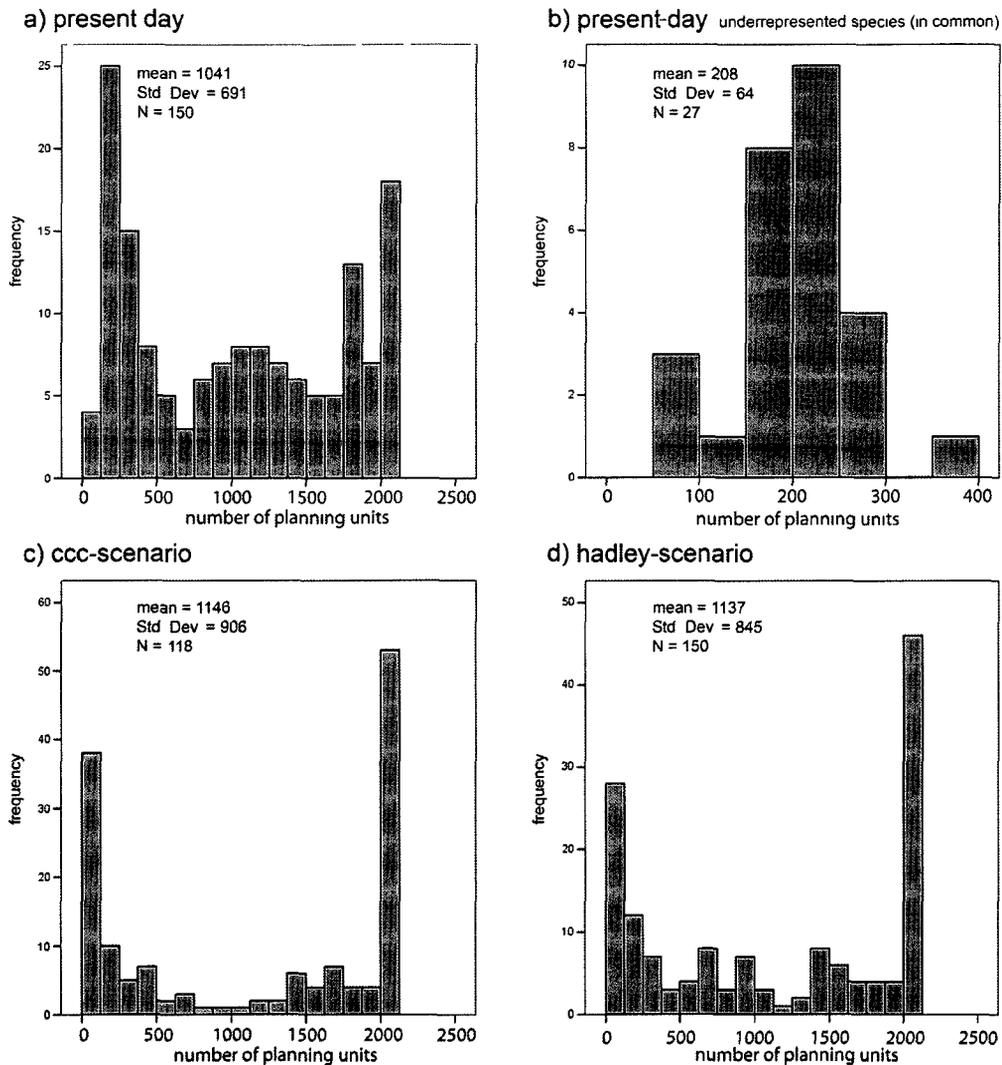


Figure 2: A histogram breakdown of species incidence within planning units (N = 2121) across the study area for a) the present-day distribution of all 150 species; b) the present-day distribution of the 27 species which do not meet conservation targets in either the CCC or Hadley scenarios; c) the CCC-scenario distribution of the 118 species remaining in the study area in this scenario; and d) the Hadley-scenario distribution of all 150 species.

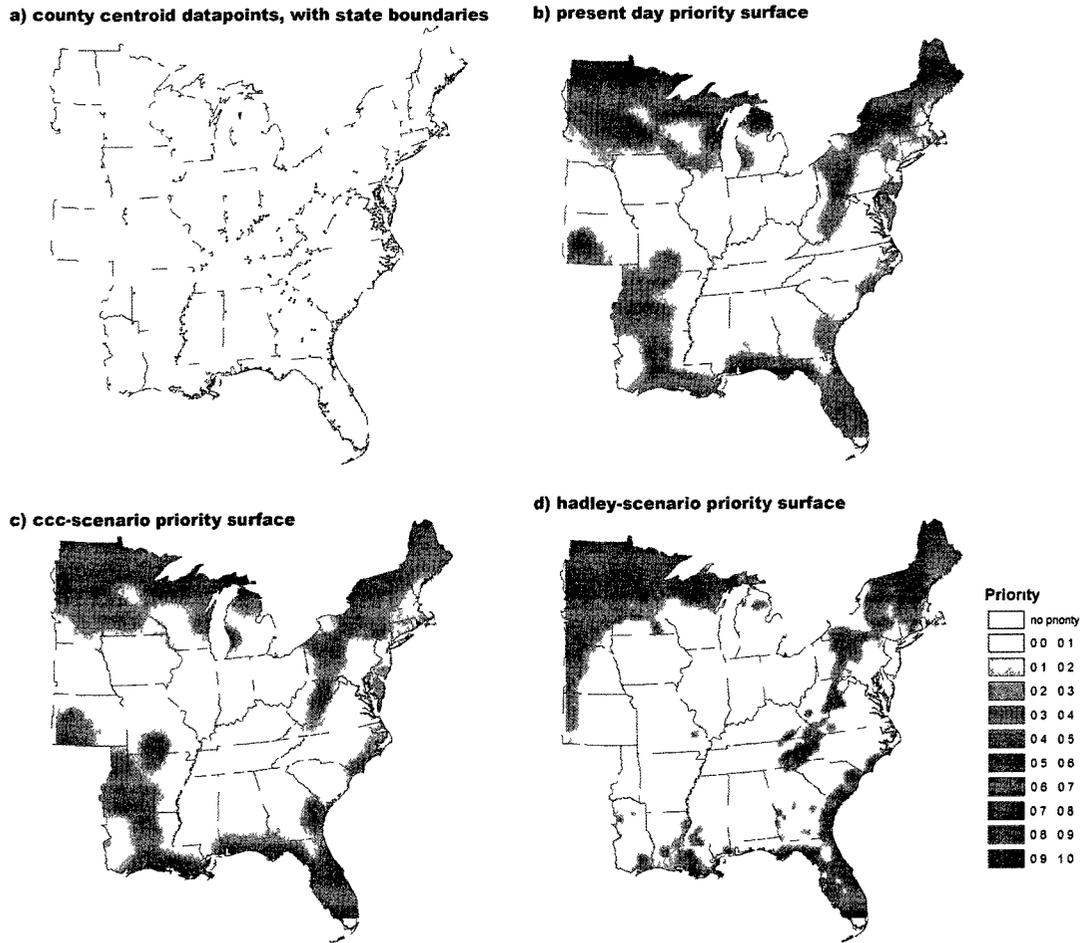


Figure 3: County centroids (a) for the study region, and interpolated conservation priority values for (b) the present-day, (c) CCC and (d) Hadley species distributions. A high priority region (approaching 1) contains rare or regionally restricted species and is required immediately at low levels of conservation (10 occurrences of each species within the reserve) while a low priority (approaching 0) indicates an area that will only be necessary to conserve at high levels of conservation effort (targets approaching 100 occurrences of each species).

Present Day Conservation Priority

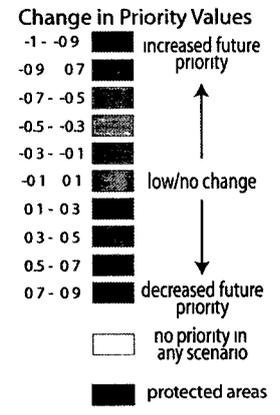
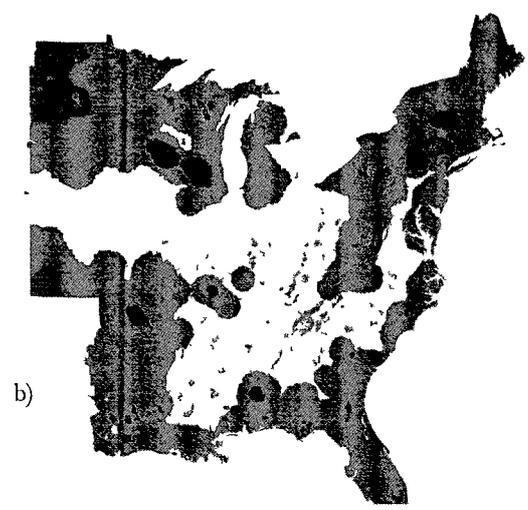
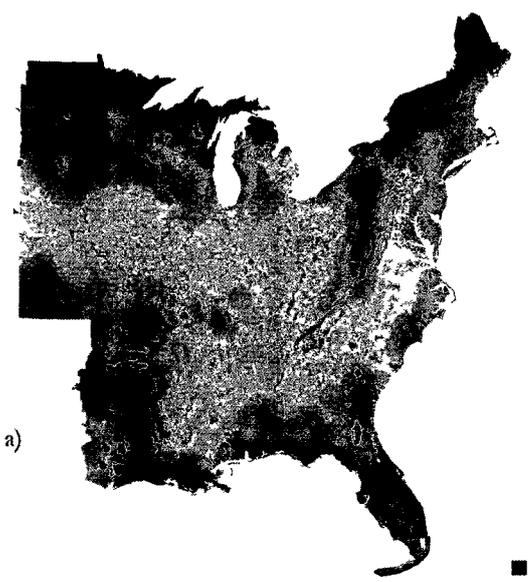
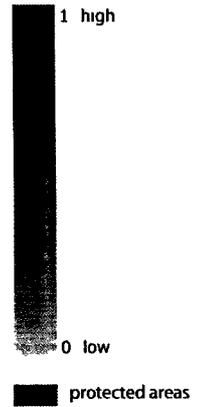


Figure 4: (a) Priority map for present-day species distributions, overlain with existing protected areas according to the CEC (2008). Priority-change surfaces generated by the subtraction of the CCC (b) and Hadley (c) predicted conservation priority surfaces from the present day priority surface (see supplemental data for original priority surfaces). Difference values near 0 show no change in priority over time. Negative differences show areas of increasing priority over time, while positive values indicate areas of decreasing priority over time. Null (white) values indicate regions with no conservation priority in any scenario. The Hadley comparison indicates finer-scale variation of greater magnitude than in the CCC case.

Chapter 2

Effects of Spatial Classification Choice When Studying Avian Biogeography

Introduction

A fundamental challenge for conservation biologists is to delimit the grain-size and spatial extent at which monitoring and management is most appropriate (Hay *et al.* 2001). Scale ‘implies a certain level of perceived detail’ (Miller 1978), and is an assumption of fundamental importance when attempting to detect patterns in biodiversity when systematically planning for conservation. The prolific use of GIS when planning may make these sorts of decisions appear trivial (as many times datasets are only made publicly available aggregated to a particular scale, due to privacy concerns or the sheer size of high resolution data) however they have direct implications on the nature of planning decisions that can be made, and on the ease and effectiveness of implementation. Too large a grain, and meaningful fine scale variation within polygons is lost (Fortin and Dale 2005). Too fine a grain, and land-use decisions run the risk of disrupting ecosystem functioning through arbitrary or unnecessary fragmentation (Van der Ryn and Cowan 1996). While scale as a geographic variable has been described as ‘almost as sacred as distance’ (Watson 1978), the adoption of single-scale research and design is often done without adequate justification (Meentemeyer 1989).

The following analyses make use of diversity data from the Ontario Breeding Bird Atlas (OBBA; Cadman *et al.* 2007) to assess the implications of the choice of spatial classification scheme on the perception of biodiversity patterning. Key questions include: How does the choice of spatial classification scheme bias our understanding of biogeographic patterns? What metrics best capture the spatial variation in bird species composition, and how does that vary across different spatial classification schemes? And what underlying spatial classification is suggested by the diversity data?

There are a variety of commonly adopted means of spatial classification that can introduce biases in diversity patterning, a result of the variety of stakeholders involved in plan-

ning for conservation and development. Varying resources, timelines and administrative capabilities place limits on the grain and extent with which conservation planners, resource users, and the general public can come together to manage land-use change (Flather *et al.* 2009). It is therefore imperative to be aware of the consequences of the spatial scales chosen for analysis and planning purposes, to better inform appropriate action (Peck 1998). Imposing a regular grid system on top of a natural diversity pattern may mask a finer-grain pattern (by treating polygons as homogeneous when they are not), or artificially fragment a larger-grain pattern (treating polygons as distinct when they should truly be managed at a broader extent). Similarly, using natural features such as watershed boundaries may not be appropriate in areas of human dominance, as land-use decisions can have overpowering effects on natural systems.

An optimal spatial analysis scheme for conservation planning will produce a tiled surface that breaks the study area into discrete units (i.e. polygons) such that it reflects true changes in the composition of biodiversity, while providing sufficient simplification to enable efficient communication with stakeholders (Holling *et al.* 1978), and sufficient flexibility to allow for the development of alternate conservation solutions (Newton *et al.* 2009). Good classifications must accurately reflect the underlying gradients and discontinuities in species diversity with as little bias or distortion as possible (Fortin and Dale 2005).

Attention to the underlying spatial distribution of biodiversity is an important component to systematic and rational conservation planning, to ensure that the decisions are made at the scales appropriate to the system under consideration. If an area contains a number of nearby points sharing very similar species composition, it would be a mistake to use a classification scheme that assigned those points to different polygons, as this would introduce arbitrary fragmentation to the observed biodiversity pattern (Peck 1998). Classification schemes should preferably define polygons that are internally homogeneous and distinct from their neighbours, so that conservation analysis and planning decisions become more straightforward and spatial results can be more directly interpreted (Gordon 1999). Homogeneous polygons are more likely to be governed by similar ecological processes (Fortin and Dale 2005),

ensuring that within-polygon conservation management strategies will be more consistent; heterogeneous polygons require additional degrees of analysis, both with respect to the intensity of monitoring, and the additional levels of ecological detail necessary to understand within-polygon diversity patterning (Shifley *et al.* 2009). Thoughtful analysis of present-day diversity patterns may suggest an appropriate spatial classification whose borders align with changes in diversity. A hierarchical analysis of species similarity may inform an appropriate clustering with which to define such a classification. However, a dataset containing hundreds of species and many thousands of samples is difficult to assess, given the extent of variation found among points across multiple dimensions. Planning units chosen without careful regard to the distribution of the features they are meant to cover may result in inefficient management strategies, and introduce wholly artificial partitions to the region as land-use planning decisions partition ecologically-uniform areas (Lindenmayer and Fischer 2006).

The choice of spatial classification scheme will influence how the diversity of a region is assessed, and how results of that assessment are translated into conservation effort. Snelder *et al.* (2008b) conclude that differing definition procedures for the large-scale environmental classification of streams and rivers produce classifications that are comparable in terms of their ability to discriminate variation of ecological characteristics, suggesting that the decisions over which classification to adopt should be based primarily on pragmatic considerations. In a study of 62 potential spatial classifications, however, Klijn and de Waal (1995) found that each failed to meet all requirements for ecological relevance, legend complexity, ease of understanding, accuracy, temporal stability and the applicability for assessments of susceptibility, significance and vulnerability for regional environmental policy decisions. Due to its multi-scale nature, biogeography often suffers from 'fundamental ambiguities' (O'Neill *et al.* 1986). In light of this, a single unifying classification is unlikely to be appropriate for all planning purposes, even in a single region. Lomolino and Davis (1997) suggest that 'simple explanations for the complex and diverse nature of most ecological systems will probably prove futile and illusionary'. Sound systematic conservation planning should involve an exploration of the

set of potential classification schemes at the initial stages of analysis design. When a particular spatial classification is chosen, an explicit acknowledgement should be made of the bias this choice will introduce.

A variety of approaches have been developed over the years to summarize and describe variation in species composition. Initial approaches focussed on the variety of species found at particular areas (termed species richness or alpha diversity; Whittaker 1960, 1972), and the difference in species composition between areas (termed beta diversity; Whittaker 1972; Lande 1996). Further developments have incorporated the abundance of individual species to describe the evenness of local species composition (described using various measures of entropy, such as Simpson's diversity metric; Keylock 2005). More recent measures describe the degree of nestedness in species composition across samples (Atmar and Patterson 1993; Rodríguez-Gironés and Santamaría 2006), and attempts have been made to explicitly describe the spatial components of variation in species composition (using 'Principal-Coordinates of Neighbour-Matrices' or PCNM; Borcard and Legendre 2002; Borcard *et al.* 2004; Dray *et al.* 2006). The patterns described by these measures may be highly influenced by the underlying spatial classification scheme; in this analysis, each metric is calculated for each of the polygons produced by each spatial classification scheme.

Large-scale volunteer biological surveys provide a powerful starting point for the study of regional biodiversity patterning; datasets such as the Ontario Breeding Bird Atlas (OBBA; Cadman *et al.* 2007) provide a high-density assessment of avian species composition and abundance across a broad extent of Ontario. Over a thousand volunteers sampled much of Ontario over the years 2001 – 2005, with point count observations allocated according to a stratified sampling regime. The southern half of the province was subdivided into 10 x 10 km 'atlas squares', and sampling points were laid out with respect to the within-square distribution of landcover types. Sampling effort in northern Ontario was sparse and often biased by river-based sampling efforts (Cadman *et al.* 2007). Although road-side observations dominate the dataset, extensive work was done to ensure sampling was representative of habitat (OBBA

2001; Smith 2005; Cadman *et al.* 2007). These abundant, wide-ranging diversity data provide an opportunity to examine and describe the distribution of avian species for a combination of extent and resolution previously unavailable for this region.

Bird Conservation Regions have been delimited across North America (NABCI 2009) and are being used as a framework to guide conservation planning for avian diversity across regions, coupled with finer scale conservation targeting within each region. The Ontario portions of Bird Conservation Regions 12 (the Boreal Transition) and 13 (the Lower Great Lakes/St. Lawrence Plain) are well covered by OBBA data, and serve as the chief bounds of the study region for the current analysis.

Techniques such as Voronoi tessellation produce tiled and easily displayed polygon surfaces from point patterns (Perry *et al.* 2002). By first classifying the points using multivariate clustering algorithms, the data can be simplified into fewer discrete classes or assemblage types, and any neighbouring Voronoi polygons which share the same classification may be merged to form a single polygon. This produces polygons whose boundaries represent substantial changes in species composition, while ensuring that similar points are grouped together, avoiding artificial fragmentation.

The question of adopting the appropriate spatial scale for regional ecological mapping has been addressed frequently over the years, and a variety of potential spatial classifications have been proposed in a variety of contexts (Walter and Box 1976; Wiken and Ironside 1977; Bailey *et al.* 1978; Bailey 1985; Forman and Godron 1981; Rowe 1980; Rowe 1984; Bernert *et al.* 1997). A variety of 'ecological' classifications have been produced using remotely-sensed environmental variables (Walter and Box 1976; Wiken and Ironside 1977; Bailey 1983; Snelder *et al.* 2008a), however in the absence of certain and consistent knowledge of a reliable relationship between these environmental variables and the observed pattern of species diversity (Peres-Neto personal communication; Parks and Mulligan 2010; Rocchini *et al.* 2010), classifications which directly arise from diversity patterns may be more appropriate for conservation planning. The opportunity presents itself to use the OBBA data to identify the biogeographic

implications of a suite of commonly adopted spatial classification schemes, and to assess the potential consequences of using each to understand and characterize biodiversity patterning.

Optimally, polygons should be derived from patterns implied by the data (Fortin and Dale 2005), with polygon edges falling along existing boundaries defined by changes to species composition; this may not be immediately intuitive from the human perspective, or particularly easy to implement on the ground, but it is a useful baseline to compare against other classification schemes derived from more practical considerations. However, the decisions made during the design of the sampling regime will have real impact here, influencing the nature of observed patterns in biodiversity. A study conducted over too coarse a sampling grain may simply fail to detect important spatial variation in diversity (Peck 1998). Once collected, it is important to maintain the minimum scale of the sampling regime, so that fine scale biogeographic patterning in the data is not lost. Aggregating too quickly may lose important detail (Flather *et al.* 2009).

The constraints of the planning process require some degree of clumping or aggregation to align with the scales at which decisions are being made (Holling *et al.* 1978). Many spatial classification schemes have developed over the years, to satisfy a wide variety of purposes. Some, such as national, provincial or municipal borders, arise out of the political process. Others are indicated by topological constraints or long-term geological processes, such as watersheds and soil classifications, respectively. Many classifications are the result of processor, memory and sensor constraints, with scale decisions made out of necessity (minimum scales based on sampling resolution, maximum scales based on processing constraints).

Potential classification schemes may also be derived from the existing stratified sampling regime used to generate the data (the OBBA squares), a post hoc / arbitrary polygon tiling (hexagons have a better perimeter to area ratio and so are often chosen for spatial planning), or purely human creations selected for jurisdictional means (municipal boundaries). Others might be based on existing topological constraints (watersheds), on a classification of natural features (ecological land classifications such as the Ecodistrict), or on the union

between these coarser delineations, to better reflect ecological processes. The lattice that these polygons create across the planning region carries with it certain implicit spatial assumptions when used to summarize data of a discrete nature, such as the occurrence of species across the region. By using fine-scale OBBA point-samples as a baseline, the impact of aggregation into different spatial classifications can be compared, and the implications for systematic conservation planning evaluated. Summarizing these data by means of diversity metrics can extract important components of biodiversity, highlighting different aspects of the pattern of variation. A comparison of these diversity metrics across different spatial classifications will reveal the confounding effect that classification schemes have on the perception of biodiversity patterning. How does the choice of spatial classification scheme bias our perception of biogeographic patterns through the use of diversity metrics? What metrics best distinguish the spatial variation in bird species composition, and how does that vary across different spatial classification schemes? And what underlying spatial classification scheme is suggested by the data?

The choice of a particular scheme may have varied effects with regards to our understanding of natural patterns, causing small isolated areas of diversity to be erroneously grouped into to a larger region, or causing broader trends to be ignored as the planning process narrows its focus to finer detail, i.e. ‘missing the forest for the trees’. Polygons with low spatial variation in species composition can be monitored and managed with straightforward designs (Kiesecker *et al.* 2009). Those with more complex spatial patterns in abundance and distribution may require further subdivision into finer units to properly observe and preserve the existing natural variation (White *et al.* 1999). Classifications defining polygons that are not adequately sampled may not be useful planning tools, regardless of their theoretical utility or ecological appropriateness. Similarly, a classification scheme may appropriately reflect the underlying spatial biodiversity patterns, but be impractical because of the number or shape of the resulting polygon units. The purpose and constraints of the planning process will be a key deciding factor when choosing between potential classifications, and knowledge of the impact

of this choice is important so that the planning process is most effectively conducted (Ferrier and Wintle 2009).

Methods

The Ontario Breeding Bird Atlas (OBBA; Cadman *et al.* 2007) provided a dense and broad spatial survey of bird abundance across much of Ontario. The data for the Ontario Breeding Bird Atlas was collected over 2001 – 2005, surveying the province of Ontario for breeding bird diversity in a rigorous and comprehensive fashion, operating under peer review. This survey split the southern portion of the province into 10 x 10 km squares, and the northern portion into 100 x 100 km blocks, conducting targeted point counts within each to attempt a stratified random sampling design where possible. Point counts consisted of a count of all birds seen and heard (within and beyond 100m) during a 5 minute period. Counts were done between dawn and 5 hours after dawn between May 24 and July 10 in good weather. Most point counts were along roads. Up to 50 random “designated” roadside point locations were shown on each volunteer reference atlas square map. Each volunteer was asked to sample 20 of these points. Some habitats, especially forest interior (>100m from an edge), were not well covered by roadside points. Volunteers were instructed to complete a minimum number of off-road point counts in each habitat for each square. Within each habitat, volunteers decided where to put off-road point counts, chosen ahead of time to avoid bias towards temporary hotspots of diversity. Count stations had to be at least 300m apart. In squares with few or no roads, or squares where roads were not shown on standard maps, volunteers were provided with information on the proportion of the square made up by each major habitat (e.g. 75% forest, 15% bog, 10% coastal marsh). Volunteers were asked to select point counts throughout the square as access allowed, and to sample the habitats proportionately to their availability in the square. Data were collected, and reviewed by an the atlas coordinators, with unlikely results flagged for validation. Unusually high species counts were flagged by OBBA personnel and either confirmed or removed (Smith 2005). These dataset is now openly available for research,

and provides a comprehensive survey of the province's avian biodiversity.

The fine scale of the southern sampling region squares were more suited to an analysis of conservation design. Bird Conservation Regions (BCRs) have been delimited across North America (NABCI 2009) and used as a framework to guide the conservation planning of avian diversity. The Ontario portions of Bird Conservation Regions 12 (the Boreal Transition) and 13 (the Lower Great Lakes/St. Lawrence Plain) are well covered by OBBA data, and serve as the chief bounds of the study region. This 50 993 point sampling of 235 species ('sites \times species') diversity dataset formed the basis of the current analyses, containing 1 002 971 observed individual birds (based on the unlimited distance point count sampling). The data were first examined using a distance-based hierarchical cluster analysis to determine the extent to which the data points could be classified based on their species composition. The spatial locations of the sampling points were subject to a variety of spatial classification schemes, used to group points together based on commonly adopted means of partitioning the landscape into polygons. These polygons were analyzed using a suite of diversity metrics commonly adopted by ecologists, then compared to denote the effect of spatial classification choice on the perceived patterning of biodiversity implied by these metrics. Null model Monte Carlo simulation was used to estimate the significance of each metric, for each polygon, for each classification scheme. The mean differences between classifications was tested for each metric using Tukey's Honestly Significant Difference T-test.

Dataset transformations: Euclidianizing the species data

The high number of species found in the dataset introduced the classic 'double-zero' problem commonly found in species diversity data (Legendre and Legendre 1998). The presence of a particular species at a pair of points suggests that those points share some intrinsic characteristics (be they ecological or geographic) that make it suitable for the species and likely for it to be found there. A shared absence of a species provides much less local information regarding the quality of particular areas; a species may not occur in a particular location for

any number of reasons (a real absence may be due to topological constraints on immigration, environmental conditions, or limited ecological niche space, or detection issues associated with the sampling method may have introduced a false negative observation).

In an abundance-based distance ordination, sites with no overlap in species composition may appear closer together than those sharing some species but differing greatly in abundance, termed the ‘Horseshoe Effect’ (Podani and Miklos 2002). Species diversity datasets (sites \times species matrices) may not satisfy many of the assumptions of normality inherent in many forms of multivariate analysis. To overcome the double-zero problem and focus the weight of analyses on the presence data, Legendre and Gallagher (2001) suggest a number of transformations for ecological data that are appropriate for traditional Euclidian statistical approaches. The Hellinger transformation is particularly well suited for clustering and ordination methods (Rao 1995), defined as

$$Y_{ij}^* = \sqrt{[Y_{ij}/Y_{i+}]}$$

where the new species value Y_{ij}^* equals the square root of the ratio of each species abundance Y_{ij} for species j at point i to the total number of individuals at point i , Y_{i+} . This maintained as much information as possible in the dataset (i.e. using all the raw data, and making use of abundance estimates to distinguish sites with similar compositions but differing densities), while allowing the use of traditional Euclidian ordination and cluster procedures. The entire 50 993 point dataset was transformed in this manner for the hierarchical cluster analysis used to produce the Avian spatial classification scheme (discussed below).

Spatial Classification schemes:

1. Voronoi Tiles (Voro)

Raw point data can be seamlessly assigned to cover an entire study region by means of a voronoi tessellation (Perry *et al.* 2002). This procedure draws polygons around each point, such that the area within each polygon is closer to that point than to any other. This produced an irregular tiled surface: Points located far from other points resulted in large polygons, while

more closely spaced sampling points yielded smaller polygons. The smallest polygon produced defines the finest spatial resolution possible for this particular dataset.

2. Avian composition classification (Avian)

A hierarchical cluster analysis of species similarity was used to classify points based on species composition and abundance. The difference between the avian species found at any two points was quantified using multivariate analyses. After transformation, the dataset was treated as a Euclidian space with regard to the Euclidian distances between all points. A distance / dissimilarity matrix was calculated, containing the distance from each point to every other point in the regional 235-dimension avian species-space (Legendre and Legendre, 1998; McArdle and Anderson 2001).

The structure of the species diversity dataset was described by analyzing this distance matrix using a hierarchical, unsupervised classification (Gordon 1999). This analysis used Ward's clustering algorithm to merge points to minimize the increase in the ratio of squared distance between clusters to that within clusters. At each step the two closest points or clusters were merged, provided this either minimized the total sum of squared distances within groups, or increased the distance between them. This hierarchical classification was then displayed as a dendrogram or tree structure, with branch lengths equal to the separation distance between the leaves in species-space, and height proportionate to the total variation in the data.

To create the avian spatial classification, points were then clustered into different groups by 'cutting' the tree across its height at regular intervals; cluster validation techniques were used to identify which clusters were sufficiently distinct (such that they should not be treated as equivalent to other clusters) and homogeneous (so that data within the cluster can be treated as variations on a single entity). No entirely reliable method exists for determining the appropriate number of clusters, so a reasonable range of cluster numbers was explored (Hennig 2004). The validity of the clusters produced by each of these cuts were compared

using the Calinski index (the ratio of between cluster to within cluster variance; Calinski and Harabasz 1974), the largest value implying the most appropriate split.

This optimal cluster-classification was then applied to the Voronoi tessellation (derived from the point location data); proximate polygons that shared the same classification were merged into a single polygon. This produced a tiled set of 'Avian planning units', classified by their species composition, and constrained by the distribution of the sampling regime.

3. OBBA Atlas squares (Square)

The OBBA used a stratified sampling approach, based on tiling the province into UTM-based 100 km² squares (with smaller, wedge shaped polygons used to fill in areas near UTM boundaries, where changes in projection introduce distortion). Sampling points were distributed within these squares, predominantly along roadsides, with off-road points selected to sample habitat types that were not otherwise accessible (OBBA 2006a).

4. Hexagons (Hex)

A hexagonal tiling produces more compact polygons than a square tiling, and has often been used in terrestrial biodiversity surveys (White *et al.* 1999; Warman *et al.* 2004; Free-mark *et al.* 2006). The increased number of edges also allows more neighbouring polygons, potentially aiding collaborative planning across polygons. This classification scheme breaks the region into the same 100 km² area as that used to define the OBBA sampling regime, but with different boundary properties. Points that originally fell within a single OBBA Square may be assigned to different neighbouring hexagons.

5. Ecodistricts (Ecod)

The Canadian Ecodistrict classification (Marshall and Schut 1999) derives from broad delineations between geologic soil types and coarse vegetation classes. This classification further subdivides the ecoregions of Canada, which are too large and too few to serve as a

flexible planning surface at the provincial extent. These polygons capture variation in habitat in a broad sense, reflecting soil chemistry and vegetation changes over the region.

6. Watersheds (Basin)

The sub-sub-basin watershed classification (NRCAN 2009) breaks the region into stream-level watersheds. Regional variation in rainfall, as well as human impacts such as stream effluent and hydroelectric projects, may make these polygons representative of broad diversity patterning across the region. However, the directional effect of water flow from upslope, to stream, to downstream, introduces a great deal of within-watershed variation in composition at the same time; upstream areas are exposed to less influx than downstream. There is some merit in using this scheme as in some regions, land is managed through conservation authorities delimited by watershed boundaries (in Ontario) or by Regional Water Management Districts (in the Canadian prairies).

7. Municipal districts (Muni)

Municipal boundaries (OMNR 2008) are often used when planning and delineating human activities. The impact of fragmented local land-use decisions may be reflected in a classification scheme based on municipal boundaries. Additionally, recommendations based on this classification will be easier to implement, as there will be no need for ‘translation’ into terms familiar with land-use planners. This classification is also familiar to the public, and may be used in an informative or interpretive fashion in public settings. In this study the ‘lower-tier’ fine scale municipal boundaries were used.

8. Union of Ecod x Basin (Ecobas)

Both Ecodistricts and sub-sub Basin watersheds produce polygons that cover broad spatial extents. Watersheds may function very differently with changes to underlying soil characteristics over their length, and groundwater flow is very dependent on the depth and nature

of the bedrock. The interaction between ecounit and vegetation characteristics and watershed processes may more strongly represent the gradient of bird diversity patterns than either one alone (i.e. the notion of 'land facets'; Wessels *et al.* 1999).

9. Union of Ecod x Basin x Muni (Ebm)

This classification comprises the cross between ecounit, watershed and society, and may more effectively reduce within-polygon habitat variation, producing more homogeneity in geology and hydrology while presenting the results in a form that is readily implemented by land-use planners, and more easily conveyed to the public.

Diversity Metrics

Species Richness or Alpha Diversity

Polygon species richness can be measured in terms of mean point richness per polygon, or overall polygon richness. Point-level species richness is simply the total number of species observed at each sampling location (A1), while polygon-level richness is the number of species found within a given polygon (A2). This has been referred to as alpha or local diversity (Whittaker 1960, 1972). The total species found within the entire study area has been termed 'gamma diversity', and refers to the total 'species pool' of species likely to be observed somewhere within the area. Richness on its own carries no information regarding the composition or abundance of species, and may mask interesting spatial trends as species composition changes, while the number of species remains constant. For each polygon, for each classification scheme, the mean and standard deviation of point-richness or A1 values, and the polygon-level (A2) value, were calculated and compared (using the 'specnumber' function in the 'vegan' package in the R software; Oksanen *et al.* 2009). A classification scheme with strong negative correlation between mean and variance in A1 per polygon is desirable, as this ensures small, isolated hotspots of spatially restricted biodiversity do not falsely represent the pattern of biodiversity found across the entire polygon. High variance within a polygon implies that it

is not homogeneous, and any planning within that polygon will require additional partitioning to be efficient.

Species Paucity or Beta Diversity

A very interesting measure is beta diversity (Whittaker 1972), the number of species absent at a particular location (Lande 1996), calculated with respect to some larger species set (e.g. those species found within some spatially defined boundary). The larger set may be thought of as the 'pool' of species that have been observed elsewhere in that particular polygon, and therefore have some probability of occurring at a given point. The absence of a species that is commonly found in the nearby area is much more interesting than the absence of any particular species from the entire polygon. The former is more likely to arise from local habitat-quality selection decisions, while the latter could result solely from resource or life history constraints.

Beta diversity is a measure of the number of species absent either from a particular point (yet found somewhere within the polygon containing the point, the difference between point richness A_1 and polygon richness A_2 ; $A_2 - A_1 = B_1$). Initially defined as the ratio of total diversity to local diversity (Whittaker 1960, 1972), modern approaches have focused on an additive formulation, as this maintains whole number values, and is commensurate with the log-transformed multiplicative form (Lande 1996; Crist *et al.* 2003) The mean and standard deviation of beta diversity were calculated for each polygon. High mean beta diversity indicates the polygon has high heterogeneity in species composition, suggesting a wide variety of habitat types or a range in habitat quality. This provides complementary information to simple species richness, as it frames richness in terms of the difference in potential occurrence (which species could conceivably be found at a location) and actual occurrence (which species were observed there).

Simpson's Diversity: Compositional Entropy Within Points

Abundance-based species heterogeneity is also an important complement to species richness. Simpson's diversity metric describes the degree of entropy or disorder in the species composition of a particular point (Whittaker 1972; Keylock 2005). High values indicate a low probability of finding two individuals of the same species, lower values indicate that some species are found in disproportionately higher abundance than other species. The entropy inherent in the distribution of species at particular points, a function of the relative frequency of different species (Keylock 1995), is a useful measure to include when comparing points with similar species numbers. Two areas may be very similar in richness, but vary dramatically in the proportionate number of individuals of each species. The degree of point-level species heterogeneity / dominance can be evaluated using Simpson's diversity D , defined as

$$D = 1 - \sum_i p_i^2$$

where p_i is the proportional abundance of species i , which when squared and summed over all species gives the probability that any two individuals, sampled from the same location, will be from different species. High diversity values indicate even distributions of individuals at given locations, while low values indicate a skewed species distribution, where individuals are more likely to be of the same species. This was calculated for each point location (using the 'diversity' function of the 'vegan' package in R; Oksanen *et al.* 2009), and averaged over each polygon, for each classification scheme.

Species Nestedness via Temperature: disorder within polygons

Nestedness is a measure of the degree of disorder observed in species composition across points within polygons. In a highly nested polygon, species found in low richness points are a subset of those species found in high richness points. Groups of samples are regarded as nested if they all could be considered subsets drawn from the same pool (Atmar and Patterson 1993). In more disordered polygons, species do not follow this pattern.

The ‘Nestedness temperature’ (defined by Atmar and Patterson 1993; explicitly described by Rodríguez-Gironés and Santamaría 2006) was calculated by first ordering the columns and rows of a boolean sites \times species matrix, producing a ‘packed’ matrix with high richness sites at the top, and high occurrence species on the left. This packed matrix was then compared to an ‘isocline of perfect order’, defined as a curve that in a perfectly nested matrix of the same size (in rows and columns) and fill (maintaining the total number of presences) would separate those cells with presence of a species, from those with absence (Rodríguez-Gironés and Santamaría 2006). Effectively, the existing sites \times species matrix is packed into the top left corner, and the isocline is defined as the smooth curve passing along the border between filled cells and empty cells. The ‘nestedtemp’ function in the R package ‘vegan’ (Oksanen *et al.* 2009) provides a recent formulation of this method. The sum of the normalized distances to the isocline from an absence above, or a presence below this curve is referred to as the ‘temperature’ of the matrix, ranging from 0 (indicating a perfectly ordered matrix) to 100 (indicating a ‘maximally unnested’ matrix). This may be interpreted as a measure of the number of ‘surprises’ or ‘discrepancies’ found in the matrix (Brualdi and Sanderson 1999), either a high richness site that is lacking in common, high occurrence species, or rare species that are found only in low richness areas.

PCNM: Within Polygon Spatial Trend

Each polygon can also be described by the degree of spatial trend in species composition, estimated here using ‘Principal-Coordinates of Neighbour-Matrices’ or PCNM (Borcard and Legendre 2002; Borcard *et al.* 2004; Dray *et al.* 2006). This analysis uses a distance-based eigenanalysis that pulls the unique spatial structure of the data apart into two-dimensional waves of increasing period. The species data are then modelled using a subset of these eigenvectors, selected in order to minimize the spatial autocorrelation of the residual values. This model is then evaluated with respect to an ‘adjusted R-square’ term (Peres-Neto *et al.* 2006).

The degree of spatial trend in species composition within polygons was assessed by

using spatial variables to explain the variance in the sites \times species matrix. Spatial eigenvectors were derived from the geographic coordinates of the sampling points, using a variation on Principal-Coordinates Analysis (PCoA) known as Principal-Coordinates of Neighbourhood Matrices (PCNM; Borcard and Legendre 2002; Borcard *et al.* 2004; Dray *et al.* 2006). This analysis is akin to a redundancy analysis, but uses a distance matrix derived from spatial coordinates as the constraints on the species ordination. Using a distance matrix focuses the analysis on the spatial relationship between points, and allows for much more fine scale variation to be teased out of the spatial sampling structure than simple two-dimensional coordinates.

To conduct a PCNM analysis, a Euclidian distance matrix was calculated from the spatial locations of point counts found within each polygon. A minimum-spanning tree was calculated (the minimum Euclidian distance required to connect all points together), and the distance matrix transformed such that all distances past this point are scaled to four times the minimum spanning distance (as per Dray *et al.* 2006), in order to reduce the influence of these points on distant points and focus the ordination on the effect of neighbouring points on species composition. This truncated distance matrix was then diagonalized according to traditional PCoA, producing the ‘spatial eigenvectors’ and associated eigenvalues. The vectors were then used in a forward selection routine (the ‘forward.sel’ function in the R ‘packfor’ package, Dray *et al.* 2009) to iteratively select those vectors that best explained the variance in the Hellinger-transformed diversity matrix (using the adjusted redundancy statistic for multivariate canonical analysis, R_{2adj} ; Peres-Neto *et al.* 2006), while minimizing the Moran’s I value (Cliff and Ord 1973) of the residuals. The result was a quantification of the amount of variance in species diversity which could be explained through strong spatial trends, on a per-polygon basis. This allows the identification of polygons with strong and weak spatial trends in diversity, and may be used to sort homogeneous polygons from those more heterogeneous polygons, which may need finer scale analysis to inform effective conservation action.

Processing issues precluded the use of this analysis with large sample sizes. It would have been very interesting if the entire dataset could have been analyzed en masse, and the full

range of spatial variation modelled together. However, the memory demands of the matrix-product multiplication (required during the forward stepwise selection procedure) were simply too severe for present facilities to process at once. Consequently, the analyses were conducted on each polygon, for each classification scheme that could be successfully held in memory: Avian, Square, Hex, Muni, Ecobas and Ebm.

Randomization testing of diversity metrics

To determine the significance of calculated diversity statistics, a randomization algorithm was used to generate 100 ‘null model’ diversity matrices (Gotelli and Graves 1996; Manly 2006; ‘oecosimu’ function of the ‘vegan’ package; Oksanen *et al.* 2009), maintaining the row and column sums of the original dataset (the total number of individuals in each species and each sampling point, individuals were randomly assigned to cells within the matrix until each constraint was satisfied). Each polygon diversity metric was calculated for the original matrix and each ‘null model’ matrix. These 100 values generated the null-distribution against which the observed value of the statistic was compared using a traditional Z-score and P-value. Results were deemed ‘significant’ if they were more extreme than 95 of the null values. This process was applied to all metrics but the PCNM analysis, as this routine contains its own significance testing through randomization of the residuals of the multivariate regression model (and therefore only significant results were returned).

Calinski index: the Ratio of Between to Within Polygon Variation

To compare alternative schemes, the Calinski index is a useful starting point (Calinski and Harabasz 1974), as it is a measure of the ‘fit’ of a classification to the diversity data. It is a pseudo F-statistic akin to the standard ANOVA, the ratio of the between group to within group sum of squared variation in multivariate species-space. It is a good measure of classification validity, increasing with cluster distinctiveness, decreasing with cluster heterogeneity (Gordon 1999). It is defined as

$$\text{Calinski Index} = (\text{SSB}/(\text{K} - 1))/(\text{SSW}/(\text{n} - \text{K}))$$

where n is the number of data points, K the number of clusters, SSB the sum of squared variation between clusters, and SSW the sum of squared variation within clusters. Like the hierarchical cluster analysis, this index was calculated using the Hellinger transformed sites \times species matrix, producing a single value for each classification scheme.

If an existing polygon has low internal variance and high external variance then it reflects a distinct region with an internally consistent species composition different from its surroundings and this may be considered as an appropriate unit for conservation species planning. If two neighbouring polygons are not sufficiently distinct with respect to species composition, this indicates that a particular classification scheme inappropriately represents the observed patterns of biodiversity, and planning decisions made at that scale will likely result in habitat fragmentation. As the Calinski index value increases, more of the variation in species composition occurs between polygons, and less variation within polygons. A classification with poor fit (low value) does not represent observed biodiversity well, and will make conservation planning more difficult due to high within polygon heterogeneity, and increase the complexity of reserve designs.

Data Manipulation and Visualization

ArcGIS (ESRI 1999 - 2006) was used for the initial projection, clipping and union processes. All further analyses were done in R 2.8.1 (R Development Core Team 2008). Many analyses required the facilities of the HPCVL-Carleton computing grid, a Sun SPARC Enterprise M4000, 4 x 4 x 2 x 2.4 GHz SPARC64 VII, with 32 GB RAM.

Output maps were created and symbolized in R using the ‘mapproj’ (Lewin-Koh *et al.* 2008), ‘spatstat’ (Baddelay and Turner 2005), ‘sp’ (Pebesma and Bivand 2005), and ‘RColorBrewer’ (Neuwirth 2007) packages. All maps were displayed using the Lambert Conformal Conic projection. To consistently display metric results, and better highlight real differences between classification schemes, each metric had its overall range of values broken at ten equi-

distant values and each class assigned to a colour gradient (using the ‘brewer.pal’ and ‘colour-map’ functions of ‘RColorBrewer’ and ‘spatstat’ packages). These classes were used to colour the polygons appropriately, with a further layer of dark hatch-marks used to delineate those polygons whose statistics could not be significantly distinguished from a random pattern (i.e. P-value greater or equal to 5%).

Polygon-level histograms were generated for each classification scheme to aid in interpretation, using the same symbology, which showed the overall breakdown of each metric across each polygon in the classification scheme. However, standard polygon-level histograms do not adequately represent the variation in data density between polygons. Some classifications may have a wide range of polygon sizes, and a corresponding range of points contained within each polygon. The point count data itself was not uniformly distributed, despite the best efforts of atlas planners, so that even uniformly distributed polygon classifications did not have the same point count densities. Some classification schemes had far fewer total polygons than others, and the summary statistics for these large polygons derive from a large number of points, which introduced a bias towards more moderate values (with an accompanying high variance). To better visualize the results among classifications, a stacked barplot was created for each metric, and each classification scheme. The total height of these barplots was equal to the total number of points in the study region, divided using the same breakpoints as the maps, with bin height equal to the number of points in that bin. This represented the overall impact of classification choice on the interpretation of biogeographic patterns, as changes in classification lump different sets of points together, skewing the diversity metrics in different ways.

Metrics were also compared using boxplots showing the median, upper and lower 25% data boundaries, and outliers. The ‘notch’ represents the 95% confidence bounds around the median value; if the notches of two boxplots do not overlap, there is strong evidence that their medians differ (Chambers *et al.* 1983). Classifications were ranked by the proportion of significant polygon values (i.e. P-value <0.05), indicating how many of these polygons contain val-

ues that are outside the expected range of randomly occurring diversity patterns. These ranks were shown by darkening the boxplots, such that darker colours indicate a higher proportion of significant polygons. High ranked polygons display a strongly non-random diversity pattern, whereas low ranked polygons show patterns that could commonly be observed under random assortment of individuals.

Tukey's Honestly Significant Difference test remains a useful tool for multiple pairwise comparisons (Chambers *et al.* 1983); the mean diversity values of each classification scheme were compared, identifying which schemes produce significantly different diversity values. This analysis uses lower critical p-values for each comparison, such that the overall alpha test value remained at 0.05. Results were shown using a coloured comparison, highlighting metrics showing strong divergence between classifications. Insignificant differences were denoted using hatching. This identified which classifications had the greatest variation in metric values overall, suggesting which may lead to substantially different interpretations of the pattern of avian biodiversity, and which ones were in agreement. This demonstrated which diversity metrics are more susceptible to bias by classification choice. This summary allows a useful and compact comparison of the effects of multiple classifications on multiple diversity metrics in a single figure.

Results

Classification Schemes

Voro

The Voronoi tessellation (Figure 1) produced polygons ranging in size from 10 km² to 1.34 million km², with larger polygons formed in areas of low sampling density. The reduced sampling in the northern region produced some tiling artifacts, where isolated points yield sets of polygons with irregular geometry. The study region boundaries formed the maximum extent of these polygons during the creation process, producing a complete tiling of the study region surface.

Avian

Hierarchical cluster analysis produced a dendrogram showing the relationship among all points, with regards to their position in species space (Figure 2). This tree was cut at ten equal intervals along its height, and the resulting branches were compared. The Calinski index suggested two clusters had the greatest ratio of between cluster to within cluster species variation (Figure 3 A; first subdivision had a between group variance 4165 times that found within groups). Merging any neighbouring Voronoi polygons that fell within the same cluster produced a spatial classification that closely mirrors the existing BCR boundaries, though with great percolation of each class into the other (Figure 4 A). While a useful validation the biodiversity patterns relevant to the BCR classification, it produced many polygons that were deemed too large for effective conservation management and monitoring. Each of the two initial clusters was cut again at regular intervals to assess whether further subdivision was warranted. The 'blue' cluster (Figure 3 B) showed consistent reductions in Calinski Index value, while the 'orange' cluster showed an interesting spike when cut at 10% of its height (Figure 3 C), which may indicate a further fine division within this cluster.

A cut of the dendrogram into four clusters produced a tiling with a much broader distribution of polygon sizes (Figure 4 B). While one extensive cluster in the north remained very large (though perforated with different classes), many of the southern polygons became distinct from their neighbours. That said there were a number of tortuously connected polygons throughout the south, where broadly similar species distributions surrounded islands of different diversity. Because the Calinski index was still comparatively high a four cluster grouping seemed reasonable (Figure 3 A); the four-cluster cut produced a functional range of polygon sizes that appeared to capture variation in the scale of species turnover), while maintaining sufficient cluster distinction to warrant management using this classification.

The four-cluster classification was used as the comparative Avian scheme, defining 8120 polygons. These polygons (with low point counts per polygon) resulted in a very low Cal-

inski index value when compared to coarser classifications (due to low between polygon variance; Figure 3 D). Some linear geometric artifacts exist as a result of the voronoi tessellation (Figure 5), but these were considered to be at a scale too fine to substantially affect analyses of biodiversity conservation.

The Avian classification produced a very wide range of polygons sizes (Figure 6), a very large polygon in the north (covering much of BCR 12), a few large, irregular polygons (around Toronto in the south), and many small to mid-range polygons distributed throughout (Figure 4B). The large number of polygons containing few point counts (Figure 7), found largely in the south, made statistical analysis of the avian classification problematic for nestedness and PCNM metrics, and the single large northern polygon had too many points to conduct a PCNM analysis. Results of the diversity metric analyses for this and other classifications are compared in Figure 8, 9 and 10. Diversity metric mappings for the Avian classification surface are included in this chapter as Figures 11 - 16; these mappings provide summaries of the distribution of diversity metrics for this classification, and serve as a guide for comparison against the other diversity metrics found in Appendices A-G.

Square

A total of 1924 OBBA squares remained after clipping to the study region boundary. Squares had a low Calinski Index value, on par with Hex and Ebm (Figure 3 D), indicating high within polygon variation, 7 times that found between polygons. Polygon sizes were mostly 100 km², with smaller polygons used to 'fill in' the grid at the projected edges of UTM zone boundaries (Figure 6). Squares had the smallest range in number of point counts per polygon (Figure 7). Diversity metric mappings for this spatial classification scheme are summarized in Figures 8 and 9, mapping results are found in Appendix A.

Hex

A regular tiling of 100 km² hexagons across the study area produced 2146 polygons that were sampled by the OBBA point counts. These polygons had consistent area throughout the study region (Figure 6). The arbitrary placement caused some polygons to be poorly sampled (Figure 7). The Calinski index value was on the same order of magnitude as the Square and Ebm classifications (Figure 3 D). Diversity metric mappings for this spatial classification scheme are summarized in Figures 8 and 9, mapping results are found in Appendix B.

Muni

The OBBA sampling data for this study region covered 681 lower-tier municipal districts (OMNR 2008). This classification contained one of the largest polygons across all classification schemes (Figure 6). In southern areas, polygons were comparatively small, but less developed northern municipal districts were much larger. Urban centers were easily pinpointed as small polygons enclosed in larger municipal districts, however these areas were poorly sampled by the OBBA survey, resulting in high variation in the number of point counts per polygon (Figure 7). The Calinski index value for municipalities showed between polygon variation 14 times that found within polygons, a result in the mid-range of the classification schemes (Figure 3 D). Diversity metric mappings for this spatial classification scheme are summarized in Figures 8 and 9, mapping results are found in Appendix C.

Basin

Sub-sub-Basin watersheds were a much coarser grain than previous classifications, with 86 polygons across the study regions. Polygons were generally large in size and well sampled by point counts (Figure 6 and 7). The Calinski index value was higher than all but Ecod, with a ratio for between to within group variation of 84 (Figure 3 D), indicating that at a broad level, there was strong separation between polygons. Diversity metric mappings for this spatial classification scheme are summarized in Figures 8 and 9, mapping results are found in Appendix D.

Ecod

Ecodistricts were the coarsest grain analyzed, with only 52 polygons that were well sampled by point counts (Figure 7), and the second largest average polygon size next to the Basin classification (Figure 6). The Calinski index value was substantially higher than the other spatial classification schemes, with between polygon variation 143 times that found within polygons (Figure 3 D). Diversity metric mappings for this spatial classification scheme are summarized in Figures 8 and 9, mapping results are found in Appendix E.

Ecobas

The union of sub-sub-Basin watersheds and Ecodistrict boundaries produced 269 polygons, with a wide range of polygon size and point count numbers (Figure 6 and 7). Ecobas had a high Calinski index value compared to the finer grain classifications, between group variation was 33 times greater than within group (Figure 3 D). Diversity metric mappings for this spatial classification scheme are summarized in Figures 8 and 9, mapping results are found in Appendix F.

Ebm

The further intersection of Ecodistricts, Basins and municipal boundaries produced 1618 unique polygons. The median polygon area for this classification scheme was lower than all but the Avian classification (Figure 6). Median number of point counts per polygon was likewise low, with moderate variance (Figure 7). Diversity metric mappings for this spatial classification scheme are summarized in Figures 8 and 9, mapping results are found in Appendix G.

The Impact of Classification on Aggregated Diversity Metrics

The choice of classification scheme had a strong influence on the values of many diversity metrics. The bias of each classification is indicated by the distribution of diversity

metric values across the entire point count dataset (Figure 8). The diversity values calculated for each polygon was applied to the points it contained, and the coloured barplots indicate the resulting distribution of diversity values. Coarse classifications with large polygons caused large numbers of point counts to be assessed together, while finer classification with smaller polygons produced diversity metric values which resulted from fewer point data. By adopting a consistent colour scheme, it is possible to see at a glance how a given classification influences the diversity metric results for the entire dataset. Polygon-level alpha diversity (species richness), beta diversity, and nestedness all showed large variation in mean values across classifications, tending to higher values with increased sample point counts and area per polygon (i.e. Basin, Ecod, Ecobas, Muni; Figure 6 and 7). Mean point richness (richmean) was low and similar in all schemes, with a bit more variation in classifications with small polygon areas (Figure 9; Avian, Square, Hex and Ebm).

The Tukey's analysis highlighted the major differences between classifications for each metric (Figure 10). Basin and Ecod classifications were indistinguishable in all cases. All other classifications were significantly different with respect to polygon level richness (classalpha), and mean beta diversity (betamean). Mean point richness (richmean) and Simpson's Diversity were not good metrics to distinguish between classification schemes overall, but do indicate a few significant differences between schemes. Nestedness showed small but significant differences, with the Avian scheme producing consistently less nested polygons than others. The PCNM results indicated that no classification produced a set of polygons that could be said to lack spatial trends entirely, however within each classification areas with extremes of low and high spatial trend were detected.

Metric description by Classification Scheme

These analyses will be best used to add important considerations of biodiversity for land-use planning. The following figures provide the particular spatial maps for each classifica-

tion scheme, and are intended to inform stakeholders, government land-use planners and the lay public by visualizing each diversity metric for each classification scheme. In the absence of adequate visualization, an understanding of the distribution of valued biodiversity will be less likely to be constructively incorporated into decision making processes.

Polygon Richness, Class Alpha Diversity

Classifications with large polygons, containing large numbers of points collected over large areas, had correspondingly high richness values. The Avian classification (Figure 11) aggregated the sample points in such a way as to produce a broad range of richness values over the study region, including polygons in the north which contained the highest diversity produced by any classification. The Avian classification was also able to distinguish areas with low species richness, something which no other classification did (Figure 8). Square and Ecobas classifications had the greatest number of polygons with richness values more extreme than that expected by chance (greater or lower than 95% of all null model values). Square values tended towards 50 species per polygon, with little variation, while Ecobas had a much wider range of species. Only Basin and Ecod classification mean values were statistically indistinguishable from each other (Figure 10).

Mean Point-Level Richness

The Avian classification identified a number of high mean richness areas (Figure 12) that were otherwise washed out of coarser grained classifications. As the Avian surface reflected the underlying gradient in species composition, many distinct high richness points were not aggregated with neighbouring low richness points. Classifications which produced larger polygons failed to detect these hotspots, as the diversity of the smaller, high richness areas were blended with their less rich surroundings. Overall, this metric was not substantially biased by classification choice (Figure 8). Few classification means could be distinguished from each other (Figure 10).

Mean Point-Level Beta Diversity

The Avian classification produced the lowest beta point-level beta diversity, with a wide range of outliers found in those larger polygons to the north (Figure 13). Square, Hex and Ebm classifications had a significantly lower median beta than other classifications (Figure 8; Figure 10). Basin and Ecod classifications had very high beta diversity overall (Figure 8). Only Basin and Ecod classification mean values were statistically indistinguishable from each other (Figure 10).

Simpson's Diversity Index

Simpson's Diversity was high throughout the study region, across all classification schemes, indicating relatively even distributions of individuals. The Avian classification (Figure 14) was able to distinguish small areas with low Simpson's diversity, all other classifications do not have the resolution to identify these areas of high single-species dominance. Only the Avian classification showed a statistically greater mean value, when compared to the Ebm, Hex and Square classification means (Figure 10).

Nestedness Temperature

Nestedness temperature was generally low throughout the study region in all classifications, with medians around 1 – 2.5. The Avian classification contained single-sample polygons for which a nestedness temperature could not be calculated (Figure 9). The Avian classification showed higher nestedness along the boundary between BCR 12 and 13 (Figure 15), however overall exhibited a lower mean nestedness than all the other classifications (Figure 10).

Internal Spatial Trend, via PCNM

The amount of variation in species composition that can be explained via the spatial arrangement of points within polygons ranged widely in all classification schemes. Median polygon adjusted R-squared terms were around 20% in all classifications; leaving aside the

Basin and Ecod classifications, which could not be analyzed), and ranged as high as 93% in the Hex classification. Ecobas had the lowest maximum value, at 62.6%, but no classification could be said to produce polygons with no spatial variation in species composition. The myriad single-sample polygons present in the Avian (Figure 16) classification prevented the use of many data points in that analysis. There were polygons in all classifications that had very low or zero spatial component to species variation.

Discussion

These analyses demonstrated the impacts of classification choice on the detection of spatial patterning of avian biodiversity, and highlight a number of potential avenues for scientific investigation. The results of the hierarchical clustering validated the existing delineations of Bird Conservation Regions in the study area, however the interface between BCR 12 and 13 exhibited great variation in richness and species composition, and suggest that management strategies in these areas should be trans-boundary. The biogeography of breeding birds in Ontario reveals a great deal of fine-scale spatial patterning. The overall distribution of avian biodiversity shows a strong divergence of the data into two clusters, roughly coinciding with the boundaries established for the Bird Conservation Regions 12 and 13, providing external validation to the previous process which defined these regions. A further partitioning reveals finer scale differentiation among these two groups, and the spatial effect is to fragment much of the southern region into a heterogeneous pattern, while large sections of the Boreal Transition region remain relatively homogeneous (albeit undersampled when compared to southern areas).

A wide range of responses to classification choice were observed across the diversity metrics examined. In general, similarly-scaled classifications exhibited similar responses, although the Avian classification generally showed idiosyncratic results. Polygon richness and beta diversity values showed the greatest variation across classification schemes. Coarse-grained classifications, such as the ecodistrict and basin classifications suffer from sample size and aggregation issues that lead to low statistical significance for diversity metrics. Fine-grained classifications

(e.g. Voro and Avian) suffer from a large volume of polygons, which precluded some diversity analyses.

The Calinski index comparison provided a good summary of this study; large aggregations of points by expert opinion (BCR) and species composition clustering (via hierarchical tree) describe a great deal of the structure in these data, followed by broad classifications of hydrology (Basin) and geomorphology (Ecod), with the union of the two (Ecobas) following thereafter, then the municipal (Muni) classification, followed by the Square, Hex and Ebm, with equal index values, and finally the Avian surface (which showed poor performance because other many spatially distinct polygons share similar species composition).

Classifying the region into even a few broad species categories produced extensive fine-grain heterogeneity, predominantly in the south. The strong initial splits of the hierarchical analysis suggested that relatively few yet very distinct species assemblages exist in this region. The spatial effect of these few classes produced a very heterogeneous arrangement of polygons, generating a finely grained network in the south, with a few larger, more extensive continuous polygons found around the greater Toronto area. Examples of each cluster type were found throughout the study region, despite a definite geographic trend following the intact northern forest, and the areas of extensive human influence. The broad separation between the clusters shown by the high Calinski index values, coupled with the spatial agreement with BCR boundaries suggested that these clusters are valid (Gordon 1999).

Large magnitude Calinski values across the range of classifications suggested that while broad-scale classifications explained a large component of the variation in avian biodiversity, many other finer groupings capture important aspects of extant biogeography. There were many potentially appropriate ways to classify this study region that make sense with regards to bird diversity patterns.

Polygon-level alpha diversity increased with mean polygon area, as expected by the species-area curve (Smith 2010). Finer-scale classifications such as Square and Hex, not generated with thought to species composition or underlying geomorphology, tended to produce

lower richness values (as they artificially separated locally biodiverse areas such that the concentration is diluted across multiple polygons); Avian and Ebm were better able to define smaller areas of high biodiversity, presumably because their borders better reflect ecological boundaries affecting diversity patterns.

Mean point richness results were also influenced by classification choice, although less dramatically. Larger classifications (Ecod, Basin and Ecobas) were not able to capture a great deal of subtle variation in mean richness, as mean values from polygons that contain a range of richness tended towards the mid range. As it did a better job of producing homogeneous polygons, the Avian classification did not suffer from this masking effect, revealing more fine variation than any other classification.

Point-level mean beta diversity may be a useful tool to detect polygons that have potential for remediation, or that are currently suffering biodiversity loss. High beta diversity indicates that some points within the polygon have high richness, but that high local diversity is not common throughout the polygon. Are species absent from a point because they cannot exist there, or because they cannot get there? In beetle assemblages, Holland (2010) has suggested that beta diversity is the result of dispersal distances. As birds are not dispersal limited to the same extent that beetles are, beta diversity may be expected to be due to differences in habitat. This may be due to a localized resource (i.e. particular breeding site conditions) or a broader disturbance (due to land-cover conversion for example). In the former case, local conservation effort may be able to increase the distribution of essential habitat characteristics. In the latter case, broader land-use strategies that contribute to ecological remediation may have a good chance of increasing polygon level richness. The identification of polygons with high mean beta diversity can guide research, ensure that remaining high richness areas are identified, monitored and protected, and suggest further investigation into the causes of nearby species paucity. Areas with low beta diversity are less informative, as a homogeneous low biodiversity polygon may have similar beta diversity to a consistently species rich area. As beta diversity is the difference from the realized to the potential species pool, a polygon with

low overall potential will tend towards small differences. Ideally, conservation and remediation efforts will target areas with high richness, and high beta diversity, with the goal of increasing the distribution of existing biodiverse hotspots.

Low Simpson's diversity indicates a highly dominated species assemblage, such as a large foraging flock, or a high density breeding area. High Simpson's diversity indicates a more even distribution on average. Classifications were generally highly even overall, with the Avian scheme detecting a number of small, low value polygons that contain high concentrations of single, dominant species. These results may simply indicate the difficulty in making accurate abundance estimates in high richness areas; a given amount of sampling effort will only detect so many individuals, so that as richness increases, the accuracy of abundance estimates declines.

Although the concept of 'nestedness' is still in its early stages, it shows strong potential to direct conservation effort towards areas that while species poor overall, contain species sets that strongly resemble those found in remnant high richness areas. Highly nested polygons are examples of potentially-equivalent natural assemblages of species which have been degraded, presumably subjected to pressures leading to a consistent pattern of biodiversity loss. These easily lost species may serve as useful indicators of historical baselines, and highly nested areas may be useful targets for remediation. Nestedness values ranged from near zero (indicating a highly ordered assemblage, with a regular pattern of species loss from high richness to low richness), to over eight, indicating a highly disordered polygon whose species composition varied unpredictably from point to point. The undersampled nature of some polygons in the Avian classification merits attention, as many polygons were unsuitable for analysis. However the principal large northern polygon was heavily sampled, and reveals a highly nested diversity structure, providing a further conformation of the validity of the hierarchical clustering (as the survey provided ample point counts from which to estimate the diversity of this polygon, yet species composition remained highly similar across all these points).

Finally, the analysis of the PCNM spatial component of species composition high-

lights a number of regions throughout the south that show very strong association with sampling distribution. High spatial structure in polygons may indicate they contain points with markedly different composition from their surroundings. It is interesting to note that larger polygons did not tend towards a greater spatial component of species variation, which indicates that they may indeed be consistent in species composition across a large extent, even if patterns of heterogeneity exists within them. The Square and Hex classifications tend towards higher values, more evidence that they may be appropriately sized, but not well placed to minimize within polygon variation in species diversity. Ecobas has the smallest spatial component overall, indicating that much of the variation in species composition within polygons does not have a strong spatial trend.

Although not particularly helpful for distinguishing between classification schemes, the PCNM results highlight areas of high spatial variability that may be used to guide further sampling efforts; both large, extensive volunteer efforts, and smaller research projects. Polygons containing large spatial components of species composition may benefit from landcover specific targeting during further sampling efforts, to ensure that fine-scale pockets of richness are not missed altogether. High point-count polygons with low spatial components are well suited to BACI experimentation (Before-After Control-Impact), provided that those areas are well monitored before landcover change takes place. Spatial variance partitioning remains a worthwhile investigative technique, as it makes few assumptions about the mechanisms driving the propagation of the patterns it assesses (Borcard *et al.* 2004), in contrast to more widely-used techniques associating diversity patterns with coarse-grain remotely sensed land-cover data, whose mechanistic relationship with individual behaviour is uncertain and inconsistent (Antrop 2007). However, recent work suggests that this technique may tend to overestimate the true strength of the spatial relationship, and the best methodology to adopt has not yet been agreed upon (Gillbert and Bennett 2010). At the regional scale, it remains a useful tool to study and describe diversity patterning in the absence of sound mechanistic theory, and can guide the development of further research studies at a scale more appropriate to direct

experimentation.

While broad-scale classifications have real merit, and are useful first pass filters when making broad planning decisions, there are substantial finer scale details that will be missed if land-use change is planned solely at this resolution, especially throughout the boundaries between BCRs. Coarse scale estimates of richness may make a location appear more important than it truly is, causing conservation efforts to squander limited resources in species-poor areas. At the other extreme, too fine a classification will require greater sampling effort to further monitor the entire region, and may preclude the use of certain informative metrics requiring larger sample sizes. Instead of selecting one particular scale at which to plan conservation reserve networks, a nested hierarchical approach may prove useful, with coarse analysis used to make broad policy decisions followed up by finer scale targeting of conservation effort (White *et al.* 1999).

The hierarchical analysis demonstrates strong division between many of the points in the south, while showing strong homogeneity amongst many of the points in the north. The lack of strong spatial structure in northern polygons in the Avian, Muni and Ecobas classifications suggests that there is little spatial variation in species composition in these areas.

The paucity of northern data in Ontario is problematic, as the coarser patterns evidenced in these analyses could indeed be the result of sampling bias and location-based artifacts. Additional volunteer surveys for invertebrate, mammal or vegetation diversity will be informative, as birds are less limited by topographic features; flight provides access to a greater extent of the world than that available to many other organisms. The diversity patterns observed here in birds may not prove to be similar to or representative of overall biodiversity.

Intensive, human-induced landcover change produces a highly fragmented pattern of remnant natural areas, placing strong spatial pressure on naturally-adapted species to use those remnants as habitat. This effect may be powerful enough to mask or override natural distribution patterns, and should be considered in conservation planning amongst human dominated areas. Given the current distribution of human-dominated landcover (fine-grained urban and

agricultural landcover in the south, perforated by the existing road network, large undisturbed areas further north) it is not unreasonable to expect similar fine-to-coarse gradients in appropriate grain when managing other forms of diversity in this region. If the primary driver of biodiversity patterning today is indeed human induced landcover change (Newton *et al.* 2009; Koh and Gahzoul 2010; Theobald 2010), then this may not be so outlandish a claim. However, many organisms are much less able to disperse themselves across the world than birds, and while flighted organisms may be able to select optimal habitat over a broad scale, many may be trapped in local maxima, unable to reach optimal areas due to dispersal limitations (Araújo and Rahbek 2006). These individuals either quickly die out, or adapt their behaviour to make do. Proximity to existing populations would understandably play a larger role in determining the distribution patterns for these less mobile organisms.

Further persistent data collection may reveal whether these observed patterns are stable over time, or whether these patterns change regularly or stochastically (Meentemeyer 1989). Many waves of development have occurred across the study region (Dean *et al.* 1998), urban expansion and road development have regularly perforated the natural landcover, and the effects of these large construction events may have longer term impacts that are not yet apparent. For example, James *et al.* (2007) have shown that spatial legacies of land-use change in boreal forests, persist over 200 years. The continual state of disorder may preclude any reliable long term predictions of biodiversity patterning, highlighting the need to delimit areas that are highly important today, and reduce the rate at which they undergo detrimental human disturbances.

The choice of which classification scheme to adopt when planning in this region will be to some extent imposed by circumstance, resources and intent (Ferrier and Wintle 2009). Many questions require broad answers, and it is simply not appropriate to focus at a fine grain. As well, diversity data is not always collected across an extent such as the OBBA, or is not generally available at this level of detail. Using these data to investigate the implications of classification selection provides a case study with which to base the design of further sampling regimes. Strong evidence exists for the presence of fine scale diversity patterns throughout the

south, more northern results suggest a coarser grain may be appropriate (a result confounded by the lighter density of northern OBBA sample points). This knowledge of the implicit biases introduced by any potential classification may guide planners and decision makers towards more considered action.

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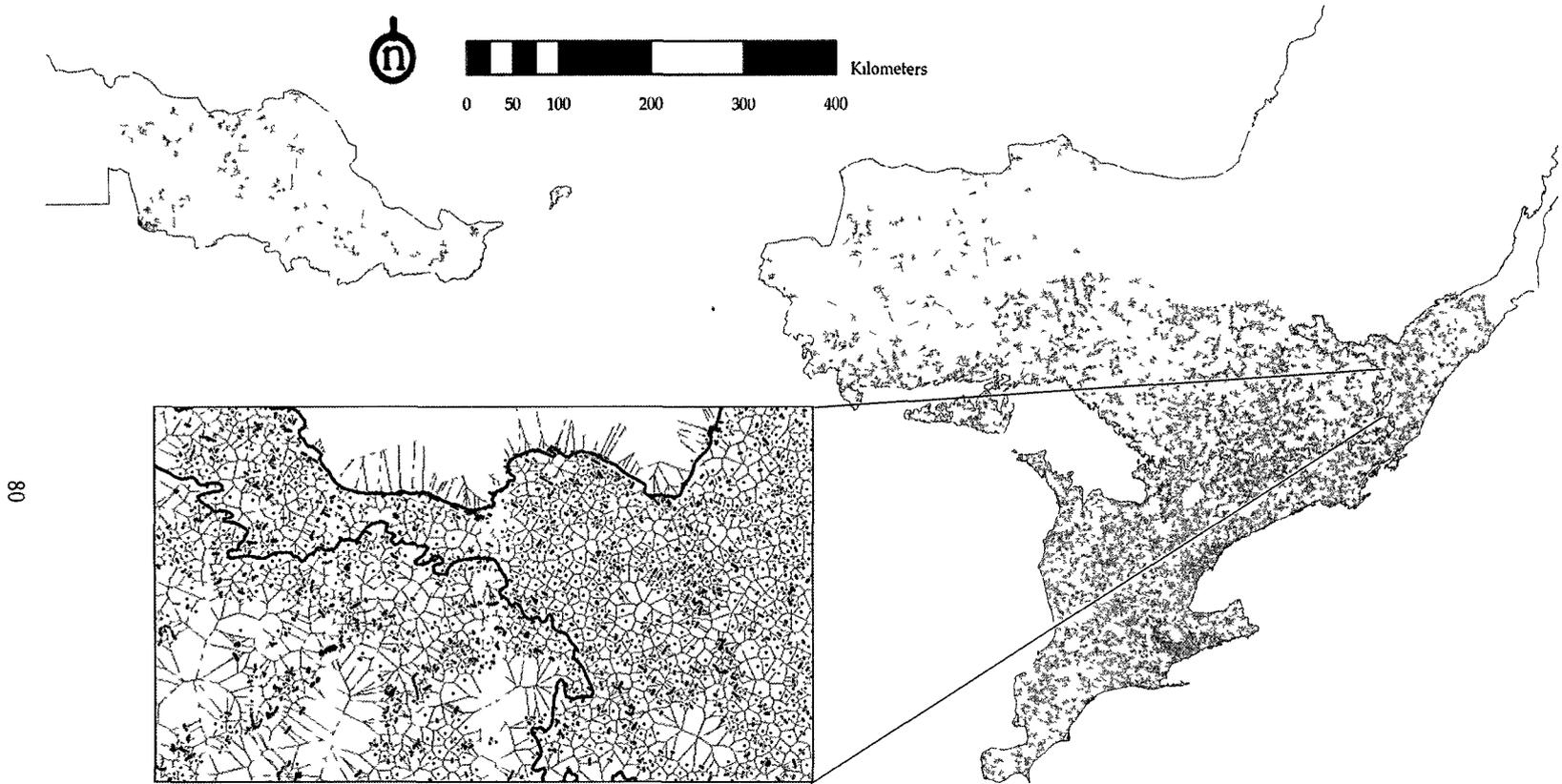
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08

Figure 1: Ontario Breeding Bird Atlas (OBBA) point counts included in these analyses (in green), with Voronoi tessellation polygons (in black) included to show spatial tiling of points across the study region. This map shows the areas covered by Bird Conservation Region 12 and 13, boundaries are shown in red. Inset reveals finer scale spatial patterning of the Voronoi tiling.

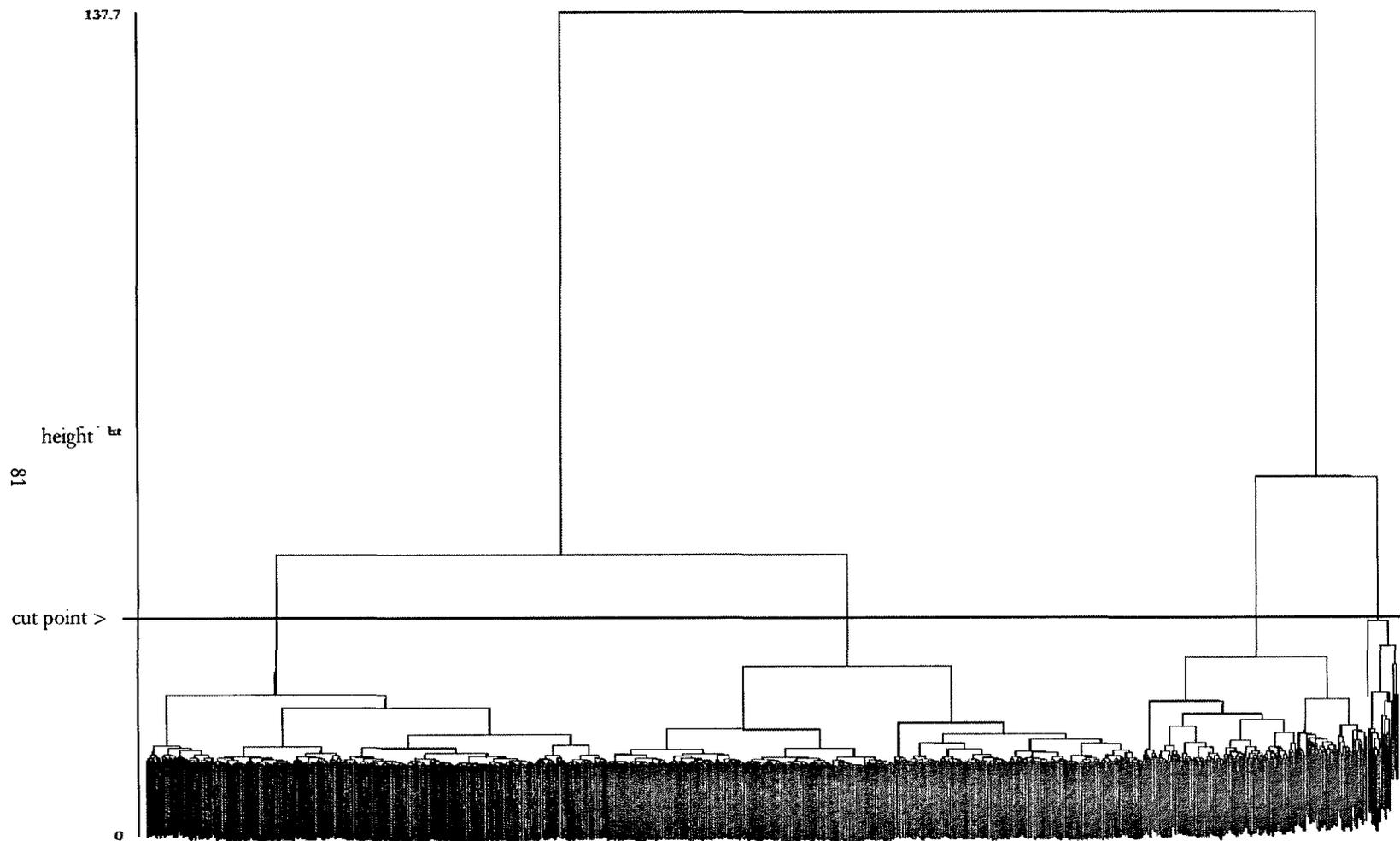


Figure 2: Dendrogram representing a hierarchical partition of 50993 Ontario Breeding Bird Atlas point counts, generated using Ward's variance-minimizing cluster algorithm on a Euclidean-distance matrix derived from a Hellinger-transformed sites-by-species abundance matrix. Colour represents the four clusters formed by a cutting the tree at 70% of its height.

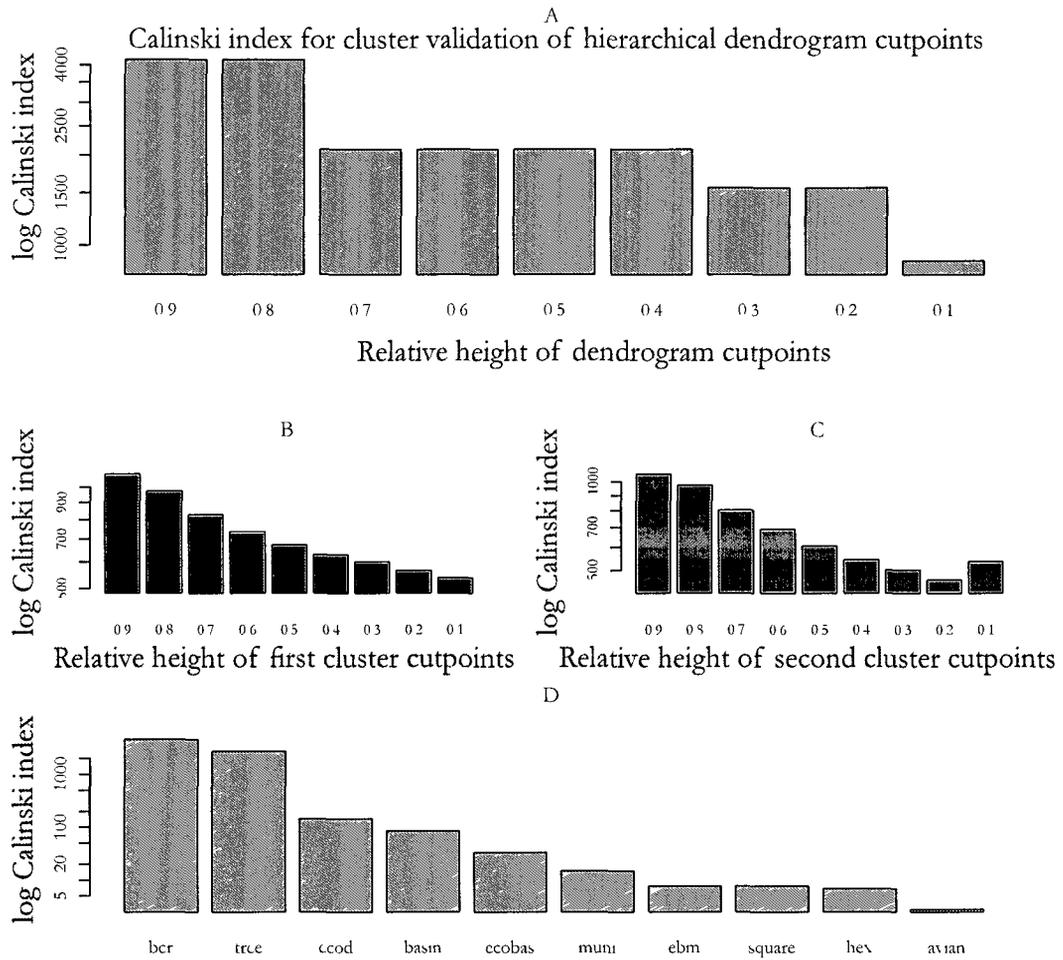


Figure 3: A. Log-transformed Calinski index values for the clusters formed from cut points spaced evenly across the height of the point dendrogram, this ratio of between to within cluster species variance indicates how well defined the clusters are, a low value indicates a poor fit. The middle figures B. and C. show a similar cutting process for each of the two clusters formed by the first cut, these clusters align closely with BCR regions 13 and 12, respectively. D. shows the index values for the chosen classification schemes. Additional broad classifications are included for reference: BCR (bird conservation regions 12 and 13, validating this division for conservation planning purposes) and tree (the four cluster class result from a hierarchical clustering).

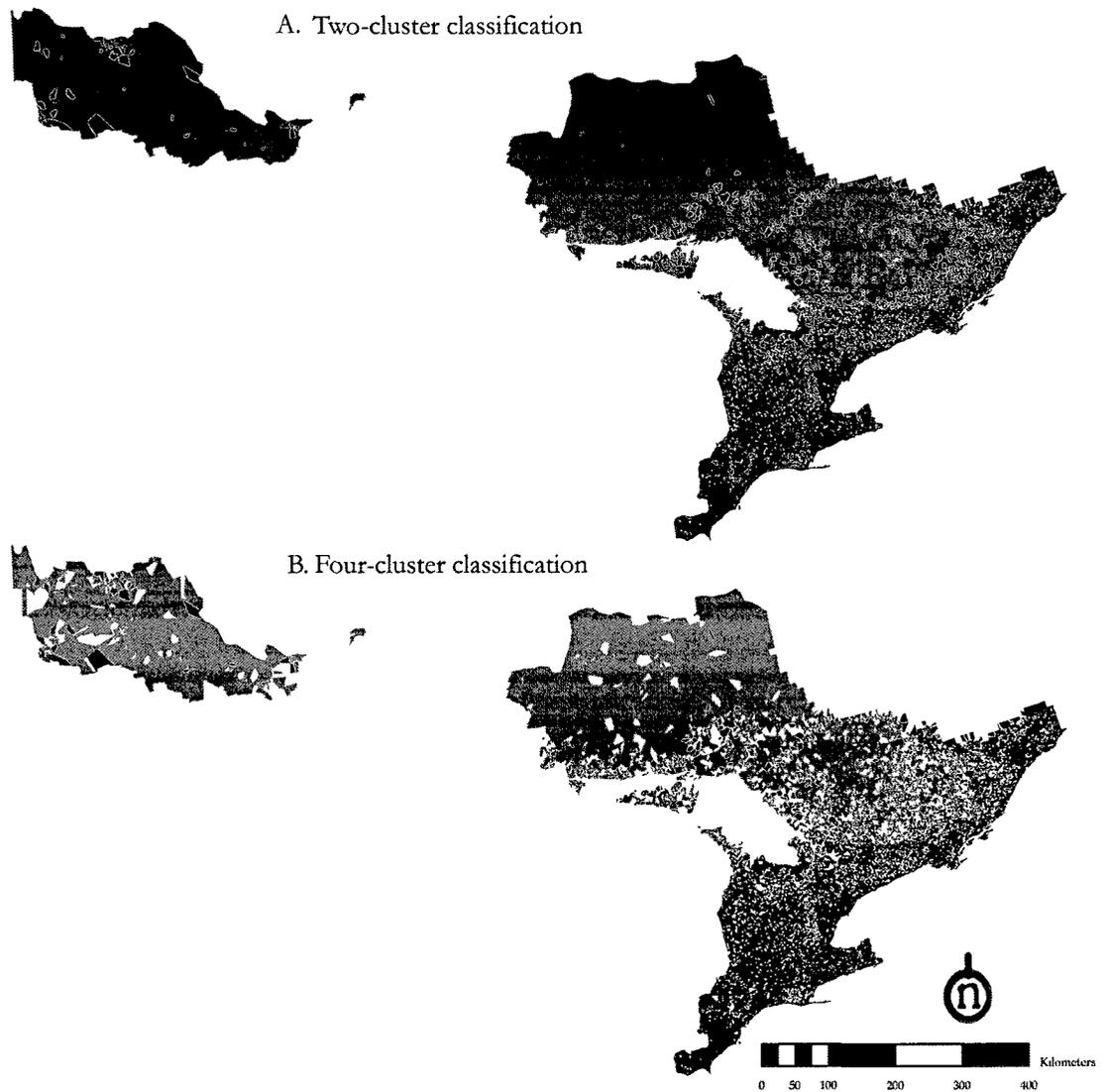


Figure 4: Spatial classification of avian biodiversity produced by merging neighbouring Voronoi polygons that share the same cluster. A. Based on two clusters. Orange areas roughly align with the boundaries of Bird Conservation Region (BCR) 12, green areas with BCR 13 B. Further subdivision into four clusters (orange and yellow, blue and green). Subsequently used as the Avian classification scheme.



Figure 5: Inset showing the fine-scale detail of the Avian classification scheme. Linear geometric artifacts are visible, as discussed in the text. Most polygons are formed of smaller neighbouring polygons in the same cluster, however there are numerous examples of single isolated polygons surrounded by a polygon of another cluster-type (see label A for example).

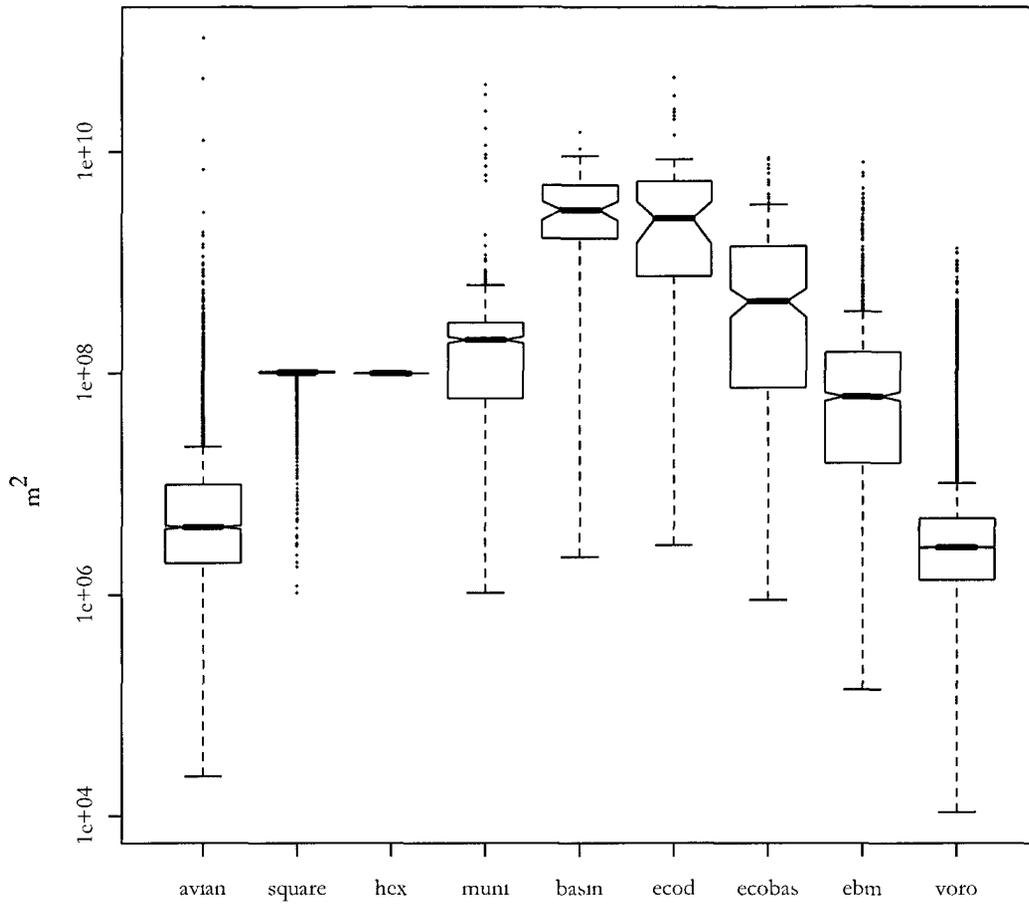


Figure 6: Boxplots of polygon areas, showing the size distribution of polygons in each classification scheme. Notches indicate the 95% confidence limits around the median. Boxes represent the interquartile range, whiskers extend 1.5 times the interquartile range, outliers beyond this range are represented with points.

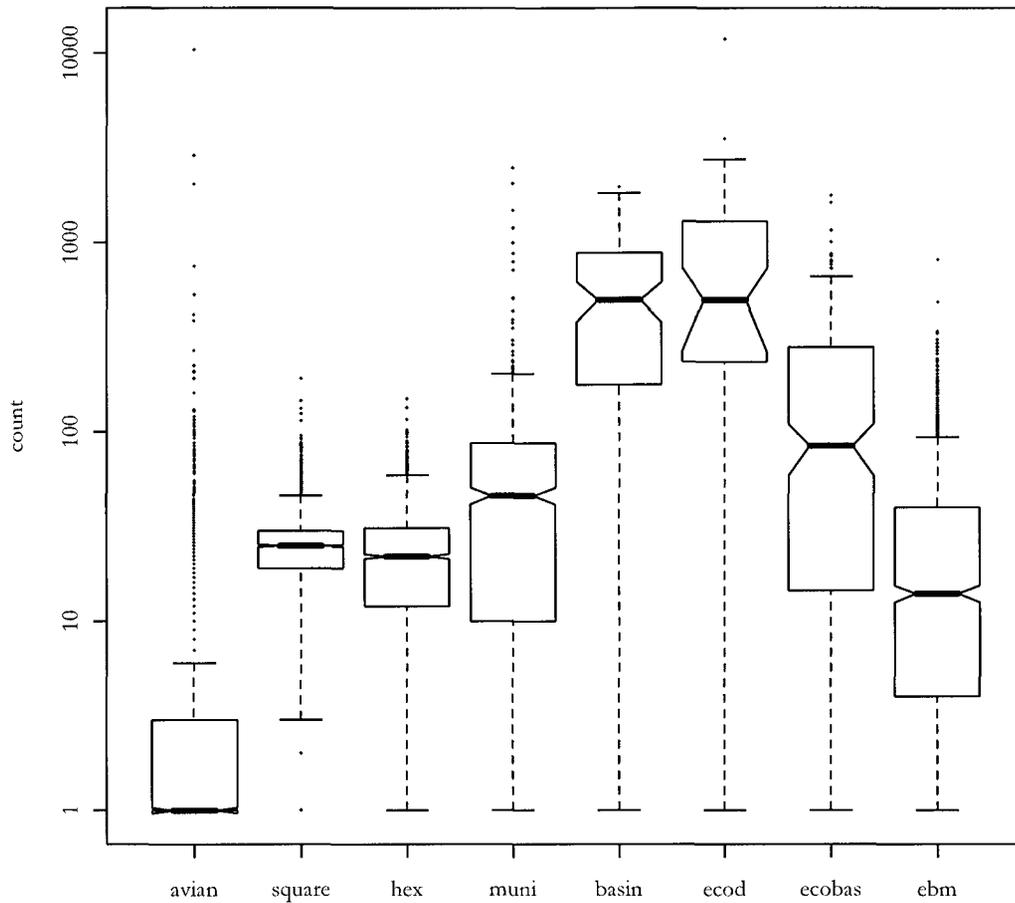


Figure 7: Boxplots of the polygon count values, the number of points assigned to each polygon in the classification scheme. Notches indicate the 95% confidence limits around the median. Boxes represent the interquartile range, whiskers extend 1.5 times the interquartile range, outliers beyond this range are represented with points.

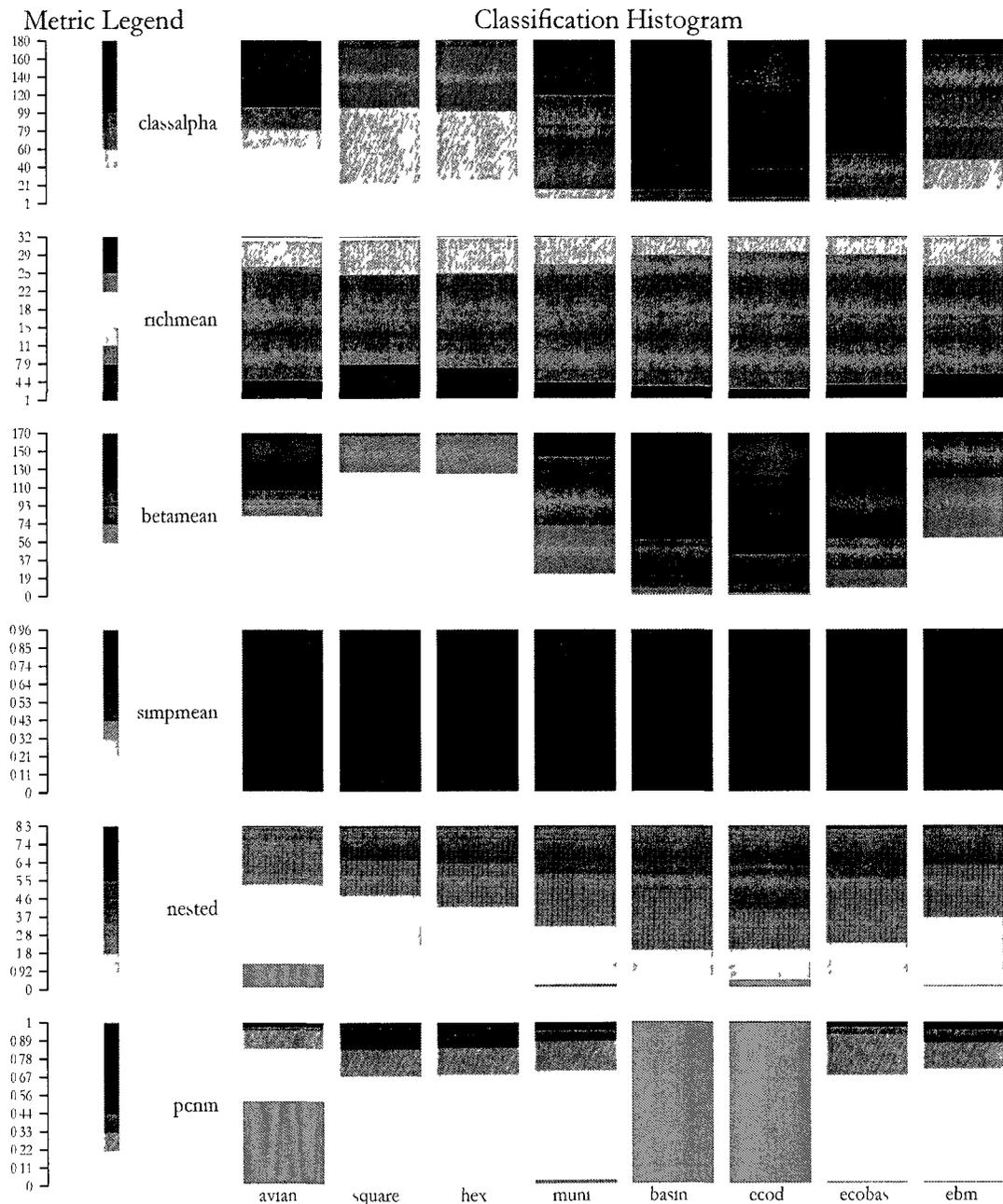


Figure 8: Classification comparison of diversity metrics: polygon richness (classalpha), mean point richness (richmean), mean point beta diversity (betamean), mean Simpson's diversity (simpmean), nestedness temperature (nested) and the proportion of within-polygon composition variance that can be explained through spatial variables (PCNM). Each metric is coloured using equal-interval breaks, and each polygon value is weighted by the total number of points that polygon contains. Each bar shows the total proportion of all points that are assigned to each range, for each classification. Grey indicates the proportion of points that could not be included in the analysis (polygons had too many or too few points).

count	628	26.5	238	75	600	1000	190	31.5
	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-
area	127	16.4	161	163	507	1730	255	49.7
	37.1	94.8	100	441	3540	5830	1090	173
pcnm	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-
	1300	22.1	0	2370	2720	9150	1560	499
nested	0.22	0.2	0.204	0.22	NaN	NaN	0.188	0.221
	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-
simpmean	0.152	0.143	0.147	0.139			0.113	0.147
	1.13	1.95	1.77	2.13	2.25	2.34	2.07	1.8
betamean	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-
	0.918	1.25	1.13	1.1	0.939	0.931	1.09	1.12
richmean	7.41	39.8	37.9	50.1	95.5	96.6	61.4	34.7
	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-
classalpha	12.5	15.8	16.8	28.8	35.3	35.9	36.9	24.5
	10.2	9.69	9.57	10.1	9.55	9.65	9.72	10.2
classalpha	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-
	17.6	49.5	47.4	60.2	105	106	71.1	44.9
classalpha	+/-	+/-	+/-	+/-	+/-	+/-	+/-	+/-
	13.2	16.7	17.7	29	34.5	34.5	37.2	24.6
	avian	square	hex	muni	basin	ecod	ecobas	ebm

Figure 9: Diversity metric summary showing mean and standard deviations for each classification, coloured using the same equal-interval symbology defined for Figure 8.

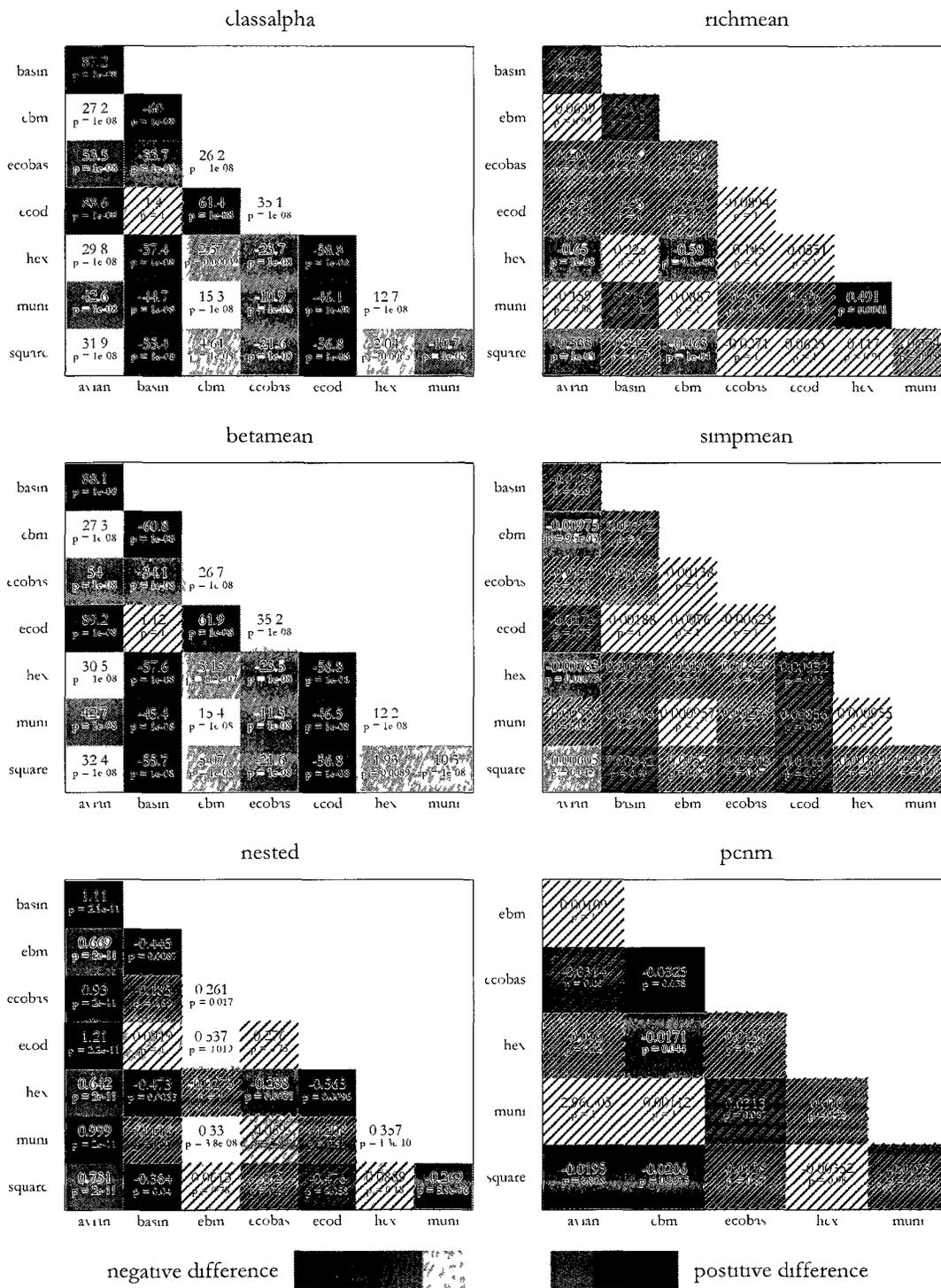


Figure 10 Tukey's Honestly Significant Difference comparisons show differences in mean metric values amongst all classifications, for each diversity metric. The differences in mean values (row minus column) are compared, and coloured to identify which classifications have the greatest difference from each other, blue for large negative differences, red for large positive differences. PCNM values could not be calculated for Ecod and Basin classifications. An overall alpha of 0.05 was maintained by reducing the pairwise alpha value in each test. Comparisons that could not be distinguished statistically from zero are denoted with hatched lines.

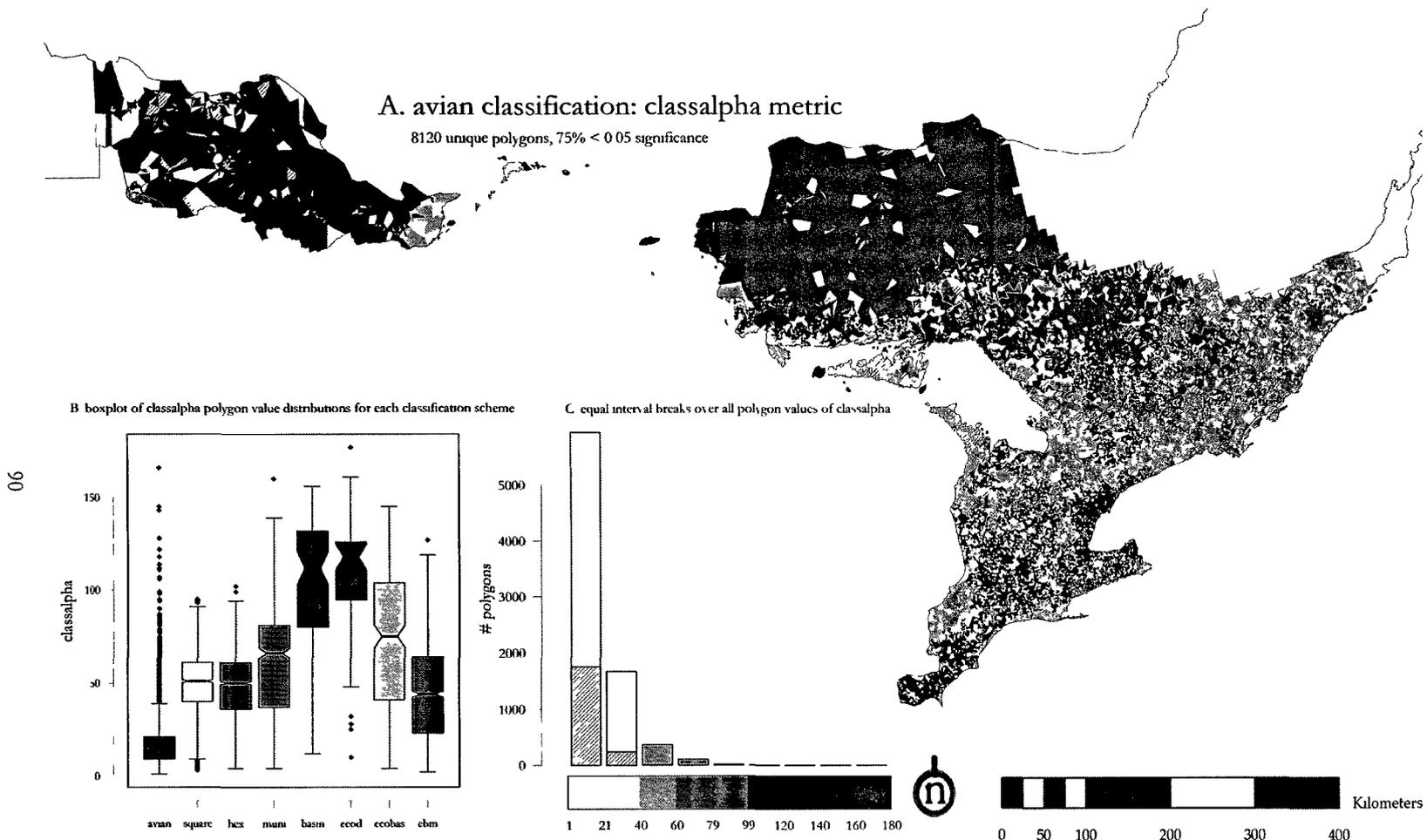


Figure 11. A. Avian classification scheme showing total polygon richness (class alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

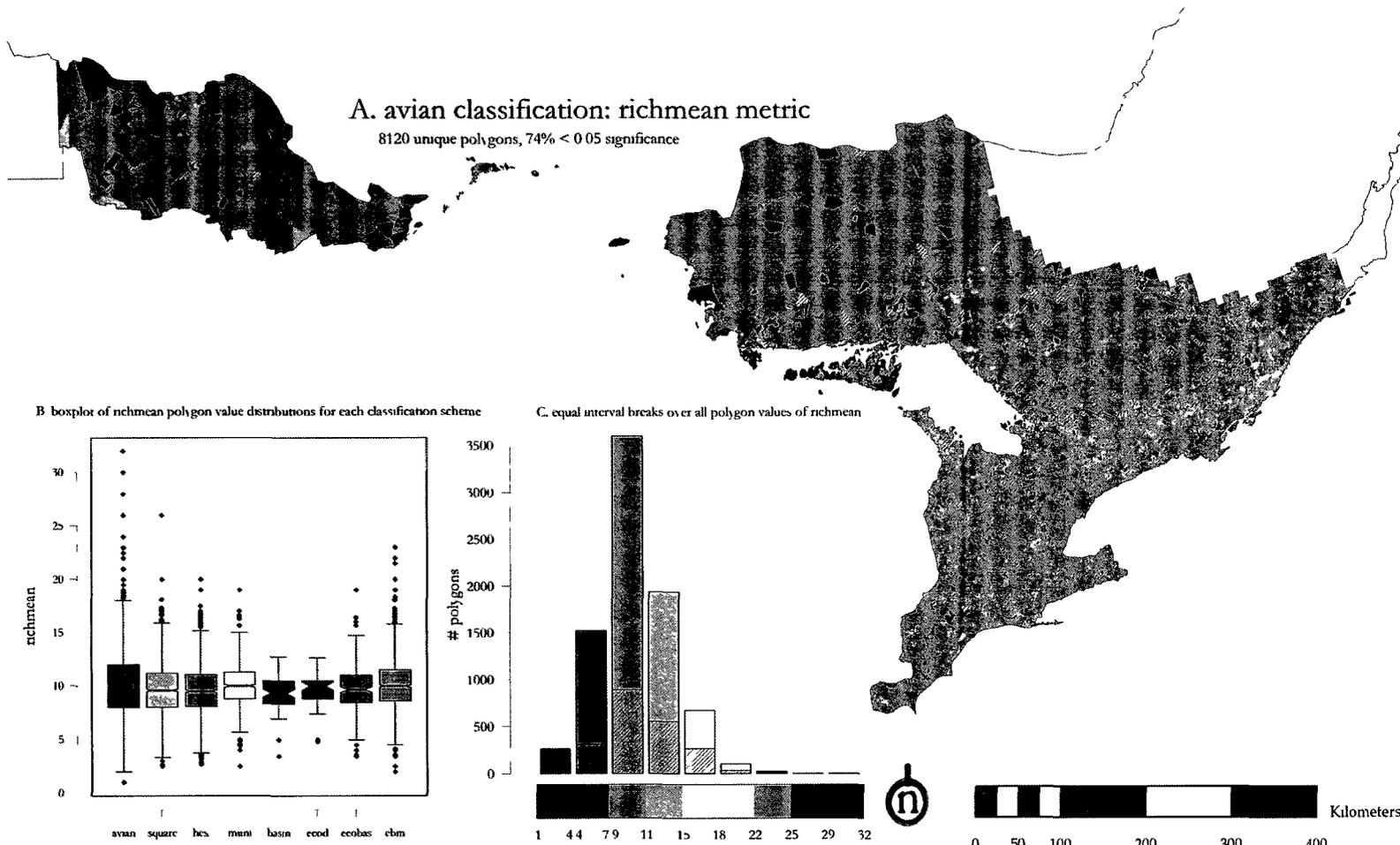


Figure 12 A Avian classification scheme showing mean point-level species richness (average point alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

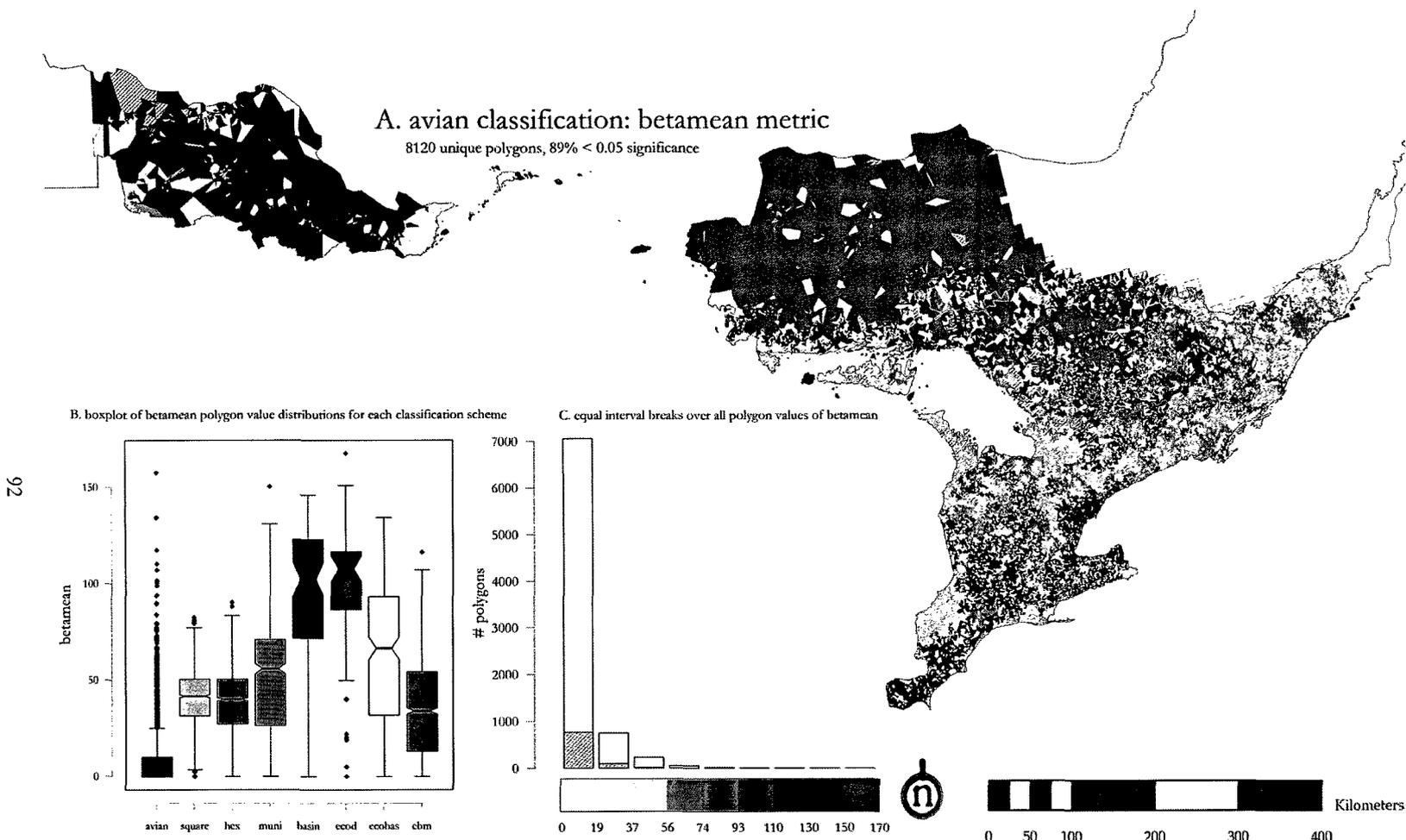


Figure 13: A. Avian classification scheme showing mean point-level beta diversity (the difference from the polygon-level species richness and the point-level richness). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

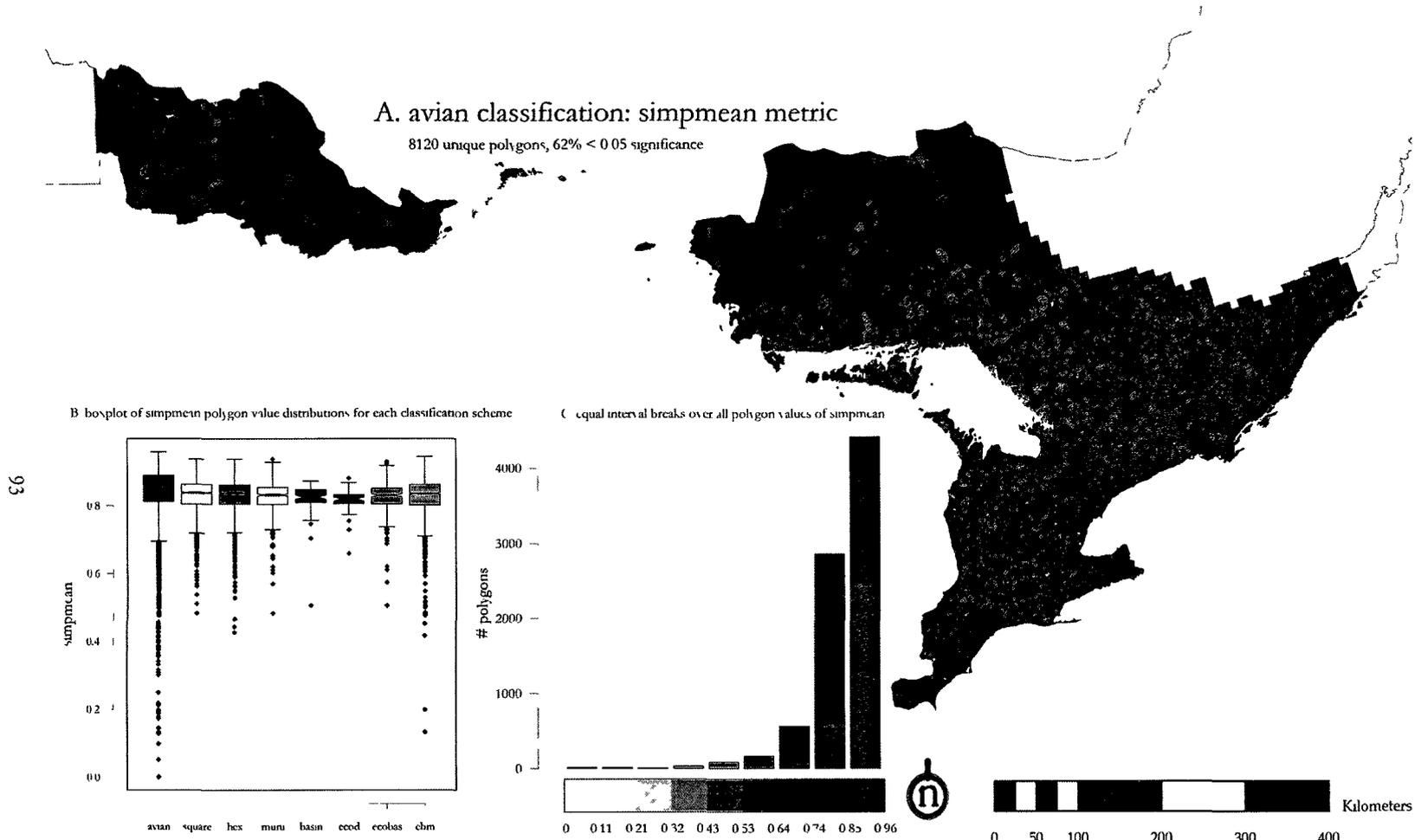
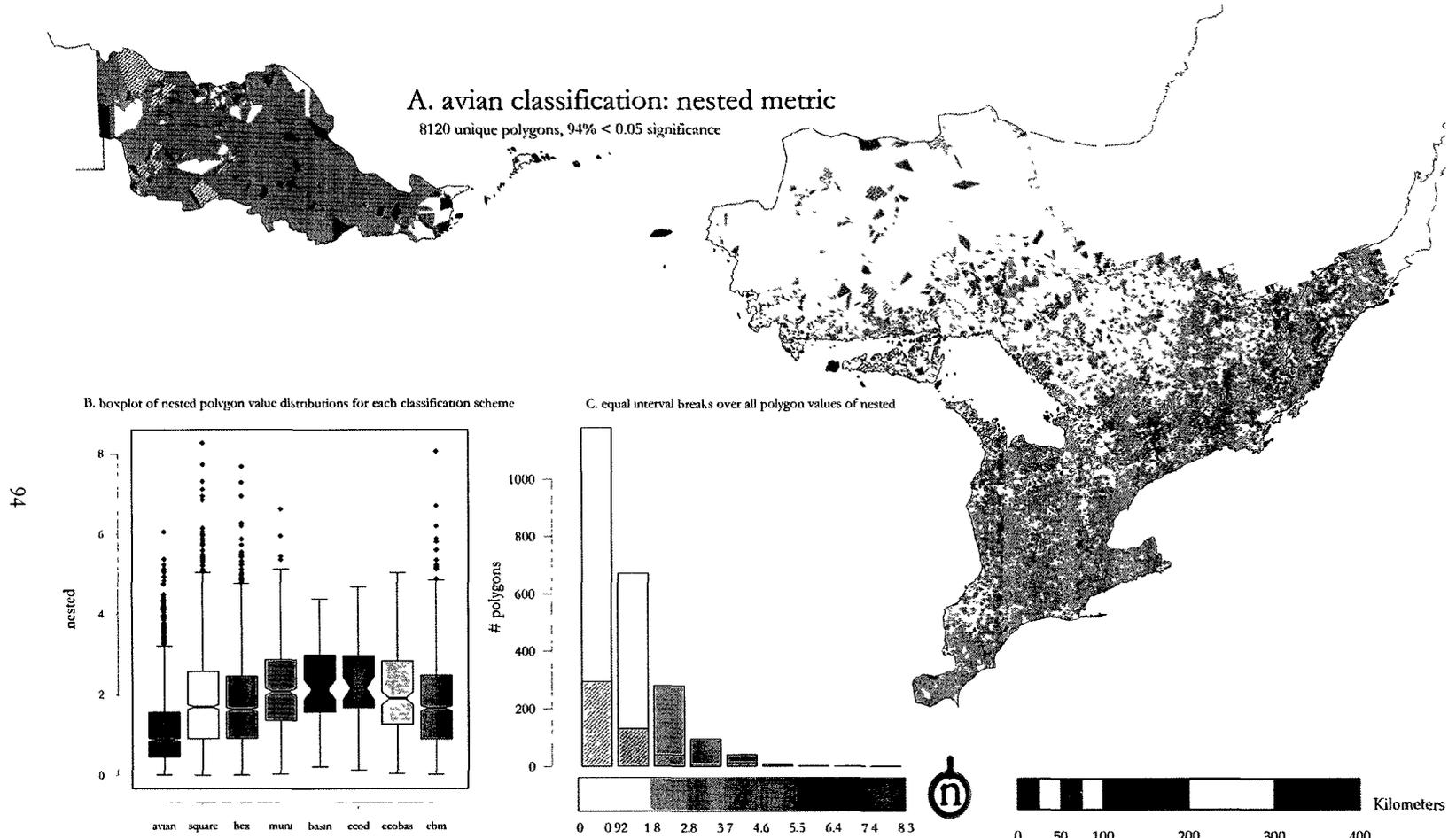


Figure 14 A Avian classification scheme showing mean point-level Simpson's diversity (the evenness of species composition). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.



94

Figure 15: A. Avian classification scheme showing nestedness temperature (a measure of the disorder in species composition within polygons; low values indicate a regular nested pattern of species loss from high to low richness points, high values reflect more disordered structures). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Light grey polygons contain less than three points, and cannot be analyzed. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

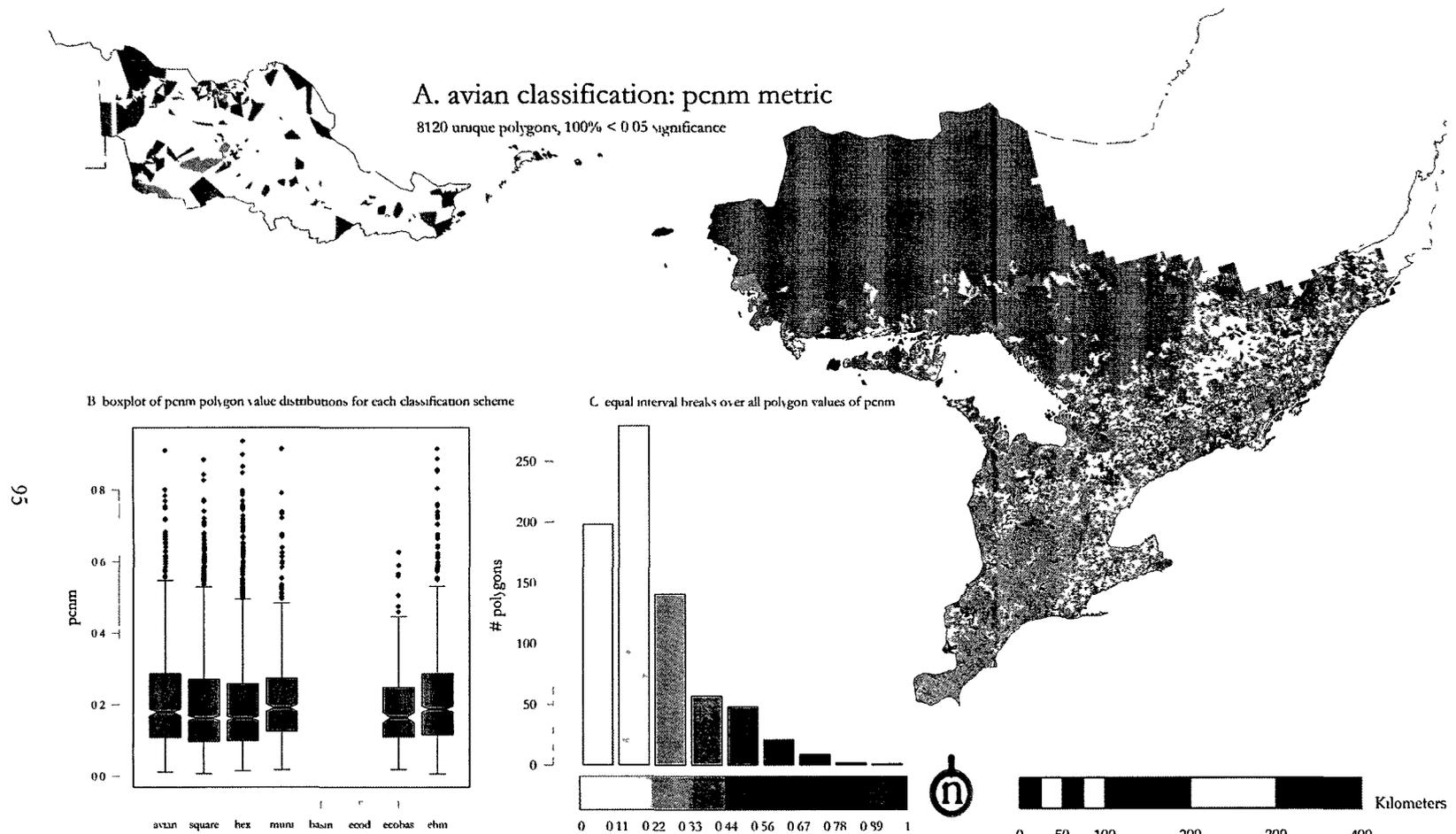


Figure 16 A Avian classification scheme showing the amount of variation in polygon species composition that can be explained using spatial components (described by an adjusted R-squared term using PCNM ordination). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Light grey polygons contain less than three points, and cannot be analysed. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

Chapter 3

Systematic Conservation Planning Using Different Species Sets, Targets and Spatial Classifications: A Case Study for Ontario

Introduction

There has been growing recognition that the existing set of protected conservation areas are insufficient to conserve extant biodiversity (Dobson *et al.* 1997; Snyder *et al.* 1999; Rodrigues *et al.* 2004; Warman *et al.* 2004). In Canada, the existing opportunistically established reserve networks have been found to be inadequate for the conservation of many species, particularly species at risk (Warman *et al.* 2004; Deguise and Kerr 2006; Freemark *et al.* 2006). The proportion of overall biodiversity that is represented by existing protected areas is highly skewed; many protected areas can be found in habitats that have historically been unproductive or isolated from human contact (Rodrigues *et al.* 2004; Warman *et al.* 2004). The present and expanding extent of human-induced land-use change makes targeting the conservation and stewardship of what remains all the more important.

In this study, a systematic conservation planning approach is adopted to derive targeted conservation solutions for a broad range of bird species. By investigating conservation solutions across a range of potential conservation targets, the sensitivity of the conservation problem can be explored. How frequently are particular areas chosen for conservation at a particular degree of conservation effort? By summarizing the frequency of selection across a range of targets, a conservation priority surface can be created. These priority surfaces are useful means of summarizing the relative contribution each area makes towards the representation of biodiversity.

However, the results of these analyses are dependent on the data which inform the conservation problem. The choice spatial classification plays an important role in determining how spatial diversity data are included in systematic conservation planning. The number and nature of 'planning unit' polygons defined by the spatial classification influence the constraints

which define the conservation planning problem. How much regional variation in priority is observed across a range of classification schemes? And what are the practical implications of planning using units defined with a non-ecological focus?

The species set chosen for conservation may also play a large role in driving the pattern of the priority surface. If conservation effort focuses on a small subset of overall biodiversity, how will this change the computed conservation priority surface? If the distribution of subset species overlaps well with the overall species set, the set of selected planning units will provide equal coverage to the whole set, 'sweeping along' other species with the targeted set (Kiestler et al. 1996; White et al. 1999). The difference in priority between these two species sets gives a visual means of distinguishing the impact of focussing on the subset.

Systematic approaches to conservation planning has flourished over the last decade, with the advent of broader, finer, and more thoroughly sampled ecological data, more powerful computing capabilities, and a move away from species-specific conservation plans towards more regional process and pattern driven efforts. 'Systematic conservation planning' has appeared as a keyword phrase 134 times in published papers in the span 1996 to October 25 2010; these papers have been cited 2579 times in that period, showing a marked increase since 2001 (Web of Science 11 November 2010). The term 'systematic conservation' refers to the selection of a set of areas for conservation in order to meet explicit and *a priori* conservation targets (Margules and Pressey 2000; Pressey 2002). The total cost of the set depends on the degree to which the areas in the set meet conservation targets, coupled with the cost of including those areas in the set (Ando *et al.* 1998). The effectiveness of a conservation design is a function of how well it meets its stated targets. The efficiency of the design is a function of how costly it is to achieve those targets.

Systematic conservation planning has been used in both marine (Leslie 2005, Game *et al.* 2008; Klein *et al.* 2008) and terrestrial contexts (Gonzales *et al.* 2003, Jenkins and Giri 2008), and has recently undergone extensive review (Moilanen *et al.* 2009). The first published example of the philosophy of complementarity underlying this technique appeared in Kirkpatrick

(1983), involving the selection of the smallest set of areas which would between them contain all the species in the study, the so-called Minimum Set or Knapsack Problem (Silvano and Toth 1990). Although at that time computation was chiefly done by hand, modern programs such as Marxan (Ball *et al.* 2009) and C-Plan (NSW-NPWS 1995 - 2002) provide powerful tools for exploring conservation planning problems, selecting planning units across a region to generate a set conservation reserve design solutions that efficiently meet *a priori* feature targets (Ball and Possingham 2000, Possingham *et al.* 2000), using a variety of algorithms (compared in Csuti *et al.* 1997 and Vanderkam *et al.* 2007). These features may be any spatially-distributed resource that can be valued in an explicit and quantified manner (see Watts *et al.* 2009 for modern extensions into multiple objective land use optimization). The explicit nature of objective cost functions makes them appealing decision support tools in multi-stakeholder land-use planning; they provide an opportunity for initial collaboration between stakeholders to define both the features, the targets, and the nature of the costs of selecting particular planning units, which in turn provide an explicit criteria for evaluating the success of a reserve set (Pressey and Bottrill 2008). By encouraging stakeholders to quantify their expectations with regards to land-use design, the functional trade-offs of any particular situation can be made apparent. By encouraging stakeholders to explicitly declare their objectives, conflicting land-use demands can be fairly and objectively addressed (Moilanen *et al.* 2009).

Systematic conservation planning operates on a regional planning unit polygon set, coupled with associated data on the extent or abundance of conservation features found within these polygons. Sets of polygons are selected randomly, and then iteratively improved to minimize an objective cost function (the sum of the total cost of the planning units selected, and the cost associated with failing to cover conservation features to the level required). Objective cost functions evaluate designs with regards to *a priori* feature targets and planning unit costs. There is a cost associated with failing to meet feature targets, and a cost of choosing a given unit of land for conservation. For any given land-use pattern, a total cost can be calculated by summing costs from target shortfalls with the cost for including each polygon in the

set. Optimal land-use designs will meet all targets and contain an efficient set of polygons; sets that meet targets with a smaller number of polygons and smaller total area will have a lower total cost. Sets which fail to include all features incur a correspondingly higher penalty cost. Similarly, sets which meet targets but have many redundant polygons that do not contribute greatly or uniquely to the targets will have a high planning unit cost. In this way, efficient sets are selected for.

The practical result of these techniques is an ability to quickly and consistently generate and compare solution sets for a wide range of conservation and land-use design problems. However, the utility of these designs is contingent on the data structure used to generate them (Pressey *et al.* 1999). The configuration of the planning unit surface, the nature of the conservation feature data, and the magnitude of the conservation targets all play a large part in constraining the range of solution sets produced with these methods. The opportunity to generate objective and explicit land-use designs is influenced by these series of often implicit decisions when designing land-use strategies (Grand *et al.* 2007). The grain and placement of planning units, the breadth of taxonomic diversity included in the data, and the confidence in the long-term fidelity of existing patterns of diversity all play important roles in determining the actual impact of the regional plan.

A high resolution spatial classification with many redundant occurrences of each species may have many examples of non-overlapping low cost reserve solution sets that meet conservation targets, and an associated low priority overall. A coarser classification with fewer polygons aggregates a great number of points into the same polygon, leading to broad regions with high diversity (through the species-area effect; *c.f.* White *et al.* 1999), and greater conservation priority. Coarser classifications constrain the potential reserve solution-space, and increase the irreplaceability of each polygon accordingly. There are fewer unique combinations of polygons which will meet conservation targets, leading to reduced solution flexibility (and increased conservation priority, as aggregated polygons containing many regionally restricted species will be important to meet even low conservation targets).

Conservation efforts can be made more effective and efficient by designing for species assemblages as a whole, selecting appropriately-sized, biologically relevant planning units for conservation, and ensuring that these units are complementary to each other with regards to their species composition (Margules and Pressey 2000). This results in reserve sets composed of planning units with low internal heterogeneity, leading to more straightforward local management strategies (Plather *et al.* 2009). When using a classification scheme that more accurately represents natural delineations of species composition, there is less need for additional constraints on reserve selection configuration; costs such as spatial proximity or total reserve boundary length do not need to be incorporated into the reserve selection process (as noted by McDonnell *et al.* 2002), producing more elegant and interpretable conservation plans. Rather than applying a series of convoluted correction factors to minimize the conservation boundaries (and so drive sets towards more compact and clustered designs), it is more appropriate to select an ecologically relevant classification. This improves interpretation, because high priority polygons are selected solely due to the species composition found within them, and not due to any additional, overriding spatial constraints.

In this analysis, species abundances serve as the spatial features which drive the selection of planning unit polygons to meet a range of conservation targets. The maintenance of avian biodiversity has been considered a valuable conservation objective in many countries (European Union 1979). The Ontario Breeding Bird Atlas (OBBA; Cadman *et al.* 2007) was collected from a five year, 1000-volunteer survey of the province, providing a dense and broad spatial survey of bird abundance across much of Ontario. The OBBA dataset for Bird Conservation Regions 12 and 13 contained 50993 point count observations of 235 species. The fine scale of the southern sampling region is more suited to the requirements of systematic conservation planning. The Ontario portions of Bird Conservation Regions 12 (the Boreal Transition) and 13 (the Lower Great Lakes/St. Lawrence Plain) are well covered by OBBA data, and serve as the chief bounds of the study region. Bird Conservation Regions (BCRs) are delimited across North America (NABCI 2009) and are being used as a framework to guide

the monitoring and management of avian diversity at a broad level.

The consistent and widespread sampling methodology of the OBBA makes these dataset particularly useful, as aggregating data from disparate collection methods introduces the potential for spatial bias in composition and abundance estimates. A great deal of effort has gone into ensuring that these dataset is a reliable estimate of bird distributions across the province (Smith 2005). The OBBA dataset is a valuable and comprehensive dataset enabling assessment of the current patterns of avian biodiversity. A previous edition of the atlas collected from 1980 – 1985 allows a coarse assessment of the temporal trend of avian biodiversity in this region (e.g. Melles *et al.* 2010). Any conservation effort should be mindful that these data are only a snapshot of an ongoing process.

The process of planning unit delineation is particularly important. The grain of the sampling regime sets the minimum size of inference possible, and practical planning is often limited to existing planning units such as municipal boundaries, watersheds or coarse-scale ecological land classifications. The question arises, what are the practical implications of planning using units defined with a non-ecological focus? How much regional variation in priority is observed across a range of classification schemes? This analysis provides an opportunity to address these questions, by investigating the impact of planning unit classification and species set selection on conservation reserve design.

There are a number of potential classification schemes that may be used to define the planning unit set, and their delineation will have a corresponding effect on the aggregation of the raw OBBA point data into polygon-level conservation feature values. This analysis uses a variety of data-driven, ecological and political classifications.

Using the OBBA data, priority surfaces can be constructed for each of the potential classification schemes using the Marxan annealing algorithm. These priority surfaces indicate the likelihood that a given polygon will be needed for a conservation network, over a range of potential conservation targets. This ranking is a useful summary of conservation potential under uncertain conservation effort. This metric represents a unit's contribution to the reserve

network, given its local species assemblage and the regional distribution of species, as a function of the degree of conservation effort directed at a given planning region.

The practical influence of spatial classification on conservation planning is reflected in how each scheme aggregates the raw point data with respect to the location and ranking of conservation priority in each polygon in each scheme, and to the overall flexibility of the polygon set. Conservation target selection implies an existing or intended degree of effort. At the most minimal goals, the goal may be simply to represent regional biodiversity within the reserve set. The resulting solution set can be regarded as the complementary set of units covering all species in the most efficient fashion. This core area is then further expanded as conservation targets increase, providing additional, redundant coverage until at some level the entire planning region saturates, and all areas containing conservation features become important. A unit selected for conservation at low target values contains more unique species than a unit that is selected only at higher targets, i.e. adding only redundancy to the reserve network. Few conservation efforts are enacted wholesale; this metric provides a visualization of the trade-offs between minimal target, representational reserves and more intensive coverage of species distributions.

A second important consideration when defining conservation reserves is the suite of species used for analysis. The species-set used for conservation planning is rarely entirely representative of the biodiversity found within a region. Funding opportunities and logistical constraints have traditionally focussed attention on a limited subset of species. The practical need to triage given investment constraints mandate a focussed and directed conservation strategy (Bottrill *et al.* 2008). To this end, each Bird Conservation Region (BCR) contains a subset of 'priority' species, those whose populations and important habitat fall chiefly or solely inside of the BCR bounds. Key questions to ask when targetting conservation action in this way include: What is the impact of focussing solely on a subset of regionally important species when designing conservation efforts? Is there strong agreement with a conservation priority surface designed for all species? The use of this subset of species when designing a regional

conservation plan may focus conservation effort on areas that are important for conservation of the subset, while missing areas important for overall biodiversity. Conversely, the areas that are important for the subset may be just as important for the larger set. This ‘sweep’ effect may result in unintended protection for a greater extent of species, which would be desirable for those wishing to maximize the effect of conservation effort (Kiestler *et al.* 1996; White *et al.* 1999).

The current analyses assess the conservation priority of each polygon defined by a suite of potential spatial classification schemes, for a set of ‘BCR Priority Bird Species’, and for the overall species set. The shifts in priority between spatial classifications indicate the extent to which the choice of classification scheme will guide or distort optimal conservation planning. The degree of agreement in priority between the BCR species subset and the full set indicate the strength of the potential ‘sweep effect’, the degree to which species distributions overlap in a complementary fashion. Are there potential shortfalls introduced by planning using only a limited subset of species, or can we expect the areas important for the existing priority species subset to cover a broad range of other species?

Methods

OBBA Point Count Method

The Ontario Breeding Bird Atlas (OBBA; Cadman *et al.* 2007) provides a dense and broad spatial survey of bird abundance across much of Ontario. The data for the Ontario Breeding Bird Atlas was collected over 2001 – 2005, surveying the province of Ontario for breeding bird diversity in a rigorous and comprehensive fashion, operating under peer review. This survey split the southern portion of the province into 10 x 10 km squares, and the northern portion into 100 x 100 km blocks, conducting targeted point counts within each to attempt a stratified random sampling design where possible. Point counts consisted of a count of all birds seen and heard at an unlimited distance during a 5 minute period. Counts were done between dawn and 5 hours after dawn between May 24 and July 10 in good weather. Most point

counts were along roads. Up to 50 random “designated” roadside point locations were shown on each volunteer reference atlas square map. Each volunteer was asked to sample 20 of these points. Some habitats, especially forest interior (>100m from an edge), were not well covered by roadside points. Volunteers were instructed to complete a minimum number of off-road point counts in each habitat for each square. Within each habitat, volunteers decided where to put off-road point counts, chosen ahead of time to avoid bias towards temporary hotspots of diversity. Count stations had to be at least 300m apart. In squares with few or no roads, or squares where roads were not shown on standard maps, volunteers were provided with information on the proportion of the square made up by each major habitat (e.g. 75% forest, 15% bog, 10% coastal marsh). Volunteers were asked to select point counts throughout the square as access allows, and to sample the habitats proportionately to their availability in the square. Data were collected, and reviewed by the atlas coordinators, with unlikely results flagged for validation. This dataset is now openly available for research, and provides a comprehensive survey of the province’s avian biodiversity.

Comparing Species Subsets

This study included all atlas points which fell within Bird Conservation Regions 12 and 13, producing 50993 point count observations, containing abundance estimates for 235 species (see Appendix G for details). A subset of these species has been designated as ‘priority for conservation’ within each BCR. These subset species are compared against the full set to identify whether they are a representative sampling of the entire set of bird species found within the study region. A hierarchical dendrogram analysis (described below) provided a useful way of summarizing the associative patterns found within the large species distribution dataset. Grouping species by their habitat preference highlighted functional differences among species. Finally, a classification based on the total abundance of each species across the study region allowed regionally restricted or rare species to be separated from more common ones. These species comparisons are used to assess how representative the BCR subset is of overall

bird diversity in the region, in terms of their spatial co-occurrence, their habitat preference, and their relative abundance.

BCR Species Subset

Each Bird Conservation Region has a list of ‘priority species’. This classification identifies species that regional managers have the primary responsibility to conserve (as the bulk of the population and breeding habitat fall within the BCR bounds), with less focus on rare species (as regionally rare species may be found at greater abundances in other locales). The combined priority subset for BCR 12 and 13 includes 107 species, 45% of the pool of 235 studied species.

Habitat ‘guild’ grouping

The Canadian Wildlife Service (CWS) maintains a species habitat classification list of those species which it has sufficient long-term data to perform a population trend analysis (CWS-MBCD 2009). This classification covers 77% of the species found in the OBBA dataset, grouping them into ‘woodland’, ‘wetland’, ‘scrubland’, ‘grassland’ or ‘urban’ sets.

Log summed-abundance categories

Species were classified by their log-transformed summed abundance into ten equal interval classes. Logged values were used to provide greater separation within the low abundance range of species.

Species-based hierarchical analysis

A 235 x 235 distance matrix was created using the Euclidean distance between all species in the 50993-dimensional geographical point-space (Legendre and Legendre 1998). The dataset was standardized using the Hellinger transformation ($Y_{ij}^* = \sqrt{Y_{ij}/Y_{i+}}$); the new species value Y_{ij}^* equals the square root of the ratio of each species abundance Y_{ij} for species j

at point i to the total number of individuals at point i , Y_i+), a standardization particularly well suited for clustering and ordination methods (Rao 1995), maintaining as much information as possible in the dataset (i.e. Using all the raw data, and making use of abundance estimates to distinguish sites with similar compositions but differing densities), while allowing the use of traditional Euclidian based ordination and cluster procedures. A hierarchical cluster analysis was then used to classify the species into groups that typically occur in similar abundance at similar locations (Gordon 1999). Ward's clustering methodology iteratively merges points or clusters to maximize the ratio of sum of squares between clusters to within clusters, relaxing the criteria at each step, until the entire dataset merged. This method was useful for describing the full structure of the species relationships, rather than specifying an *a priori* clustering.

Spatial Classification Scheme Comparisons

To provide flexibility to conservation and land-use planners, who may need to plan at a particular grain, the current analysis considered a variety of potential classifications, rather than selecting a 'most appropriate' surface that may be biologically relevant but not be operationally useful. There are a number of potential spatial classifications that were identified as appropriate for use in conservation planning (see Chapter 2 for full discussion). Some were derived from the raw point data, such as a Voronoi tessellation (*Voro*), or a clustering-based classification derived using a hierarchical analysis of species composition (*Avian*). Other classifications resulted from the OBBA sampling squares (*Square*; OBBA 2006a,b), or from a hexagon tiling *Hex*, often used in conservation planning to where connectivity and area are concerns (White *et al.* 1999, Warman *et al.* 2004, Freemark *et al.* 2006). Municipal boundaries may be appropriate when planning for conservation (*Muni*; OMNR 2008). Ecological land classifications such as the Ecodistrict (*Ecod*; Marshall and Schut 1999), or sub-sub basin watersheds (*Basin*; NRCAN 2009) were considered, as a range of ecological, topological and environmental variables were correlated with this grain. These latter two classifications are quite coarse however, in comparison to the former classifications. A spatial union between ecodistrict and basin

produced a finer scale classification (*Ecobas*), subdividing ecodistricts by watershed. Finally, a union of ecodistricts, watersheds and municipal boundaries (*Ebm*) produced an even finer scale classification that partitioned the land into parcels that reflect the underlying ecological and topological features of the planning region, while respecting existing planning boundaries.

Assigning Point Data to Planning Unit Polygons

Data from the 50993 points by 235 species abundance matrix were assigned to planning unit polygons in each classification scheme by a ‘median or mean’ technique. Each polygon was assigned a species abundance equal to the median species abundance value for points within that polygon, unless this equaled zero. If so, the mean abundance value was used, so as not to lose species occurrence data for rarely occurring species. These summary datasets were used, along with polygon shapefiles of each classification scheme (Voro, Avian, Square, Hex, Muni, Ecobas, EBM, Ecod, Basin), as inputs for the Marxan simulated annealing algorithm. Individual runs of the Marxan software and additional summary analysis was scripted in R 2.8.1 (R Development Core Team 2008).

Marxan analysis comparisons

Abundance data was used to split the species set into ten classes, defined using equal intervals over the range of log-transformed summed species abundances. Ten conservation targets were defined by the minimum summed species abundance of each class. The first target was simply the presence of an individual of every species within the reserve set. Polygon selection in this case was primarily driven by the presence of rare and regionally-restricted species. Larger targets required greater numbers of individuals, and therefore a greater total numbers of polygons within the solution set; this introduced greater redundancy across the reserve set, while reducing the range of possible combinations of polygons which would achieve the targets.

For each target value, Marxan selected sets of units that most efficiently included all species to the specified target abundance. Efficiency was estimated by using polygon area as a cost to offset the gain of species to the solution set. An initial set was randomly generated, including 50% of all polygons in the solution set. At each step, a polygon was selected at random and added or removed from the set, with 1000000 iterative improvement steps per Marxan run. The modified set was compared to the previous set using an objective cost function, a measure of the total cost of the solution, defined as the total area included in the reserve, plus the total penalty cost associated with failing to include each species at the required conservation target. An initial range of species penalty factors was tested to select the value which balanced the target penalty with the planning unit cost; a species penalty factor of 10000 produced solutions which satisfied all species targets with the lowest increase in total cost, as per Marxan best practices (Watts *et al.* 2009). The total cost function was

$$\text{cost}_{\text{total}} = \sum_{\text{pu}} \text{km}_{\text{pu}}^2 + 10000 * \sum_{\text{spp}} (\text{target}_{\text{spp}} - \text{amount}_{\text{spp}})$$

Simulated annealing routines initially permit costly changes to the solution set (Cerny 1985); the magnitude of disordered changes permitted is reduced with each subsequent iteration, such that changes made near the end of the run should be a direct improvement over the previous step. In this way, initial random patterns may escape local minima yet still be honed to arrive at an efficient solution set. Using 100 initial random seeds, followed by iterative improvement under simulated annealing, produced 100 unique conservation reserve sets for each conservation target.

Defining Conservation Priority

Conservation priority may be defined as the proportion of times a site is selected for conservation, across a broad range of conservation targets. High conservation priority indicated that the unit was selected across all target values due to its unique and regionally re-

stricted species composition; those selected at higher target values add increasing redundancy to the conservation plan, but bring no regionally restricted species into the reserve set. In this analysis, a series of 100 solution sets were produced in Marxan for each of 10 target values, and a 'priority surface' was calculated for each classification as the proportion of times each polygon was selected over the full range of 1000 surfaces (*sensu* Wilhere *et al.* 2008).

Conservation priority surfaces were generated with Marxan for each planning unit classification scheme, using both the BCR priority subset and the full species dataset. For each point, the mean priority value was calculated across all classifications and a surface created using the Voronoi-based spatial classification. These surfaces were then compared by Pearson correlation coefficients (Becker *et al.* 1988), by the proportion of points assigned to each priority level, and by the spatial distribution of conservation priority values across the region. Finally, difference maps were created for each classification, showing the difference in conservation priority between the BCR subset and the overall species set. Higher value differences indicate an area which is more important to the BCR subset, lower values highlight regions which are more important to the full set of species.

Results

Species Subset Comparisons

The hierarchical cluster analysis split the species set into two major divisions, chiefly a result of abundance differences (Figure 1a). Low abundance species tended to cluster together, as all were very close to the origin in the 50993-dimensional point space. A second partition further divided this group into species with less than 281 observed individuals, those predominantly in the range of a few thousand individuals, and a few common species. The higher-abundance, right-most arm of the dendrogram contained species with greater differentiation between groups, resulting from splits which occurred higher up the tree. All these species had many thousands of observations within the data, a further split separated the ubiquitous species, with greater than 26 000 observed individuals.

The BCR priority subset of 107 species appears to represent a wide range of the species diversity found in this region, containing many low abundance species, and a number of higher abundance species, across the full range of available habitat guild classifications (Figure 1b).

The bulk of observed species in this region were of the woodland guild (Wood; 76 species; Figure 1c). Wetland species (Wet) were also prevalent. Scrubland or successional species (Scrub) were frequent (30 species), but this may have resulted from a tendency to lump odd species into this broad category. Urban and grassland (Grass) species made up a small fraction of all species (12 and 14 species, respectively). The CWS classification contained only those species for which adequate data exists to calculate a population trend, hence many species with few observations within the OBBA dataset were not assigned to a habitat guild (50 in total). However, there were also a few high abundance habitat generalist species that also remained unassigned. Ten equal interval classes across the range of log summed abundance values split the species into classes with a somewhat even distribution (Figure 1d).

Reserve Cost Across Target Values

All classifications displayed similar initial costs at lowest target values, and saturate at the same maximum cost at highest values (Figure 2). However, the relationship between target value and reserve cost varied substantially among classification schemes. Ecod displayed a marked increase in cost as soon as targets began to increase, saturating at target level 5. Basin and Ecobas showed a very similar increase in total cost. Muni showed a stepped pattern in mid range values. Square, Hex and Ebm classifications showed very similar smooth trends. Avian showed a flat response in cost across low- to mid-range target values, while point-level selection in the Voro classification displayed the lowest cost overall, with a steeper increase in cost over target values of 7 to 9.

Priority Values for the BCR Species Subset Across Classification Scheme

The conservation priority of bird survey points varied across classification schemes (Figure 3). By applying the polygon level priority values to the bird survey points they contained, an equally weighted comparison of the difference in priority could be made. Coarse-grained classifications (e.g. Basin, Ecod) tended to skew the entire surface towards high priority values; with more points aggregated together, more polygons were produced which contained the only examples of certain species, and thus these polygons were then required to meet even low conservation targets. Similarly, small polygons tended to contain few points, increasing the likelihood that the few points containing rare and influential species will be found in different polygons, reducing the priority of those polygons. Classifications which assign the extant biodiversity of a region to a finer scale produce redundant and flexible sets of polygons, which will in turn produce lower priority conservation surfaces overall. The Square, Hex, Ecobas and Ebm classifications produced a broad range of priority values, with no zero priority polygons. Some polygons of the avian, muni and voro classifications had no priority value, indicating low numbers of common species were all that was observed in those areas. The mean point-level priority results show that most areas frequently contribute to conservation solutions, however very high priority values are rarely seen, occurring only in small, restricted areas. Mean results showed extensive fine scale differences in priority between neighbouring polygons, indicating that high priority areas are likely to be restricted to fine scales.

Differences Between BCR Subset and All Species Priority Surfaces

Classification schemes showed general agreement in conservation priority surfaces for the BCR subset and the entire species set (Figure 4). The Mean results showed strong agreement between the two surfaces, yet identified a number of polygons which are more important for one or the other of the subsets. The Voro point-level classification showed finely distributed differences in priority across the area, showing agreement in the large number of zero priority values, and many small polygons with higher priority for the BCR subset.

The Ecobas classification showed a strong sweep effect, with only positive differences noted, indicating that focussing on subset ‘priority’ species using the Ecobas classification identifies polygons that meet conservation targets for both the subset, as well as the overall species set.

Mean or Consensus Classification

The priority values of each classification were applied to the bird survey points they contain, and a mean point-level conservation priority value was calculated (Figure 5). This may be thought of as the consensus surface, highlighting areas that were consistently high priority regardless of the spatial classification used. This surface highlighted a number of fine-scale, higher priority areas throughout the region, which were obscured by coarser classifications.

The mean difference surface shows little difference overall between the BCR subset and overall species priority (Figure 6). A Pearson correlation of 0.77 ($P < 0.05$) reflected this. Although there were minor positive and negative differences in priority throughout the region, the mean consensus priority values were consistent across species sets.

Voro Classification

The raw point data, mapped using a Voronoi tessellation, produced a unique priority surface (Figure 7). As each point-polygon stood on its own, without any summarization or aggregation, the systematic algorithm was afforded the greatest degree of freedom when selecting planning units. The pattern that resulted reflects this, with generally low priority throughout, yet with a number of very important polygons (as the few point observations of regionally restricted species were required in all designs). At the same time, no points were included in reserve sets for reasons other than their species composition. This produced a striking heterogeneity across the entire region, as over 6000 polygons were not included at any conservation target. This highlighted a fine-scale variation in bird diversity that was not observed in other classifications.

The difference surface indicates that many polygons were more important from the

perspective of the BCR subset than for overall bird diversity (although again, substantial fine-scale peppering occurs throughout the surface; Figure 8). The Pearson correlation between the two surfaces was 0.71 ($P < 0.05$). The bulk of polygons had zero priority in either the subset or the full species set.

Avian Classification

The avian classification highlighted a number of zero priority regions that contained no examples of rare or regionally restricted species (Figure 9). The bulk of polygons were assigned a low priority, however there were numerous higher priority values, often in small and isolated polygons, with a number of higher priority large polygons around the greater Toronto area, the north-western portion of BCR 12, and the boundary between the two BCRs.

This classification showed general agreement between the subset and all species priority surfaces, but the priority for the BCR subset was generally higher for northern polygons (Figure 10), the Pearson correlation between these surfaces was 0.53 ($P < 0.05$). Using the entire species set shifted conservation priority away from larger northern polygons containing many examples of BCR subset species, towards smaller polygons in southern Ontario that contain species on the northern edge of their range. This implies that conservation planning directed towards overall avian biodiversity may distract from conservation efforts better directed towards species which breed and dwell primarily within the region.

Square Classification

This classification tended toward mid-range priority values, with a few isolated squares at high priority along shorelines and near the boundaries of BCR 12 and 13 (Figure 11). As some squares were not sufficiently sampled (due to lakes and other geographic constraints), there were a number of gaps across the planning region.

The square classification did not perform well with respect to the sweep effect. Many squares showed large shifts in priority between the subset and all species surfaces, both posi-

tive and negative, across the study region (Figure 12). The Pearson correlation between these surfaces was 0.58 ($P < 0.05$), but the spatial peppering of these differences (without an appreciable spatial trend) suggested that the subset should not be consistently relied upon to represent all species. There were considerable differences between the priority areas selected for the subset and for the overall set.

Hex Classification

The Hex classification demonstrated the effect of subtle spatial shifts on the aggregation of data for design purposes. Although polygon area was consistent between the Square and Hex classifications, the tiling produced by these polygons causes the data points to be grouped together in different ways. This produced a much different spatial pattern of priority, as targets were met using different sets of polygons. A similar overall distribution of priority values was seen, but the exact spatial location of high priority values shifted considerably (Figure 13). This highlights the dangers of using an arbitrary tiling for planning purposes; the impact was often subtle but the solution sets were substantially different.

As with the Square classification, the difference between the subset and all species surfaces in the Hex case produced a pattern peppered with disagreements (Figure 14). A correlation of 0.54 ($P < 0.05$) between these surfaces suggested a significant yet inconsistent sweep effect.

Muni Classification

The Muni priority surface contained one large northern polygon that was never included in a solution set (Figure 15). This was likely a combination of its large area and presumably uniform habitat. This polygon is firmly within the Boreal Transition, and was similar to other neighbouring polygons; other examples of the species found within it were achievable without the costly inclusion of this polygon. The rest of the surface showed a normal distribution of priority values, with a number of small, important municipalities throughout the

region, and many that contributed substantially to conservation targets.

The Muni difference surface was generally negative in the north (northern polygons were more important for conserving the overall species set than for the BCR subset; Figure 16), and with a range of values across the south. A Pearson correlation of 0.66 ($P < 0.05$) between polygon priority values was observed.

Basin Classification

Watersheds showed high priority overall, the few low priority polygons were small, clipped edges of larger watersheds that extend beyond the study bounds. Highest priority occurred in the periphery of the study region, along the study bounds and the shoreline regions (Figure 17).

With a Pearson correlation between priority values of 0.62 ($P < 0.05$), the Basin classification showed definite spatial differences between surfaces, but generally of lower magnitude than that found in other classifications (Figure 18). There was lower variation in priority than seen in other schemes.

Ecod Classification

The Ecod classification showed the greatest proportion of the total area at high priority values (Figure 19). The surface quickly saturated at relatively low target levels (Figure 3); the large size of the polygons grouped together so many data points that local, regionally restricted occurrences were inflated to cover much larger regions.

The difference surface revealed fairly broad disagreement between values (Figure 20), although a large central portion showed no difference. A correlation of 0.58 ($P < 0.05$) between the surfaces revealed that when differences did occur, they were often large magnitude disagreements.

Ecobas Classification

The Ecobas classification showed a broad range of priority values (Figure 21), including a number of important, high priority polygons, located along the shoreline and at the boundaries of BCR 12 and 13.

The most striking feature of the Ecobas classification was the very high consistency between the subset and all species priority surfaces (Figure 22). A correlation of 0.96 ($P < 0.05$) between polygon values indicated that those areas selected as important for the subset coincided with those needed for all species. With minor exception, all differences were positive, suggesting that a focus on a limited subset of species highlighted areas that were important for overall diversity as well.

Ebm Classification

The Ebm classification produced a surface with generally low priority values, while highlighting a number of small polygons that were important to meet conservation targets (Figure 23). The union of watersheds, ecodistricts and municipalities produced many small polygons in the south, while larger polygons still dominated the north. High priority values tended to fall roughly along the BCR 12 and 13 boundary.

The difference surface revealed a great deal of variation between the BCR subset and all species priority values (Figure 24). A correlation of 0.61 ($P < 0.05$) reflected this, with large negative differences in the north, and a heterogenous distribution throughout the south.

Discussion

The results of this study demonstrate the strong, confounding effect of spatial classification choice on the outcomes of systematic conservation planning. The scale and layout of planning units greatly impacts the calculated conservation priority surfaces for each classification. The aggregation of samples into coarse classifications (such as the Ecod and Basin schemes) inflate priority values by reducing the number of possible polygon solution sets that

may be chosen, reducing the flexibility of the solution, and causing more and more polygons to be irreplaceable. Finer scale classifications produce a greater range of priority values, with Square, Hex and Ebm each showing a similar response to each other. Avian and Voro classifications have generally low priority throughout, with a smaller number of high priority polygons. This is due to the flexibility accorded by prioritizing using fine-scale planning units. The average conservation priority of each point across all analyzed classifications may represent a useful starting point to target general areas where conservation priority is consistently high. By assessing the effect of classification schemes across a broad range of potential conservation targets, the sensitivity and flexibility of potential conservation solutions can be addressed. Adopting a single target a priori without exploring the bounds of the problem may cause the conservation solution to be inefficient. Too low a target, and the resulting solutions will miss species rich areas (which may not add new species but bring important redundancy to the conservation solution). Too high a target, and the conservation solution will include areas which add little benefit at a high cost to conflicting land-uses. A strong conservation planning process will consider the full range of targets, from simple representation (all species are at least included in the solution) up to full saturation (where all examples of studied species are included).

Ecobas shows the greatest ‘sweep’ effect (Kiestler *et al.* 1996; White *et al.* 1999), with strong correlation between the BCR subset priority surface and that for all species. This indicates that BCR prioritized conservation effort delimited using the intersection between watershed and ecotype has a good chance of benefiting the overall set of birds. No other classification achieves this level of spatial agreement. This surface would be well-used as a tool to direct regional conservation plans, and may be an appropriate tool to guide further research. Having identified polygons which seem to consistently represent avian biodiversity, the next step should be to survey these polygons to identify the local conditions which lead some to be centers of biodiversity and others not. Having identified areas which contain high or low priority assemblages of species, the environmental and topological constraints which determine

the different assemblages may be investigated.

Conservation planning surfaces can be used for a variety of purposes, often conflicting ones. For example, the Ecodistrict classification priority surface would suggest that most places in the region are unique and important. In contrast, the Basin, EcoBas, Muni and Ebm priority surfaces highlight regions of regionally-restricted and irreplaceable biodiversity, and may be more effective at fostering a sense of urgency by focussing attention on critical areas. However, if the goal is to generate a flexible set of planning units for targeting conservation effort, then it may be more useful to make use of a classification scheme with lower priority values, such as the Avian or Voro schemes, as these surfaces have more options for achieving effective investment.

The point-level results indicate that regardless of the factors driving larger scale patterns, there are fine-scale variations in species composition that are not necessarily apparent from simple richness or heterogeneity. Large numbers of points do not contain regionally restricted or important species, or indeed large numbers of individuals at all. The Voro and Avian schemes also produced spatially efficient reserve sets, if small total reserve area is not an issue. A less Boolean approach might use these areas as cores of more flexible conservation land-use management, allowing a certain range of land-use activities within a distance of high priority point-polygons. The first step identifies core areas of existing biodiversity; the next step encourages the remediation of surrounding lands to encourage increased biodiversity across a broader area (Twedt *et al.* 2006).

Following a higher-level regional priority assessment, conservation focus on the local scale will require further field validation of the biogeographic patterns used to derive the prioritization. Areas with high priority should be assessed to confirm the high or regionally unique biodiversity found there in the OBBA surveys. Areas with low priority should be assessed in conjunction with additional local knowledge to ensure that existing hotspots of biodiversity have not simply gone undetected. A consistent sampling methodology should be encouraged in this region, such that subsequent monitoring can contribute to a trend analysis

of avian biodiversity. Incorporating temporal dynamics to select areas of conservation investment may ensure a long term regional benefit, while identifying increasing concentrations of biodiversity so as to respond in step may prove important. The Voro classification had the most zero priority polygons of all the classifications, in either the BCR subset or the full species set; these low-value areas may reflect an widespread pattern of bird diversity loss due to habitat or environmental degradation. The coarser nature of other classifications occluded this pattern.

Areas rated as low priority should be treated with caution. All that can be said of low priority areas is that based on these survey results, there is less evidence of the biological importance of 'low priority' areas than there is in 'high priority' areas with observed concentrations of biodiversity. This does not mean that low priority regions should be ignored! Birds may not adequately 'sweep along' other taxa, such that areas with low priority for birds may be essential areas for other forms of diversity. However, priority areas defined for a specific taxa do tend to cover a higher-than-random amount of other taxa; Warman *et al.* (2004) found significant and positive correlations for species richness amongst all five studied taxa, while Freemark *et al.* (2006) found that priority sites selected for species at risk represented 72 - 91% of species in other taxa.

The prioritization defined in this study is based on the abundance of observed birds, and plans in this region should be prepared to incorporate supplementary data where available, so as to properly assess the value of the region. Due to the difficulty of obtaining true absences when conducting diversity surveys (Kéry & Schmidt 2008), there may be valid caution against using these results to identify regions which do not require conservation focus at all. Priority maps are based on observed bird abundance, and as such are prone to under-detection of rare or cryptic species. As well, larger topographic, climatic and hydrological factors play a large part in maintaining overall ecosystem function, which may not be adequately represented by a five year estimate of diversity and abundance.

These priority surfaces are by their very nature a result of the data analyzed, and

should be regarded as a single facet of a much larger suite of competing interests and land-uses, rather than solely focussing on species diversity. Many additional constraints and pressures exist that drive human land-use, and decisions made solely with regard to avian biodiversity may miss important factors that may impede or bolster the success of conservation efforts as a whole (Scott *et al.* 1993; Bojorqueztapia *et al.* 1995). The vulnerability of a species assemblage is not necessarily emergent from the results of biodiversity surveys alone.

For comparison's sake, the target definitions were kept constant between classification schemes, but as polygon size goes down, targets may be met in smaller and smaller total areas. The current method does not address the species-area effect issue associated with fine resolution data. At the population level, the smaller the area selected for reserve, the greater the potential loss of biodiversity (Woolhouse 1983; Adler *et al.* 2005; Fridley *et al.* 2005). While efficiency is achieved by using polygon area as a planning unit cost, a linear relationship between the two causes the algorithm to prefer the smallest area possible, leading to designs which may capture the required amount of biodiversity, but not include sufficient habitat to maintain it. A threshold or curvilinear cost-area relationship could be used to drive up the cost of small sized polygons, or down-weight their contribution towards species targets, offsetting the preference for smaller areas. The notion of a 'boundary length modifier' has been suggested as a means of encouraging clustered reserves (Game and Grantham 2008). While this may be necessary for uniform or arbitrary classifications such as hexagons (White *et al.* 1999), it may be more sensible to directly delimit the bounds of potential planning units first and choose between them, rather than trying to 'grow' them from finer scale units.

This assumes some predictable or consistent relationship between reserve area and species persistence, which should not be assumed to remain constant across such a broad region, containing varied habitat impacted by a wide range of threats. The mechanisms by which these species perceive and interact with the fine-scale structure of their individual habitat has not been well established (With 1994; Mitchell *et al.* 2001). The fact that a remnant piece of habitat may not be sufficient in and of itself to maintain biodiversity does not mean that it

contributes nothing to persistence, simply that the persistence of biodiversity depends on the suitability of the surrounding land as well.

These results should be seen as an iterative step of an on-going process to improve our perception and understanding of biodiversity, with the addition of newer and more thorough data prompting further reanalysis and reinterpretation. The success of systematic conservation planning will come from guiding land-use decisions using a strategy of informed opportunism (Pressey and Bottrill 2008) to make the best decisions in the moment with the clearest picture of the moment. This work provides practical justification for near-term conservation efforts, and should further inform the decisions of the stakeholders of Ontario.

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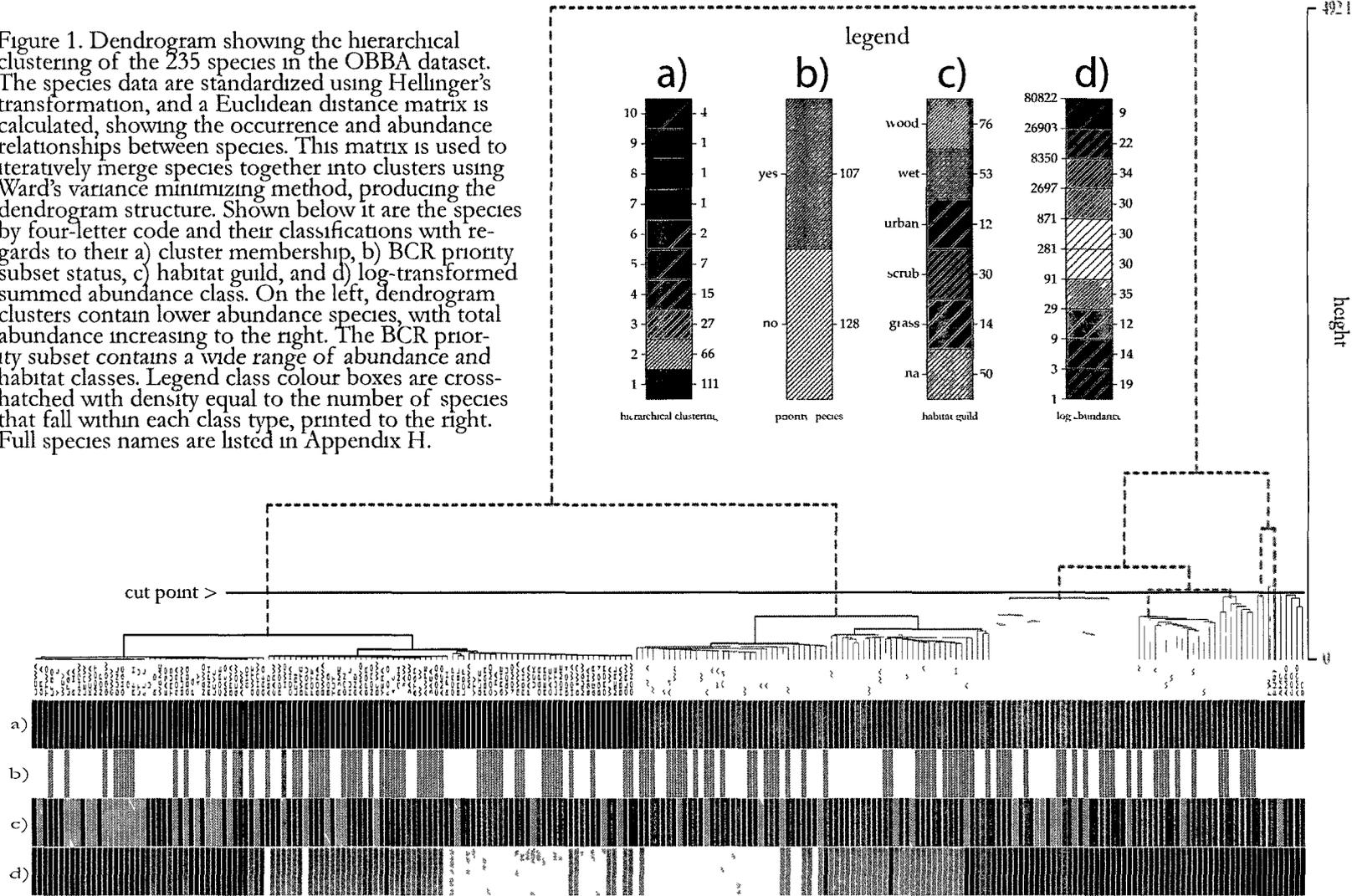
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Figure 1. Dendrogram showing the hierarchical clustering of the 235 species in the OBBA dataset. The species data are standardized using Hellinger's transformation, and a Euclidean distance matrix is calculated, showing the occurrence and abundance relationships between species. This matrix is used to iteratively merge species together into clusters using Ward's variance minimizing method, producing the dendrogram structure. Shown below it are the species by four-letter code and their classifications with regards to their a) cluster membership, b) BCR priority subset status, c) habitat guild, and d) log-transformed summed abundance class. On the left, dendrogram clusters contain lower abundance species, with total abundance increasing to the right. The BCR priority subset contains a wide range of abundance and habitat classes. Legend class colour boxes are cross-hatched with density equal to the number of species that fall within each class type, printed to the right. Full species names are listed in Appendix H.



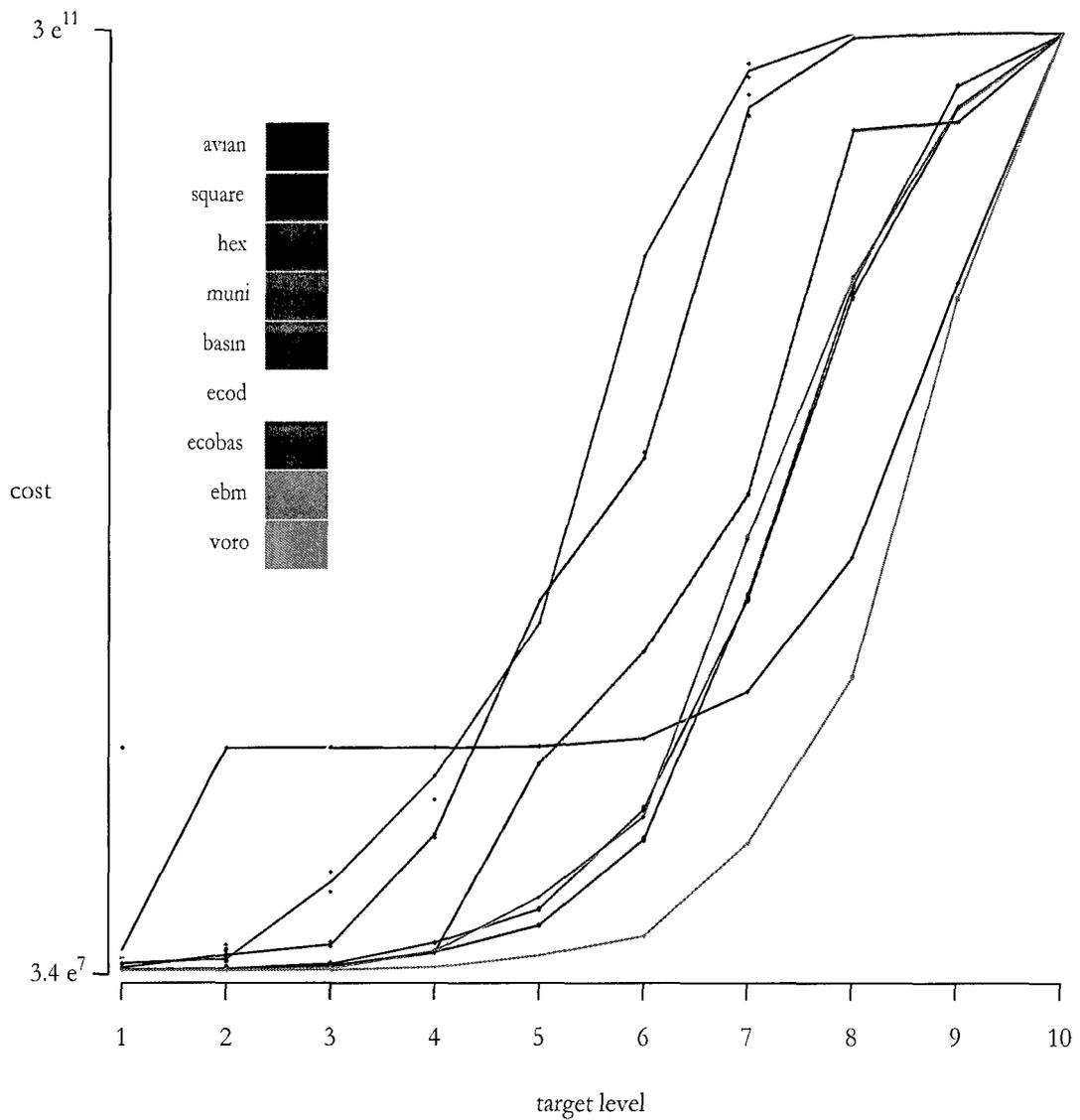


Figure 2: Relationship between conservation target level and the associated total cost of reserve sets that meet those targets for the BCR priority species set. Cost is calculated as the reserve area in square kilometers plus the weighted difference between each species target value and the actual abundance of each species found within the solution set (see methods for additional detail).

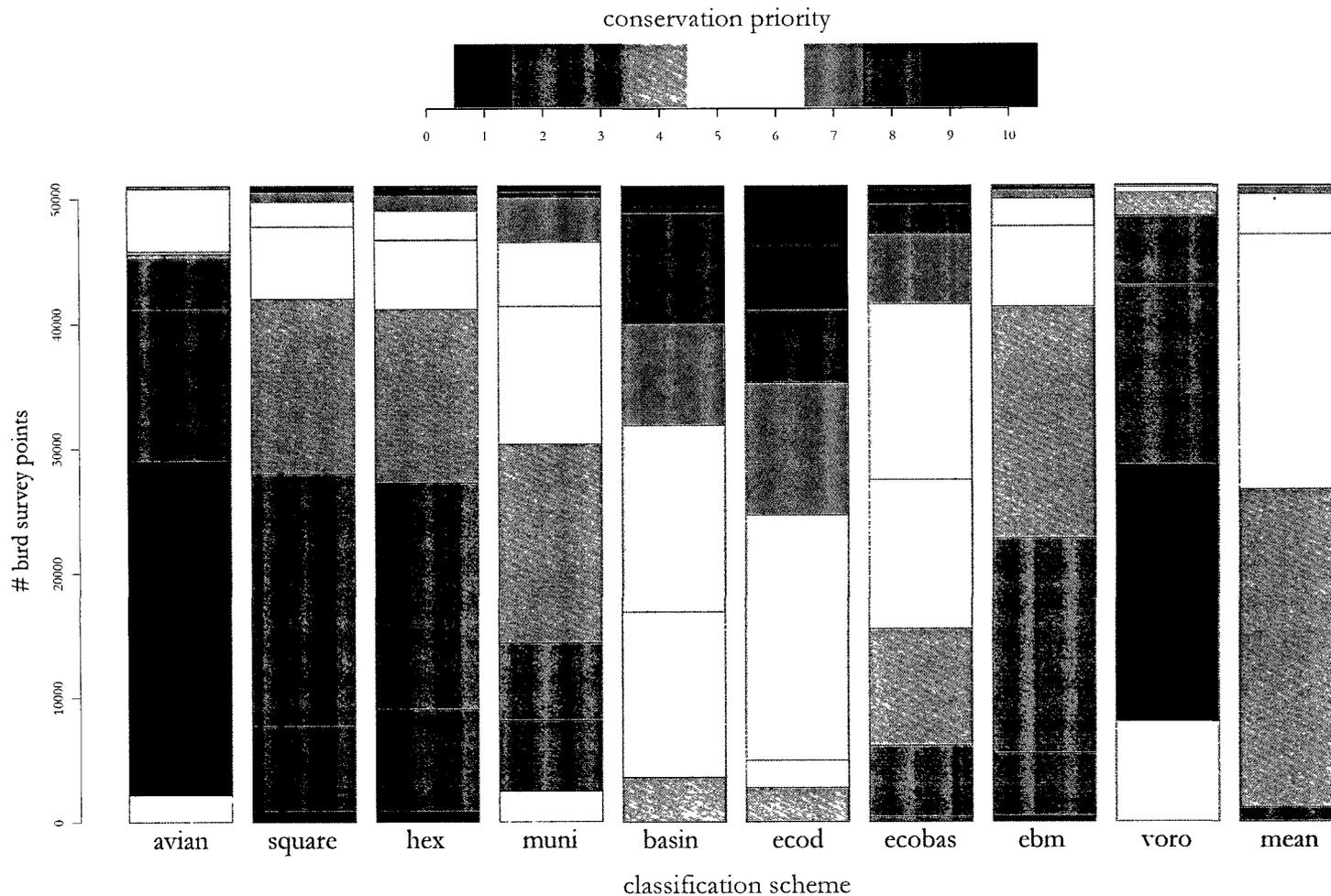


Figure 3: Point-weighted barplot-histogram of conservation priority values for the BCR species subset, for each classification scheme. Each stacked barplot shows the proportion of bird survey points in each priority level, from 0 (white, never selected for conservation at any target value) to 1 (red, selected immediately at low target values, and remained important across all target values).

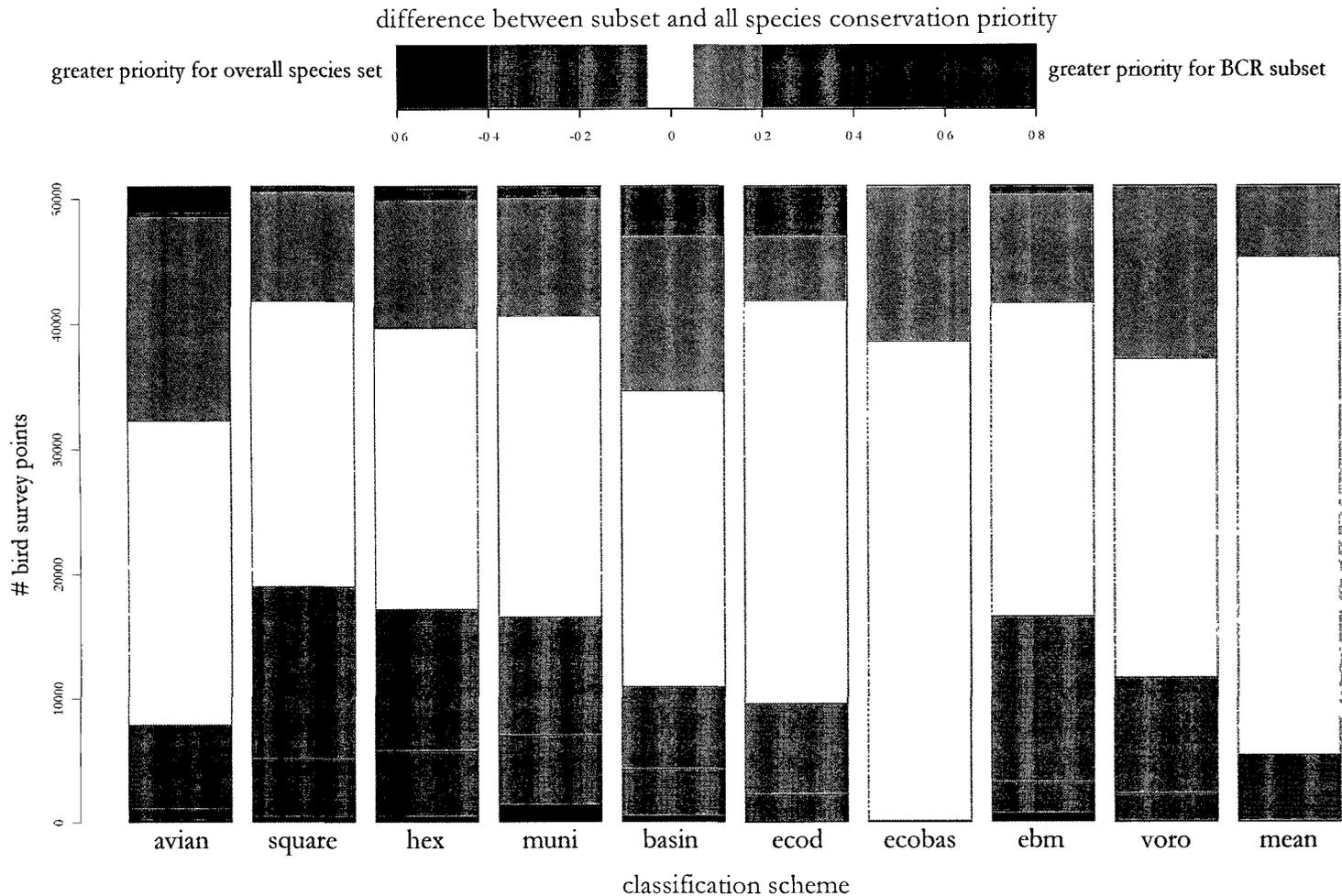


Figure 4: Point-weighted difference between conservation priority values for the BCR species subset and for all species, for each classification scheme. Each stacked barplot shows the proportion of points in each difference range, from -0.6 (purple, greater priority for all species) to 0.6 (dark orange, greater priority for BCR subset species). White indicates no difference between the two surfaces.

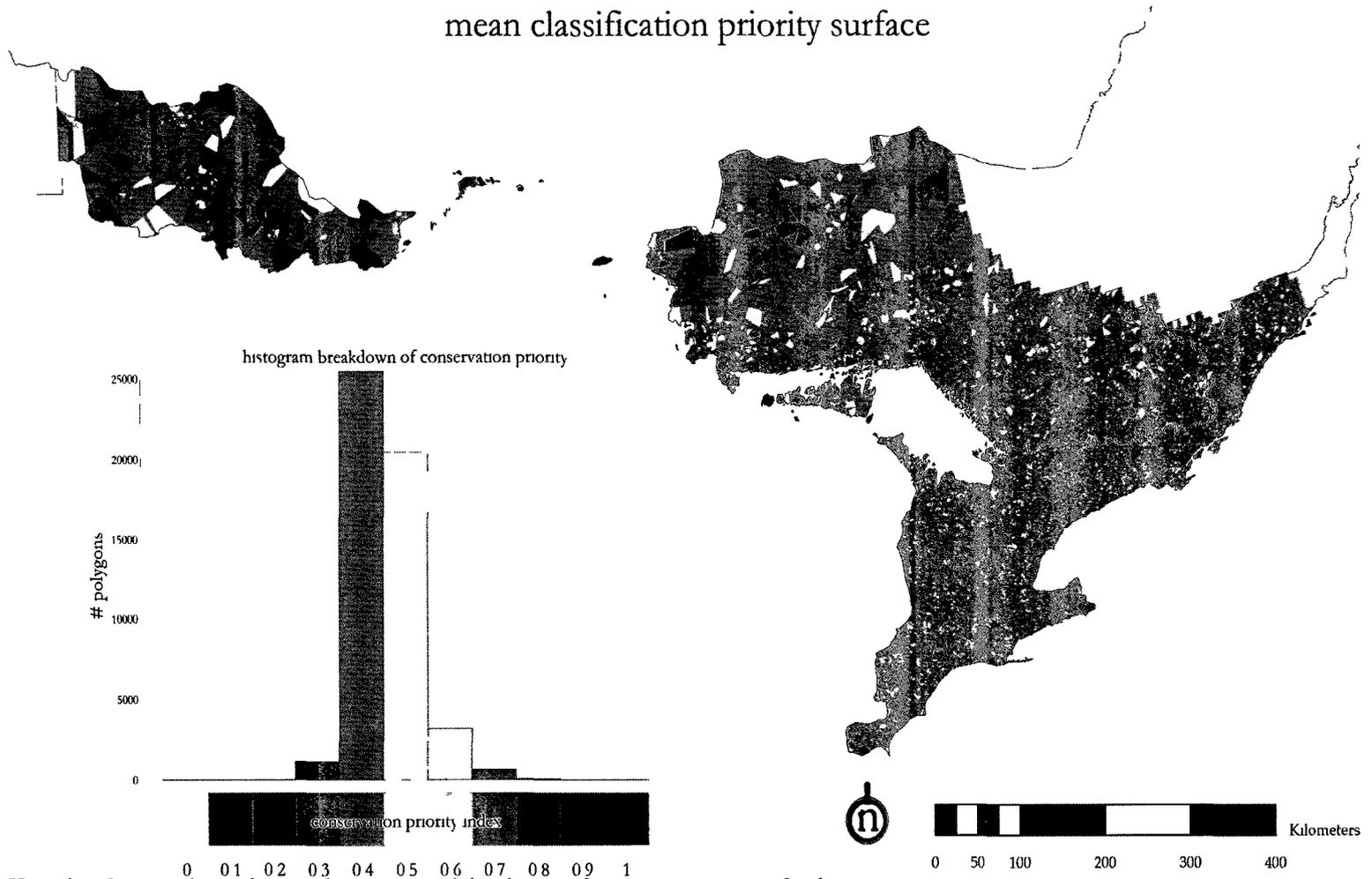
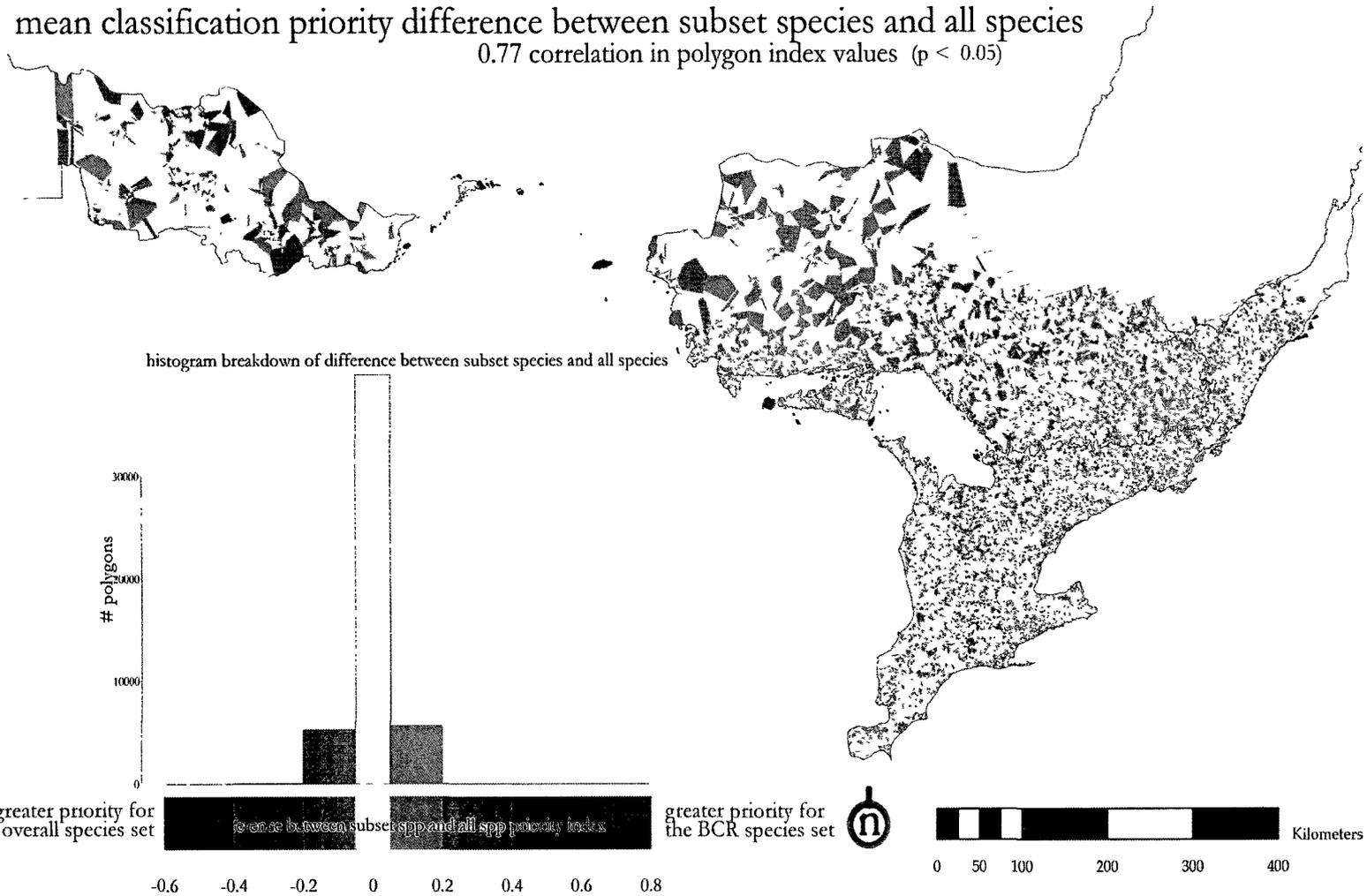


Figure 5 Voro classification scheme showing the mean spatial distribution of conservation priority for the BCR species subset across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority values across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

mean classification priority difference between subset species and all species
 0.77 correlation in polygon index values ($p < 0.05$)



132

Figure 6: Voro classification scheme showing the mean difference between a conservation priority surface calculated for BCR 'priority' subset species, and a priority surface calculated for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

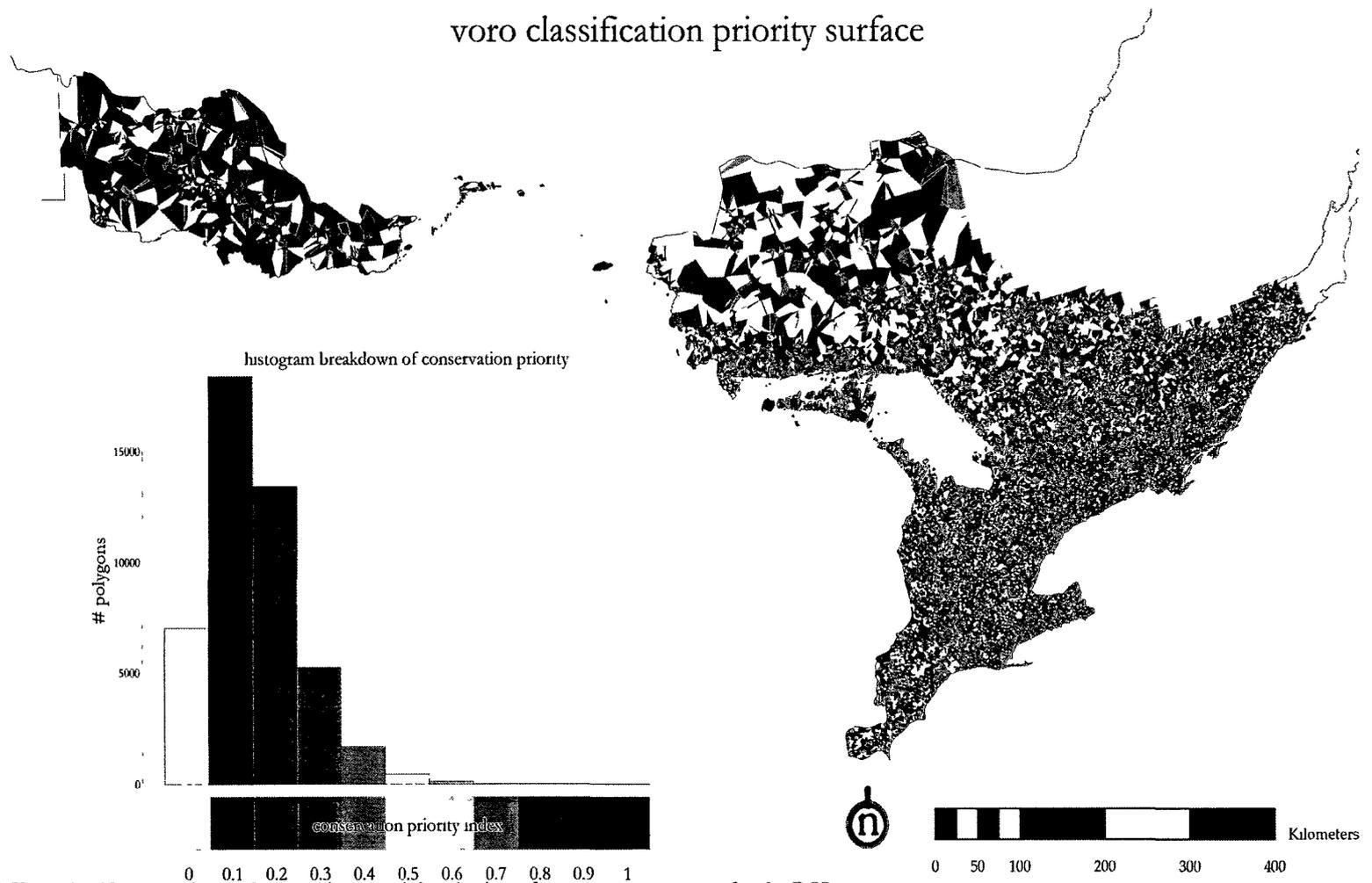


Figure 7: Voro classification scheme showing the spatial distribution of conservation priority for the BCR species subset across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority values across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

voro classification priority difference between subset species and all species
 0.71 correlation in polygon index values ($p < 0.05$)

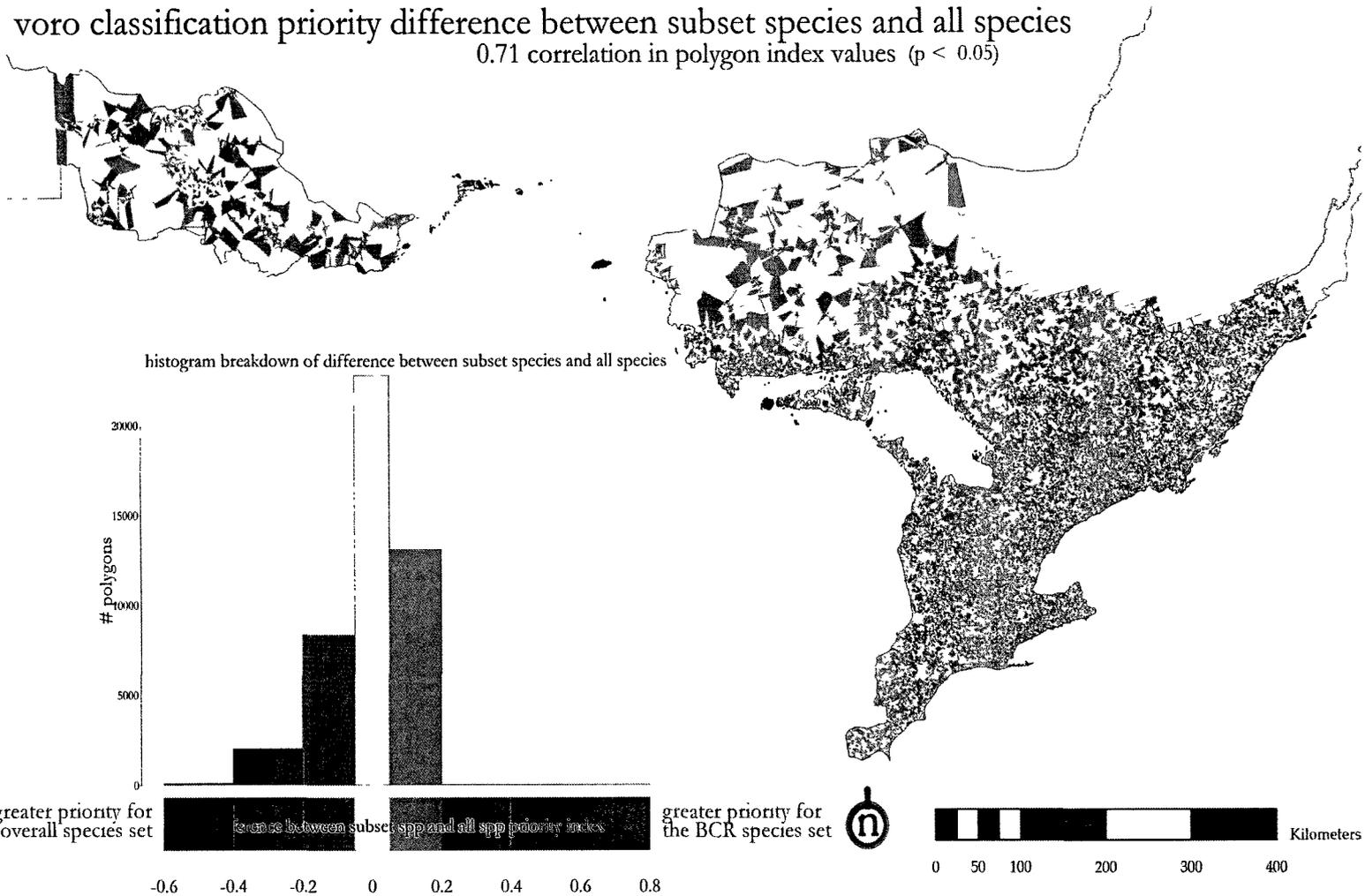


Figure 8: Voro classification scheme showing the difference between a conservation priority surface calculated for BCR 'priority' subset species, and a priority surface calculated for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

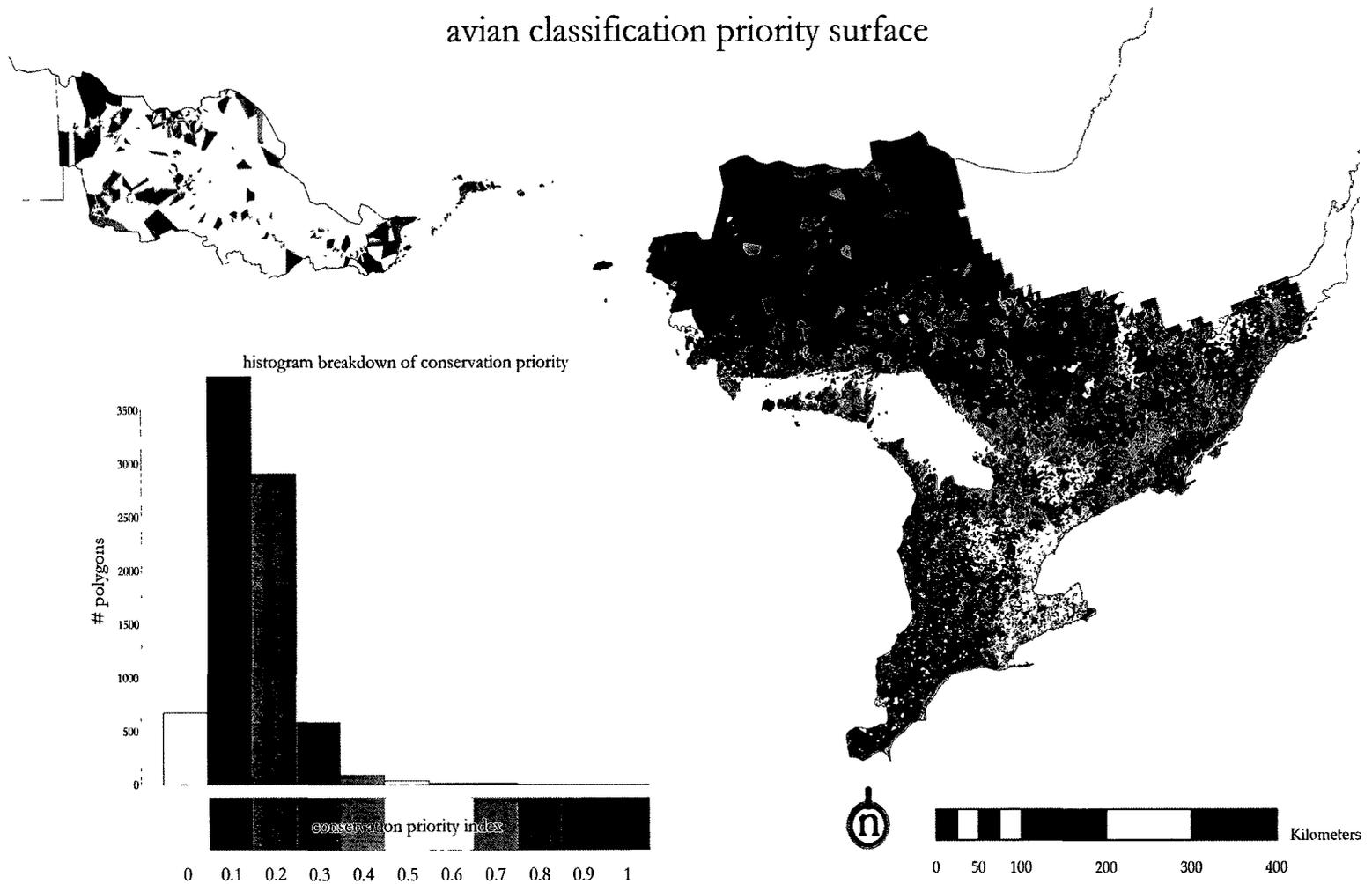


Figure 9: Avian classification scheme showing the spatial distribution of conservation priority for the BCR species subset across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority values across the study region, with legend.

avian classification priority difference between subset species and all species
 0.53 correlation in polygon index values ($p < 0.05$)

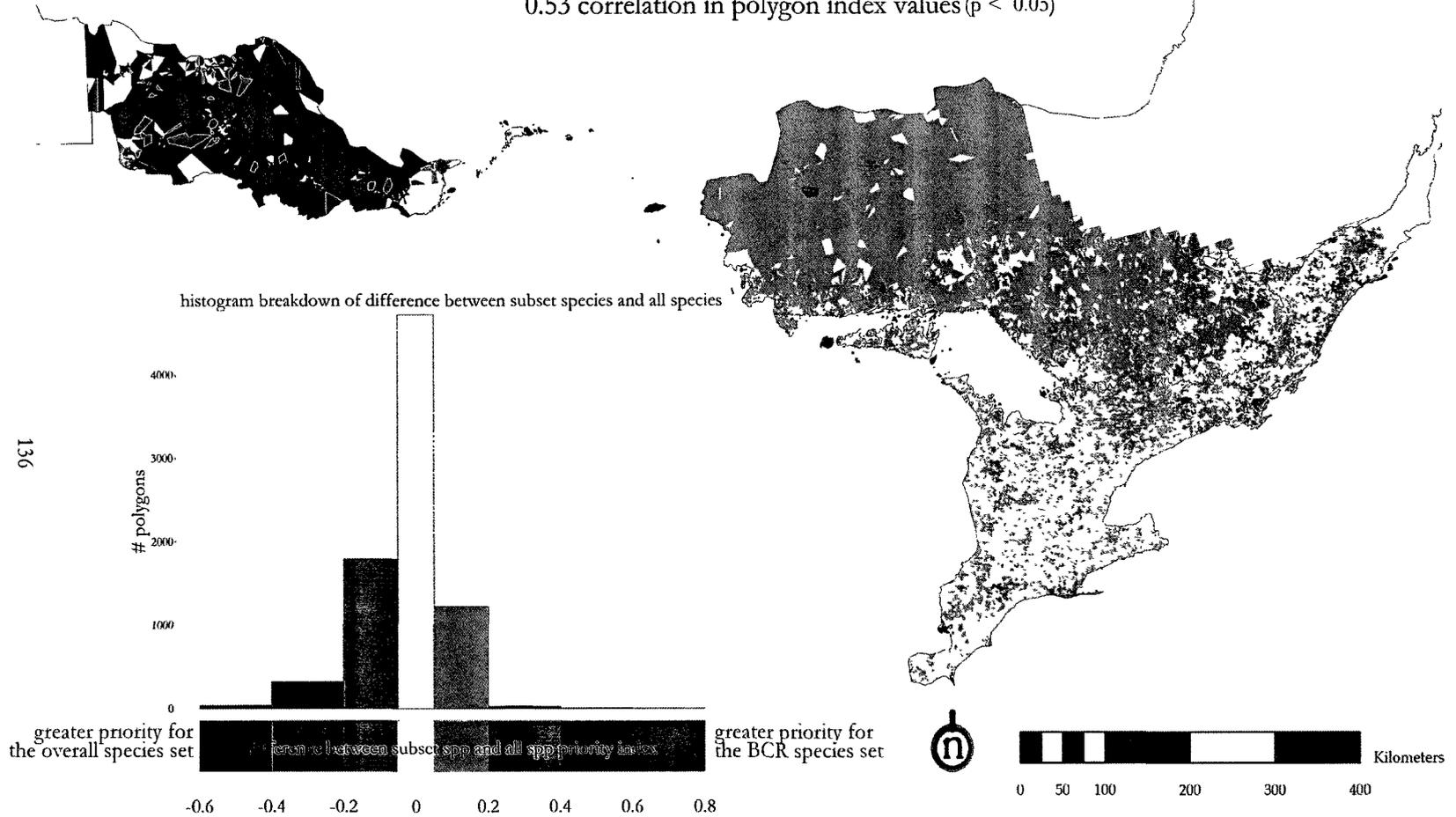


Figure 10: Avian classification scheme showing the difference between a conservation priority surface calculated for BCR 'priority' subset species, and a priority surface calculated for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend.

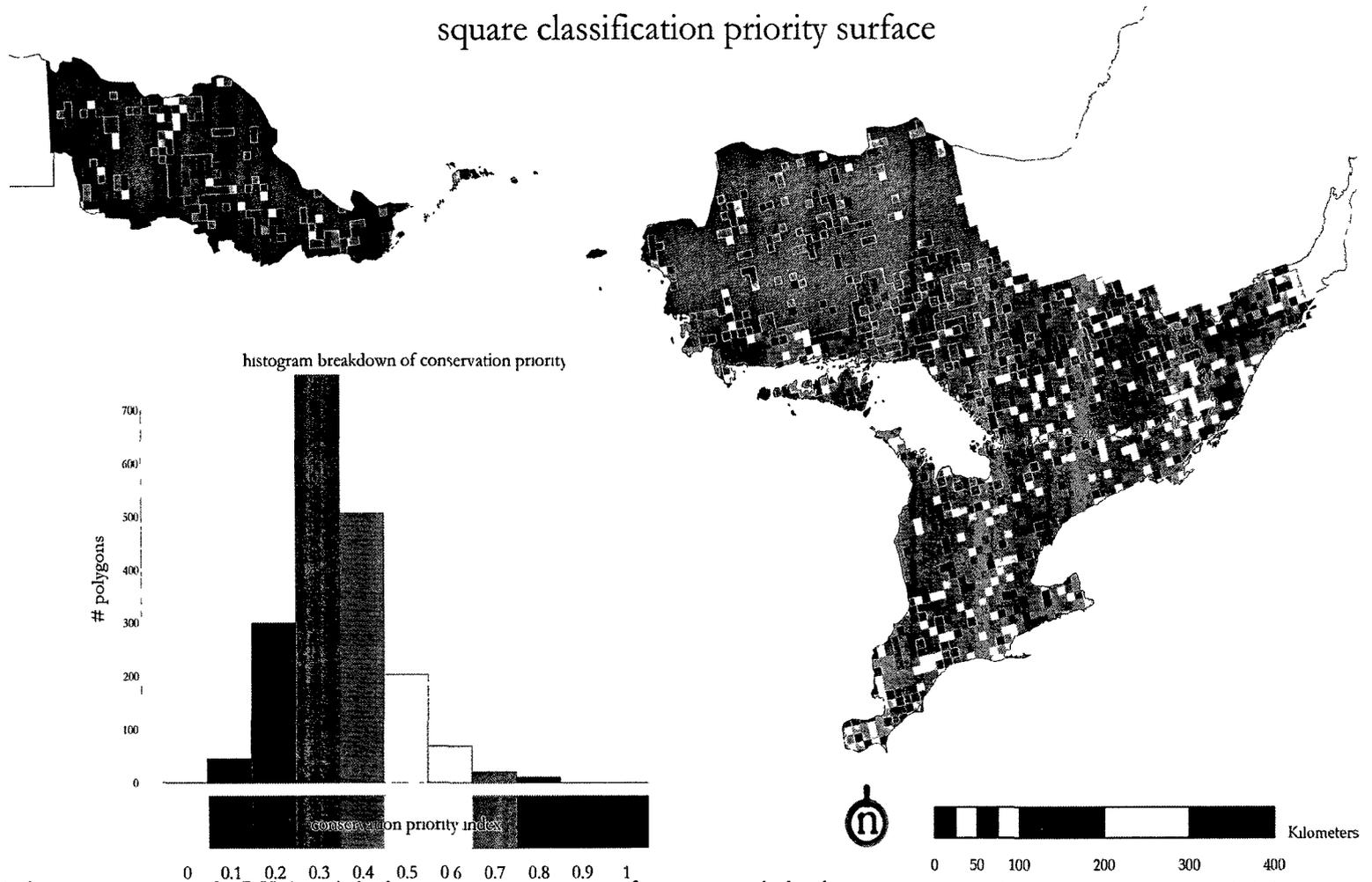
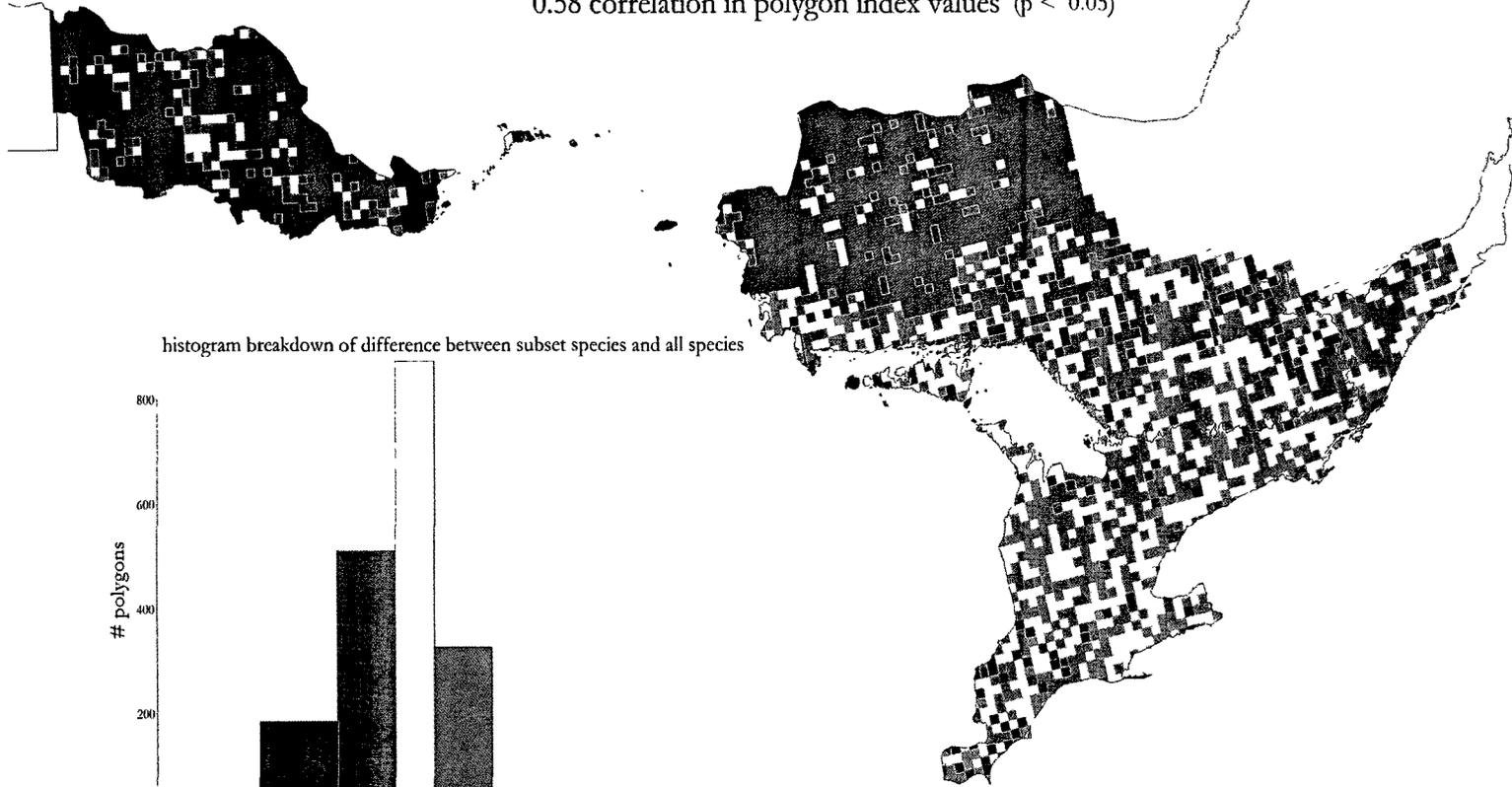
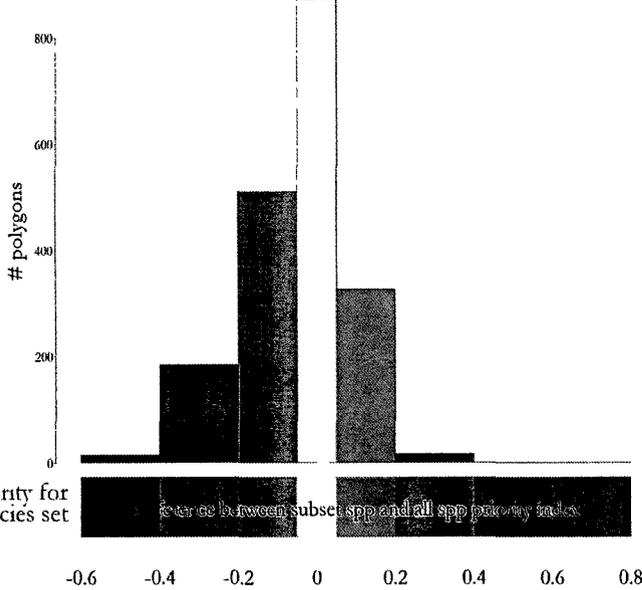


Figure 11: Conservation priority for BCR 'priority' subset species across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority values across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

square classification priority difference between subset species and all species
 0.58 correlation in polygon index values ($p < 0.05$)



histogram breakdown of difference between subset species and all species



138

Figure 12: Difference between the conservation priority surface calculated for BCR 'priority' subset species, and the priority surface for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

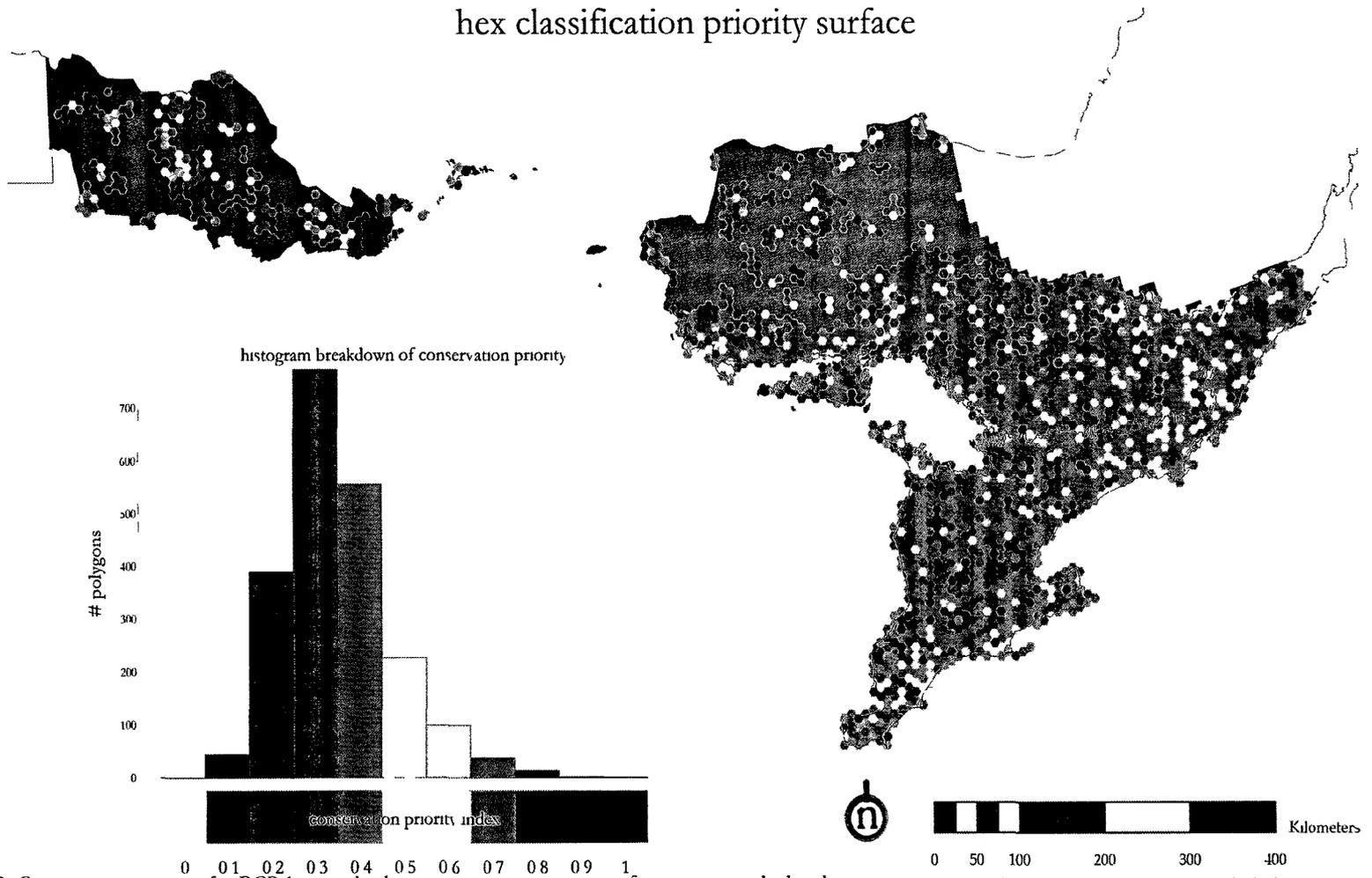


Figure 13 Conservation priority for BCR 'priority' subset species across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon level histogram summarizing the distribution of priority values across the study region, with legend. Dark regions are those polygons that are not covered by OBBV survey points.

hex classification priority difference between subset species and all species
 0.54 correlation in polygon index values ($p < 0.05$)

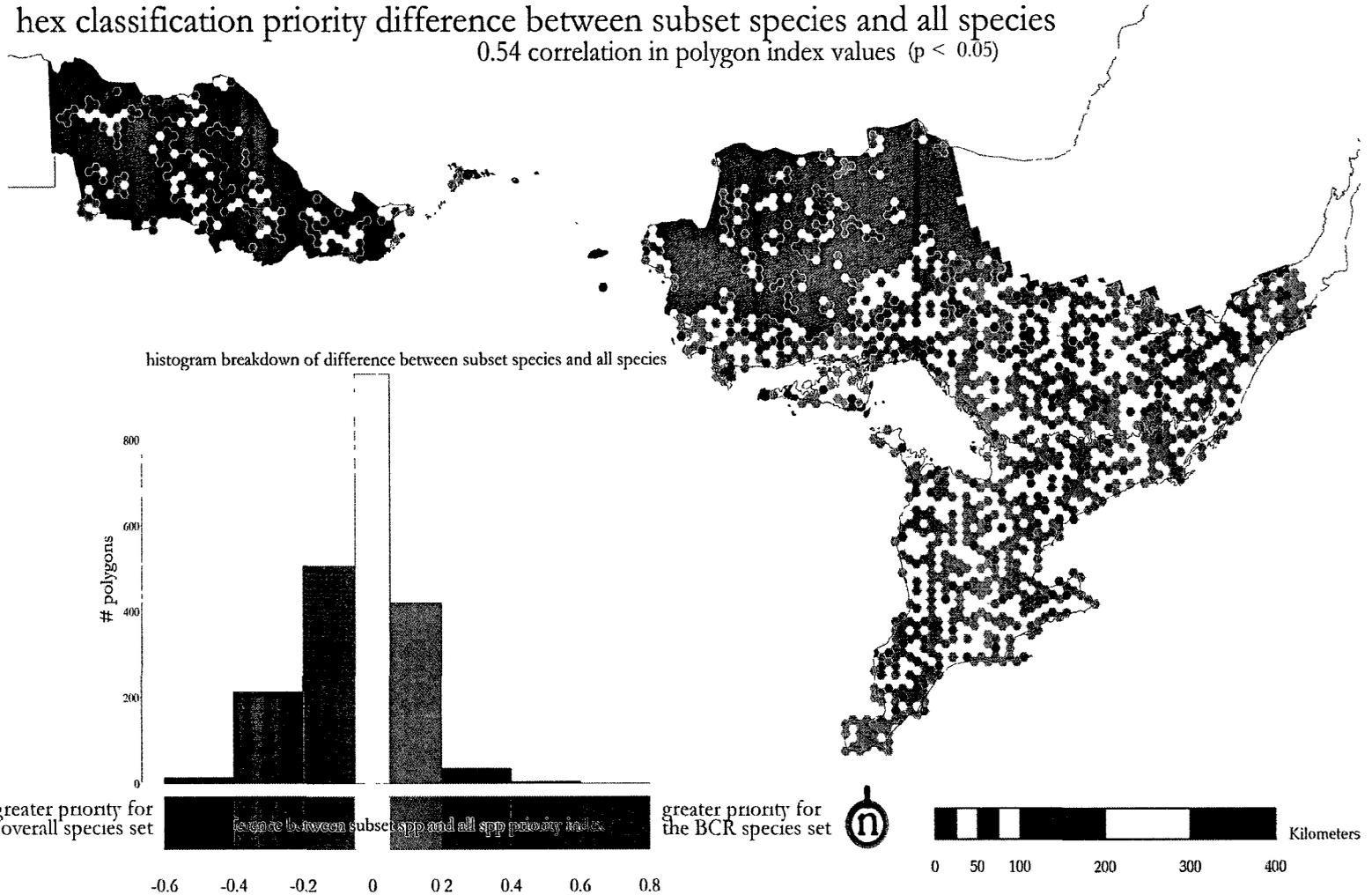


Figure 14: Difference between the conservation priority surface calculated for BCR 'priority' subset species, and the priority surface for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

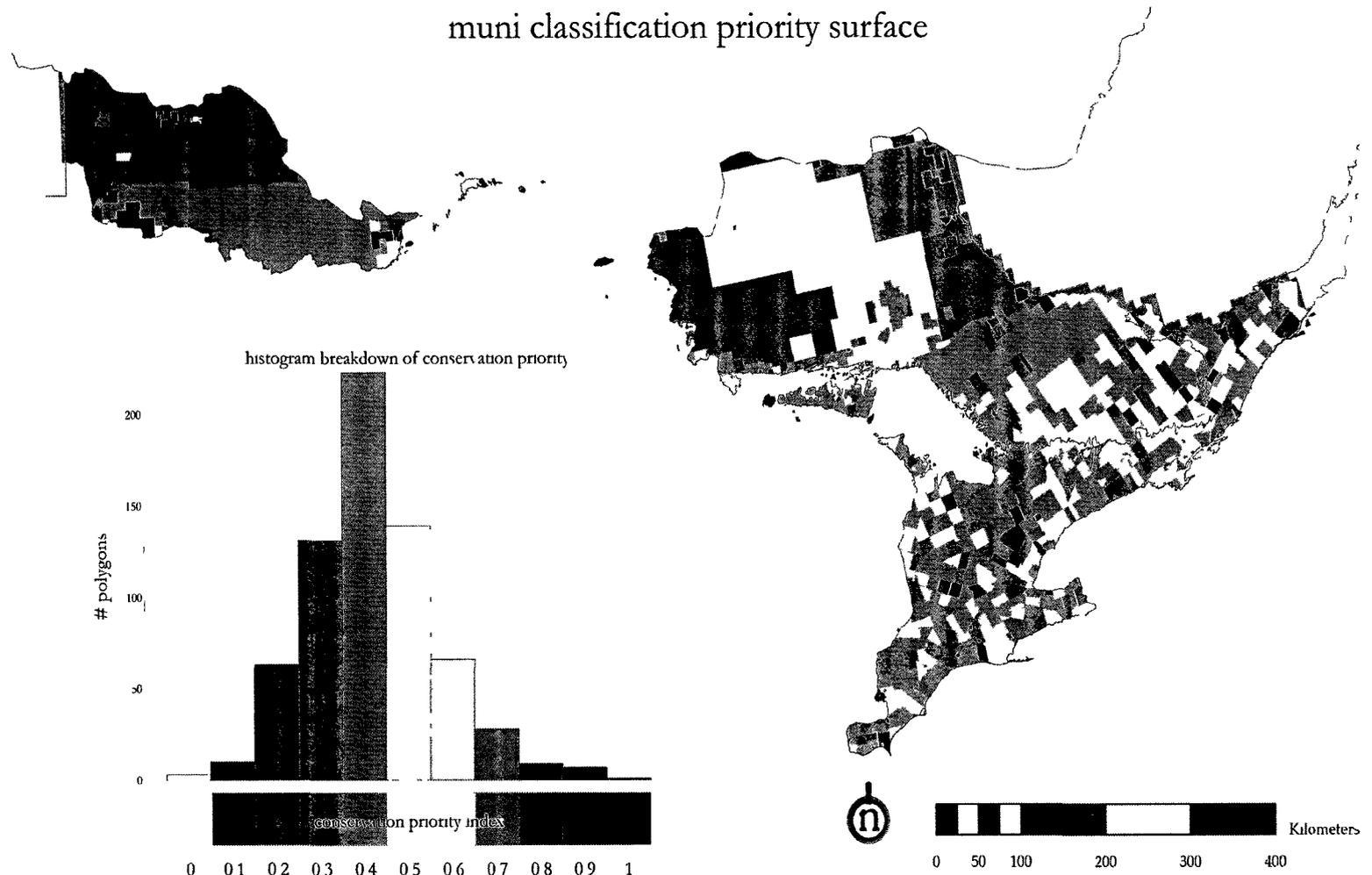
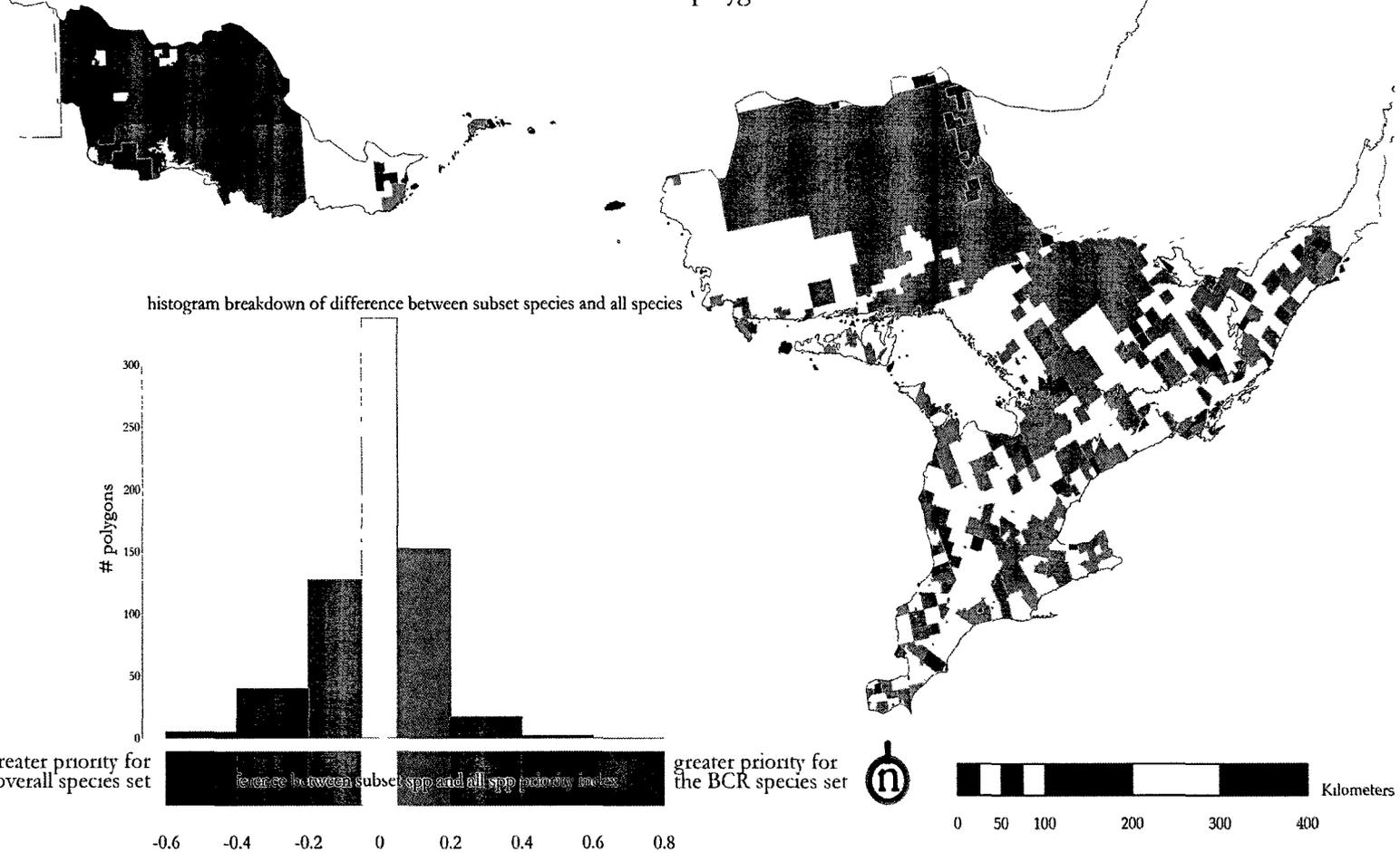


Figure 15 Conservation priority for BCR 'priority' subset species across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority values across the study region, with legend. Dark regions are those polygons that are not covered by OBB\A survey points.

muni classification priority difference between subset species and all species
 0.66 correlation in polygon index values ($p < 0.05$)



142

Figure 16: Difference between the conservation priority surface calculated for BCR 'priority' subset species, and the priority surface for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

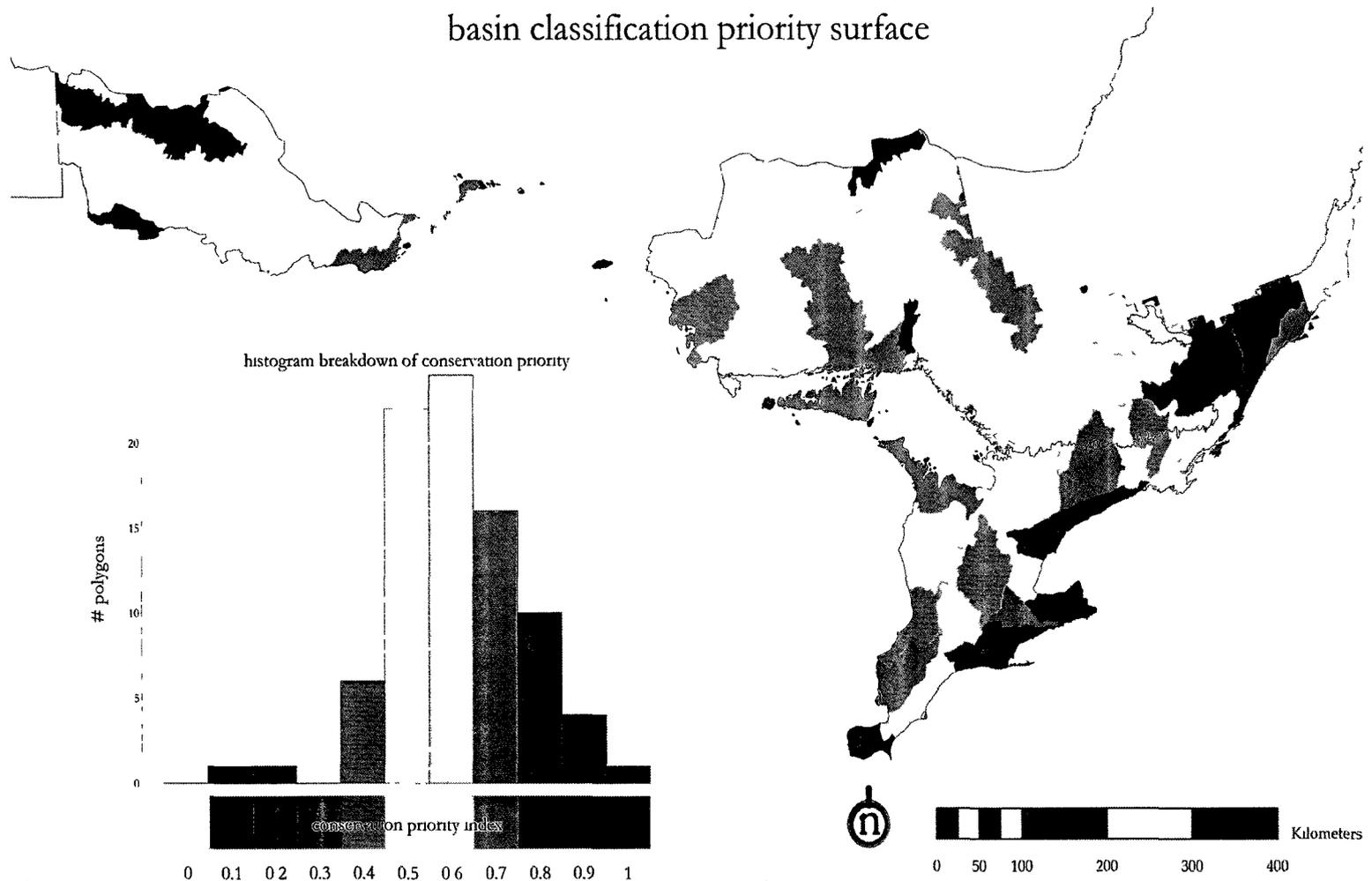


Figure 17. Conservation priority for BCR 'priority' subset species across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south) Inset shows a polygon-level histogram summarizing the distribution of priority values across the study region, with legend Dark regions are those polygons that are not covered by OBBA survey points. Dark regions are those polygons that are not covered by OBBA survey points.

basin classification priority difference between subset species and all species
 0.62 correlation in polygon index values ($p < 0.05$)

144

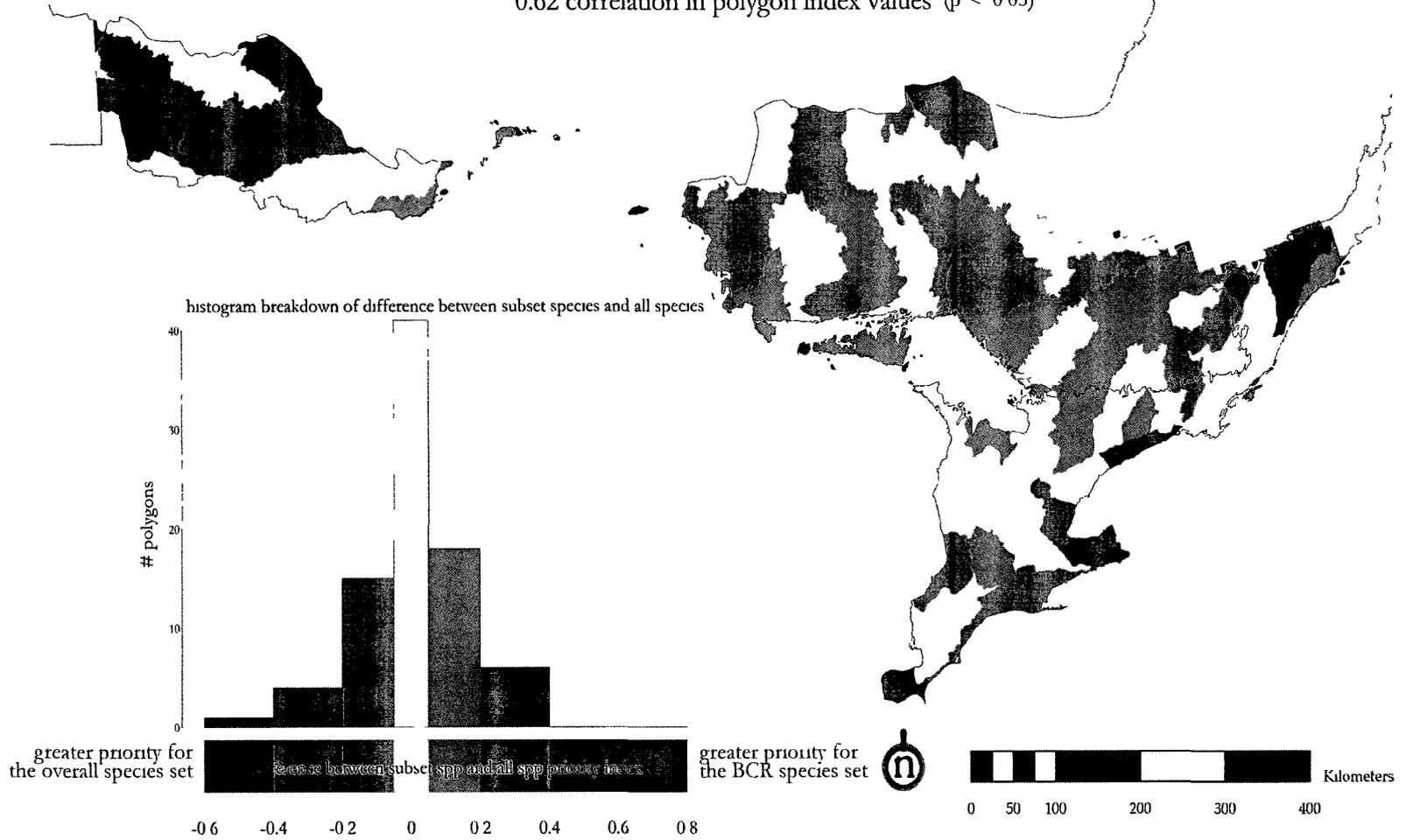


Figure 18: Difference between the conservation priority surface calculated for BCR 'priority' subset species, and the priority surface for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

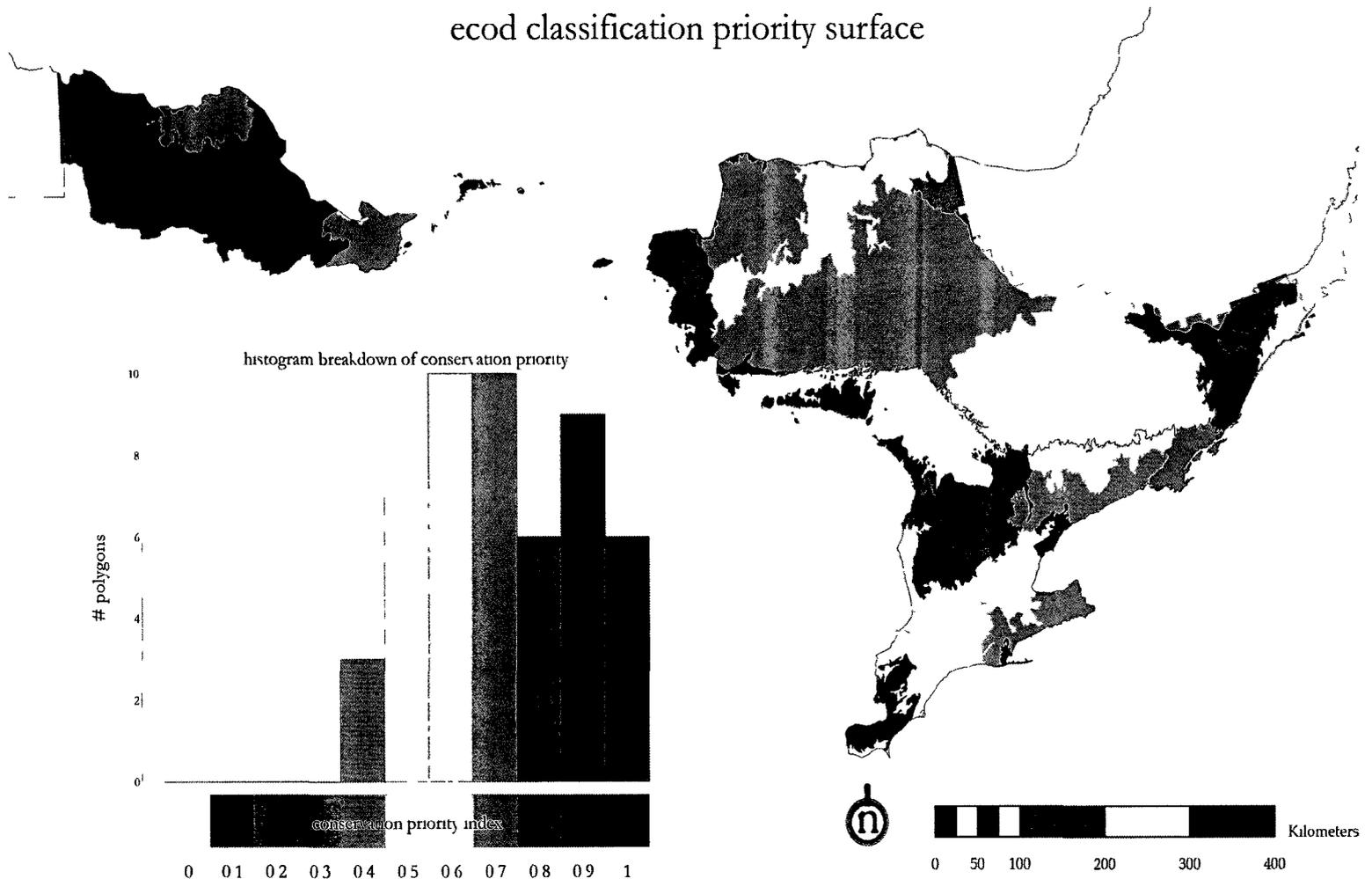


Figure 19 Conservation priority for BCR 'priority' subset species across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority values across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

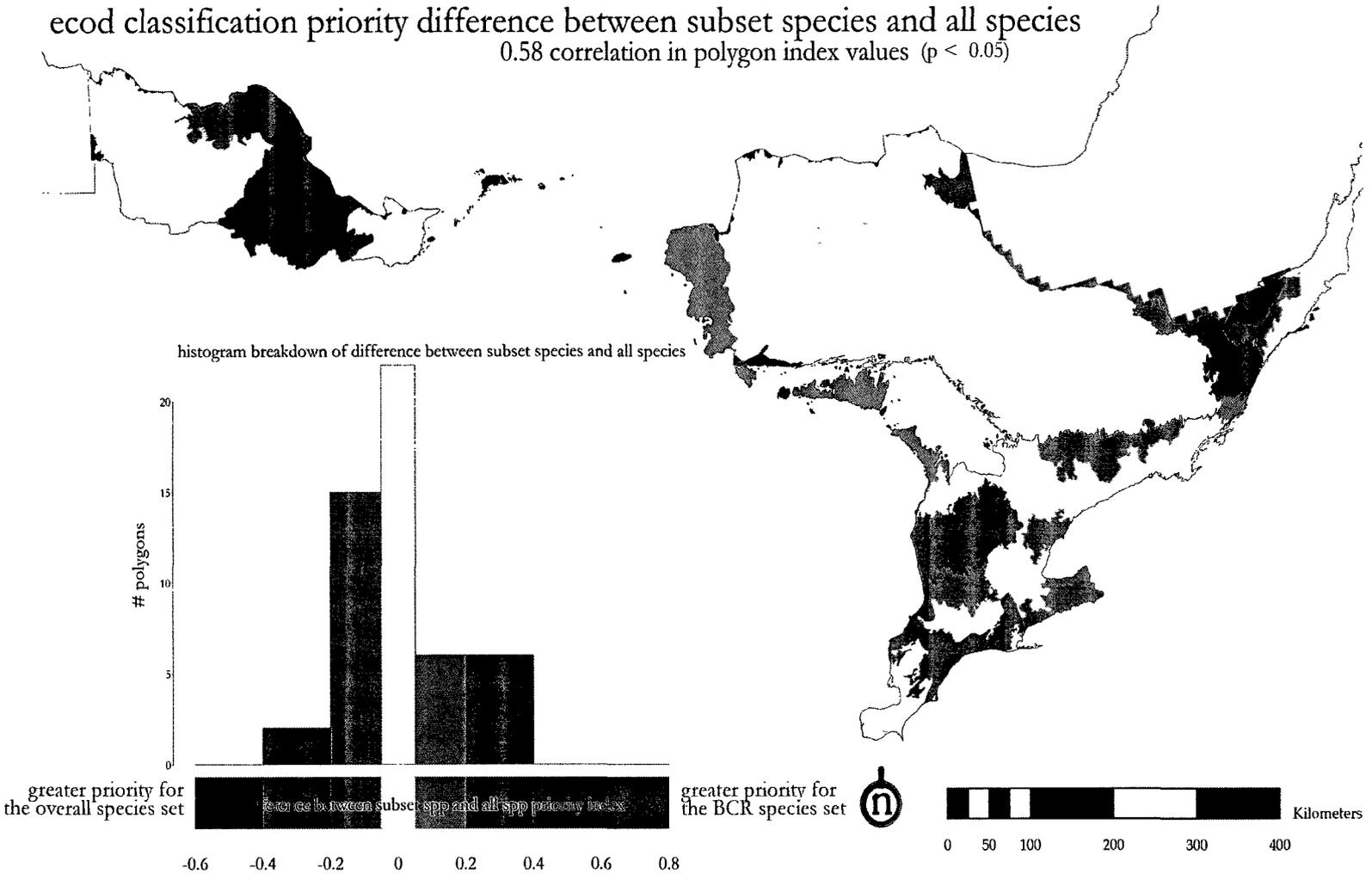


Figure 20: Difference between the conservation priority surface calculated for BCR 'priority' subset species, and the priority surface for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

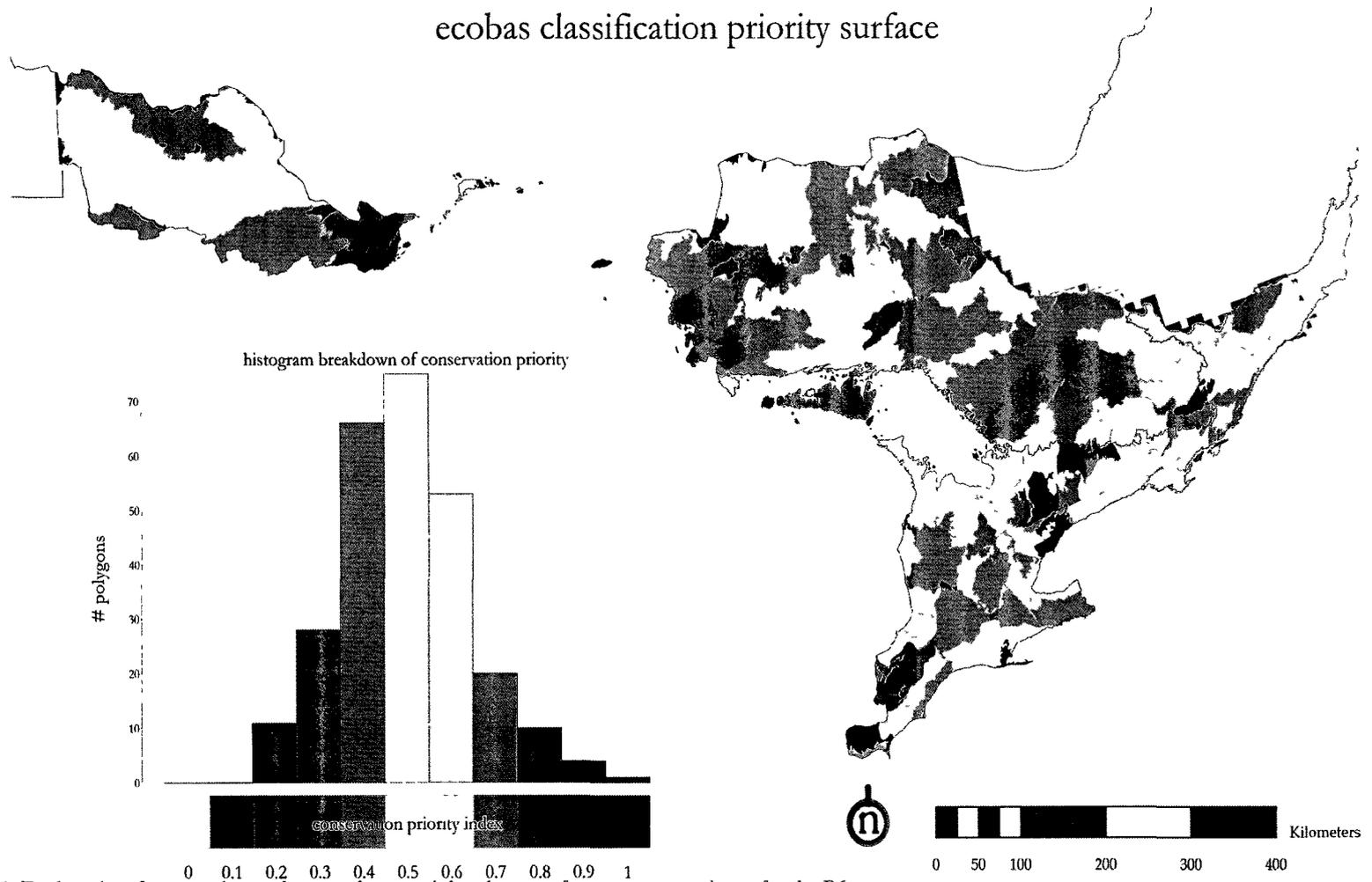


Figure 21: Ecobas classification scheme showing the spatial distribution of conservation priority for the BCR species subset across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority values across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

ecobas classification priority difference between subset species and all species
 0.96 correlation in polygon index values ($p < 0.05$)

148

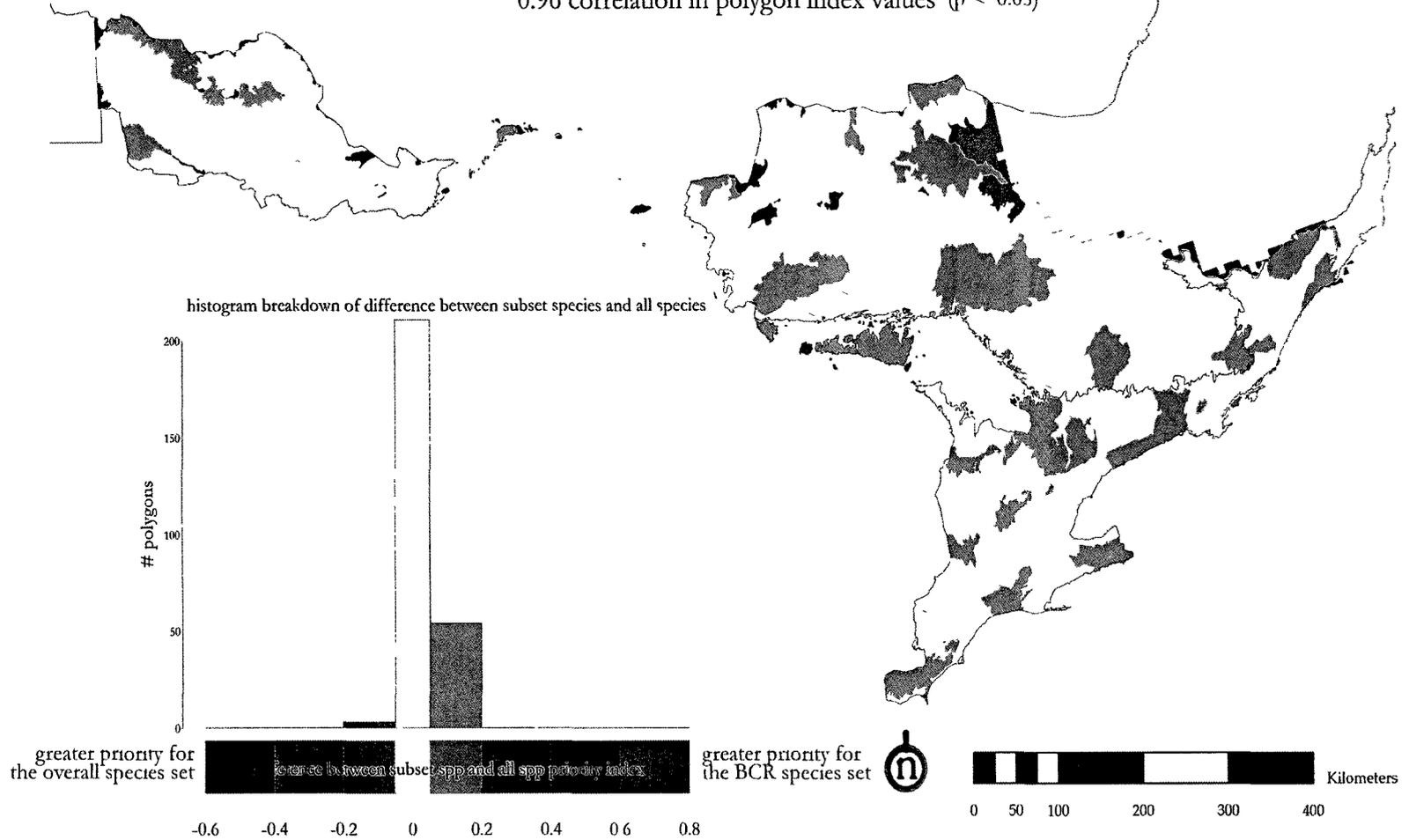


Figure 22: Ecobas classification scheme showing the difference between a conservation priority surface calculated for BCR 'priority' subset species, and a priority surface calculated for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

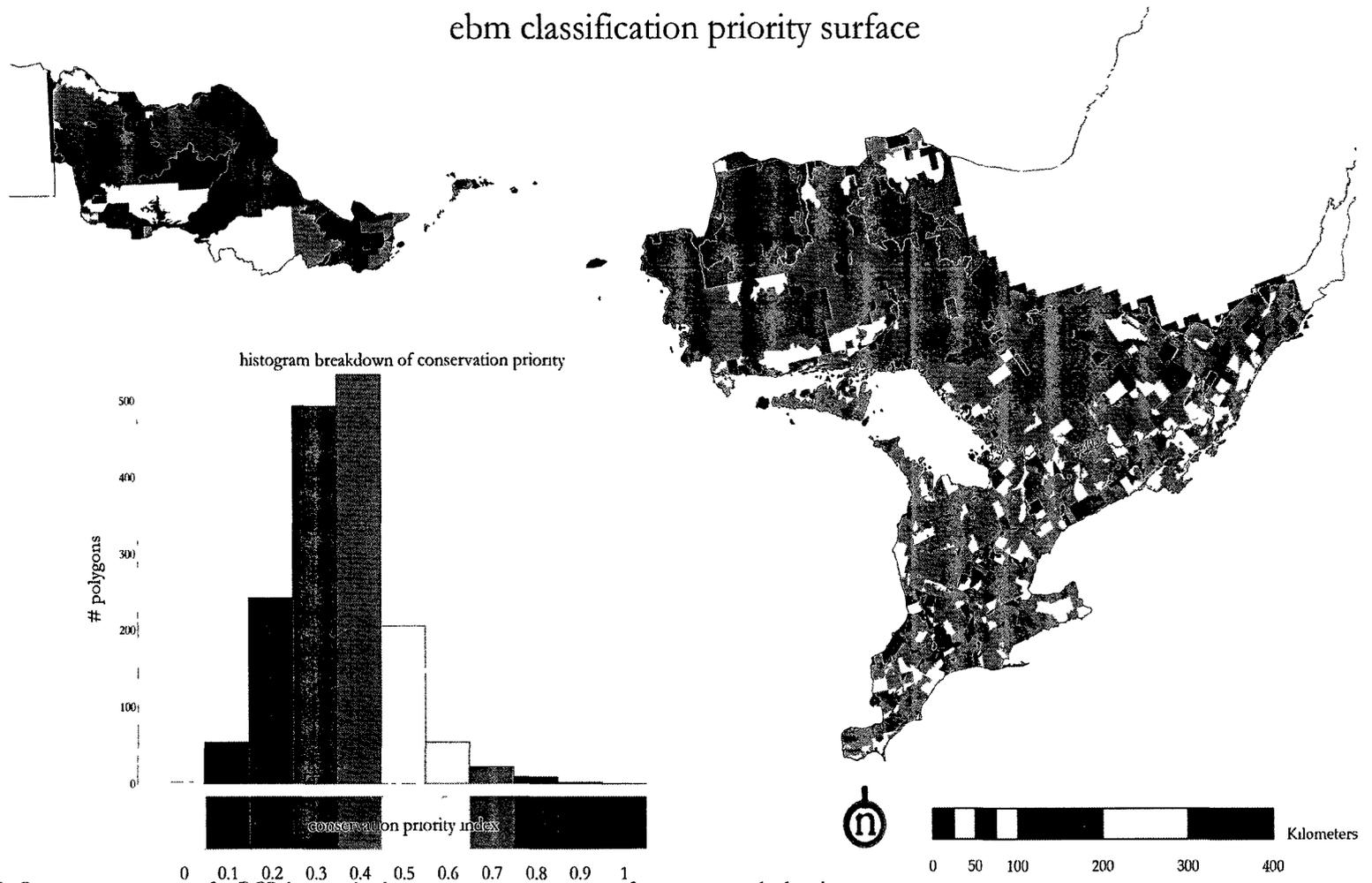


Figure 23: Conservation priority for BCR 'priority' subset species across a range of ten targets, calculated as the proportion of times each polygon is included in a systematic reserve solution set, across all targets. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority values across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points

ebm classification priority difference between subset species and all species
 0.61 correlation in polygon index values ($p < 0.05$)

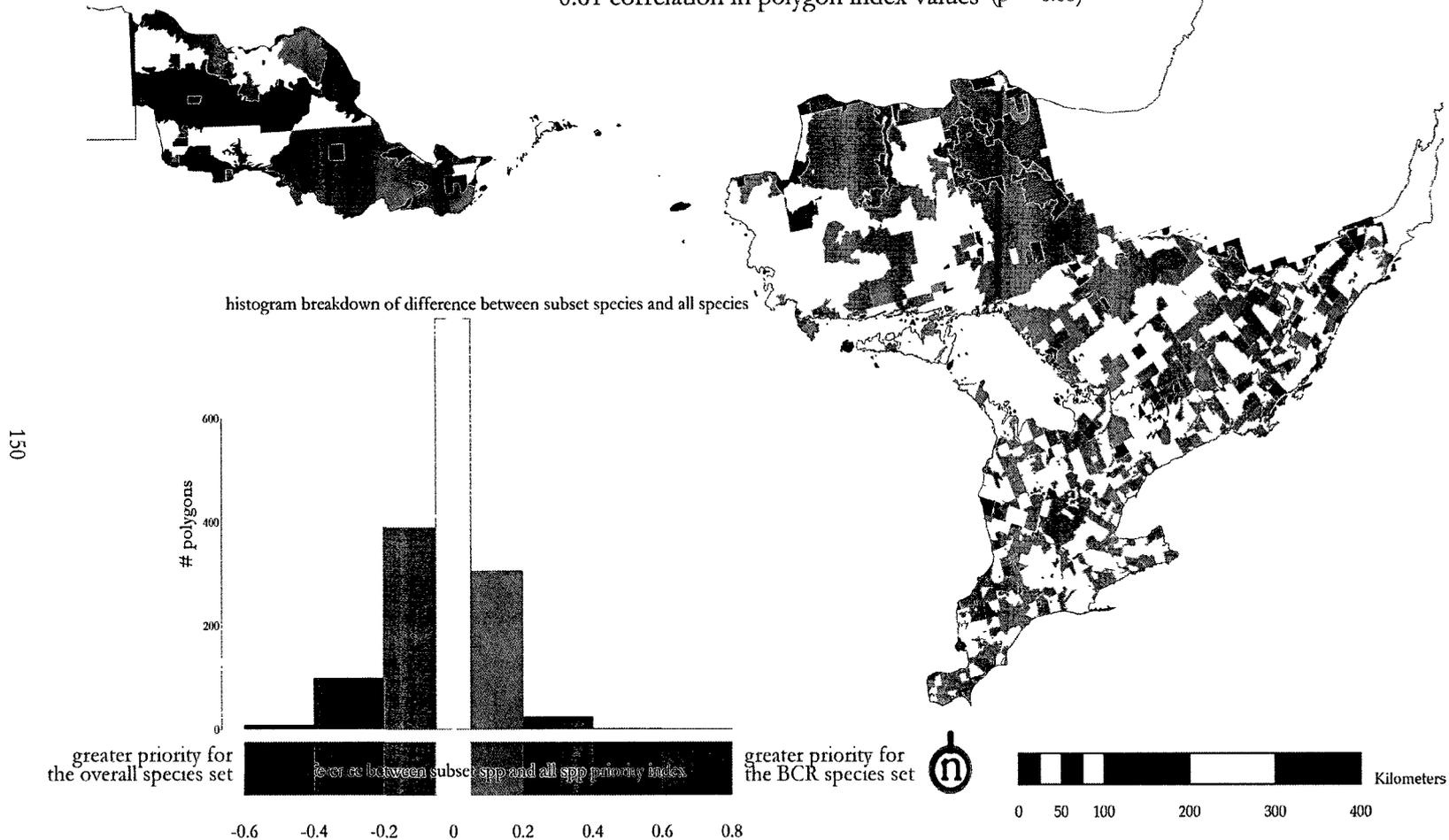


Figure 24: Difference between the conservation priority surface calculated for BCR 'priority' subset species, and the priority surface for all species. Red outlines the boundaries of Bird Conservation Region 12(north) and 13(south). Inset shows a polygon-level histogram summarizing the distribution of priority differences across the study region, with legend. Dark regions are those polygons that are not covered by OBBA survey points.

Conclusion

The field of systematic conservation planning has grown substantially in recent years as there are a broad range of applications to which systematic design is appropriate (Pearce *et al.* 2008; Smith *et al.* 2008; Fraschetti *et al.* 2009; Klein *et al.* 2009), and there is a growing recognition of the need to transparently and efficiently target conservation planning efforts (see Moilanen *et al.* 2009 for a comprehensive review of the subject). Many variant methods are available today, but tend to produce similar results when compared (Carwardine *et al.* 2007). However, the results of these methods are all highly dependent on the datasets used to formulate the reserve selection problem (Shriner *et al.* 2006; Grand *et al.* 2007; Langford *et al.* 2009; Underwood *et al.* 2010). This study investigates four important aspects of the analysis design for systematically optimized conservation planning: the temporal stability of conservation features, the conservation target levels adopted, the choice of planning units, and the feature set chosen for planning. These are critical aspects of ‘best-practices’ for systematic conservation planning for all manner of spatially-distributed features, including birds, as highlighted in this study.

Regardless of the eventual magnitude of climate-driven changes in species distribution, the distributions of many species targeted by conservation efforts are expected to shift over time (Oetting *et al.* 2006; Rayfield *et al.* 2008; Edwards *et al.* 2010). Whenever possible, the temporal stability of conservation features should be estimated, and the likely range of changes should be incorporated into the analysis design. The methods proposed by Hannah *et al.* (2007) present a sensible way forward. Projected future distributions can be appended to known distributions, optimizing conservation designs to cover both present and future distributions. This will produce solutions which meet existing targets while ensuring that future distributions are adequately covered. This requires confidence in the projected distributions, as biased and incorrect projections will lead to biased and ineffective designs (Grand *et al.* 2007). However, in the face of uncertainty, it is possible to incorporate multiple future scenarios, weighted by their likelihood, as independent conservation feature sets, to ‘hedge the bet’ when making long-term conservation plans.

Within the range of variation projected at the time, the results of Chapter One suggest

that areas identified today (which contribute significantly to the immediate goal of conserving known distributions of extant species) continue to cover a substantial portion of analyzed species under potential climate change. This underwrites the value of present-day conservation efforts, as they are likely to continue to play an important roll in conservation over time. However, those conservation efforts will need to be monitored, evaluated and adapted as species respond to changing conditions (Rayfield *et al.* 2008). Historically or presently important centres of biodiversity may not remain so, despite our best efforts. This may be mitigated by the iterative identification of newly important regions as they develop, however there is likely to be a ‘cost of waiting’ due to the inefficiency of a multi-stage selection procedure (Hannah *et al.* 2007). This will require ongoing and thorough monitoring of the patterns of biodiversity, so that species range shifts can be detected, and resulting shifts in the composition of species assemblages can be understood.

The need for widespread and intensive biodiversity data requires that samples be broadly and routinely collected over a wide area. Barring extensive investment in distributed sensor networks (Porter *et al.* 2005; Borgman *et al.* 2007) and lightweight and long-range tracking devices (Cooke *et al.* 2004), collaborative volunteer surveys such as the Ontario Breeding Bird Atlas remain the most feasible method to achieve this extensive data density. In less populated northern areas with little urban presence, collaboration between resource extraction industries (mining, timber, oil and gas development, etc.) and the regulatory bodies who manage their practice may remain the primary source of research and short-term monitoring.

A widely-used method to supplement or substitute for fine-scale, broadly-distributed diversity data is the process of species-specific habitat suitability modelling (Zielinski *et al.* 2006). Carvalho *et al.* (2010) show that reserve selection procedures are indeed sensitive to the kind of species distribution data available, and a mixed approach (including both known and modelled distributions) can produce an acceptable compromise between species representation and implementation cost, in areas where data are lacking. Ban (2009) has shown that reserve selection results are robust to limited data, but biotic data tends to serve as a better surrogate for abiotic data than the reverse; his results suggest that a combination of biotic and abiotic data may better represent

both species and habitats than either alone. Parks and Mulligan (2010) outline a similar approach to identifying and protecting areas of geodiversity as a surrogate for scant biodiversity data.

People may value diversity itself (Fuller *et al.* 2007) or individual species that are particularly charismatic (Richardson and Loomis 2009) or rare (Tisdell and Nantha 2007; Angulo and Courchamp 2009). However, recent work has demonstrated that the loss of more common and broadly-distributed species has important consequences for ecosystem functioning (Gaston and Fuller 2008). There is evidence however that in at least some ecosystems, conservation planning for those species at risk may provide adequate coverage to other species as well (Warman *et al.* 2004; Freemark *et al.* 2006; Drummond *et al.* 2010).

In Ontario, an analysis of the biogeography of breeding birds reveals a great deal of fine-scale spatial patterning. The overall distribution of avian biodiversity shows a strong divergence of the data into two clusters, roughly coinciding with the boundaries established for the Bird Conservation Regions 12 and 13, providing external validation to the previous process which defined these regions. A further partitioning reveals finer-scale differentiation among these two groups, and the spatial effect is to fragment much of the southern region into a heterogeneous pattern, while large sections of the Boreal Transition region remain relatively homogeneous (albeit under-sampled when compared to southern areas). Coarse-grained classifications, such as the ecodistrict and basin classifications suffer from sample size and aggregation issues that lead to low statistical significance for diversity metrics. Fine-grained classifications (e.g. Voro and Avian) suffer from a large volume of information. A productive use of the results of Chapter Two is as a survey tool to highlight regions of high and low diversity and disorder, to select regions of homogeneity for control-impact studies. This broad assessment of biodiversity patterning may guide further fine-scale research, targeted in those areas which may be fruitfully investigated using controlled experimentation.

The relationship between species composition and spatial variables in each classification scheme exhibited a wide range of responses, as evidenced by the PCNM analyses. Although many show low to moderate amounts of variation in species composition explained by spatial eigen-

vectors, some polygons in every classification showed a strong relationship, indicating that no classification produced a polygon set that was devoid of significant internal spatial trend. These spatially diverse areas may be productive avenues for further observation and direct experimentation, to determine which factors may be driving this variation. Given the degree of spatial variation in biodiversity found in this study, conservation planning may benefit from multiple layers of nested planning, with a coarse first pass during the planning phase supplemented by finer scale assessment of highly variable areas leading up to implementation. Others (White *et al.* 1999; Payet *et al.* 2010) have suggested that the most efficient conservation plans would first consider coarse-scale biodiversity surrogates to guide broad conservation plans, and use fine-scale species data to complement and target planning at a local level. Huber *et al.* (2010) found similar complementary benefits by aggregating the disparate conservation priority values found at different scales, this approach parallels the ‘mean surface’ mapping used in this analysis.

By assessing the effect of classification schemes across a broad range of potential conservation targets, the sensitivity and flexibility of potential conservation solutions can be addressed. Adopting a single target *a priori* without exploring the bounds of the problem may cause the conservation solution to be inefficient. Too low a target, and the resulting solutions will miss species rich areas (which may not add new species but bring important redundancy to the conservation solution). Too high a target, and the conservation solution will include areas which add little benefit at a high cost to conflicting land-uses. A strong analysis will consider the full range of targets, from simple representation (all species are at least included in the solution) up to full saturation (where all examples of studied species are included).

In BCR 12 and 13, the choice of planning unit classification had a strong effect on the distribution of conservation priority, as reflected in the range of priority values seen across the potential planning unit surfaces assessed in Chapter Three. Scale has been shown to have a strong effect on reserve species representation, richness and spatial configuration (Shriner *et al.* 2006; Kiesecker *et al.* 2009). This was observed in the current study of Ontario.

The aggregation of samples into coarse classifications (such as the Ecod and Basin

schemes) inflate priority values by reducing the number of possible polygon solution sets that may be chosen, reducing the flexibility of the solution, and causing more and more polygons to be irreplaceable. Finer scale classifications produce a greater range of priority values, with Square, Hex and Ebm each showing a similar response to each other. Avian and Voro classifications have generally low priority throughout, with a smaller number of high priority polygons. This is due to the flexibility accorded by prioritizing using fine-scale planning units. The average conservation priority of each point across all analyzed classifications may represent a useful starting point to target general areas where conservation priority is consistently high. The challenge will then be to further delimit the boundaries of the conservation areas from these more general starting points.

The Avian classification is a useful tool when planning for the conservation of the existing avian biodiversity pattern. By merging only those neighbouring points with similar species composition, small areas with distinct species are not incorporated into larger neighbouring polygons, preventing the diversity data for the distinct area from artificially inflating the priority of neighbouring polygons. This targets conservation using the finest data available while ensuring that areas sharing similar species are not fragmented. The Avian classification map products may not have the visual impact of classifications with a greater proportion of high priority values (such as the Ecodist and Basin results), but this classification allows greater design flexibility when selecting solution sets for conservation targets, and ensures that spatially uniform species sets are not fragmented by that selection process (as may happen when using biologically-irrelevant, spatially-uniform schemes such as the Hex and Square classifications). The change in the priority distribution between Hex and Square indicates that shifting planning units spatially is sufficient to change the solution constraints, even while maintaining the same planning unit scale.

The conservation priority results from the Voro classification paint an alarming picture, as many areas are not selected even at the highest conservation targets. This indicates that existing patterns of avian biodiversity are perforated by areas with low or no apparent conservation value. The finding that this result is not revealed until the finest possible resolution indicates that conservation effort may need additional fine-scale delineation, regardless of the coarseness of the

chosen classification. At the finest scale possible, the conservation priority surface is peppered with low value areas; the task of conservation managers in this region will be to encourage and redevelop these species poor areas, while maintaining the existing priority hotspots. At present, these results confirm that a suite of conservation tools may prove beneficial, combining a limited-access 'protected area' approach in higher priority hotspots, with a 'matrix management' approach mandating best practices in lower priority areas.

The Ecobas classification is potentially the most appropriate scheme for conservation planning in this region targeted at a broad range of bird species. A wide range of priority values were observed in this classification, identifying critical areas to target immediate conservation efforts, as well as low priority regions that warrant further investigation and may benefit from remediation to improve existing or restore historical habitats. The relatively low spatial component to species variation in Ecobas, found in Chapter Two, indicates that for the most part, this classification produces internally uniform polygons, with respect to their bird species distribution.

The strong sweep effect observed in the Ecobas classification in Chapter Three suggests that this classification provides a consistent basis for conservation planning across a broad range of bird species. This makes this classification appealing with regards to return on conservation investment, and increases the number of additional species that may benefit from conservation efforts at this grain. This sweep effect indicates that these polygons track a consistent pattern of biodiversity across a wide range of species, suggesting that they may delimit underlying factors which play a role in the distribution bird diversity. Assuming that these factors remain consistent in other locations, some manner of union between geophysical and hydrological boundaries may prove a beneficial starting point for conservation planning elsewhere (these have been referred to as 'Land Facets', sensu Wessels *et al.* 1999; Parks and Mulligan 2010).

The present analyses provide a foundation for the systematic conservation planning of avian diversity in the province of Ontario, and this methodology may be usefully applied elsewhere for a broad range of conservation features. Many additional environmental, topological and social factors will no doubt also need to be incorporated into a real world application of system-

atic design in Ontario (Ban *et al.* 2009; Christensen *et al.* 2009; Meynard *et al.* 2009; Lagabriele *et al.* 2010). Current results provide an important overview of bird diversity to inform conservation effort in the short-term, and to guide investment in stewardship and monitoring over the longer term. Given the large proportion of migratory species, avian conservation success in the province will also depend on the continued maintenance of habitat outside of the study region (e.g. Hazlitt *et al.* 2010). Pressure from ongoing human land-uses will also need to be included in order to properly prioritize between potential conservation areas. Political and jurisdictional issues may play a strong role in determining what spatial classification scheme is used for near term planning; in part it is for this reason that a broad range of classifications were analyzed. Once the most appropriate or preferred scheme has been selected, the results for that classification can be used to target conservation investment in those terms, hopefully maximizing the usefulness of the current analysis to as broad a range of stakeholders as possible.

Recent developments, including this thesis, move the systematic reserve design approach beyond simple conservation planning into the realm of multi-objective land-use planning (Ban *et al.* 2009; Christensen *et al.* 2009; Watts *et al.* 2009; Lagabriele *et al.* 2010). Conservation should be regarded as an iterative process which follows and reacts to changing circumstance, rather than a static effort to hold on to historical patterns. To the greatest extent possible, natural processes should be provided for so that societies have the time to integrate more robust feedback mechanisms into the development of conservation strategies. Conservation planning may benefit from a new perspective; a shift from an emphasis on preserving already rare or declining species to a focus on maintaining present biodiversity patterning and the processes which drive those patterns. Legal requirements presently direct conservation efforts towards more threatened species, conservation efforts directed towards these species will likely have a broadly beneficial impact on biodiversity as a whole. Data on the occurrence of rare species may be best used as an indicator of habitat quality, rather than as the principal focus of conservation planning. This will be true for those species that are associated with high quality habitat or low human disturbance, but not necessarily for those remnant species which have been pushed into marginal habitat by habitat

loss. Species which are not presently found within optimal habitats will make poor choices as umbrella species, and models based on their known present distributions may not identify their preferred habitat. These analyses suggest a number of productive approaches to ensuring that the results of systematic conservation planning produce useful and unbiased conservation solutions. Conservation planners should explicitly acknowledge the confounding effects of spatial classification, conservation target level, and the species set chosen for analysis when formulating systematic conservation planning analyses.

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Appendix A

Biogeographic Mappings

10 km² OBBA Sampling Square Classification

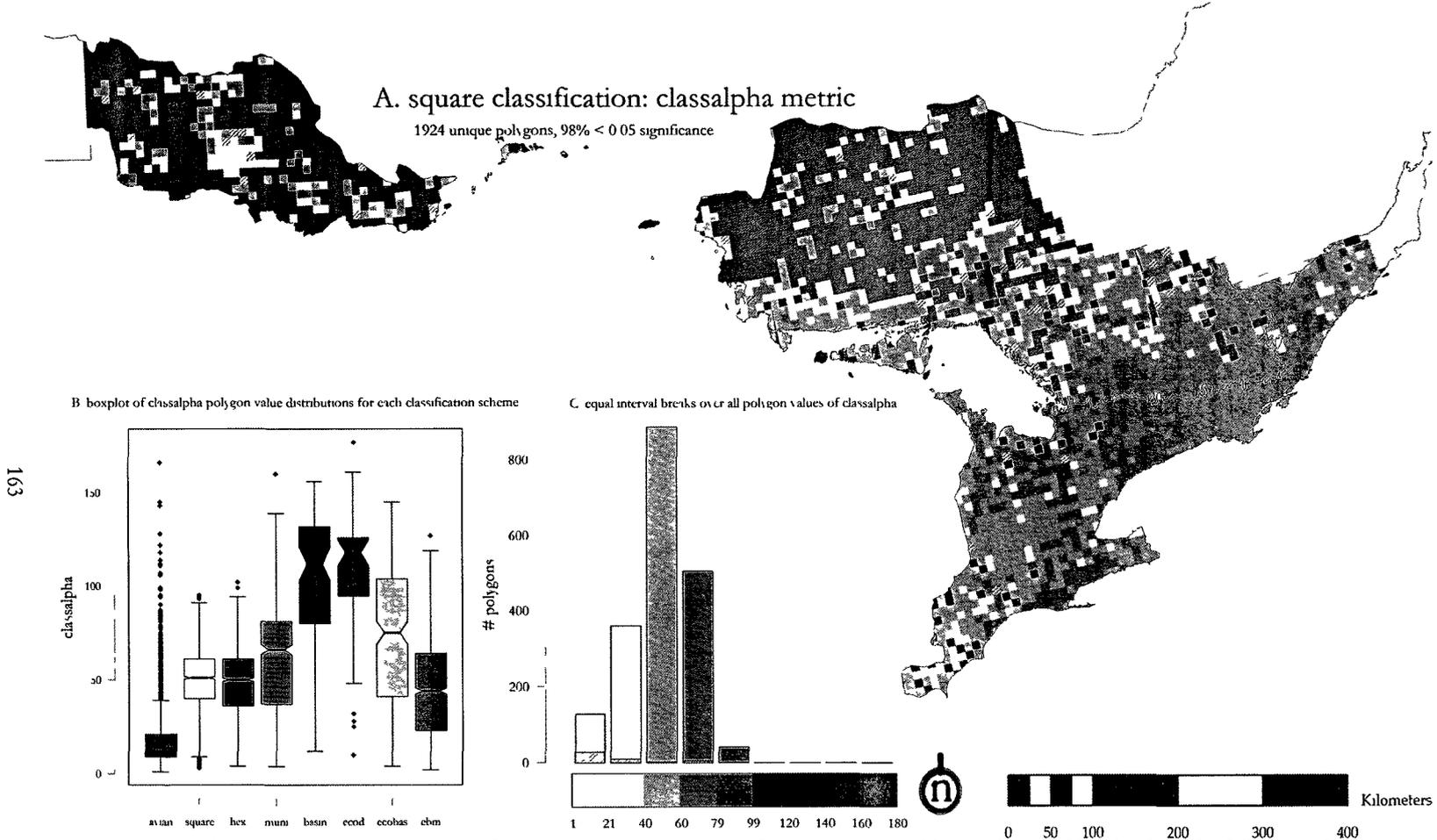


Figure A 1 A Results summary for total polygon richness (class alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the classification, and associated colour scheme. Hatched areas show the proportion of non-significant polygon values.

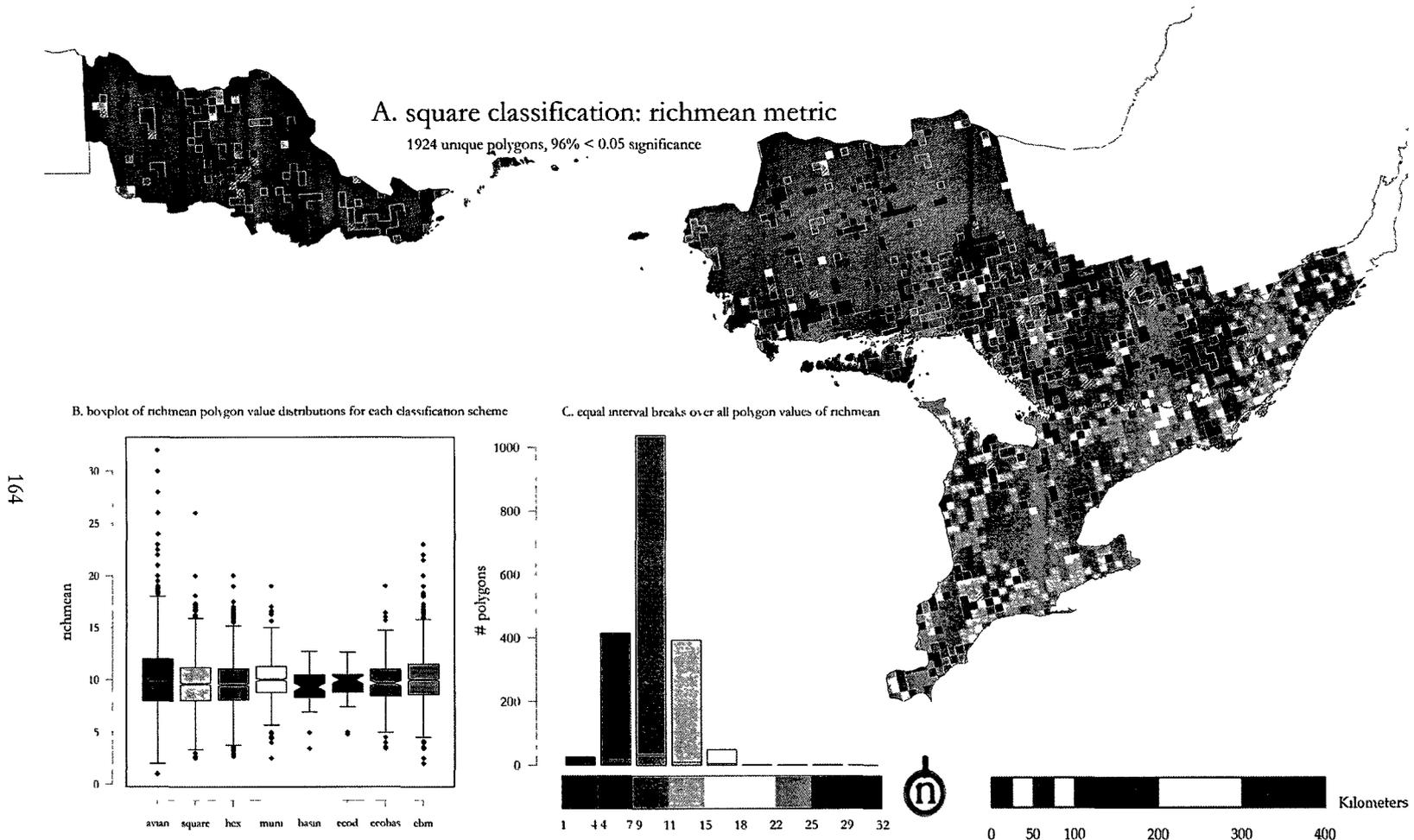


Figure A.2: A. Results summary for mean point-level species richness (average point alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the classification, and associated colour scheme. Hatched areas show the proportion of non-significant polygon values.

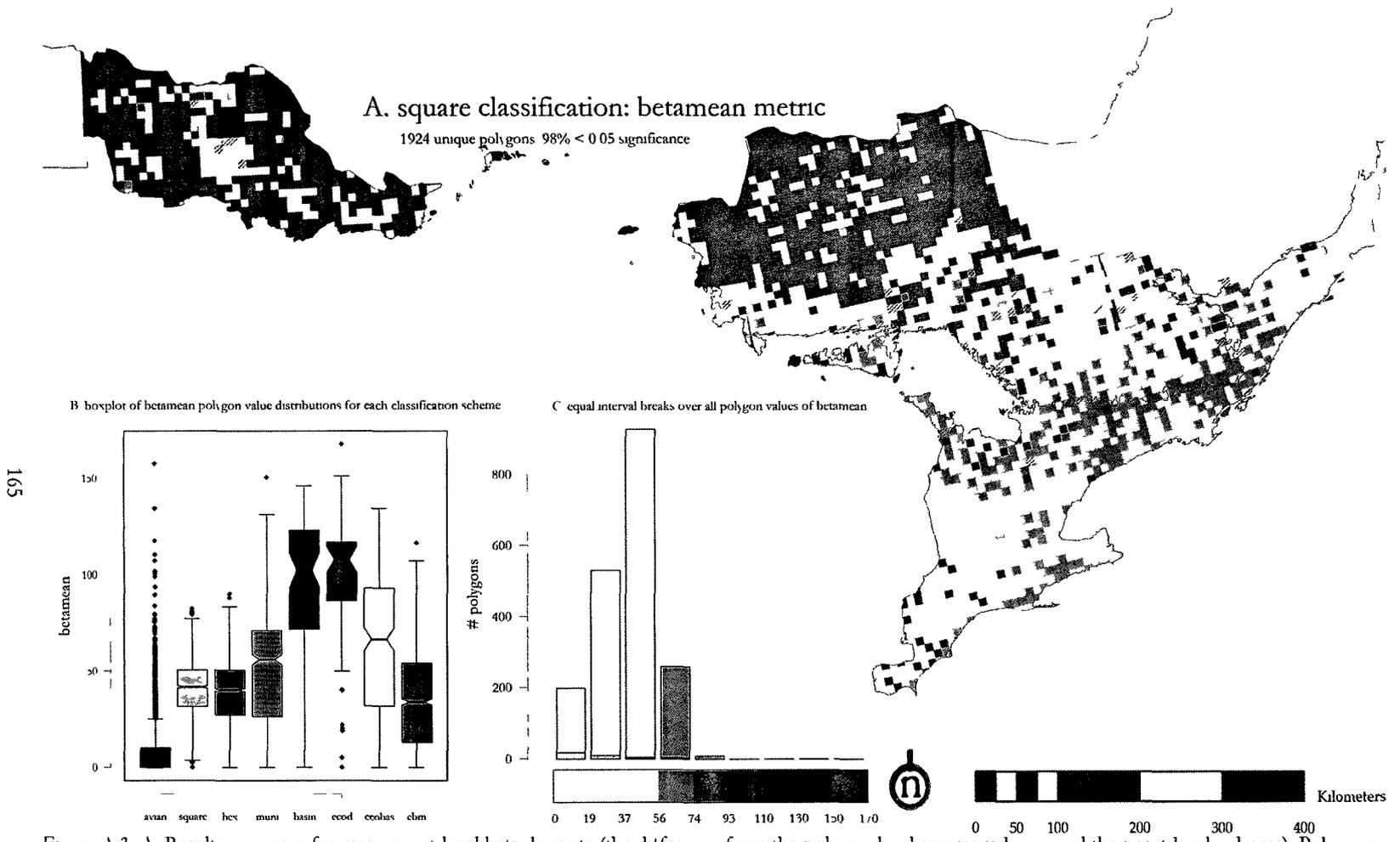


Figure A 3 A Results summary for mean point-level beta diversity (the difference from the polygon level species richness and the point level richness) Polygons are coloured by equal interval breaks along the full range of values Dark grey polygons are within the study region but contain no OBB A points Hatched areas denote polygons containing values that are indistinguishable from a random null model B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark C Polygon level histogram showing the distribution of values across the classification, and associated colour scheme Hatched areas show the proportion of non significant polygon values

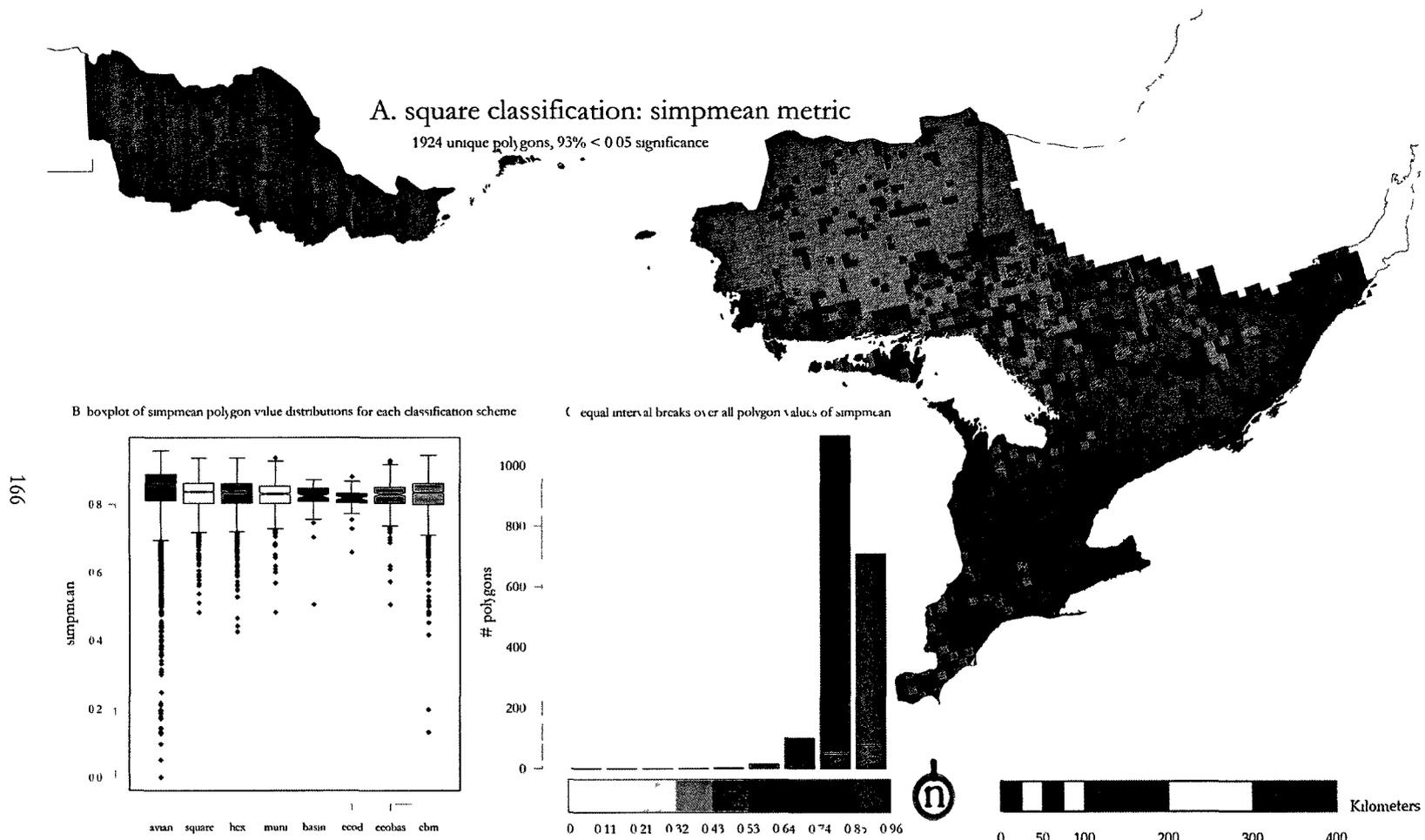


Figure A 4 A Results summary for mean point-level Simpson's diversity (the evenness of species composition). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the classification, and associated colour scheme. Hatched areas show the proportion of non-significant polygon values.

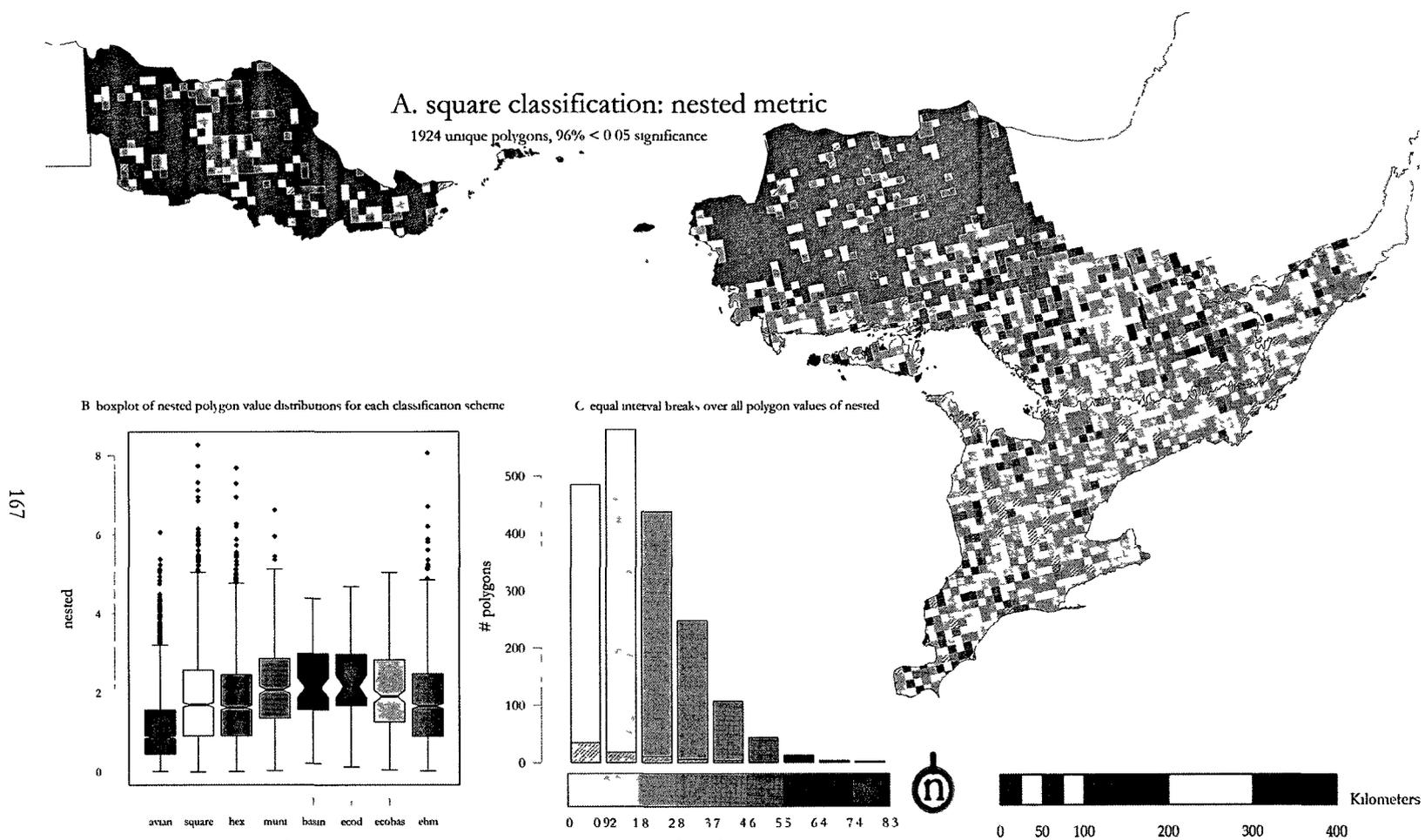


Figure A.5: A. Results summary for nestedness temperature (a measure of the disorder in species composition within polygons, low values indicate a regular nested pattern of species loss from high to low richness points, high values reflect more disordered structures). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Light grey polygons contain less than three points, and cannot be analyzed. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the classification, and associated colour scheme. Hatched areas show the proportion of non-significant polygon values.

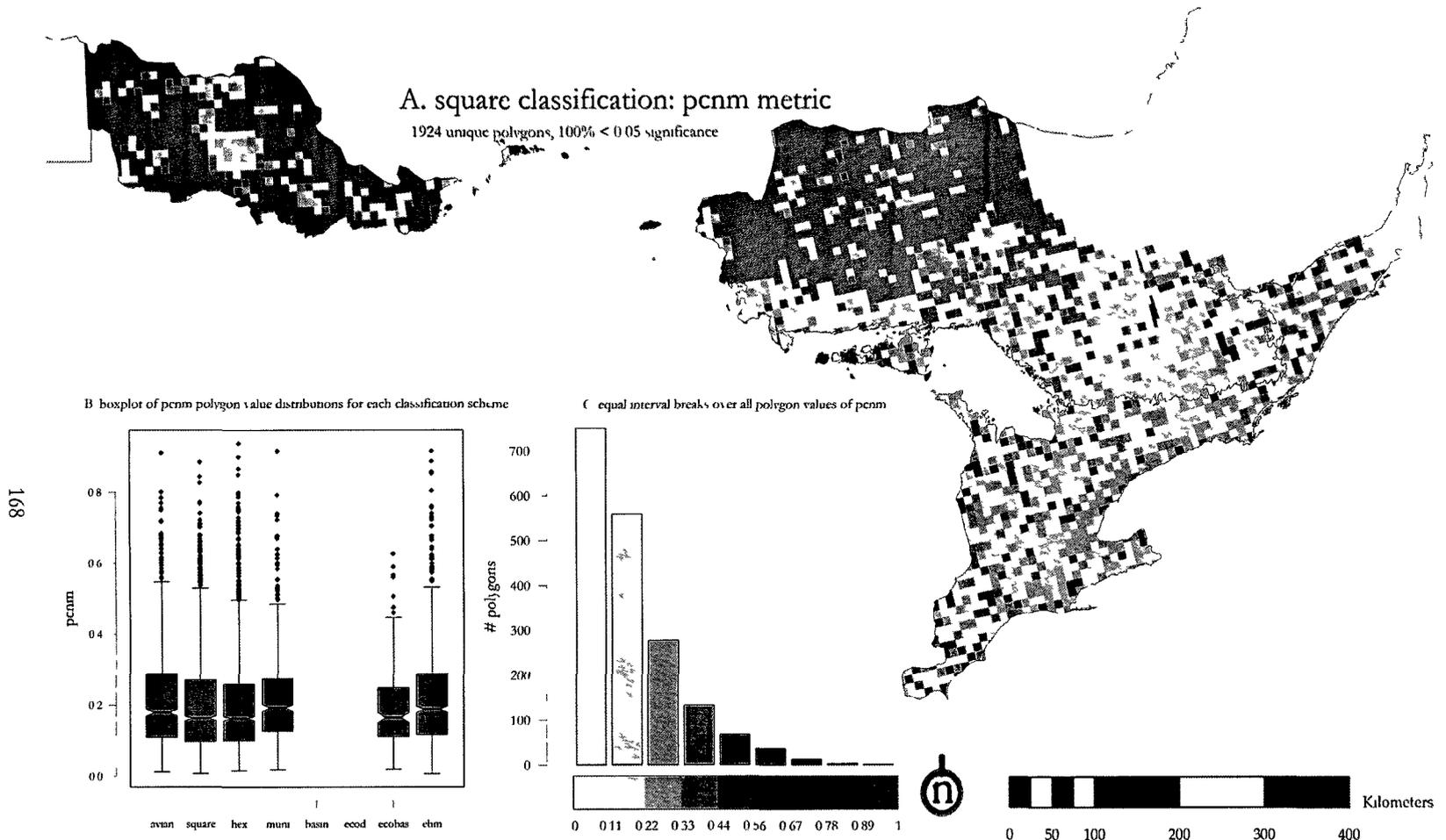


Figure A 6 A Results summary for the amount of variation in polygon species composition that can be explained using spatial components (described by an adjusted R squared term using PCNM ordination). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Light grey polygons contain less than three points, and cannot be analysed. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon level histogram showing the distribution of values across the classification, and associated colour scheme. Hatched areas show the proportion of non significant polygon values.

Appendix B

Biogeographic Mappings

10 km² Hexagon Classification

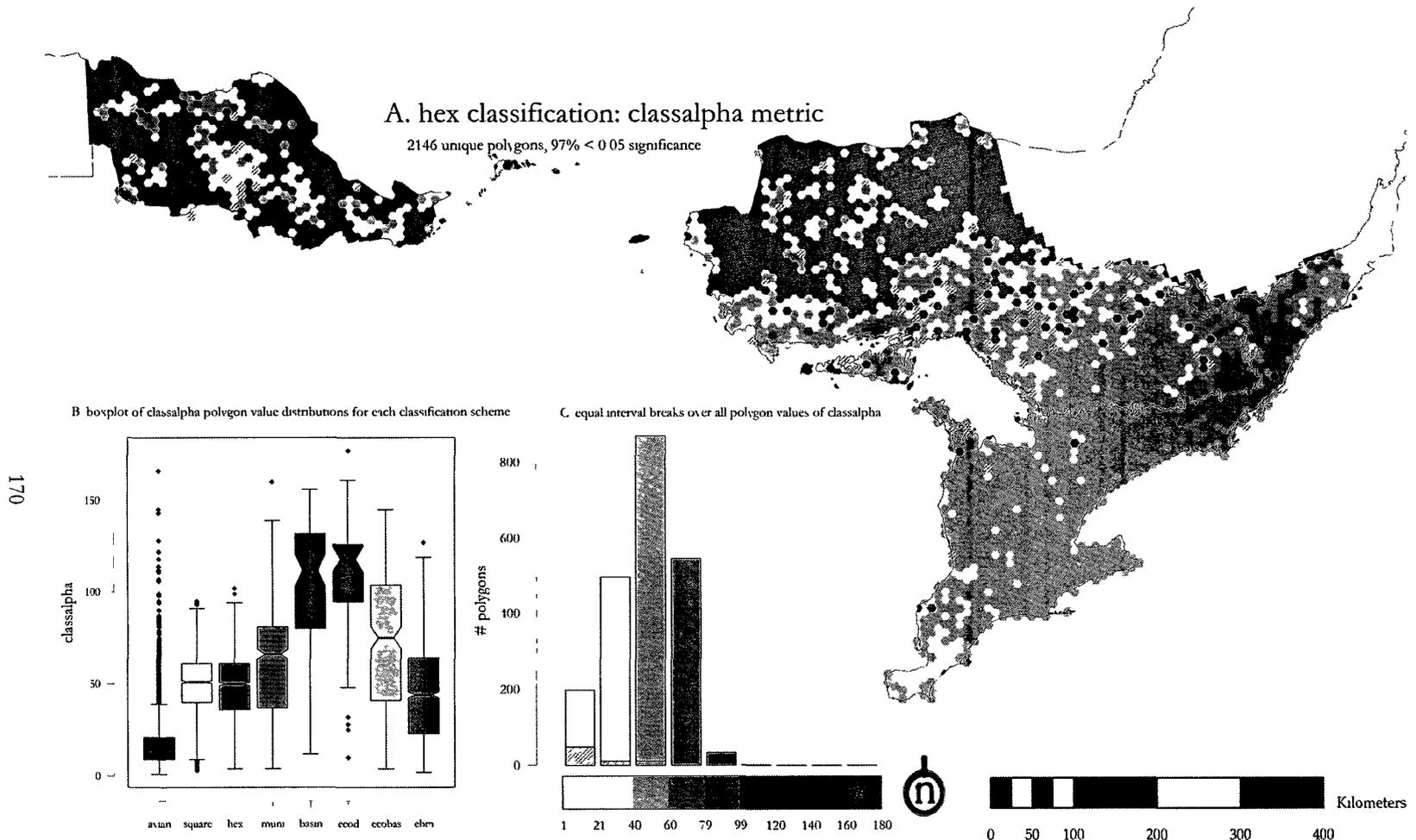
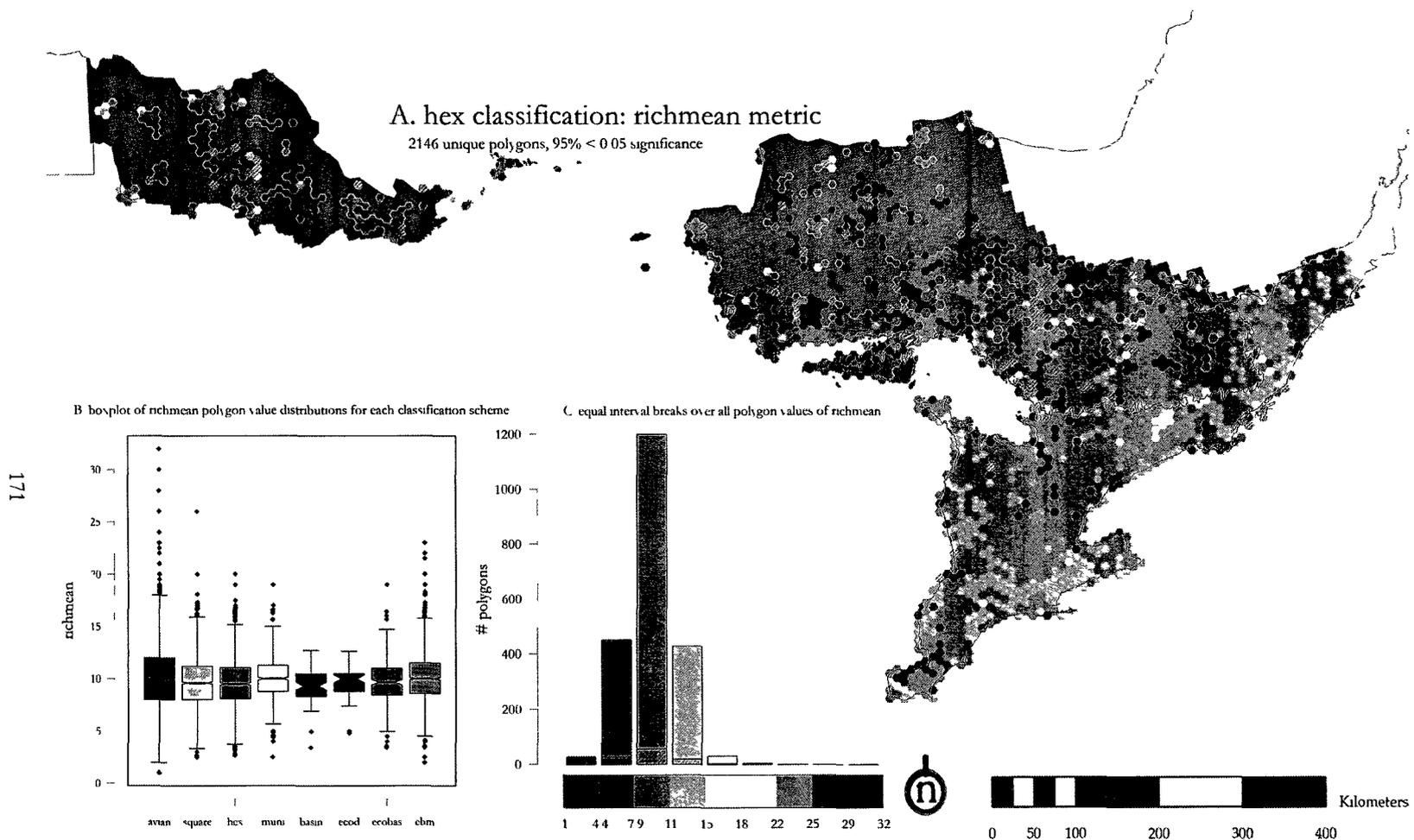


Figure B.1. A. Results summary for total polygon richness (class alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.



171

Figure B.2. A Results summary for mean point-level species richness (average point alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non significant polygon values.

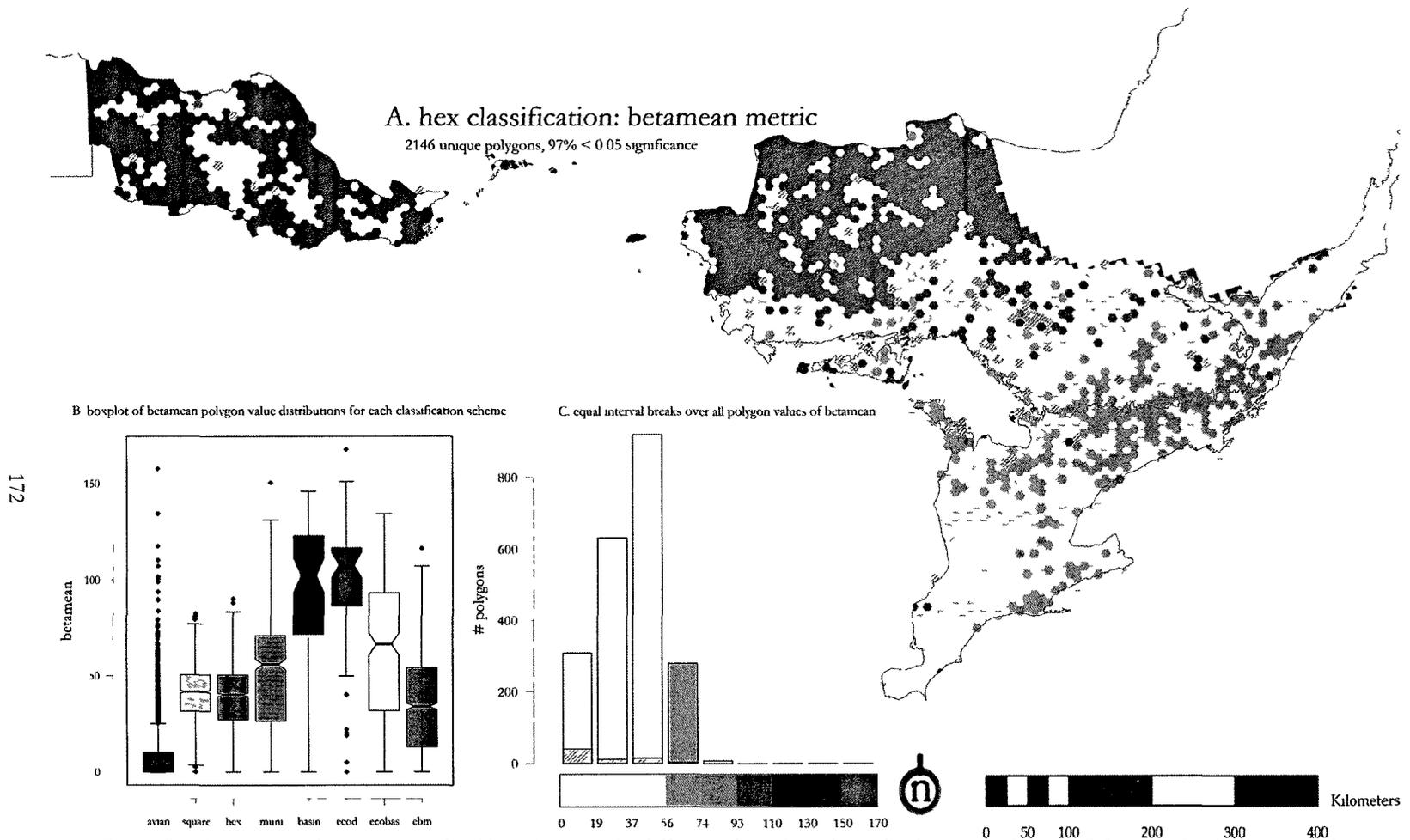


Figure B.3. A. Results summary for mean point-level beta diversity (the difference from the polygon-level species richness and the point-level richness). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

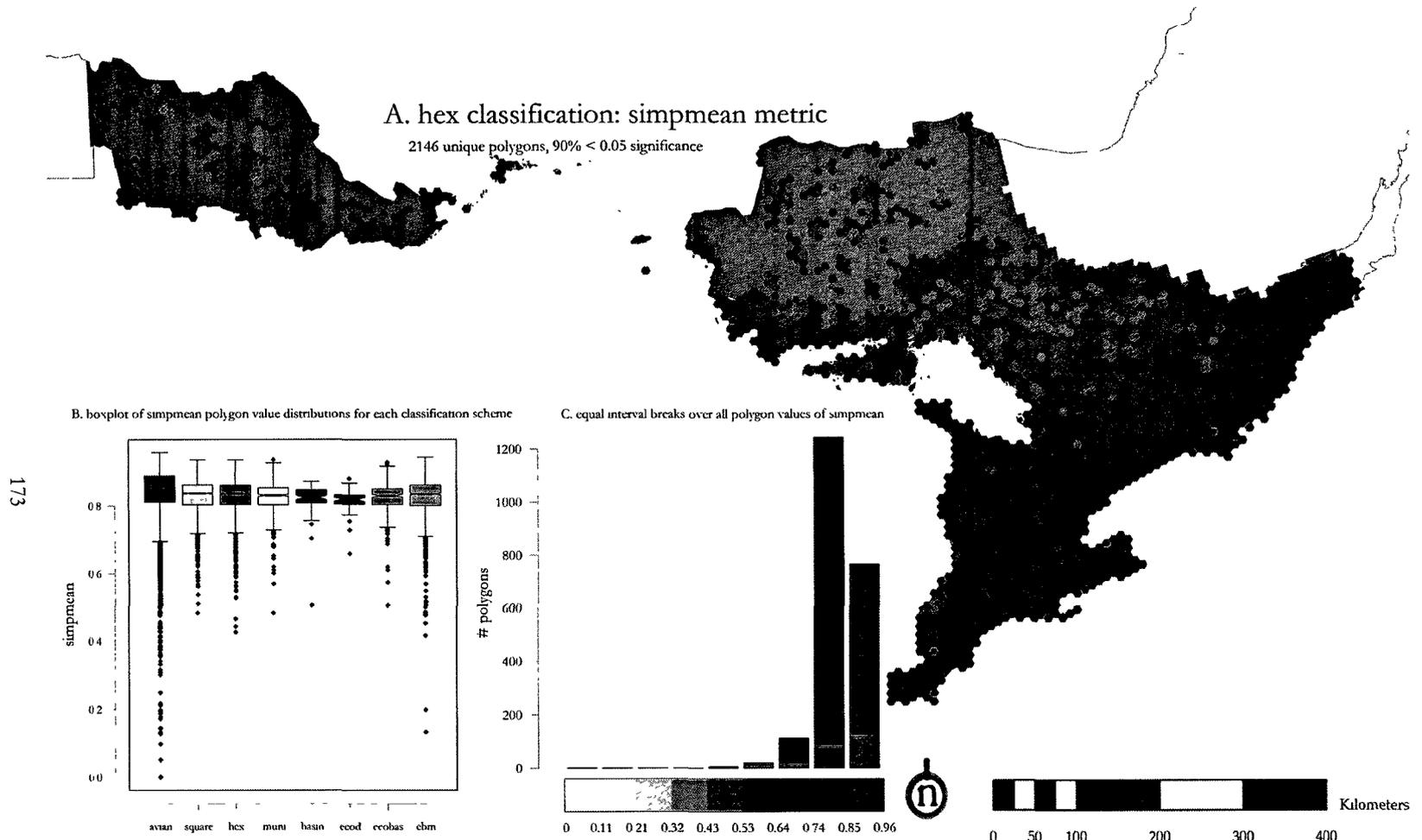


Figure B.4: A. Results summary for mean point-level Simpson's diversity (the evenness of species composition). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

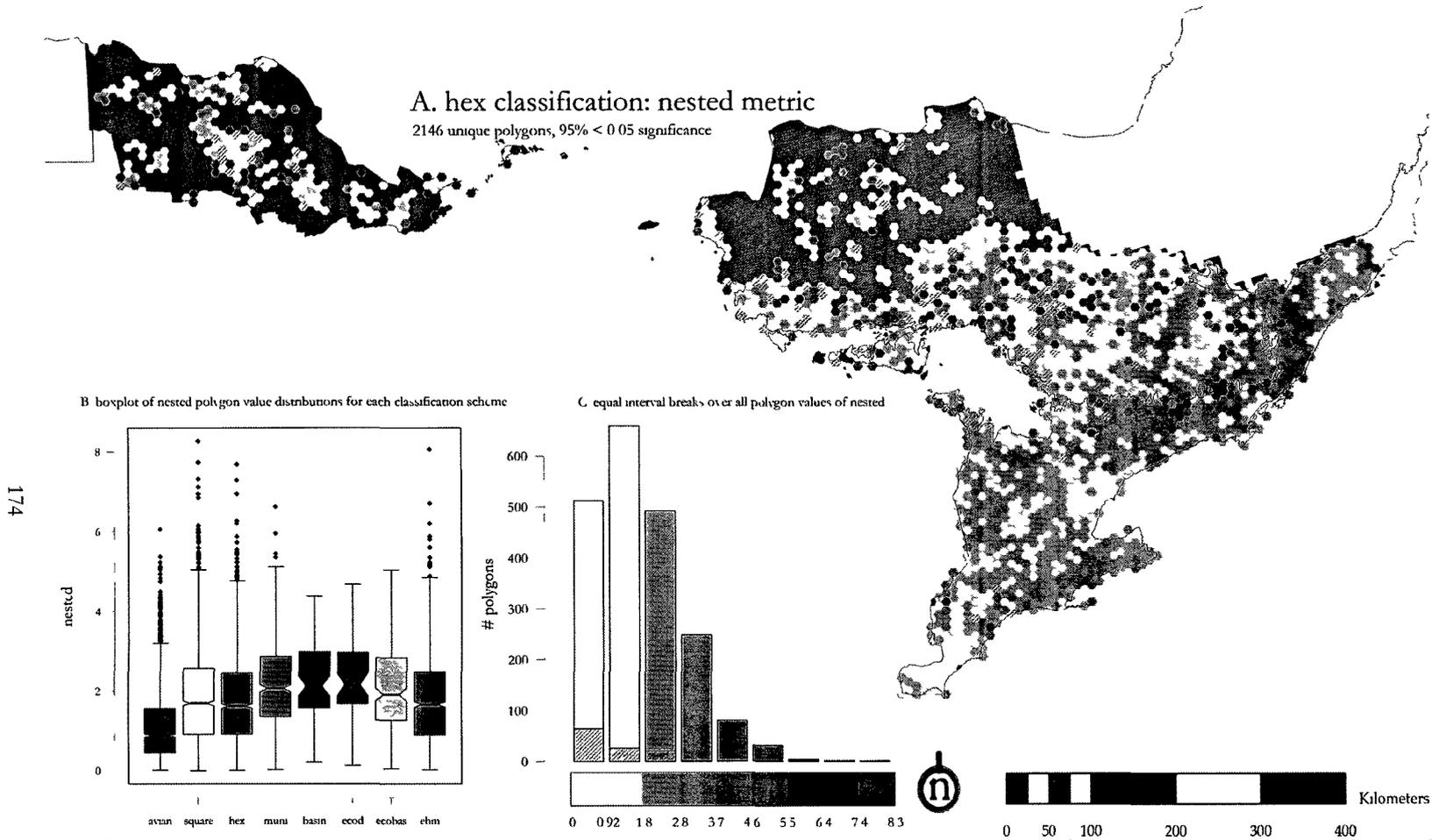


Figure B 5 A Results summary for nestedness temperature (a measure of the disorder in species composition within polygons, low values indicate a regular nested pattern of species loss from high to low richness points, high values reflect more disordered structures) Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Light grey polygons contain less than three points, and cannot be analyzed. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

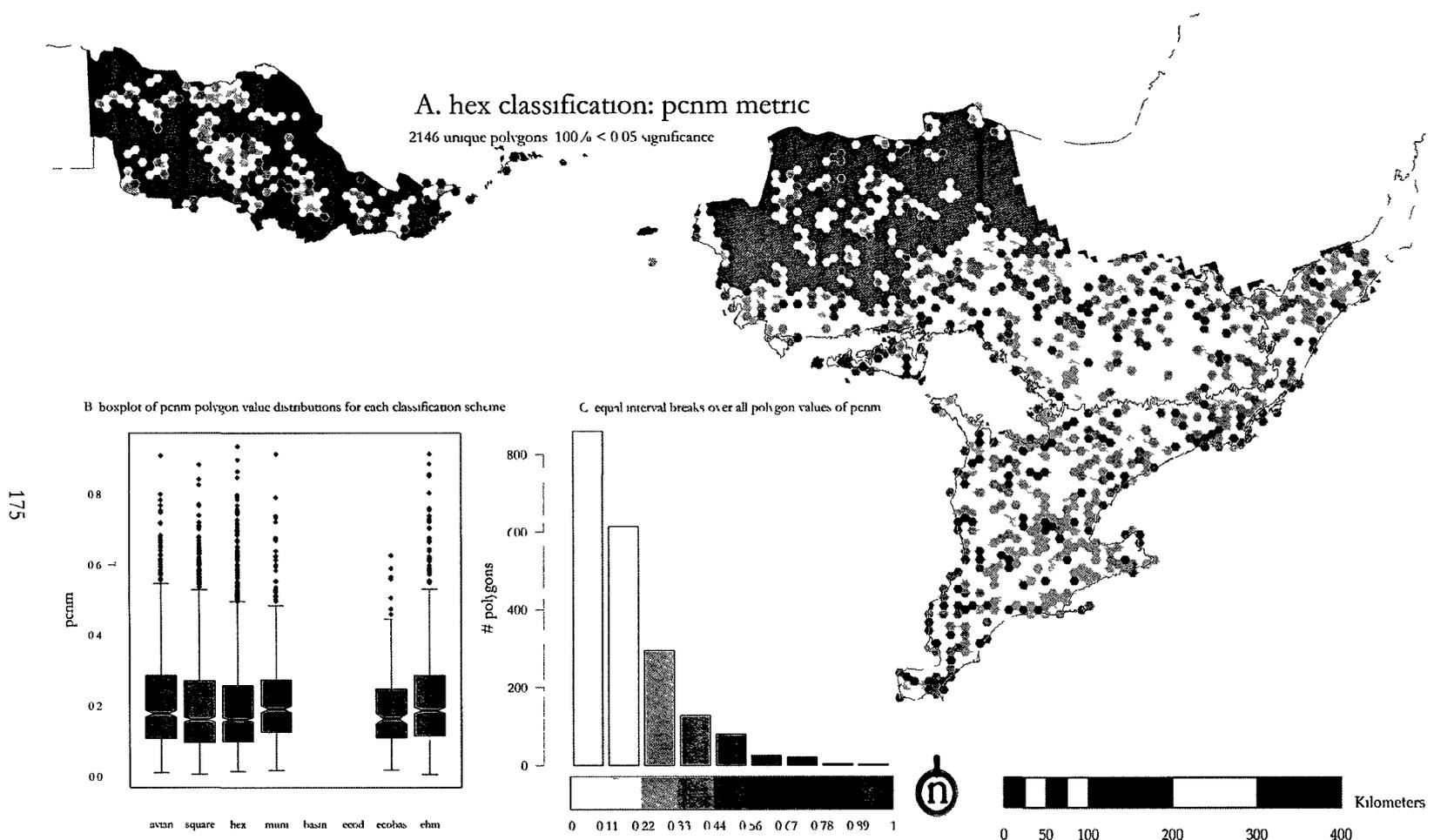
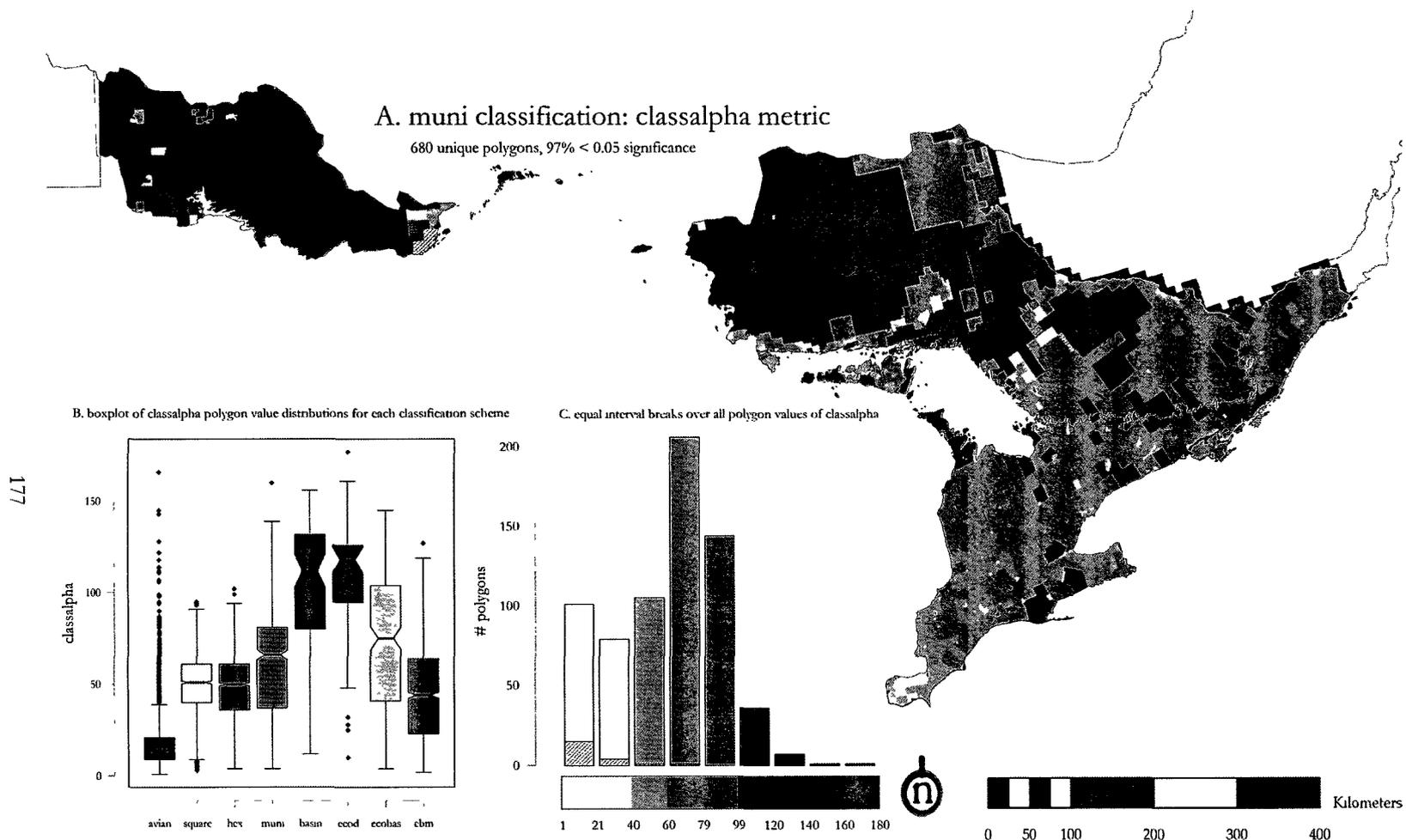


Figure B.6 A Results summary for the amount of variation in polygon species composition that can be explained using spatial components (described by an adjusted R squared term using PCNM ordination) Polygons are coloured by equal interval breaks along the full range of values Dark grey polygons are within the study region but contain no OBBA points Light grey polygons contain less than three points, and cannot be analysed Hatched areas denote polygons containing values that are indistinguishable from a random null model B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark C Polygon level histogram showing the distribution of values across the study region, and associated colour scheme Hatched areas show non significant polygon values

Appendix C

Biogeographic Mappings

**Lower Tier Municipal Boundary
Classification**



177

Figure C.1: A. Results summary for total polygon richness (class alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

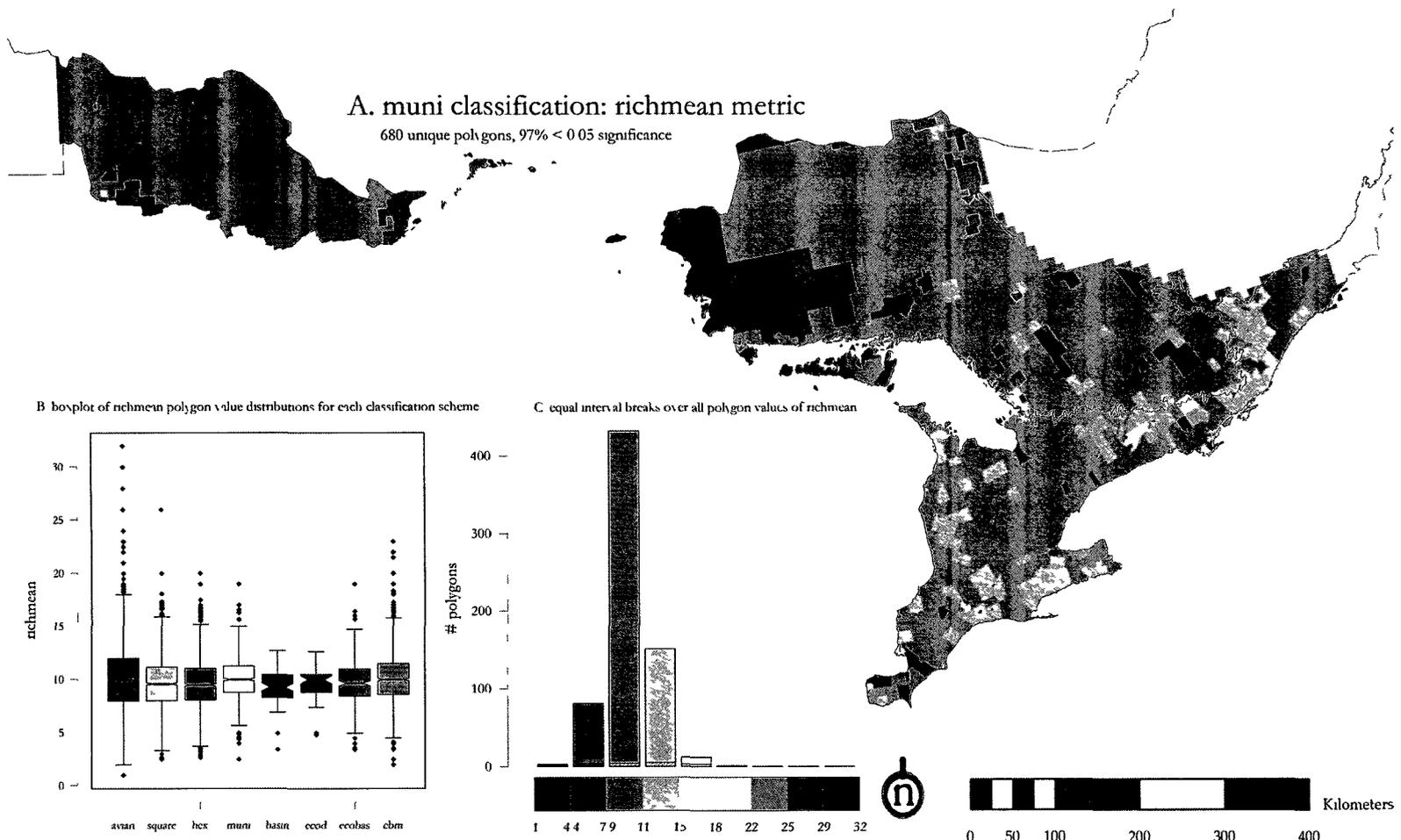


Figure C.2 A Results summary for mean point-level species richness (average point alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

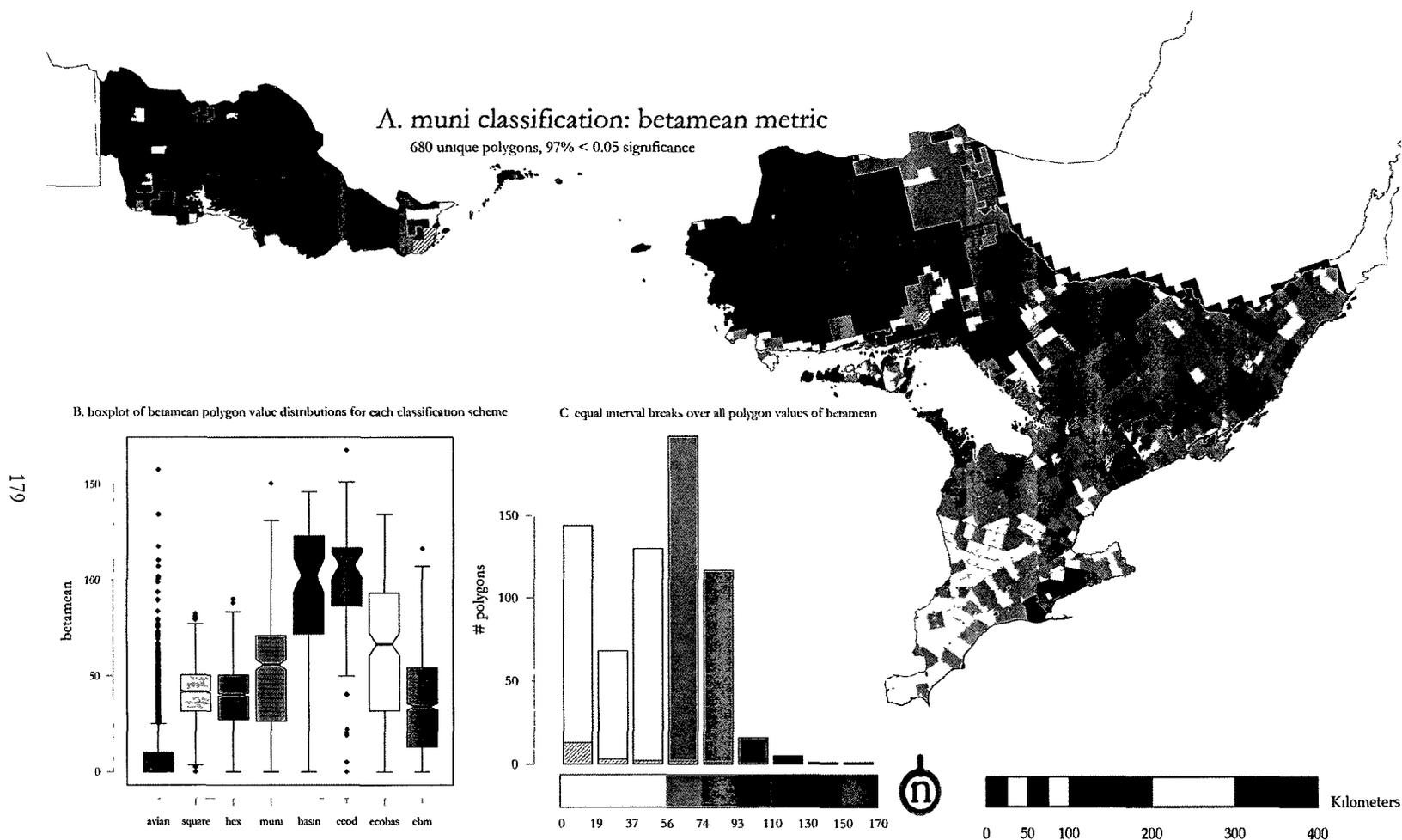
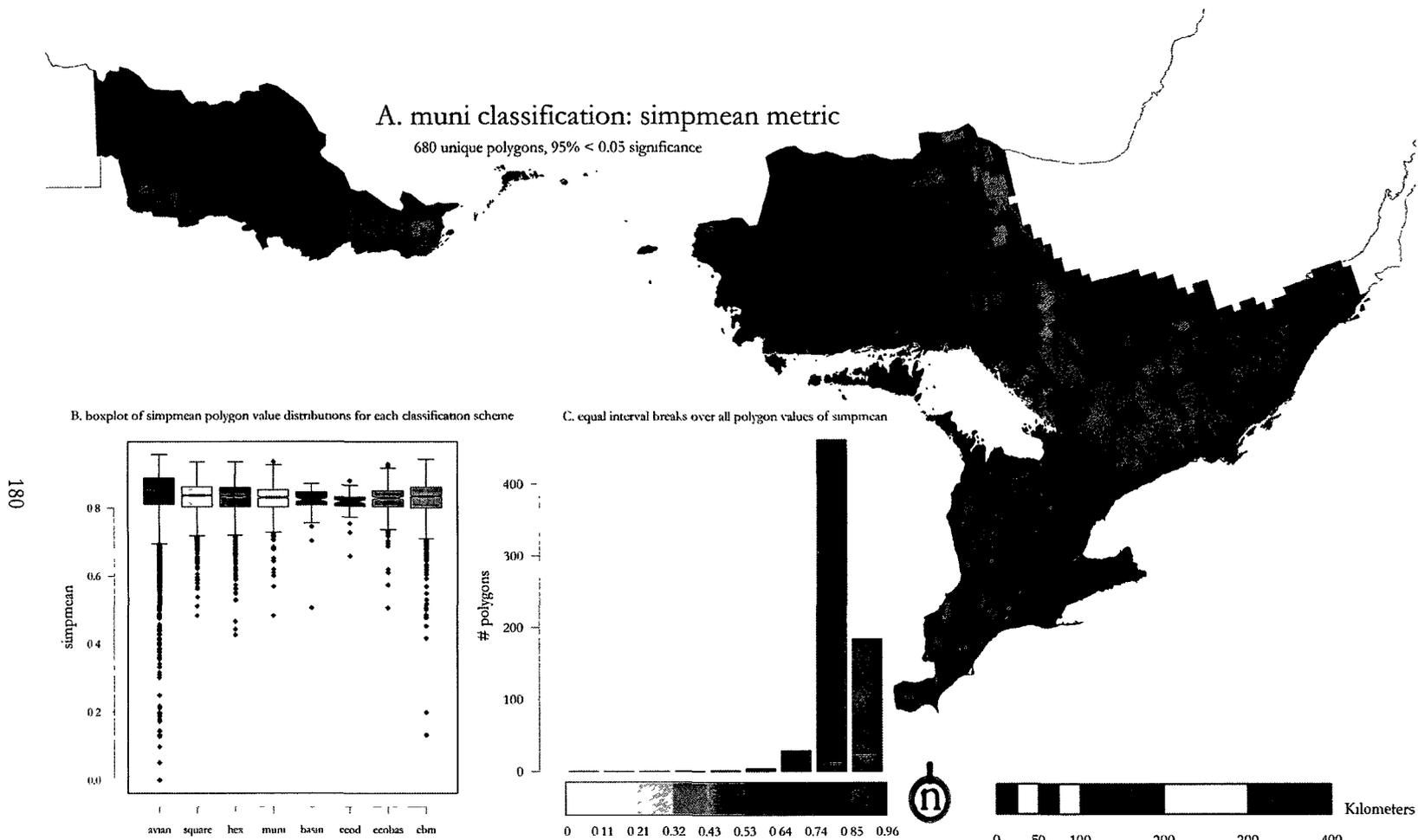


Figure C.3: A. Results summary for mean point-level beta diversity (the difference from the polygon-level species richness and the point-level richness). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.



180

Figure C.4: A. Results summary for mean point-level Simpson's diversity (the evenness of species composition). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

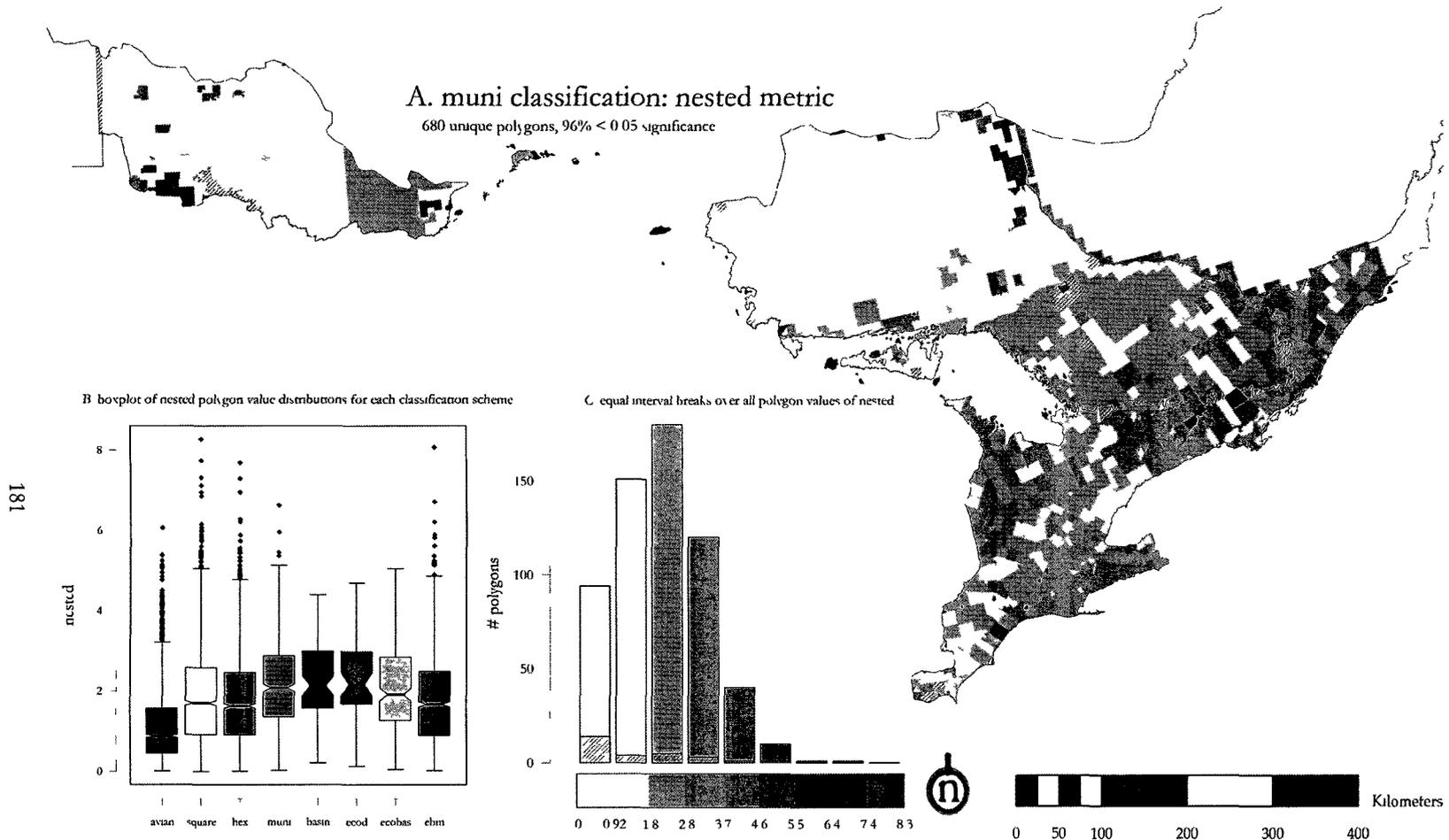


Figure C 5 A Results summary for nestedness temperature (a measure of the disorder in species composition within polygons, low values indicate a regular nested pattern of species loss from high to low richness points, high values reflect more disordered structures) Polygons are coloured by equal interval breaks along the full range of values Dark grey polygons are within the study region but contain no OBBA points Light grey polygons contain less than three points, and cannot be analyzed Hatched areas denote polygons containing values that are indistinguishable from a random null model B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark C Polygon level histogram showing the distribution of values across the study region, and associated colour scheme Hatched areas show non-significant polygon values

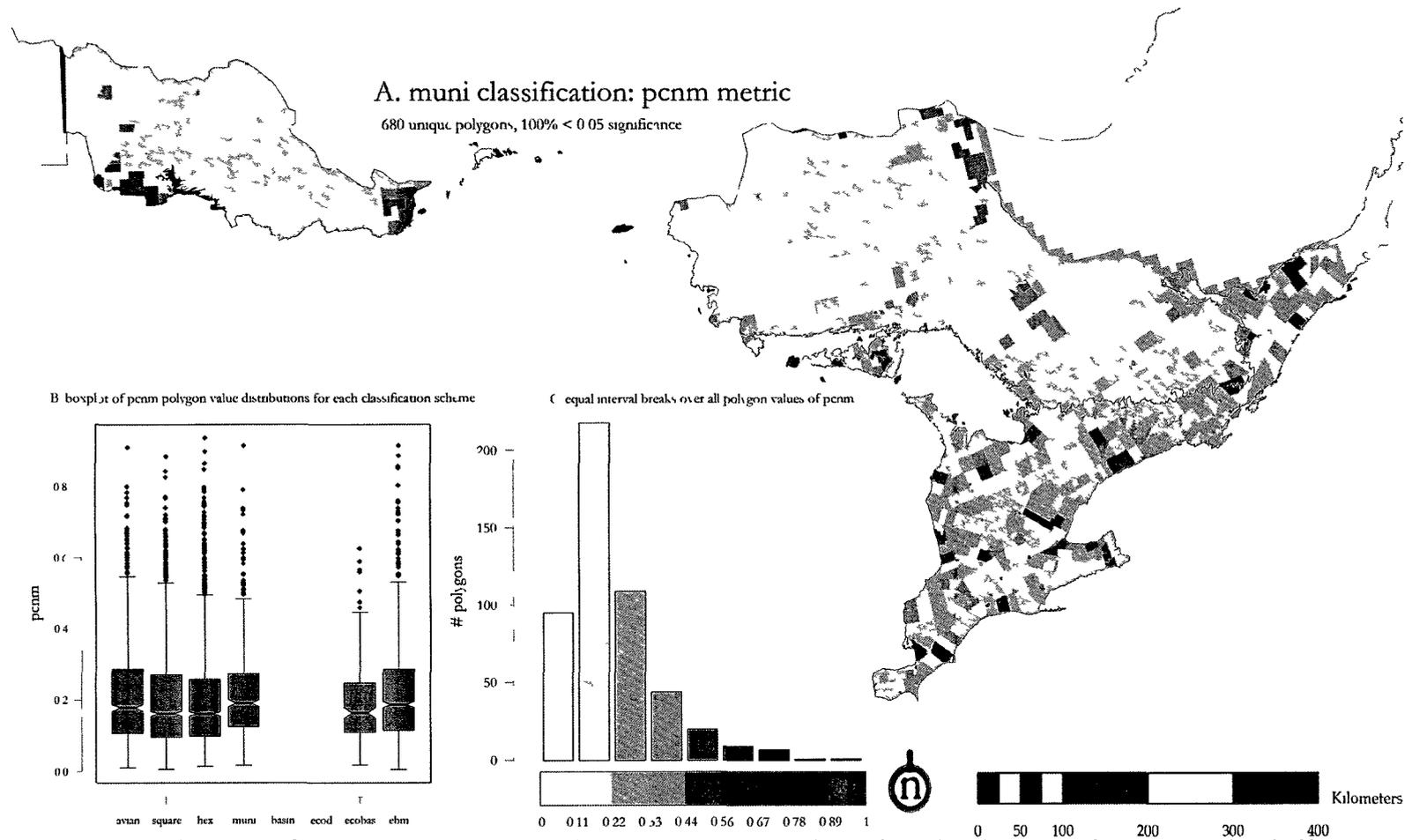


Figure C.6 A Results summary for the amount of variation in polygon species composition that can be explained using spatial components (described by an adjusted R squared term using PCNM ordination). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Light grey polygons contain less than three points, and cannot be analysed. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non significant polygon values.

Appendix D

Biogeographic Mappings

Sub-Sub Basin Watershed Boundary Classification

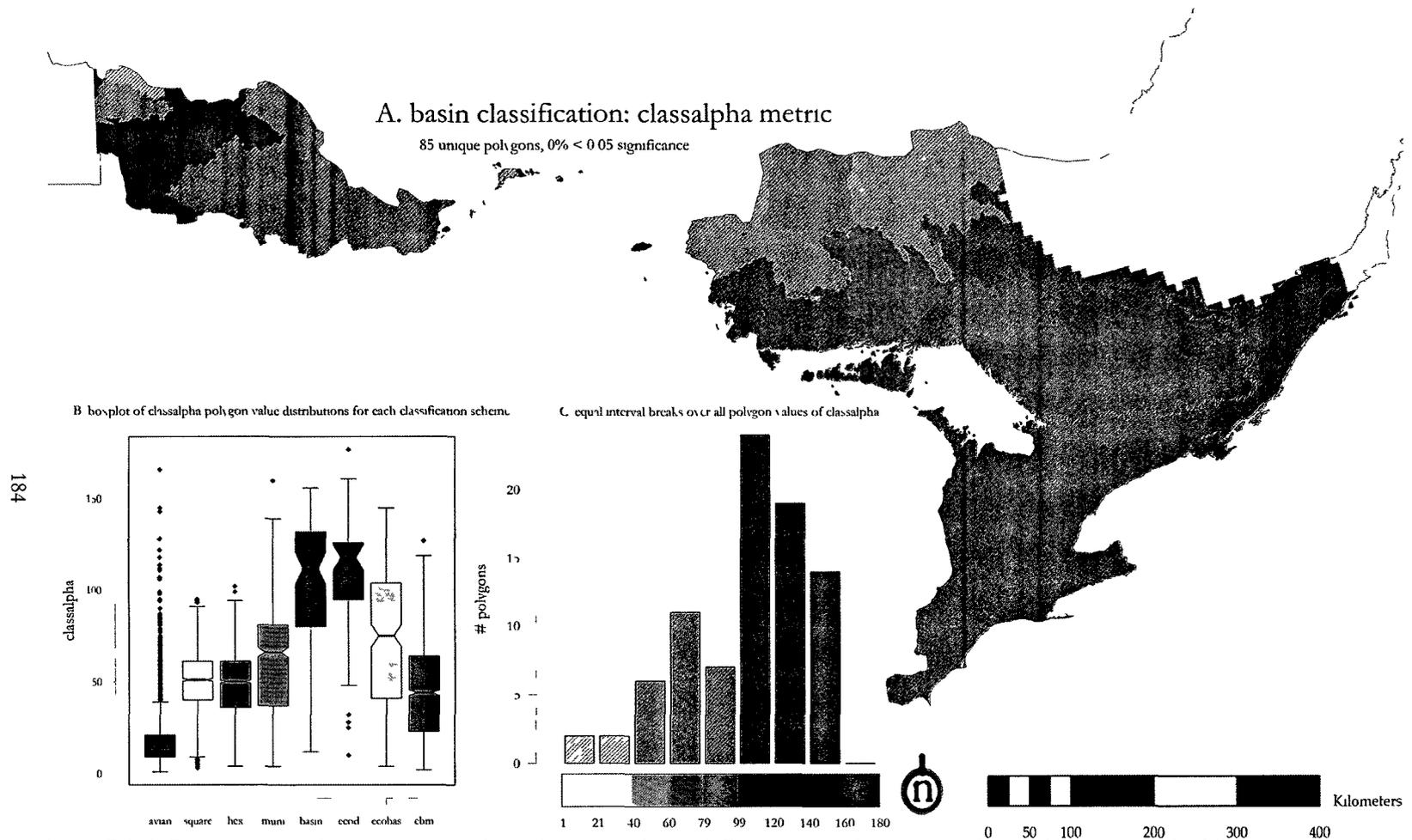


Figure D1 A Results summary for total polygon richness (class alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non significant polygon values.

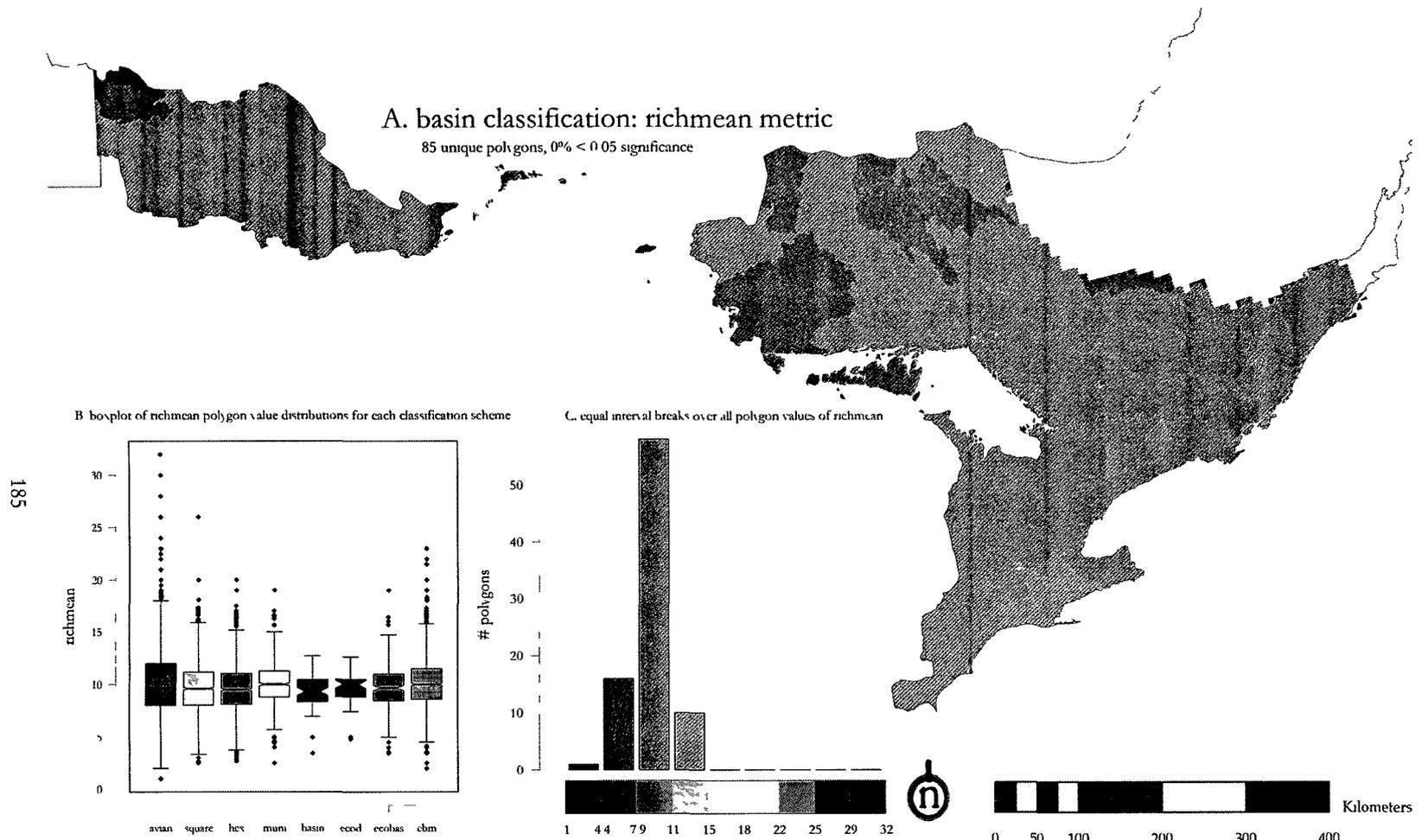


Figure D2. A Results summary for mean point level species richness (average point alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non significant polygon values.

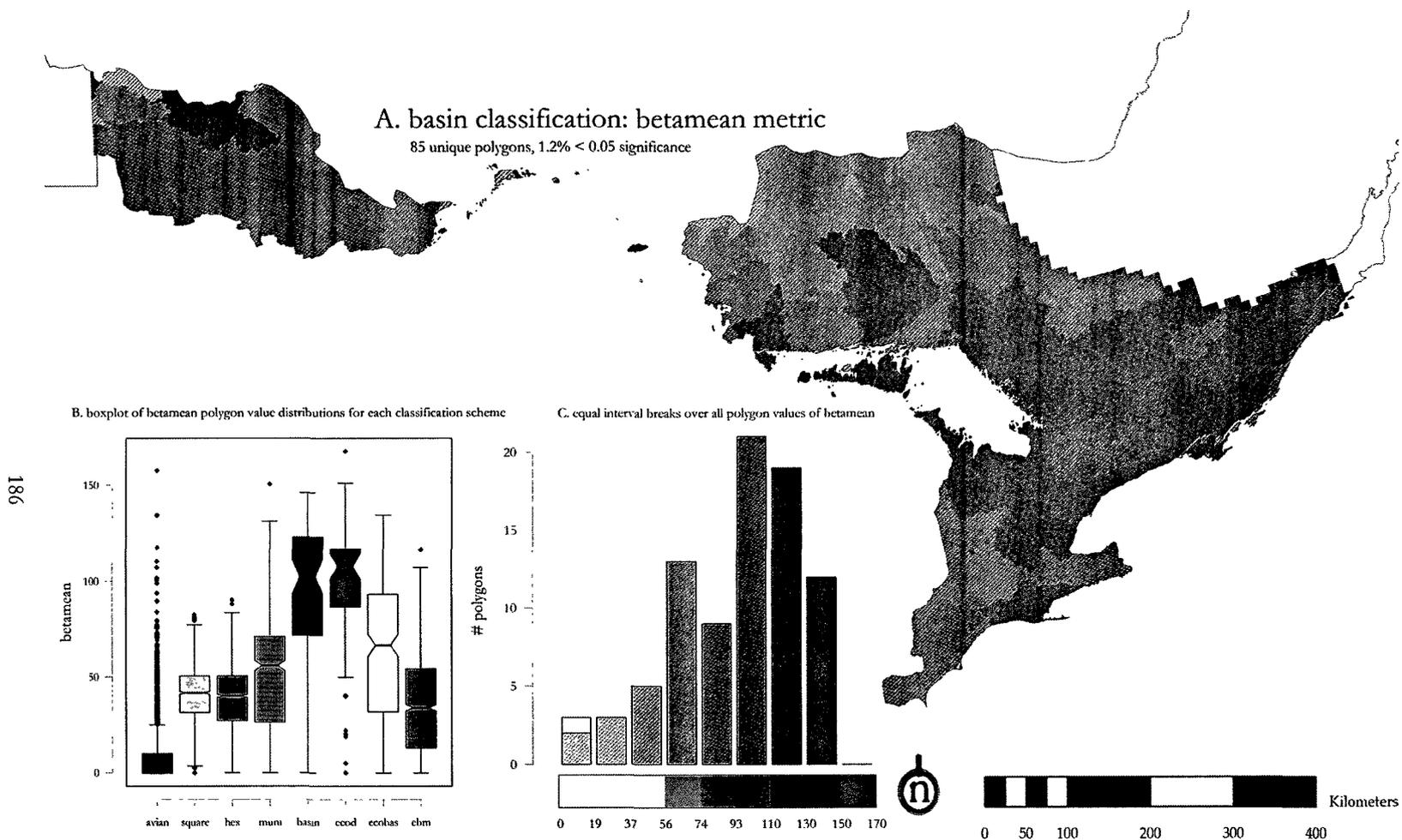


Figure D.3: A. Results summary for mean point-level beta diversity (the difference from the polygon-level species richness and the point-level richness). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

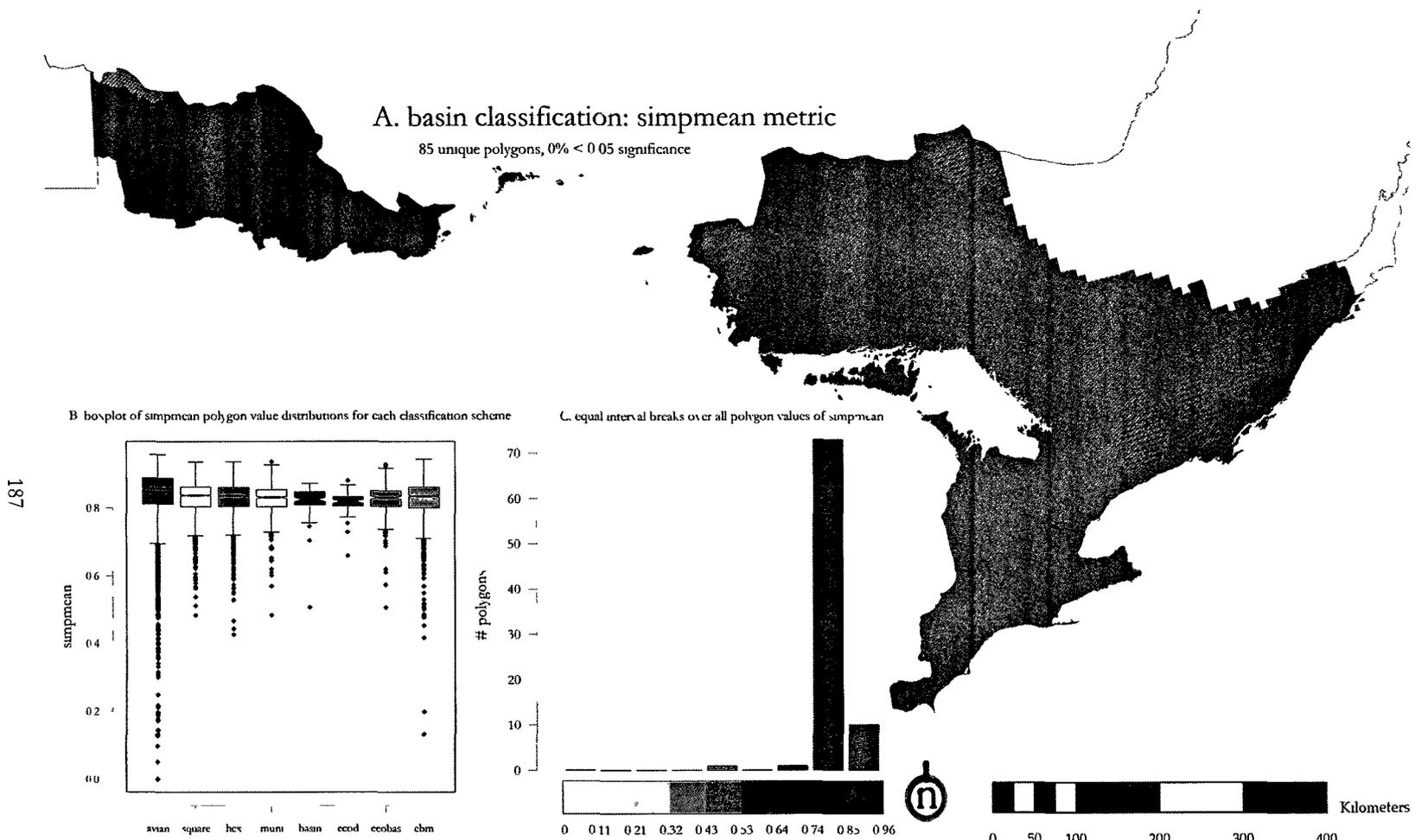


Figure D4 A Results summary for mean point-level Simpson's diversity (the evenness of species composition). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBB \ points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

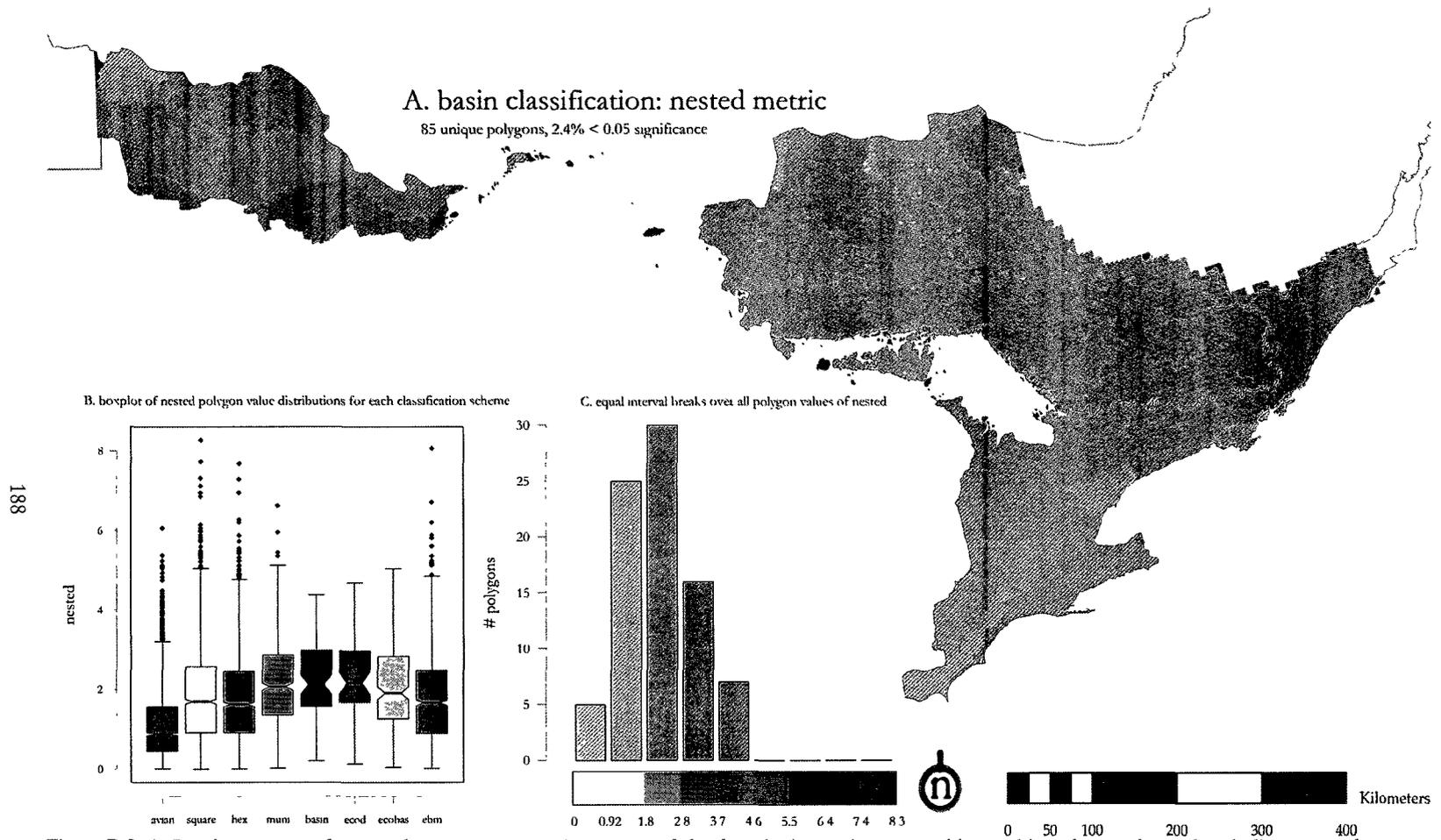


Figure D.5: A. Results summary for nestedness temperature (a measure of the disorder in species composition within polygons; low values indicate a regular nested pattern of species loss from high to low richness points, high values reflect more disordered structures). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

Appendix E

Biogeographic Mappings

Ecodistrict Classification

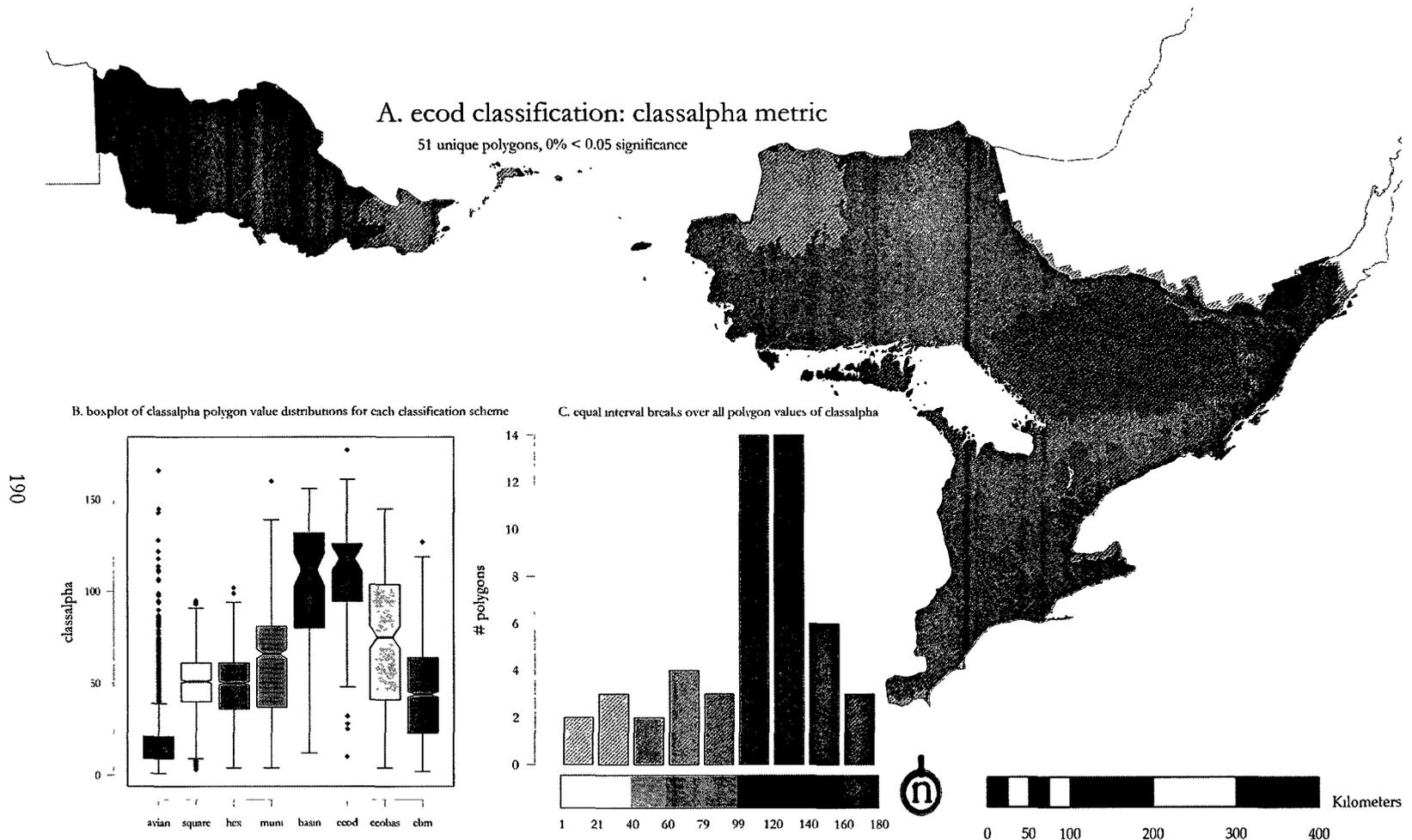


Figure E.1: A. Results summary for total polygon richness (class alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

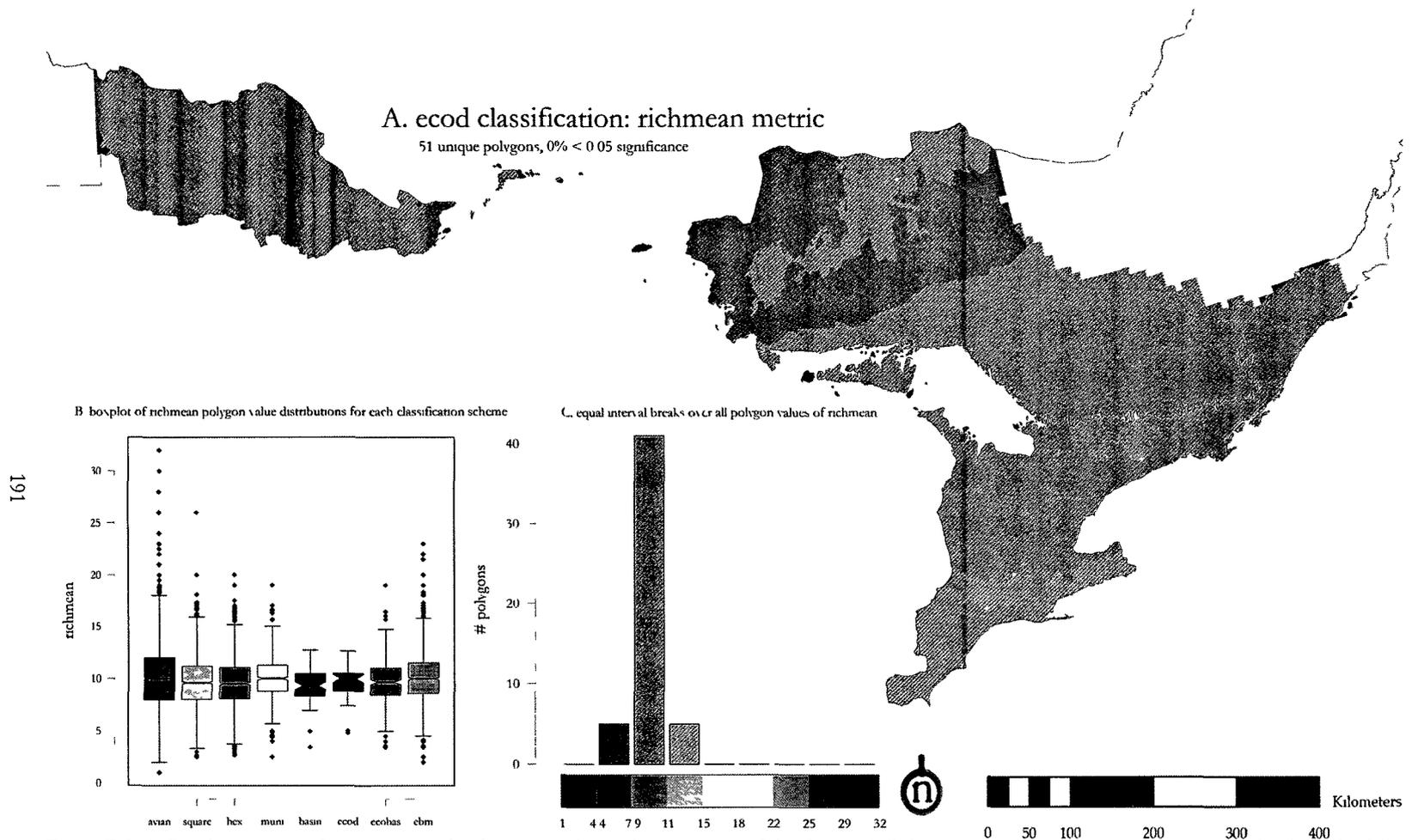


Figure E.2 A Results summary for mean point-level species richness (average point alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

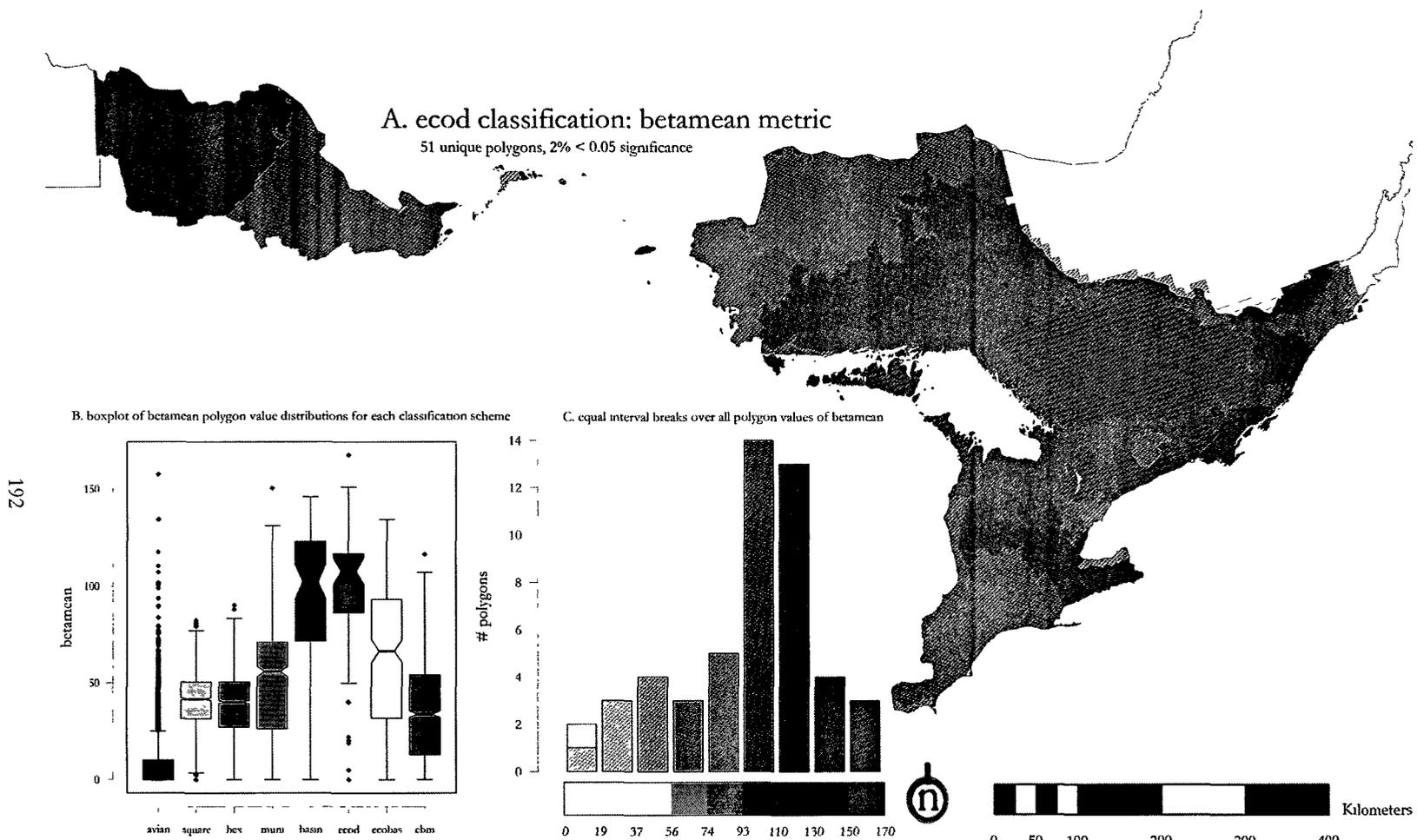


Figure E.3: A. Results summary for mean point-level beta diversity (the difference from the polygon-level species richness and the point-level richness). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

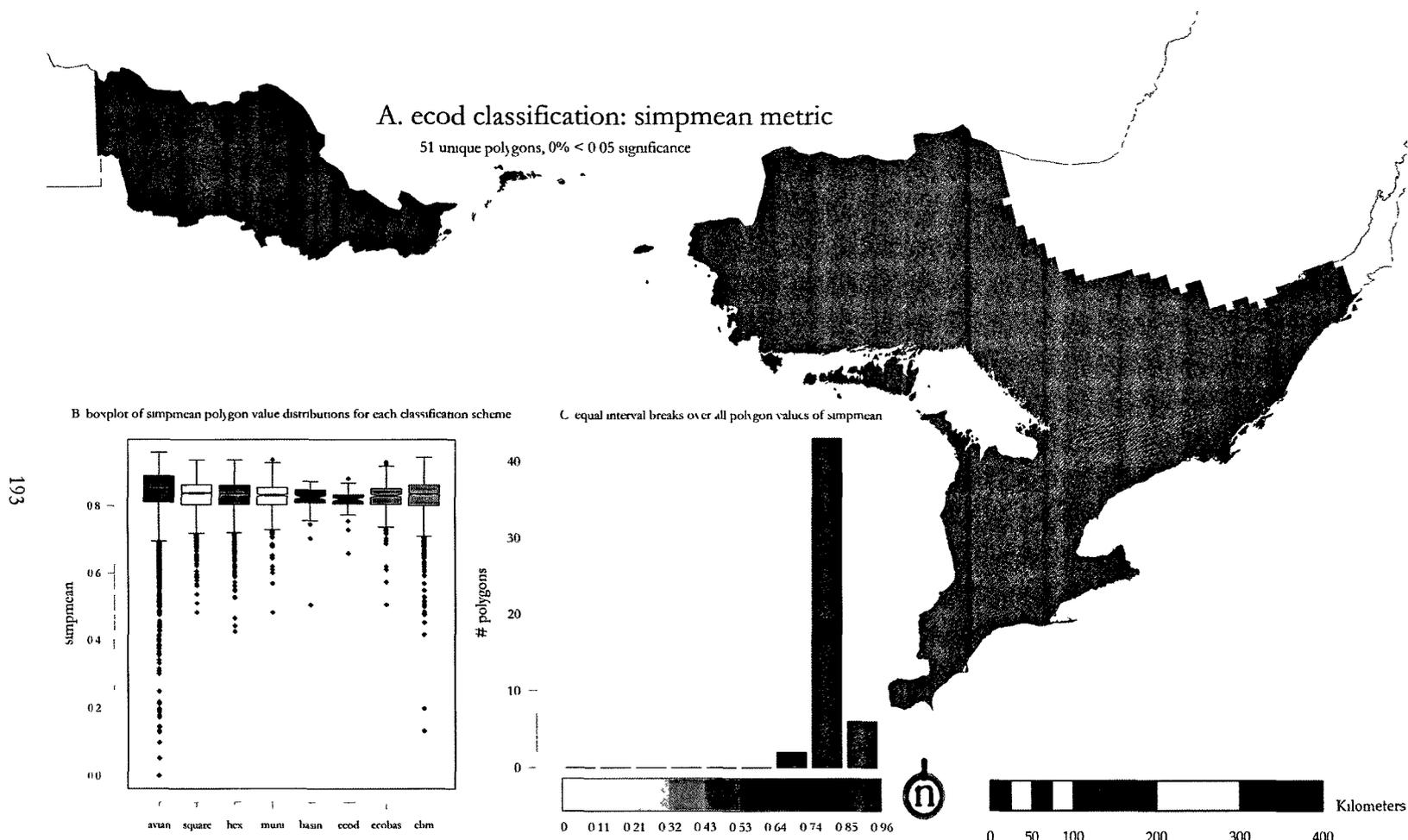


Figure E 4. A. Results summary for mean point-level Simpson's diversity (the evenness of species composition). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

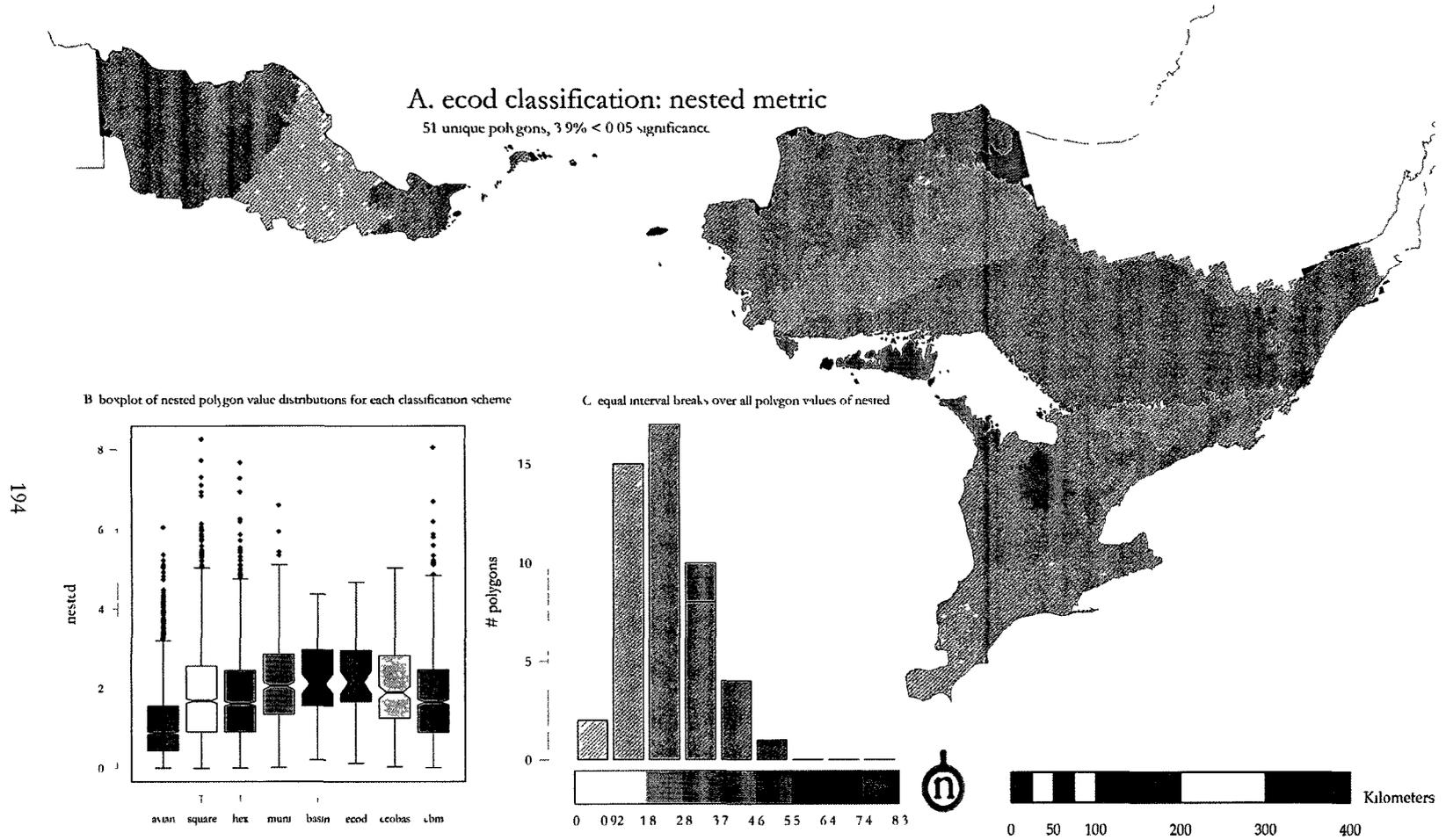


Figure E.5. A. Results summary for nestedness temperature (a measure of the disorder in species composition within polygons; low values indicate a regular nested pattern of species loss from high to low richness points, high values reflect more disordered structures). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBΛ points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

Appendix F

Biogeographic Mappings

Ecobas Classification

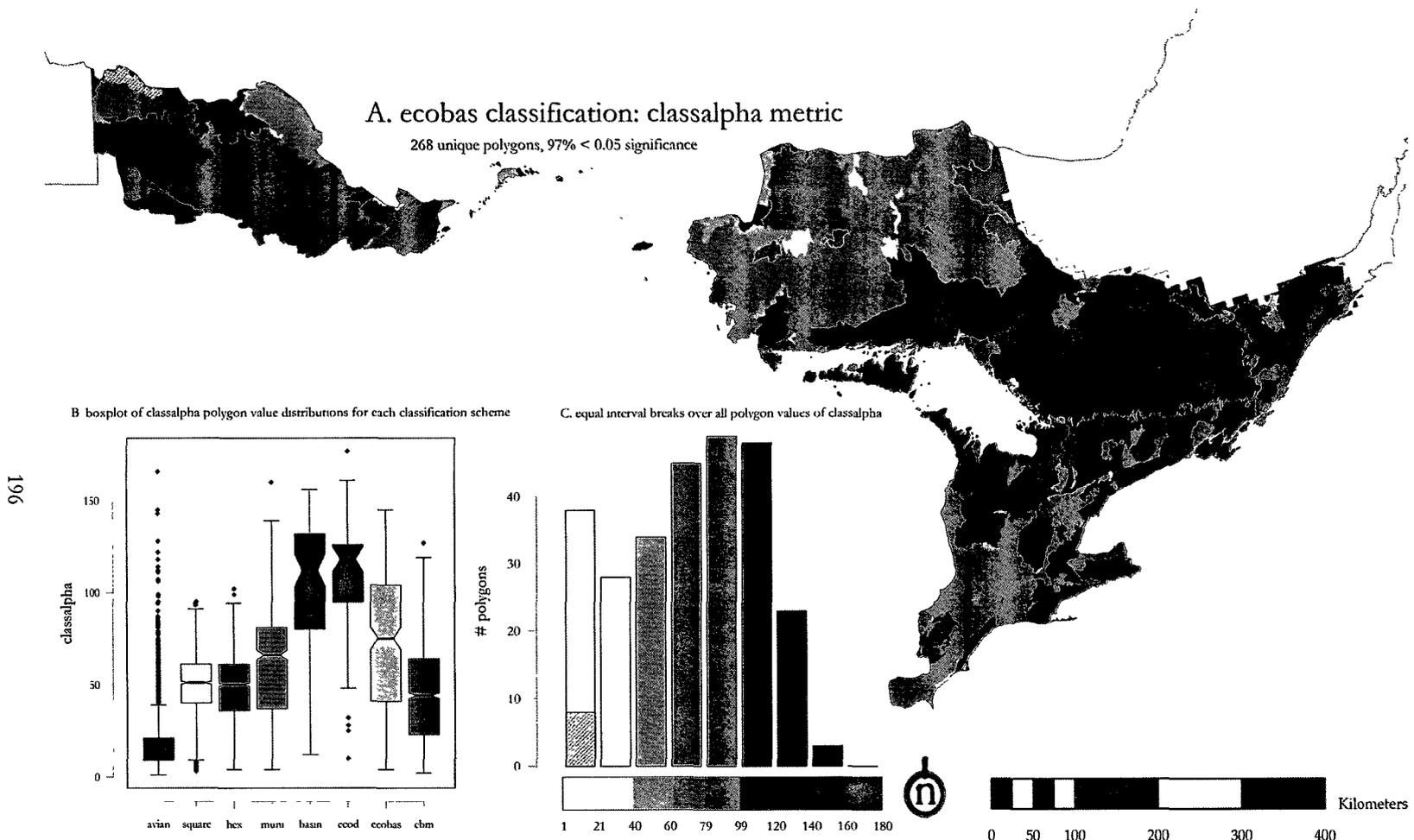


Figure F.1: A. Results summary for total polygon richness (class alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

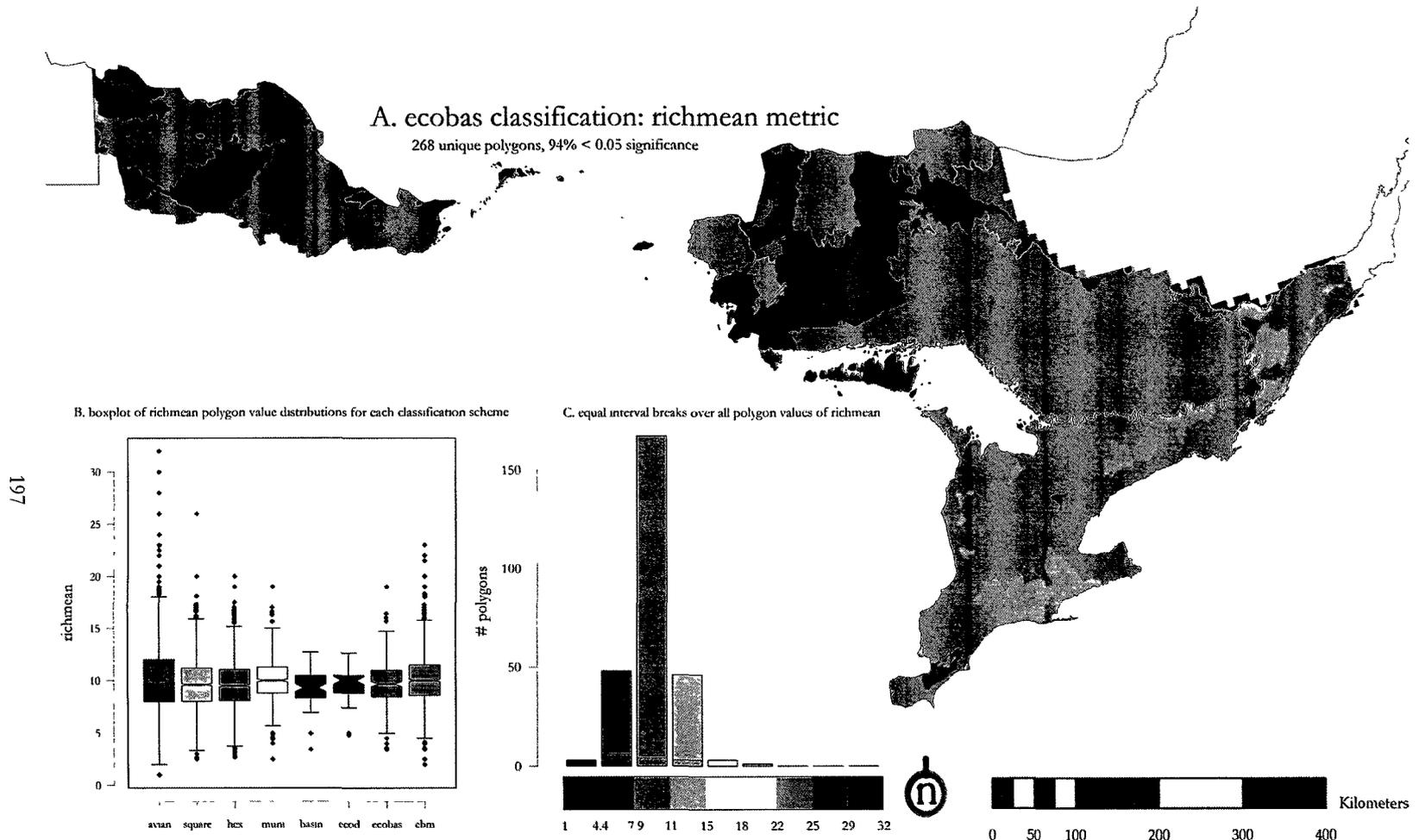


Figure F2: A. Results summary for mean point-level species richness (average point alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

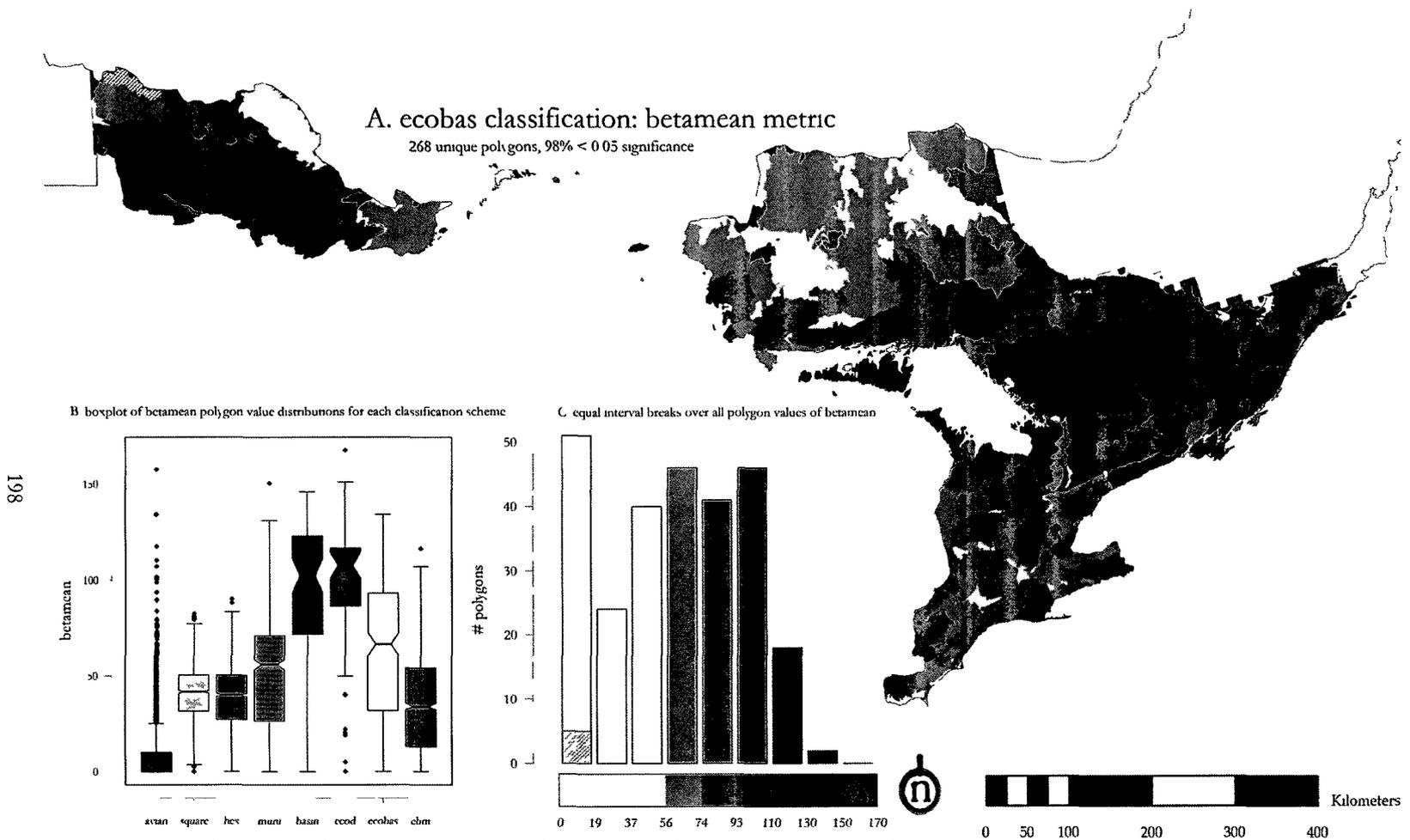


Figure 12.3 A Results summary for mean point-level beta diversity (the difference from the polygon-level species richness and the point level richness) Polygons are coloured by equal interval breaks along the full range of values Dark grey polygons are within the study region but contain no OBBA points Hatched areas denote polygons containing values that are indistinguishable from a random null model B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark C Polygon level histogram showing the distribution of values across the study region, and associated colour scheme Hatched areas show non-significant polygon values

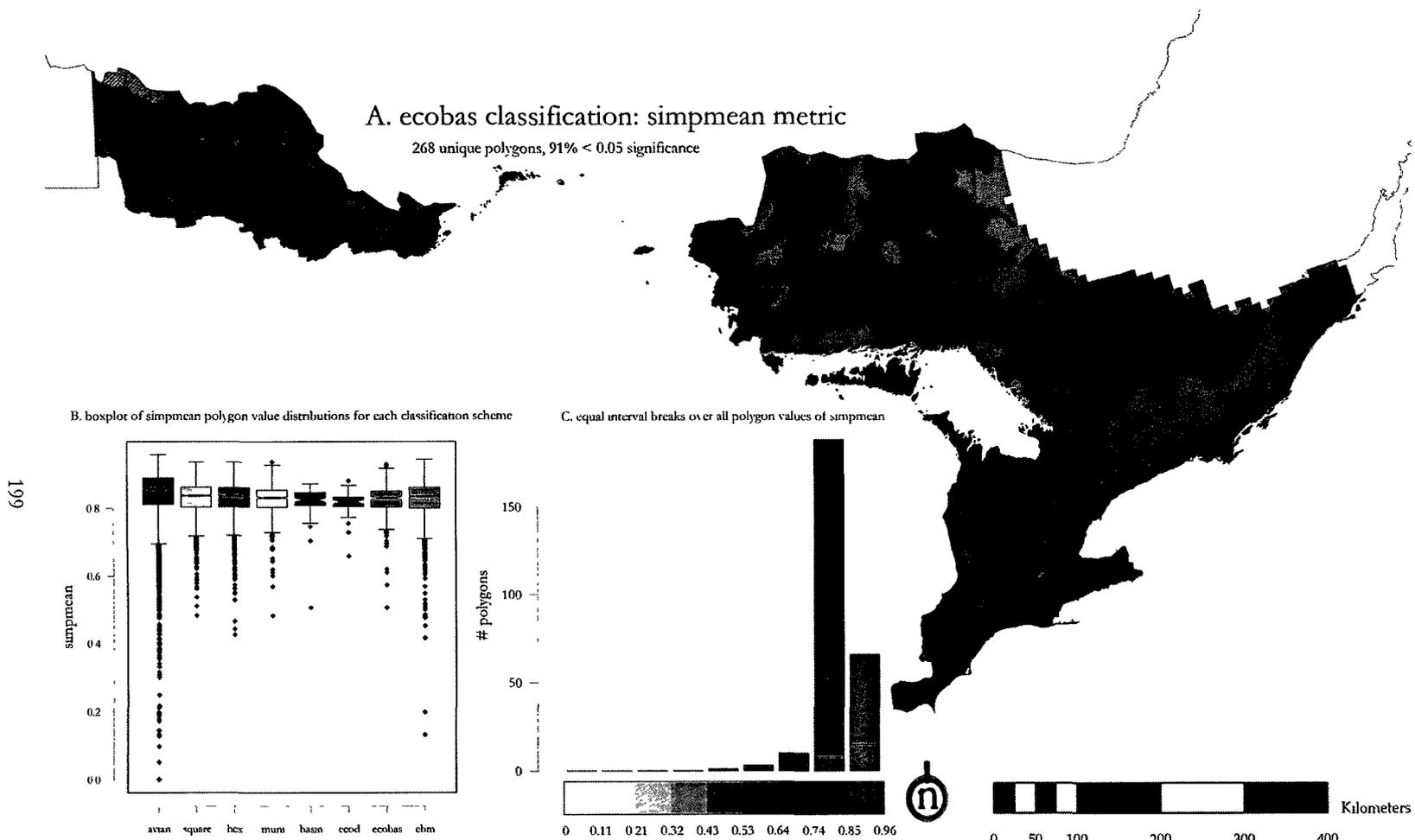


Figure F.4: A. Results summary for mean point-level Simpson's diversity (the evenness of species composition). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

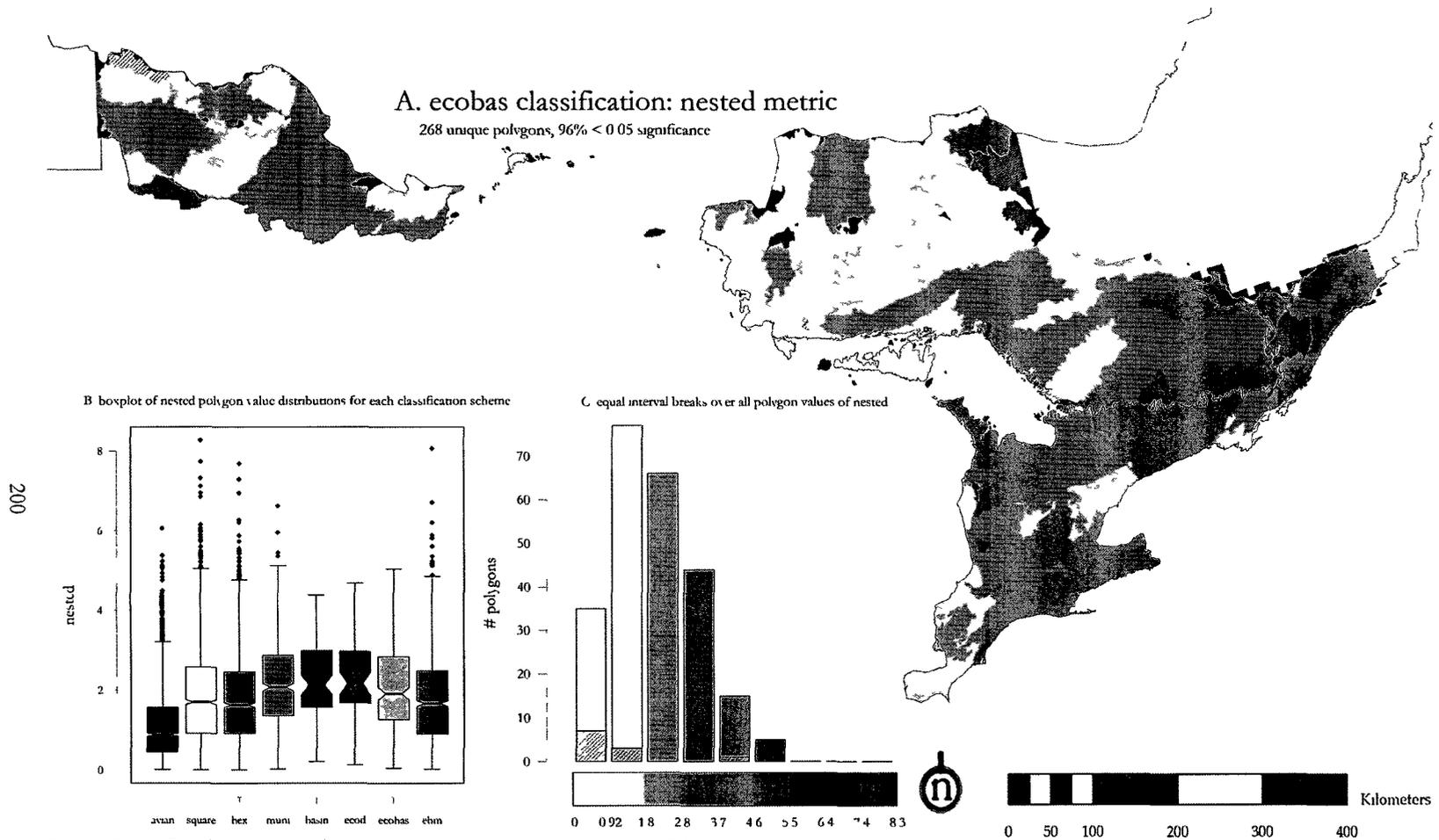


Figure F5. A Results summary for nestedness temperature (a measure of the disorder in species composition within polygons, low values indicate a regular nested pattern of species loss from high to low richness points, high values reflect more disordered structures). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

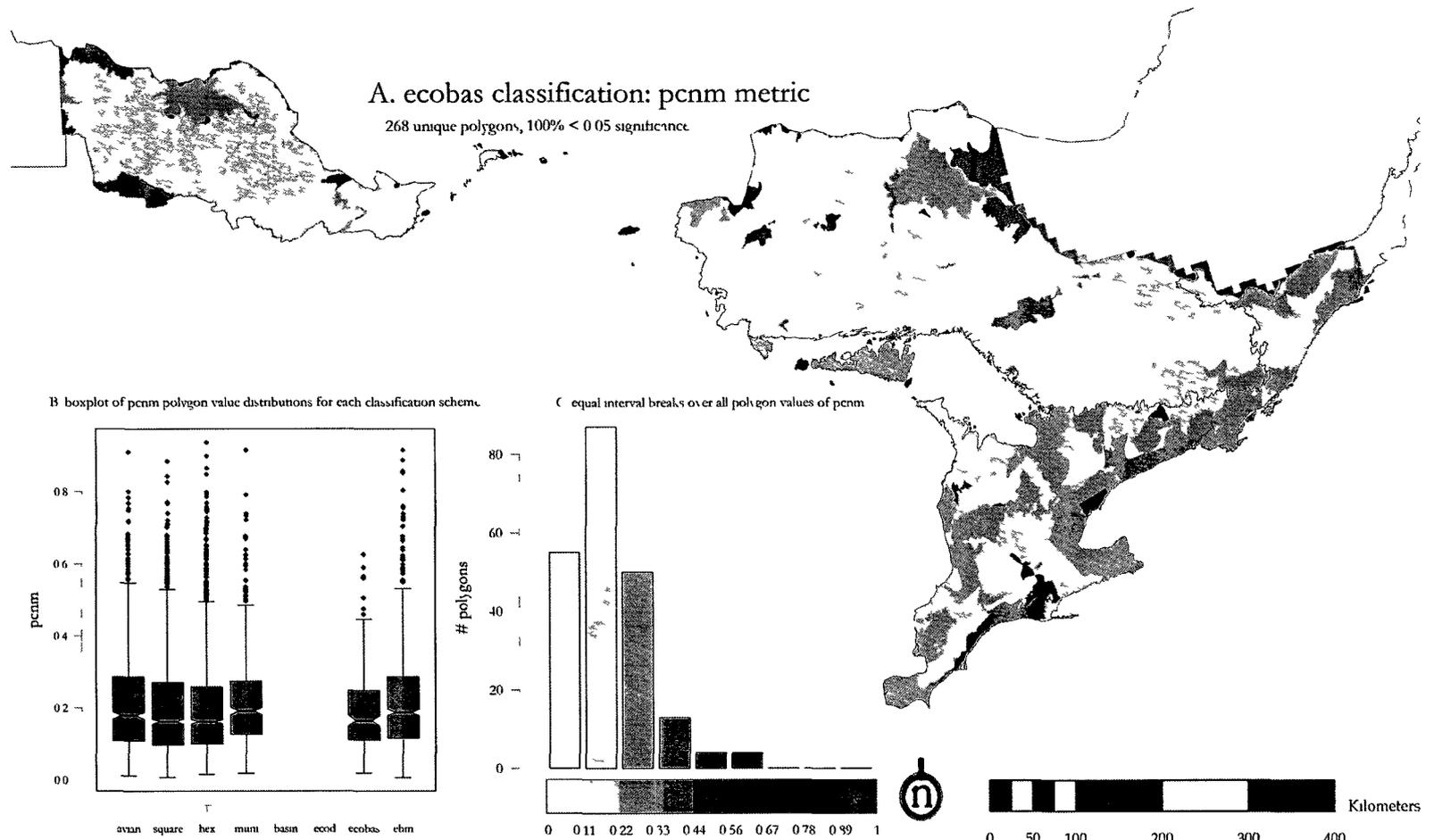


Figure F6 A Results summary for the amount of variation in polygon species composition that can be explained using spatial components (described by an adjusted R squared term using PCNM ordination) Polygons are coloured by equal interval breaks along the full range of values Dark grey polygons are within the study region but contain no OBBA points Hatched areas denote polygons containing values that are indistinguishable from a random null model B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark C Polygon level histogram showing the distribution of values across the study region, and associated colour scheme Hatched areas show non significant polygon values

Figure G 6 A Results summary for the amount of variation in polygon species composition that can be explained using spatial components (described by an

Appendix G

Biogeographic Mappings

Ebm Classification

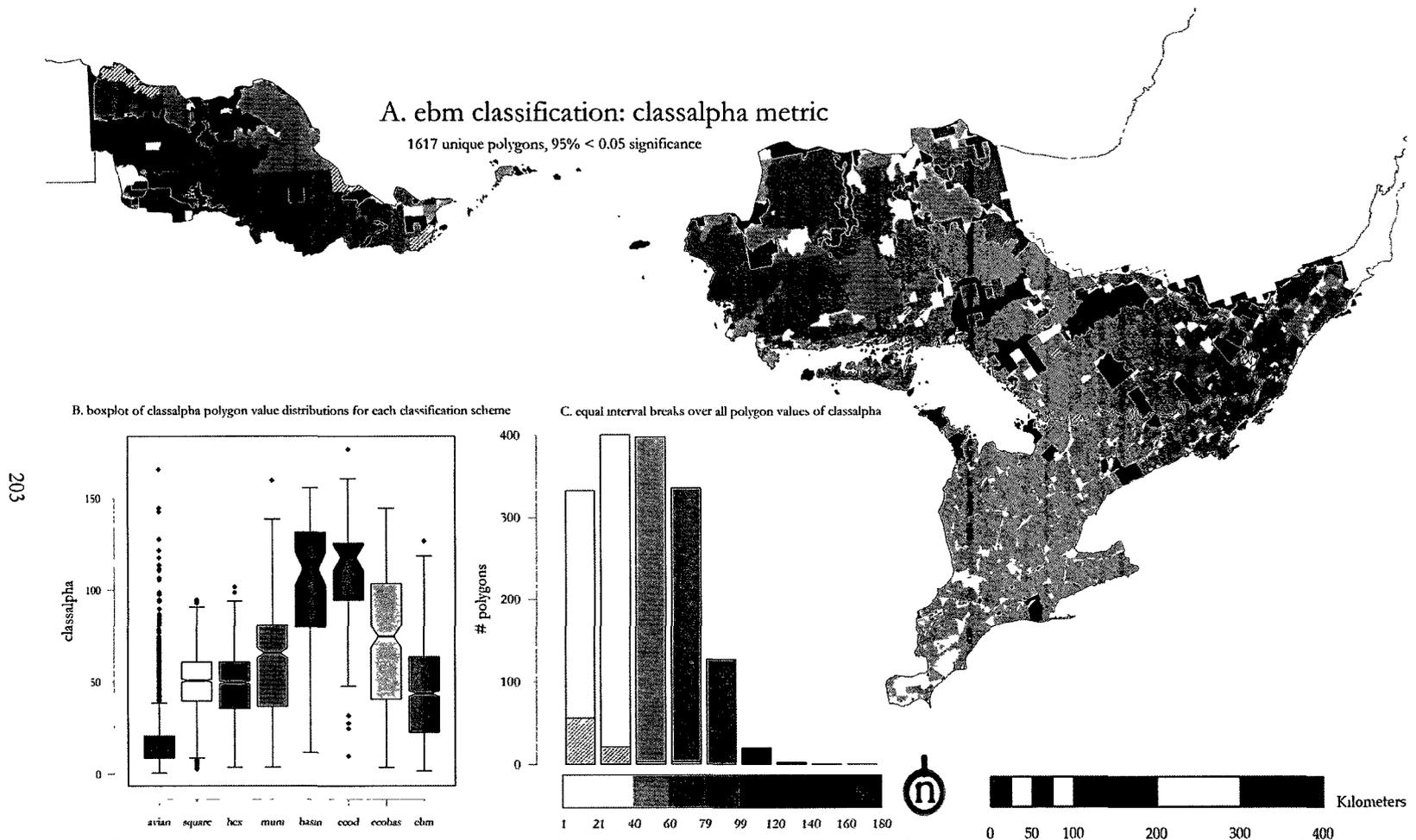


Figure G.1: A. Results summary for total polygon richness (class alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

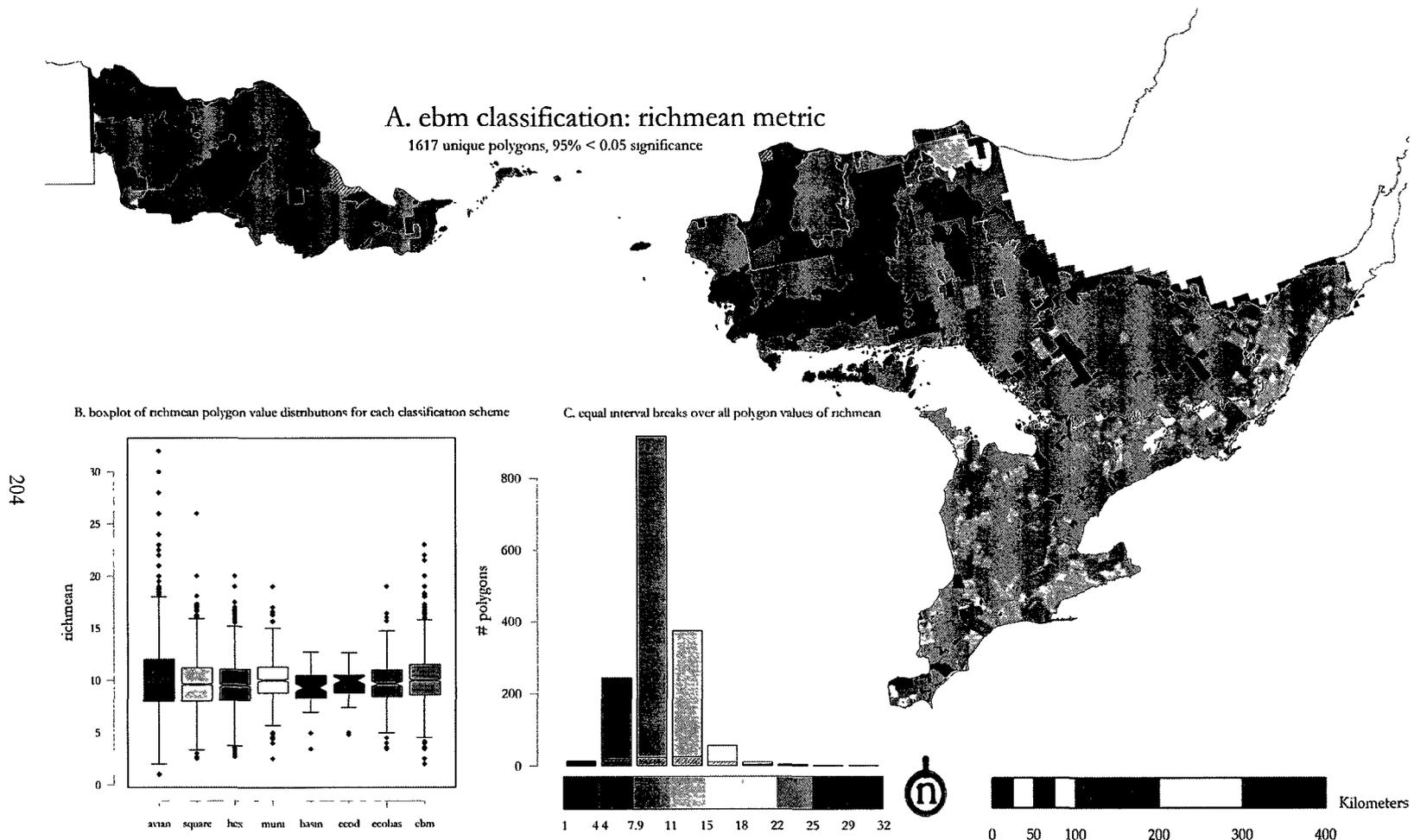


Figure G.2: A. Results summary for mean point-level species richness (average point alpha diversity). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

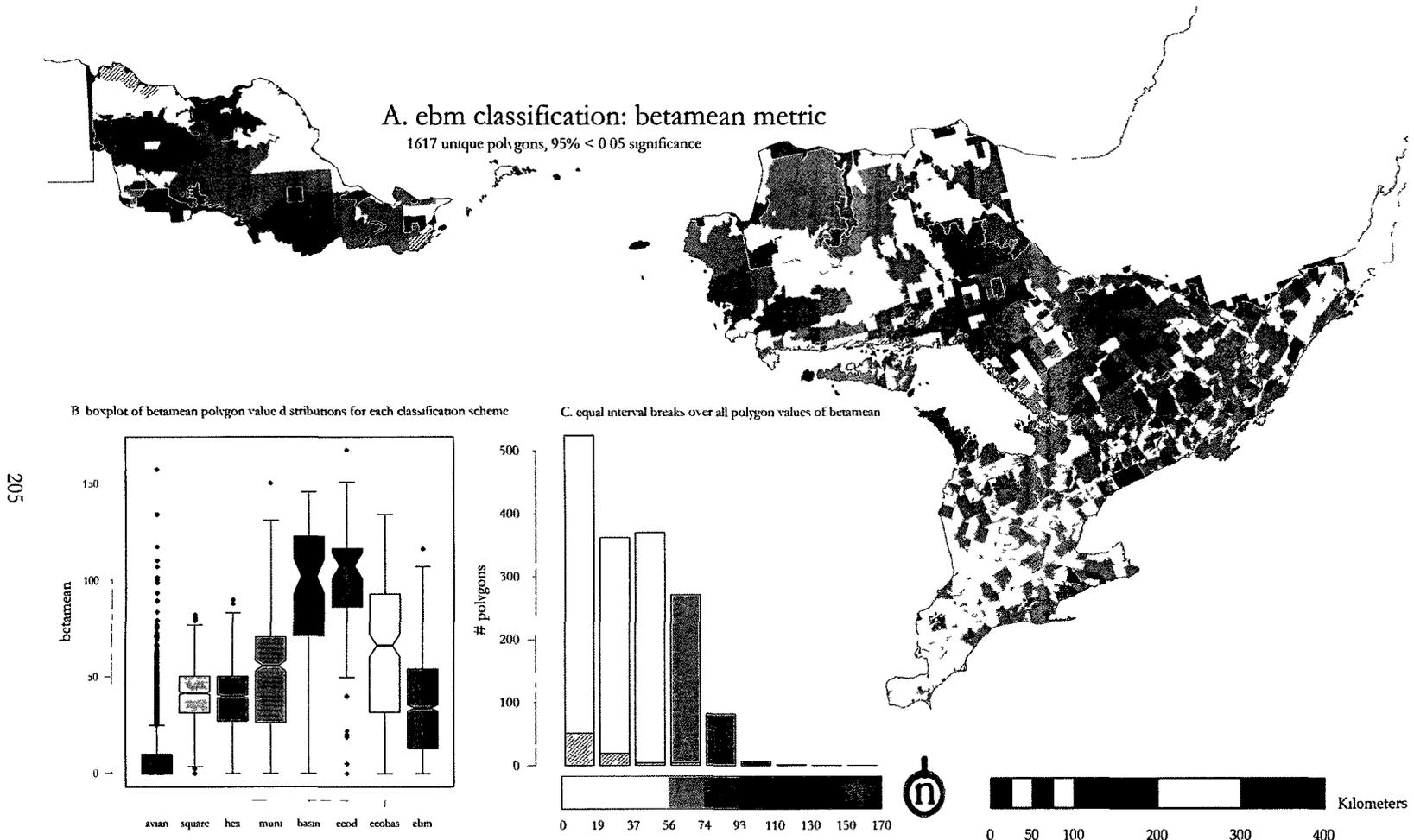


Figure G 3 A Results summary for mean point-level beta diversity (the difference from the polygon-level species richness and the point-level richness) Polygons are coloured by equal interval breaks along the full range of values Dark grey polygons are within the study region but contain no OBBA points Hatched areas denote polygons containing values that are indistinguishable from a random null model B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark C Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme Hatched areas show non-significant polygon values

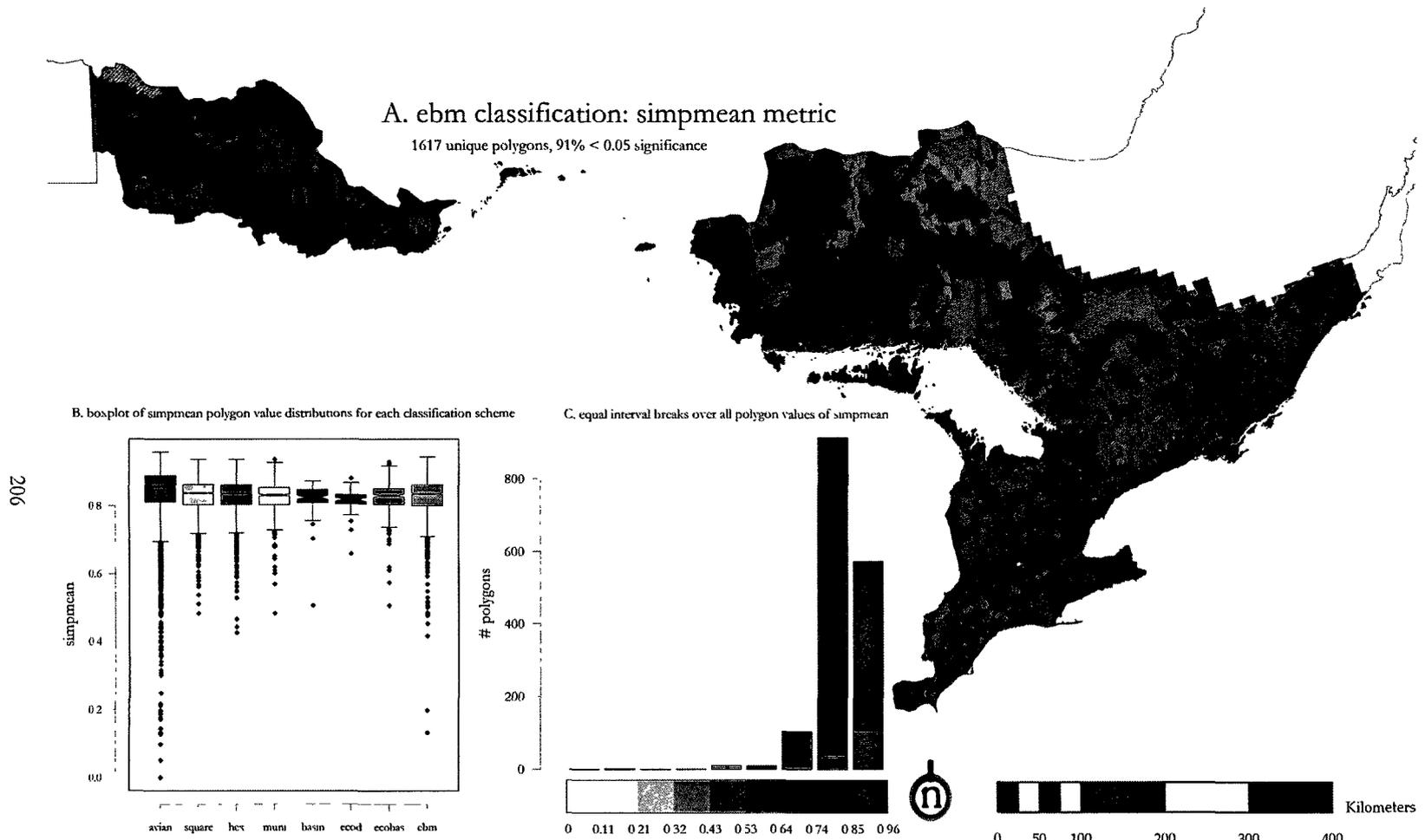


Figure G.4: A. Results summary for mean point-level Simpson's diversity (the evenness of species composition). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

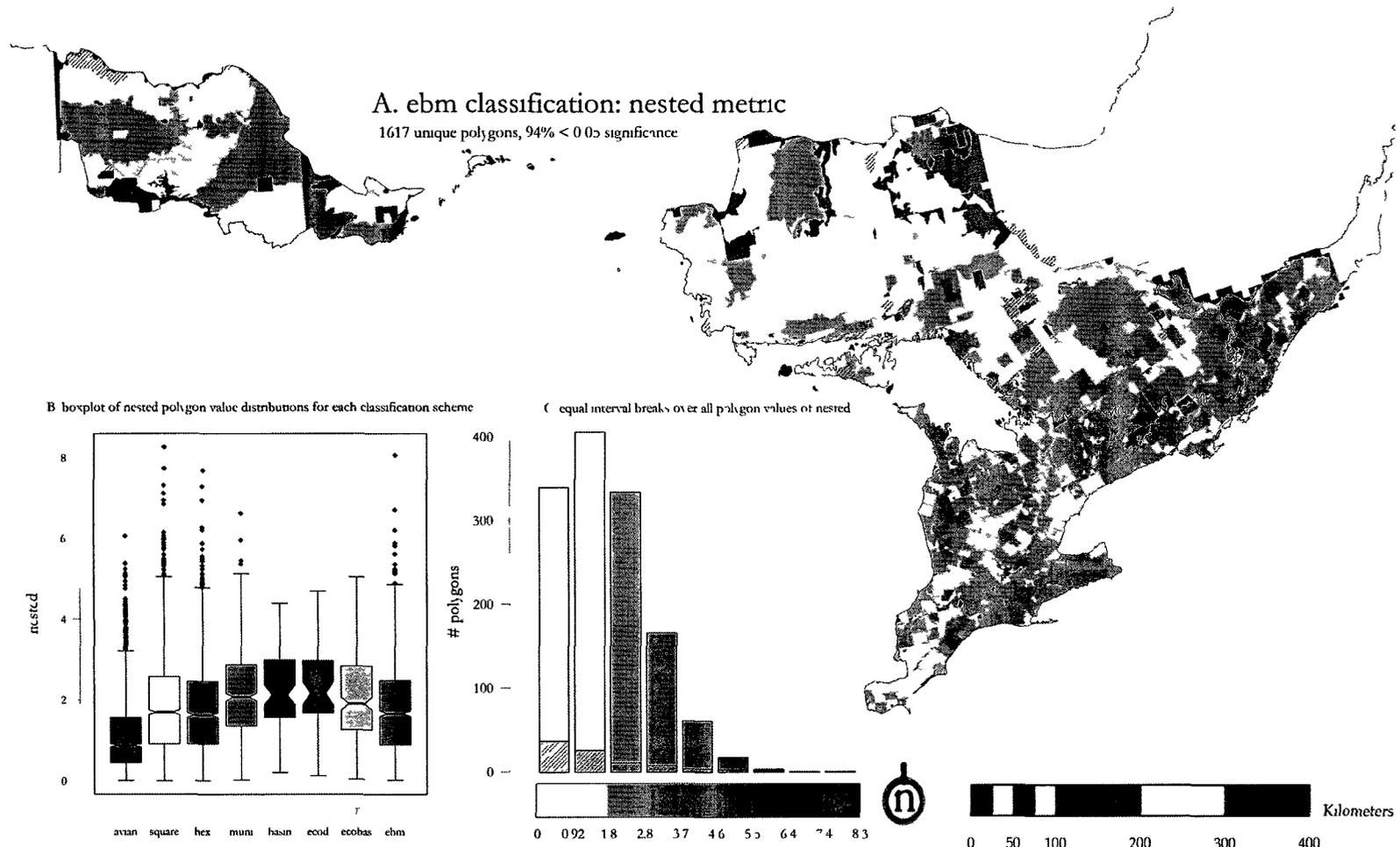
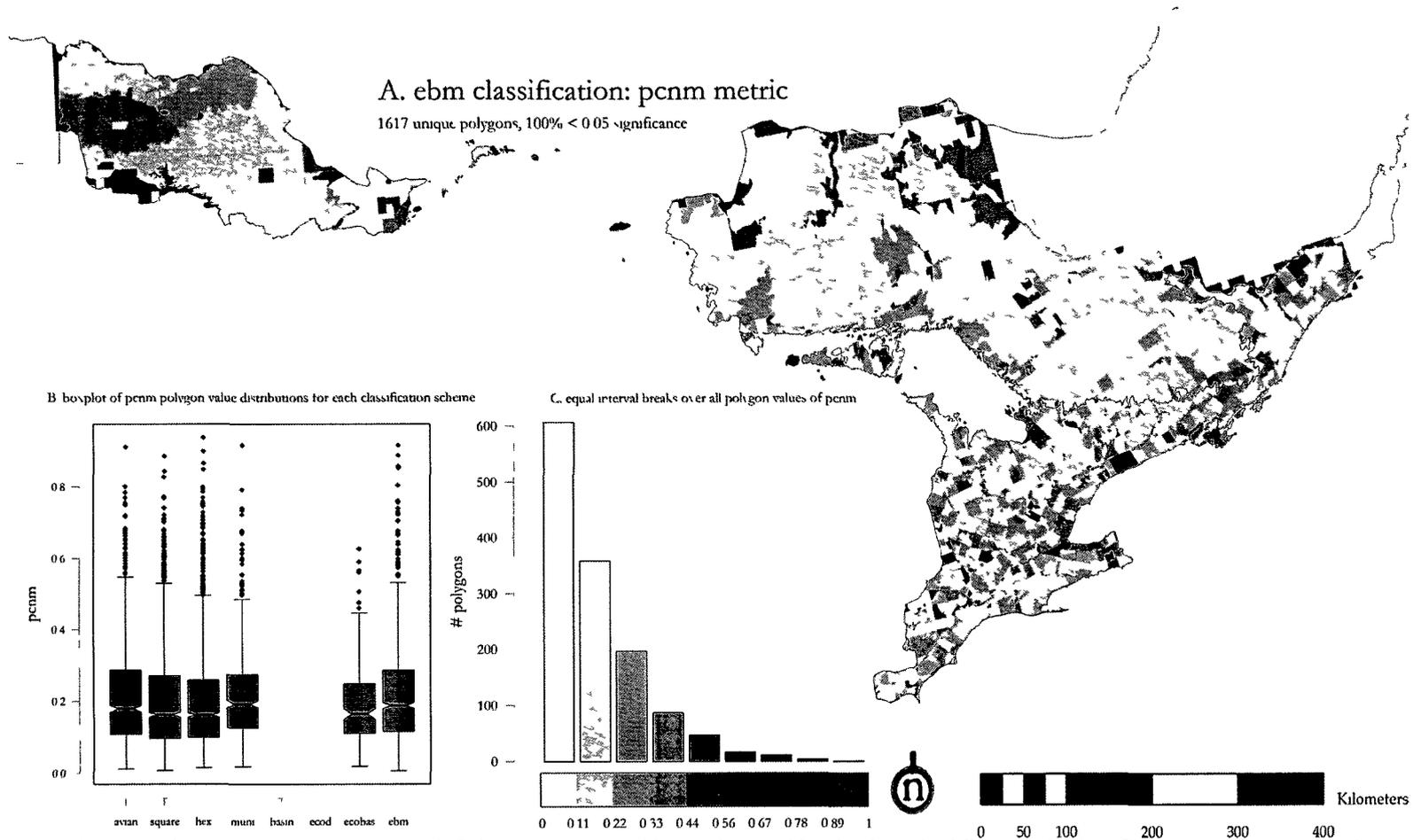


Figure G 5 A Results summary for nestedness temperature (a measure of the disorder in species composition within polygons, low values indicate a regular nested pattern of species loss from high to low richness points, high values reflect more disordered structures) Polygons are coloured by equal interval breaks along the full range of values Dark grey polygons are within the study region but contain no OBBA points Light grey polygons contain less than three points, and cannot be analyzed Hatched areas denote polygons containing values that are indistinguishable from a random null model B Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark C Polygon level histogram showing the distribution of values across the study region, and associated colour scheme Hatched areas show non significant polygon values



adjusted R-squared term using PCNM ordination). Polygons are coloured by equal interval breaks along the full range of values. Dark grey polygons are within the study region but contain no OBBA points. Light grey polygons contain less than three points, and cannot be analysed. Hatched areas denote polygons containing values that are indistinguishable from a random null model. B. Boxplot comparisons across all classification schemes, the proportion of polygons that are significant is indicated from high to low by shading from light to dark. C. Polygon-level histogram showing the distribution of values across the study region, and associated colour scheme. Hatched areas show non-significant polygon values.

Appendix H

**Names For 235 Analyzed Species From the Ontario Breeding
Bird Atlas Data for Bird Conservation Regions 12 and 13.
Species hierarchical clustering, BCR priority status, habitat as-
sociation and log abundance data found in Chapter 2: Figure 1**

AOU code	Common Name	Scientific Name
ABDU	American Black Duck	<i>Anas rubripes</i>
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>
AMBI	American Bittern	<i>Botaurus lentiginosus</i>
AMCO	American Coot	<i>Fulica americana</i>
AMCR	American Crow	<i>Corvus brachyrhynchos</i>
AMGO	American Goldfinch	<i>Carduelis tristis</i>
AMKE	American Kestrel	<i>Falco sparverius</i>
AMRE	American Redstart	<i>Setophaga ruticilla</i>
AMRO	American Robin	<i>Turdus migratorius</i>
AMWT	American Wigeon	<i>Anas americana</i>
AMWO	American Woodcock	<i>Scolopax minor</i>
AWPE	American White Pelican	<i>Pelecanus erythrorhynchos</i>
BAEA	Bald Eagle	<i>Haliaeetus leucocephalus</i>
BANS	Bank Swallow	<i>Riparia riparia</i>
BAOR	Baltimore Oriole	<i>Icterus galbula</i>
BARS	Barn Swallow	<i>Hirundo rustica</i>
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>
BBCU	Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>
BBMA	Black-billed Magpie	<i>Pica hudsonia</i>
BBWA	Bay-breasted Warbler	<i>Dendroica castanea</i>
BBWO	Black-backed Woodpecker	<i>Picoides arcticus</i>
BCCH	Black-capped Chickadee	<i>Parus atricapillus</i>
BCNH	Black-crowned Night-Heron	<i>Nycticorax nycticorax</i>
BDOW	Barred Owl	<i>Strix varia</i>
BEKI	Belted Kingfisher	<i>Ceryle alcyon</i>
BGGN	Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>
BGWW	Blue/Golden Winged Warbler	<i>Vermivora sp.</i>
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>
BHVI	Blue-headed Vireo	<i>Vireo solitarius</i>
BLBW	Blackburnian Warbler	<i>Dendroica fusca</i>
BLJA	Blue Jay	<i>Cyanocitta cristata</i>
BLPW	Blackpoll Warbler	<i>Dendroica striata</i>
BLTE	Black Tern	<i>Chlidonias niger</i>
BOBO	Bobolink	<i>Dolichonyx oryzivorus</i>
BOCH	Boreal Chickadee	<i>Parus hudsonica</i>
BOGU	Bonaparte's Gull	<i>Larus philadelphia</i>
BRBL	Brewer's Blackbird	<i>Euphagus cyanocephalus</i>
BRCR	Brown Creeper	<i>Certhia americana</i>
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>
BRWA	Brewster's Warbler	<i>Vermivora pinus x chrysopt.</i>
BTBW	Black-throated Blue Warbler	<i>Dendroica caerulescens</i>
BTNW	Black-throated Green Warbler	<i>Dendroica virens</i>
BUFF	Bufflehead	<i>Bucephala albeola</i>
BVHA	Broad-winged Hawk	<i>Buteo platypterus</i>
BWTE	Blue-winged Teal	<i>Anas discors</i>
BWWA	Blue-winged Warbler	<i>Vermivora pinus</i>

AOU code	Common Name	Scientific Name
CAGO	Canada Goose	<i>Branta canadensis</i>
CARW	Carolina Wren	<i>Thryothorus ludovicianus</i>
CATE	Caspian Tern	<i>Hydroprogne caspia</i>
CAWA	Canada Warbler	<i>Wilsonia canadensis</i>
CCSP	Clay colored Sparrow	<i>Spizella pallida</i>
CEDW	Cedar Waxwing	<i>Bombycilla cedrorum</i>
CERW	Cerulean Warbler	<i>Dendroica cerulea</i>
CHSP	Chipping Sparrow	<i>Spizella passerina</i>
CHSW	Chimney Swift	<i>Chaetura pelagica</i>
CLSW	Cliff Swallow	<i>Petrochelidon pyrrhonota</i>
CMWA	Cape May Warbler	<i>Dendroica tigrina</i>
COGO	Common Goldeneye	<i>Bucephala clangula</i>
COGR	Common Grackle	<i>Quiscalus quiscula</i>
COHA	Cooper's Hawk	<i>Accipiter cooperii</i>
COLO	Common Loon	<i>Gavia immer</i>
COME	Common Merganser	<i>Mergus merganser</i>
COMO	Common Moorhen	<i>Gallinula chloropus</i>
CONI	Common Nighthawk	<i>Chordeiles minor</i>
CONW	Connecticut Warbler	<i>Oporornis agilis</i>
CORA	Common Raven	<i>Corvus corax</i>
CORE	Common Redpoll	<i>Carduelis flammea</i>
COSN	Common Snipe	<i>Gallinago gallinago</i>
COTE	Common Tern	<i>Sterna hirundo</i>
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>
CSWA	Chestnut sided Warbler	<i>Dendroica pensylvanica</i>
CUCK	Cuckoo	<i>Coracina</i> sp.
CWWI	Chuck will's widow	<i>Caprimulgus carolinensis</i>
DCCO	Double crested Cormorant	<i>Phalacrocorax auritus</i>
DEJU	Dark eyed Junco	<i>Junco hyemalis</i>
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>
DUNL	Dunlin	<i>Calidris alpina</i>
EABL	Eastern Bluebird	<i>Sialia sialis</i>
EAKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>
EAME	Eastern Meadowlark	<i>Sturnella magna</i>
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>
EASO	Eastern Screech Owl	<i>Megascops asio</i>
EATO	Eastern Towhee	<i>Pipilo erythrophthalmus</i>
EAWP	Eastern Wood Pewee	<i>Contopus virens</i>
EUST	European Starling	<i>Sturnus vulgaris</i>
EVGR	Evening Grosbeak	<i>Coccothraustes vespertinus</i>
FISP	Field Sparrow	<i>Spizella pusilla</i>
FOTE	Forster's Tern	<i>Sterna forsteri</i>
FRGU	Franklin's Gull	<i>Larus pipixcan</i>
GADW	Gadwall	<i>Anas strepera</i>
GBBG	Great Black backed Gull	<i>Larus marinus</i>
GBHE	Great Blue Heron	<i>Ardea herodias</i>

AOU code	Common Name	Scientific Name
GCFL	Great Crested Flycatcher	<i>Myiarchus cineritus</i>
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>
GGOW	Great Gray Owl	<i>Strix nebulosa</i>
GHOW	Great Horned Owl	<i>Bubo virginianus</i>
GRAJ	Gray Jay	<i>Perisoreus canadensis</i>
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>
GREG	Great Egret	<i>Ardea alba</i>
GRHE	Green Heron	<i>Butorides virescens</i>
GRPA	Gray Partridge	<i>Perdix perdix</i>
GRSC	Greater Scaup	<i>Aythya marila</i>
GRSP	Grasshopper Sparrow	<i>Ammodramus savannarum</i>
GRYE	Greater Yellowlegs	<i>Tringa melanoleuca</i>
GWTE	Green-winged Teal	<i>Anas crecca</i>
GWVA	Golden-winged Warbler	<i>Vermivora chrysoptera</i>
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>
HERG	Herring Gull	<i>Larus argentatus</i>
HETH	Hermit Thrush	<i>Catharus guttatus</i>
HOFI	House Finch	<i>Carpodacus mexicanus</i>
HOGR	Horned Grebe	<i>Podiceps auritus</i>
HOLA	Horned Lark	<i>Eremophila alpestris</i>
HOME	Hooded Merganser	<i>Lophodytes cucullatus</i>
HOSP	House Sparrow	<i>Passer domesticus</i>
HOWA	Hooded Warbler	<i>Wilsonia cirina</i>
HOWR	House Wren	<i>Troglodytes aedon</i>
INBU	Indigo Bunting	<i>Passerina cyanea</i>
KEWA	Kentucky Warbler	<i>Oporornis formosus</i>
KILL	Killdeer	<i>Charadrius vociferus</i>
LCSP	Le Conte's Sparrow	<i>Ammodramus lecontei</i>
LEBI	Least Bittern	<i>Ixobrychus exilis</i>
LEFL	Least Flycatcher	<i>Empidonax minimus</i>
LEOW	Long-eared Owl	<i>Asio otus</i>
LESA	Least Sandpiper	<i>Calidris minutilla</i>
LESC	Lesser Scaup	<i>Aythya affinis</i>
LEYE	Lesser Yellowlegs	<i>Tringa flavipes</i>
LISP	Lincoln's Sparrow	<i>Melospiza lincolni</i>
LTDU	Long-tailed Duck	<i>Clangula hyemalis</i>
MAGO	Marbled Godwit	<i>Limosa fedoa</i>
MALL	Mallard	<i>Anas platyrhynchos</i>
MAWA	Magnolia Warbler	<i>Dendroica magnolia</i>
MAWR	Marsh Wren	<i>Cistothorus palustris</i>
MERL	Merlin	<i>Falco columbarius</i>
MODO	Mourning Dove	<i>Zenaida macroura</i>
MOOT	Common Mudhen	<i>Fulica sp.</i>
MOWA	Mourning Warbler	<i>Oporornis philadelphia</i>
MUSW	Mute Swan	<i>Cygnus olor</i>

AOU code	Common Name	Scientific Name
NAWA	Nashville Warbler	<i>Vermivora ruficapilla</i>
NHOW	Northern Hawk Owl	<i>Surnia ulula</i>
NOBO	Northern Bobwhite	<i>Colinus virginianus</i>
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>
NOEL	Northern Flicker	<i>Colaptes auratus</i>
NOGO	Northern Goshawk	<i>Accipiter gentilis</i>
NOHA	Northern Harrier	<i>Circus cyaneus</i>
NOMO	Northern Mockingbird	<i>Mimus polyglottos</i>
NOPA	Northern Parula	<i>Parula americana</i>
NOPI	Northern Pintail	<i>Anas acuta</i>
NOWA	Northern Waterthrush	<i>Seiurus noveboracensis</i>
NRWS	Northern Rough winged Swallow	<i>Stelgidopteryx serripennis</i>
NSHO	Northern Shoveler	<i>Anas clypeata</i>
NSWO	Northern Saw whet Owl	<i>Aegolius acadicus</i>
OCWA	Orange crowned Warbler	<i>Vermivora celata</i>
OROR	Orchard Oriole	<i>Icterus spurius</i>
OSFL	Olive sided Flycatcher	<i>Contopus cooperi</i>
OSPR	Osprey	<i>Pandion haliaetus</i>
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>
PAWA	Palm Warbler	<i>Dendroica palmarum</i>
PBGR	Pied billed Grebe	<i>Podilymbus podiceps</i>
PHVI	Philadelphia Vireo	<i>Vireo philadelphicus</i>
PIGR	Pine Grosbeak	<i>Pinicola enucleator</i>
PISI	Pine Siskin	<i>Carduelis pinus</i>
PIWA	Pine Warbler	<i>Dendroica pinus</i>
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>
PRAW	Prairie Warbler	<i>Dendroica discolor</i>
PUEF	Purple Finch	<i>Carpodacus purpureus</i>
PUMA	Purple Martin	<i>Progne subis</i>
RBGR	Rose breasted Grosbeak	<i>Pheucticus ludovicianus</i>
RBGU	Ring billed Gull	<i>Larus delawarensis</i>
RBME	Red breasted Merganser	<i>Mergus serrator</i>
RBNU	Red breasted Nuthatch	<i>Sitta canadensis</i>
RBWO	Red bellied Woodpecker	<i>Melanerpes carolinus</i>
RCKI	Ruby crowned Kinglet	<i>Regulus calendula</i>
RECR	Red Crossbill	<i>Loxia curvirostra</i>
REDH	Redhead	<i>Aythya americana</i>
REVI	Red eyed Vireo	<i>Vireo olivaceus</i>
RHWO	Red headed Woodpecker	<i>Melanerpes erythrocephalus</i>
RPH	Ring Necked Pheasant	<i>Phasianus colchicus</i>
RLHA	Rough legged Hawk	<i>Buteo lagopus</i>
RNDU	Ring necked Duck	<i>Aythya collaris</i>
RNGR	Red necked Grebe	<i>Podiceps grisegena</i>
RNPH	Red necked Phalarope	<i>Phalaropus lobatus</i>
RODO	Rock Dove	<i>Columba livia</i>
RSWA	Red shouldered Hawk	<i>Buteo lineatus</i>

AOU code	Common Name	Scientific Name
RTHA	Red-tailed Hawk	<i>Buteo jamaicensis</i>
RTHU	Ruby-throated Hummingbird	<i>Archilochus colubris</i>
RUBL	Rusty Blackbird	<i>Euphagus carolinus</i>
RUDU	Ruddy Duck	<i>Oxyura jamaicensis</i>
RUGR	Ruffed Grouse	<i>Bonasa umbellus</i>
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>
SACR	Sandhill Crane	<i>Grus canadensis</i>
SAVS	Savannah Sparrow	<i>Passerculus sandwichensis</i>
SCTA	Scarlet Tanager	<i>Piranga olivacea</i>
SEOW	Short-eared Owl	<i>Asio flammeus</i>
SEPL	Semipalmated Plover	<i>Charadrius semipalmatus</i>
SEWR	Sedge Wren	<i>Cistothorus platensis</i>
SORA	Sora	<i>Porzana carolina</i>
SOSA	Solitary Sandpiper	<i>Tringa solitaria</i>
SOSP	Song Sparrow	<i>Melospiza melodia</i>
SPGR	Spruce Grouse	<i>Falcapennis canadensis</i>
SPSA	Spotted Sandpiper	<i>Actitis macularius</i>
SSHA	Sharp-shinned Hawk	<i>Accipiter striatus</i>
STGR	Sharp-tailed Grouse	<i>Tympanuchus phasianellus</i>
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>
TEWA	Tennessee Warbler	<i>Vermivora peregrina</i>
TRES	Tree Swallow	<i>Tachycineta bicolor</i>
TRUS	Trumpeter Swan	<i>Cygnus buccinator</i>
TTWO	American Three-toed Woodpecker	<i>Picoides tridactylus</i>
TUTI	Tufted Titmouse	<i>Baeolophus bicolor</i>
TUVU	Turkey Vulture	<i>Cathartes aura</i>
UPSA	Upland Sandpiper	<i>Bartramia longicauda</i>
VEER	Veery	<i>Catharus fuscescens</i>
VESP	Vesper Sparrow	<i>Pooecetes gramineus</i>
VIRA	Virginia Rail	<i>Rallus limicola</i>
WAVI	Warbling Vireo	<i>Vireo gilvus</i>
WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>
WEME	Western Meadowlark	<i>Sturnella neglecta</i>
WEVI	White-eyed Vireo	<i>Vireo griseus</i>
WIFL	Willow Flycatcher	<i>Empidonax traillii</i>
WITU	Wild Turkey	<i>Meleagris gallopavo</i>
WIWA	Wilson's Warbler	<i>Wilsonia pusilla</i>
WIWR	Winter Wren	<i>Troglodytes troglodytes</i>
WODU	Wood Duck	<i>Aix sponsa</i>
WOTH	Wood Thrush	<i>Hylocichla mustelina</i>
WPWI	Whip-poor-will	<i>Caprimulgus vociferus</i>
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>
WWCR	White-winged Crossbill	<i>Loxia leucoptera</i>
YBCU	Yellow-billed Cuckoo	<i>Coccyzus americanus</i>
YBFL	Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>
YERA	Yellow Rail	<i>Coturnicops noveboracensis</i>
YHBL	Yellow-headed Blackbird	<i>Xanthocephalus xanthocephalus</i>
YRWA	Yellow-rumped Warbler	<i>Dendroica coronata</i>
YTVI	Yellow-throated Vireo	<i>Vireo flavifrons</i>
YWAR	Yellow Warbler	<i>Dendroica petechia</i>