

1 Title: Detecting spatial regimes in ecosystems

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44 **Abstract**

45 Research on early warning indicators has generally focused on assessing temporal transitions with
46 limited application of these methods to detecting spatial regimes. Traditional spatial boundary
47 detection procedures that result in ecoregion maps are typically based on ecological potential (i.e.
48 potential vegetation), and often fail to account for ongoing changes due to stressors such as land use
49 change and climate change and their effects on plant and animal communities. We use Fisher
50 information, an information theory based method, on both terrestrial and aquatic animal data (U.S.
51 Breeding Bird Survey and marine zooplankton) to identify ecological boundaries, and compare our
52 results to traditional early warning indicators, conventional ecoregion maps, and multivariate
53 analyses such as nMDS and cluster analysis. We successfully detected spatial regimes and
54 transitions in both terrestrial and aquatic systems using Fisher information. Furthermore, Fisher
55 information provided explicit spatial information about community change that is absent from other
56 multivariate approaches. Our results suggest that defining spatial regimes based on animal
57 communities may better reflect ecological reality than do traditional ecoregion maps, especially in
58 our current era of rapid and unpredictable ecological change.

59 **Introduction**

60 The possibility of multiple regimes for ecosystems is now well documented, and methods to detect
61 temporal regime shifts have received a great deal of attention (Scheffer & Carpenter 2003; Dakos *et al.*
62 *et al.* 2008; Guttal & Jayaprakash 2008). Less well developed is the application of these tools to the
63 identification of spatial regimes that reflect the boundary between two types of ecosystems (though
64 see Kéfi and others 2014). Spatial data has unique challenges in that while it is not necessary for
65 data points to be equally spaced (Dai *et al.* 2013; Cline *et al.* 2014), sufficient spatial sampling
66 resolution is needed to distinguish one spatial regime from another. The identification of spatial
67 regimes is increasingly important due to habitat fragmentation, which increases the proportion of
68 boundaries in landscapes (Kent *et al.* 2006), and anthropogenic climate change, which is expected to
69 shift ecological boundaries. Studies have already shown rapid altitudinal shifts in montane
70 ecological boundaries in response to climate change (Allen & Breshears 1998; Beckage *et al.* 2008).
71 Similarly, climate-driven boundary shifts are being detected in marine systems as both spatial shifts
72 in primary production and in individual species ranges, as well as in phenological shifts and changes
73 in community composition (Beaugrand *et al.* 2002; Edwards & Richardson 2004; Grebmeier *et al.*
74 2006). Because ecological boundaries in terrestrial systems typically demarcate the distribution of
75 vegetation and ecosystem type, they provide critical information about the extent and rate of the
76 biological processes shaping the boundary and driving the maintenance of the regime within the
77 boundary (Yarrow & Salthe 2008). This has implications for both environmental management and
78 biological conservation (Kent *et al.* 2006).

79 Boundary identification has been an active area of research in terrestrial ecology and biogeography,
80 and is generally both data intensive and statistically challenging, particularly when it involves
81 vegetation sampling (Kent *et al.* 2006). The use of remotely-sensed data is less laborious than field
82 work, but the method is poor at distinguishing between physically similar but floristically different
83 vegetation; hence, it may require labor-intensive ground-truthing to verify ecological transitions in
84 plant assemblages (Kent *et al.* 2006). Boundary detection is further complicated by the multiplicity

85 of scales at which different processes and physical patterns are expressed (Fagan *et al.* 2003; Strayer
86 *et al.* 2003), and that the relationship between abiotic variables such as climate, and biotic variables
87 such as vegetation, is often non-linear across boundaries (Danz *et al.* 2012). Typically, terrestrial
88 ecological boundaries defined for ecoregion maps such as those used by U.S. federal agencies are
89 based on potential plant communities, which in turn reflect differences in bedrock, soil, altitude,
90 temperature, and moisture (Bailey 1983; Omernik 1987). Terrestrial plant communities may not
91 respond as rapidly as animal communities to direct anthropogenic change and climate change
92 (Pearson 2006; Pearman *et al.* 2008), therefore defining the boundaries between animal
93 communities may better represent current biotic and abiotic conditions. Variation in animal
94 population dynamics provides information on the stability of ecosystem mechanisms, processes, and
95 linkages, and may serve as an early warning signal of shifting regimes (Cline *et al.* 2014).

96 Pelagic marine ecological boundaries are typically defined by primary production characteristics
97 (Longhurst 1998) which reflect aquatic properties such as currents, temperature, salinity, nutrients,
98 and bathymetry, but are complicated by the ephemeral nature of features such as oceanographic
99 fronts. Landforms, such as straights, may create another form of boundary between biological
100 communities. Advection across fronts or through physical constrictions between water masses can
101 serve as a driver of both physical and ecological homogeneity, though the degree of connectivity can
102 vary rapidly in space and time (Wassmann *et al.* 2015). There is much current discussion of
103 appropriate variables by which to track marine ecological change (Rice & Rochet 2005; Samhuri *et*
104 *al.* 2009; Rombouts *et al.* 2013). *A priori*, it is difficult to know which individual taxa or processes
105 represent a spatial regime and thus ecological boundaries. Because of the central role played by
106 zooplankton as a prey item and a grazer, zooplankton data have commonly been used (Hooff &
107 Peterson 2006; Pace *et al.* 2013), although Scheffer *et al.* (2003) warn that zooplankton community
108 composition and abundance may be too chaotic to be useful for regime shift prediction except at
109 very high level aggregate states.

110 Ideally, a monitoring program should be able to forecast far-reaching change such as a regime shift.
111 However, too often monitoring focuses on particular species of interest, effectively barring
112 community-level or ecosystem-level analyses. We use spatially explicit avian and zooplankton
113 community species composition data to test for the identification and location of spatial regimes
114 using Fisher information, an information-theory method with no strict data requirements that is a
115 powerful tool for understanding system-level change within a location, or over space.

116 *Regime shifts and Fisher information*

117 There is widespread acceptance in the scientific community that some ecosystems exhibit multiple
118 regimes, and that the transition between regimes can be abrupt and discontinuous (though see
119 Fukami & Nakajima, 2011; Hastings & Wysham, 2010). Statistical indicators of regime shifts that can
120 act as an early warning signal are thought to represent generic properties that behave in similar and
121 predictable ways across system types (Dakos *et al.* 2011), and are proposed to have the added
122 advantage that detailed mechanistic knowledge is not necessary for their use. The indicators include
123 critical slowing down, which can manifest as slower recovery rates from perturbation, increased
124 autocorrelation, and increased variance (Scheffer *et al.* 2009); changing skewness (Guttal &
125 Jayaprakash 2008); conditional heteroscedasticity (Seekell *et al.* 2011), and the variance index (Brock
126 & Carpenter 2006).

127 These indicators have transformed our ability to identify variables that change in response to
128 exogenous or endogenous drivers and signal an impending regime shift. However, much remains
129 uncertain. For example, although the various indicators have been tested on model systems and
130 historical data sets with known temporal regime shifts (Lindgren *et al.* 2012), their performance is
131 not consistent (Seekell *et al.* 2011; Perretti & Munch 2012; Batt *et al.* 2013; Dakos *et al.* 2013) and
132 their ability to predict future regime shifts is unknown (Boulton *et al.* 2014). Some methods, such as
133 conditional heteroscedasticity, require large, high resolution samples (Seekell *et al.* 2011) and their
134 applicability to complex systems with multivariate data is questionable because most studies have

135 been conducted using either simulated data or very simple systems (Scheffer *et al.* 2009; Drake &
136 Griffen 2010; Dai *et al.* 2012; Dakos *et al.* 2012). When models have incorporated realistic levels of
137 ecological noise, the indicators tend to perform poorly (Perretti & Munch 2012). A difficulty in
138 developing early warning indicators is that the critical variables driving system transitions are
139 typically unknown. Brock and Carpenter (2012) cite this lack of knowledge as a “fundamental
140 problem” in leading indicators research.

141 Researchers have urged that multiple ecosystem variables should be evaluated when interpreting
142 indicators for real systems (Carpenter *et al.* 2009; Lindegren *et al.* 2012). For example, Litzow *et al.*
143 (2013) found that when analysing rising variance in catch data from fisheries, trends in individual
144 fisheries largely failed to be statistically significant, while pooling multiple populations increased
145 their ability to detect a collapse. The variance index (VI) was developed to capture dominant
146 variance trends in multivariate systems (Brock & Carpenter 2006). VI should spike prior to a
147 transition, but results from this index are sometimes unclear (Eason *et al.* 2014).

148 Fisher information may address some of the issues listed above. Fisher information is an
149 information theory approach (Fisher 1922) that captures patterns in system dynamics as evidenced
150 by the trends in variables that characterize the system’s condition. The approach collapses the
151 behavior of multiple variables into an index that can be used to track changes in dynamic order,
152 including regimes and regime shifts. Historical applications of information theory-based approaches
153 include assessing ecosystem functioning, stability, complexity, and diversity (Anand & Orloci 2000;
154 Svirezhev 2000; Fath & Cabezas 2004; Patricio *et al.* 2004). More recently, Fisher information has
155 been employed for sustainable environmental management at various spatial scales (Karunanithi *et*
156 *al.* 2011; Eason & Garmestani 2012) and to examine temporal patterns in both terrestrial (Mayer *et*
157 *al.*, 2007; Eason and Cabezas, 2012;) and aquatic systems (Mantua 2004; Spanbauer *et al.* 2014;
158 Eason *et al.* 2016).

159 While other methods like time series analysis requires a sufficient resolution of data to separate
160 noise from a genuine signal of an impending regime shift, the data requirements for Fisher
161 information are more lenient. A strength of Fisher information is that it can readily incorporate a
162 wide variety of data types and variables and has been used to identify regime changes in various
163 types of systems with data resolutions from relatively small and moderate (Eason & Cabezas 2012)
164 to quite large (Spanbauer *et al.* 2014). Furthermore, there is no minimum or maximum number of
165 variables needed to compute the index. When assessing a complex system characterized by multiple
166 variables, methods like Spearman rank order correlation have been used in conjunction with Fisher
167 information to determine which variables or groups of variables are critical for shaping the Fisher
168 information signal (Eason & Cabezas 2012). Accordingly, one of the key limitations of traditional
169 statistical indicators is avoided because there is no need to make assumptions about which variables
170 best act as indicators of an impending regime shift, particularly when much is uncertain and our
171 knowledge is limited.

172 *Purpose*

173 Our goal is to identify spatial regimes in avian and zooplankton community data using Fisher
174 information, and compare the extent to which Fisher-identified regime boundaries are coincident
175 with our *a priori* understanding of where these ecological boundaries exist, as per classification
176 systems such as Bailey's (1983) and Omernik's (1987) for terrestrial systems, and marine domain
177 descriptions found in Carmack *et al.* (2010) and Archambault *et al.* (2010). The terrestrial ecoregion
178 maps rely heavily on *potential* natural vegetation based on underlying geological and climatic
179 variables, so significant discrepancies between actual land use, actual vegetative cover, and
180 potential vegetation can exist, and should be reflected in the composition of the animal community.
181 Boundaries in marine systems are not as spatially constrained as in terrestrial systems and the key
182 habitat determinants of species' distributions and community structure are not as easily defined. It
183 is important to note that we are not trying to identify regime shifts that represent a critical transition

184 (e.g. Scheffer 2009), but rather the geospatial point or region at which one ecosystem type
185 transitions into another.

186 Although Fisher information is suited to multivariate data encompassing a wide range of biotic and
187 abiotic data that characterize any given regime, we used a single taxon dataset from each system
188 (birds and zooplankton). Limiting the data in this way had the benefit of making this a conservative
189 test of the performance of Fisher information that reflects the data readily available to others
190 working on similar problems. We compared the Fisher information results with a range of early
191 warning indicators (critical slowing down, captured by the lag-1 autocorrelation coefficient; variance;
192 kurtosis; skewness; and the variance index), and multivariate methods commonly employed by
193 community ecologists (nMDS (Oksanen 2013), and cluster analysis).

194 **Methods**

195 *Terrestrial data*

196 We used USGS Breeding Bird Survey data (BBS) from 30 survey routes along a ~ 1900 km transect.
197 Each BBS route is 41 km long and has 50 stop points located at 800 m intervals; at each stop point, a
198 3-minute point count of sighted and heard birds is recorded, and data from each stop point are
199 totalled for the route (Sauer *et al.* 2014). The routes begin in the Rocky Mountains, move due east
200 through the central prairie region, and then veer north into Minnesota, terminating at the western
201 border of Lake Superior (Figure 1A). The species abundance data are a snapshot of the 2007 bird
202 community at each route location. The routes are located in 5 Omernik Level III ecoregions
203 (Omernik 1987), but were selected such that there were roughly an equal number of routes in four
204 gross ecosystem types: 8 routes from the Southern Rockies (montane forest), 7 from the High Plains
205 (grassland), 3 from the Central Great Plains and 4 from the Western Cornbelt Plains (total of 7 routes
206 from grassland-agriculture matrix), and 8 from the Northern Lakes and Forest ecoregion (northern
207 forest-wetland matrix). The unequal number of routes among ecosystems was due to data
208 availability; not all routes are covered in all years, as route coverage relies on volunteers. Although

209 we used the Omernik ecoregions as an underlying map layer when selecting routes, there are
210 multiple ecoregion maps used by U.S. land agencies, with sometimes substantial differences
211 between them. None are 'right' per se, but all are best approximations of potential vegetation
212 based on areas with similar geology, physiography, vegetation, climate, soils, land use, wildlife,
213 water quality, and hydrology (United States Department of the Interior). We downloaded the
214 complete species abundance list for each route (Sauer *et al.* 2014) and used it to create a route-
215 species abundance matrix, where abundance is the number of individual birds for each species at
216 each route, with values ranging from 0 – 293.

217 Sampling biases are an issue with BBS data, resulting primarily from under detection of wary, rare,
218 and aquatic species, as well as differences between observers. However, those biases are present
219 across all routes and should not impact the very coarse pattern extracted from the
220 absence/abundance data. Remotely-sensed data for land cover type is also available for a 400 m
221 buffer around each route (Sauer *et al.* 2014). The land cover data provides a sense of the
222 heterogeneity of the habitat type for each ecoregion. We averaged the percent of each land cover
223 type across all routes for each of the five Omernik ecoregions.

224 *Marine data*

225 Zooplankton community surveys were conducted in 2008, and samples analysed under the auspices
226 of the International Polar Year program, Canada's Three Oceans project (Carmack *et al.* 2008). The
227 survey traverses 12,000 km from coastal British Columbia just north of Vancouver Island to the
228 Labrador Sea on the eastern side of Canada, crossing through 6 oceanic domains: the Gulf of Alaska,
229 the Bering Sea, the Chukchi Sea, the Beaufort Sea Shelf, the Canadian Arctic Archipelago, and
230 terminates in the Davis Strait/Labrador Sea (Figure 1B). Although these oceanic domains share some
231 zooplankton species, they are known to be distinct from each other to varying degrees (Archambault
232 *et al.* 2010; Pomerleau *et al.* 2011, 2014). There were 44 sampling locations irregularly spaced along
233 the transect.

234 Mixed zooplankton samples were collected from August to September by vertical net hauls with a
235 236 micron net (typically to 100 m or 7 metres above the bottom), and were preserved in 95%
236 ethanol and 10% buffered formalin. The zooplankton samples were keyed out to the lowest possible
237 taxonomic unit and enumerated and 4th root transformed, as is standard for marine zooplankton
238 data. When possible, the developmental stages of each taxa was counted separately. A site-taxa
239 abundance matrix was created. Sites were ordered from western-most to eastern-most station.

240 *Statistical Methods*

241 Fisher information was developed by Fisher (1922) as a measure of the amount of information about
242 a particular parameter (or system characteristic) that can be obtained by observation. The form of
243 Fisher information used in this work is based on the probability of observing various conditions ($p(s)$)
244 of the system (Fath *et al.* 2003; Mayer *et al.* 2007).

$$245 \quad I = \int \frac{ds}{p(s)} \left[\frac{dp(s)}{ds} \right]^2 \quad (1)$$

246

247 This is appropriate for our study because we are interested in determining patterns of change in the
248 condition (or state: s) of a system. From this equation, note that Fisher information is proportional
249 to the change in the probability of observing a system state ($dp(s)$) over the change in state ds
250 (i.e. $I \propto \frac{dp(s)}{ds}$). The significance of this proportionality may be examined using two cases. The first
251 example is a system in which the overall condition does not change from one observation to the
252 next. While such a system may fluctuate within a basin of attraction, it is considered stable because
253 the overall conditions are predictable and the patterns are evident; accordingly, the probability of
254 observing a particular state of the system is high and Fisher information tends toward infinity. The
255 exact opposite is true of a system that is constantly changing. In this case, the system displays no
256 bias toward a particular condition and there are no distinct patterns useful for characterizing the

257 way the system behaves; hence, there is equal probability of the system functioning in any state and
258 Fisher information is zero (Pawlowski & Cabezas 2008).

259 Karunanithi et al (2008) adapted Equation 1 to handle empirical data from real systems. Through a
260 series of derivation steps, Fisher information (henceforth denoted as FI) is numerically estimated as:
261

$$262 \quad FI = 4 \sum_{s=1}^n [q_s - q_{s+1}]^2 \quad (2)$$

263
264 where $p(s)$ is replaced by its amplitude ($q^2(s) \equiv p(s)$) to reduce calculation errors from very small $p(s)$.
265 Further details on the derivation and calculation may be found in (Mayer *et al.* 2007; Karunanithi *et*
266 *al.* 2008; Cabezas & Eason 2010).

267 Fisher information has traditionally been used to explore temporal patterns, however, the method
268 can be applied to examine spatial dynamics. The core of the FI approach is to assess patterns in data
269 based on tracking systematic changes in line with some ordering principle such that trends are
270 evaluated over a series of points (e.g., point a, point b, etc.). This sequence may be defined
271 temporally or spatially. The key distinction is that rather than using time as the basis for assessing
272 changes, spatial location is the ordering principle. The basic algorithm for computing FI is as follows:

273 (1) select variables (e.g. x_i , $i = 1 : n$ variables) that characterize the condition of the system (in this
274 case various animal species) and gather data (i.e., species abundance) from each sampling location
275 (l_j) across the route: ($x_i(l_j)$), $j = 1 : m$ sampling locations), such that the abundance of each species
276 at each site defines one point (e.g.. $pt_1(l_1): [x_1(l_1), x_2(l_1), x_3(l_1), \dots, x_n(l_1)]$); (2) assemble the data
277 into a $m \times n$ matrix and divide it into a sequence of overlapping windows that advances one route
278 location per iteration; (3) determine the measurement uncertainty for each variable (UX_i) and use
279 this to define a boundary (tolerance) around each system state. If the measurement uncertainty is
280 unknown then the variation in a stable portion of data may be used as a proxy. This boundary (size
281 of states) defines how much a measurement can vary within a particular state; (4) Use the size of
282 states to determine which points are similar (dimensions stay within the boundary defining a

283 minimum range of variation) and group (bin) similar points together into discrete states; (5)
284 Compute $p(s)$ by counting the number of points binned in each state and dividing this value by the
285 total number of points in the window; (6) compute $q(s)$ and calculate FI using Equation 2. This
286 process is repeated for each window. Based on empirical assessments, a $hwin \geq 8$ was suggested
287 (Cabezas & Eason 2010), however, it is generally set based on the amount of data available.
288 Increasing the $hwin$ tends to decrease the magnitude of the FI result and number of FI points, but
289 the basic trends remain intact (Cabezas & Eason 2010).

290 Different system regimes are controlled by fundamentally distinct processes and exhibit unique
291 patterns. Tracking FI affords the ability to assess changes in these patterns. Regimes are identified
292 as periods over time or across space in which FI is non-zero and the values are relatively stable (i.e.,
293 $dFI/dl \approx 0$). While steadily increasing FI indicates rising dynamic order, less change and possible
294 movement to more consistent patterns, declining FI signifies unstable dynamics, loss of resilience
295 and may provide warning of an impending shift (Eason et al. 2014). Although FI typically declines
296 prior to a regime shift (Mayer *et al.* 2007; Eason & Cabezas 2012; Eason *et al.* 2014), researchers
297 examined model dynamics to study the behavior of FI in the neighbourhood of a tipping point and
298 found that the behavior of FI depends heavily on the trends in the variables as the system
299 approaches a shift (Eason *et al.* 2014; Gonzalez-Mejia *et al.* 2015). It is therefore possible for FI to
300 increase as a system transitions from one regime to another. Such a result is in line with Seekell et
301 al. (2011, 2012), who found both increasing and decreasing trends in early warning indicators prior
302 to a shift.

303 Once a shift has been identified, the underlying variables can be explored to determine (or compare)
304 the condition of the system in its new state (Eason & Garmestani 2012). Although higher FI values
305 are generally associated with a greater degree of dynamic order, the level of dynamic order is not as
306 important as the ability of the system to remain stable within a desirable regime. When interpreting
307 FI, a regime is denoted by a relatively stable FI trend (i.e., $dFI/dl \approx 0$) with a high mean ($\hat{\mu}FI$) and low

308 standard deviation in FI ($\downarrow\sigma FI$) or low coefficient of variation in FI ($\downarrow cvFI = \frac{\sigma FI}{\mu FI}$) (Gonzalez-Mejia 2011;
309 Eason & Garmestani 2012). Transitions are identified as periods outside of stable regimes characterized
310 by relatively high σFI and $cvFI$.

311 The traditional temporal early warning indicators (variance, skewness, and kurtosis) were computed
312 using standard functions. The spatial variants (Moran's I spatial autocorrelation and spatial variance
313 and skewness) were not used because the sequential one-dimensional ordering of the sampling
314 stations lent itself to a space-for-time substitution. Since critical slowing down can be understood as
315 increases in short-term autocorrelation, the lag-1 autocorrelation coefficient was used as an
316 estimate (Dakos *et al.* 2008). The VI was computed as the maximum eigenvalue of the covariance
317 matrix from the dataset (Brock & Carpenter 2006). Note that the VI and traditional indicators are
318 expected to spike or increase prior to a regime shift, while FI tends to decline (Eason *et al.* 2014).
319 Fisher information and the traditional indicators were computed in MATLAB (v. 2014b) using a 5
320 station moving window that advanced one station at a time, where a station was either a BBS route
321 or a plankton sampling site. A window size of 5 ensured that there were FI results for each
322 ecoregion for both studies; using smaller or larger windows resulted in similar trends in the FI
323 results, similar to other studies (Cabezas & Eason 2010). Multivariate analyses were conducted
324 using metaMDS and ordcluster from package 'vegan' (R Development Core Team 2013). The
325 distance matrices for the nMDS were created using Bray-Curtis, and multiple dimensions were
326 plotted in a scree diagram to find the lowest dimensionality with an adequate ordination fit as
327 expressed by a stress value (<0.2 , (Clarke 1993)). The mean, standard deviation, and the coefficient
328 of variation (CV) in FI were calculated for each regime to explore regime stability.

329 **Results**

330 *Terrestrial data*

331 Fisher information detected four regimes and two transition zones which are roughly congruent with
332 *a priori* expectations based on ecoregion maps, but diverge in significant ways (Figure 2). The total

333 drop in FI between the high point in regime 1 and the low point in transition 1 is greater than that
334 between regime 2 and regime 3 (ΔFI of 2.05 and 0.98, respectively), suggesting that the difference in
335 FI between the Southern Rocky Mountains and the 3 Plains ecoregions is greater than the difference
336 among the Plains regions, which is to be expected. Likewise, the total drop in FI between regime 3
337 (all Plains routes) and regime 4 (Northern Lakes and Forest) is the largest of all (ΔFI of 2.51),
338 indicating that the greatest variation in bird community structure exists between these two regimes.

339 The declining trend in FI from west to east means avian community structure is losing order, which
340 aligns with the reality of increasing intensive agricultural land use. FI classified the community
341 structure in the first High Plains route as being similar enough to the eastern Southern Rocky
342 Mountains to include it in the first regime. There followed a steady loss of order, as reflected in the
343 FI value, across the western High Plains. When FI did stabilize, indicating a new regime, that regime
344 captured routes from both the eastern High Plains and western Central Plains ecoregions, indicating
345 a blurring of the distinction between the two Plains ecoregions in terms of vegetative cover and
346 avian community structure. Similarly, the third regime incorporates routes from the eastern Central
347 Plains and most of the Western Cornbelt Plains ecoregions, indicating that avian community
348 structure did not significantly differ between the two Plains ecoregions. This is not an unexpected
349 result, given that those two ecoregions are, in reality, a grassland-agriculture matrix.

350 The traditional indicators did not provide clear results and yielded graphs with no interpretable
351 pattern (Figure 3), however, VI provided results that were complementary to FI (Figure 2). The VI
352 peaks in several places which are congruent with regime shifts identified by FI (routes 10, 18, and
353 21). In general, the VI provides complementary information that supports the trend captured by FI,
354 but is significantly more difficult to interpret when evaluated alone because it is not possible to
355 ascertain whether a peak marks the beginning or end of a stable regime or of a transition zone.

356 While all three descriptive statistics (mean (μFI), standard deviation (σFI), and coefficient of variation
357 ($cvFI$ in FI) indicate relative stability in each of the first three regimes, the fourth regime, wholly

358 comprised of routes from the Northern Lakes and Forest region, has a lower mean, higher standard
359 deviation, and higher coefficient of variation in FI than the other regions, indicating that there is
360 greater variation in community structure within this ecoregion (Figure 4). Furthermore, the two
361 transition zones have a higher CV than the regimes (except the 4th regime), indicating zones of high
362 variability as community structure transitions from one regime to another.

363 The results of the multivariate analyses suggest that while the nMDS (stress value of 0.080 for 2
364 dimensions) and cluster analysis (not shown on Figure 5 because results are identical to the nMDS)
365 identifies distinct communities that align with the *a priori* expectations of the Omernick ecoregions,
366 they do not distinguish between the High Plains and Central Plains communities. The nMDS (Figure
367 5) shows the dissimilarity in community structure in terms of the relative position of each route to
368 every other in ordination space, as well as how those routes align with ecoregion expectations by
369 drawing polygons that connect the routes belonging to each Omernik-defined ecoregion. The routes
370 from the three Plains ecoregions are closer to each other in ordination space than either the
371 Southern Rockies or Northern Lakes and Forest routes, indicating that they are more similar in
372 community structure. The first route of the Northern Lakes and Forest region, indicated by FI as part
373 of a long transition zone between regimes, is also very proximate in ordination space to the Cornbelt
374 Plains routes, reflecting their closeness in geographic space. However, the High Plains and Central
375 Plains overlap each, indicating that the nMDS does not perceive them as dissimilar.

376 *Marine data*

377 Fisher information detected two regimes and two transition zones, which partially align with the *a*
378 *priori* expectations for the locations of the oceanic domains (Figure 6). FI is low and rises steadily
379 throughout two-thirds of the Bering Sea domain. Since FI never stabilizes in this domain, much of
380 the Bering Sea is classified as a transition zone. The first regime extends from the northern Bering
381 Sea through the Chukchi Sea. As the transect enters the Beaufort Sea, FI climbs steeply without
382 stabilizing, indicating increasing dynamic order in community structure and classifying the Beaufort

383 Sea as a second transition zone. The second regime extends from the more geographically closed-in
384 waters of the Canadian Arctic Archipelago through the sixth oceanic domain, the Davis
385 Strait/Labrador Sea. The entire distance from the western edge of the Archipelago to the Labrador
386 Sea is represented by only 12 stations, so it is relatively under-represented compared to the western
387 half of the survey.

388 Like the terrestrial case study, when the FI trends are compared to the traditional regime shift
389 indicators, only the VI was able to provide sensible results (Figure 6). The Variance Index peaks at
390 the boundary of the Bering Sea, the Chukchi Sea, and to a lesser extent the Beaufort Sea Shelf.
391 However, it does not distinguish whether the increased variance denotes the beginning of a stable
392 regime, or signals a transition zone. The descriptive statistics support an overall picture of change in
393 community structure which reflects successive patterns of an ecoregion with high variability (i.e.
394 high σ FI and cv FI) transitioning into a more stable regime (high μ FI, and low σ FI and cv FI) (Figure 7).

395 The multivariate analyses support the FI results, and suggest that the boundaries between the *a*
396 *priori* defined ecological domains are soft, particularly between the Bering Sea and Chukchi Sea.
397 When viewed in ordination space, the nMDS places the stations so they more or less flow from west
398 to east along the arc, but there is also strong overlap in community structure at sampling locations
399 near the edges of the domains (Figure 8; (stress value of 0.121 for 3 dimensions)). The cluster
400 analysis (Figure 8; pruned to 6 clusters) divides the stations of the Bering Sea into two clusters, and
401 places two of the Bering Sea stations in the Chukchi cluster, as well as fails to distinguish between
402 the Canadian Arctic and the Davis Strait/Labrador Sea. The overall result is that the zooplankton
403 communities do not have crisp boundaries which fully align with the *a priori* defined domains
404 described in the methods, but have softer boundaries with considerable overlap in community
405 structure between domains. Furthermore, FI communicates a richer story of community structure
406 transitioning across space than either the nMDS or cluster analysis. However, unlike the BBS case
407 study, the transition zones were marked by a rise in FI, as opposed to a drop, which may suggest a

408 possible slowing down of changes in community structure before the patterns destabilized and the
409 system organized into a new regime. Further work on the underlying system dynamics would be
410 instructive.

411 **Discussion**

412 *Detecting spatial regimes with Fisher information*

413 Given animal community data, we found that Fisher information was able to detect spatial regimes
414 and transitions between spatial regimes in both terrestrial and aquatic ecosystems, across regional
415 scales (1900 and 12,000 kilometres respectively). These studies were an important step towards
416 determining the utility of FI in detecting spatial regimes in both aquatic and terrestrial systems, even
417 given data limitations. In contrast, the traditional indicators we examined, such as variance,
418 skewness, kurtosis, and critical slowing down, were unable to detect spatial regimes, though this
419 was unsurprising as they are not suited for multivariate data. The VI helped to confirm general
420 trends, but it does not reveal details about the regime dynamics that are useful for assessing the
421 behavior of the system, e.g., whether there is a stable regime between two peaks, or whether
422 changes in the VI are capturing a transition. Our results suggest that Fisher information can be a
423 powerful, easy-to-use tool to assess regime shifts in animal (or other) community data, providing a
424 biological link between anthropogenic disturbances such as land use and climate change and spatial
425 shifts in ecological communities.

426 *The ecological reality of community regimes*

427 Our analyses demonstrated that the bird community boundaries only roughly coincided with the
428 expectations of ecoregion maps. There are substantial differences between the potential vegetation
429 underpinning the ecoregion classifications, and the actual spatial locations of stable avian
430 communities. If FI were to fully coincide with the ecoregion maps, then we would expect to see a
431 stable FI value through the center of each ecoregion, with evidence of increasing variability at the
432 borders, indicated by declining FI. Instead, the High Plains had high variability in community

433 structure throughout the core of the ecoregion. And rather than FI identifying three distinct Plains
434 regimes, as per the ecoregion expectation, it identified two regimes, each of which straddled routes
435 from the Central Plains. In other words, the avian community structure was simplified relative to
436 ecological expectations, with a blurring of the boundaries between what are considered distinct
437 ecoregion types by US land agencies. Indeed, the difference in FI between regime 2 and regime 3 is
438 such that the argument could be made that the entire Great Plains is one regime, with a slow but
439 steady loss of order as one moves from west to east, corresponding with an increasing intensity of
440 agriculture. The transitions to and from the Plains are both much steeper than that between the
441 two Plains regimes, as would be expected.

442 The land cover summary (Table 1) supports the findings of FI as it demonstrates that the three
443 prairie landscapes exist on a gradient of actual vegetative cover. As we move east from the High
444 Plains to the Cornbelt Plains, the percent grassland cover drops dramatically from 60% to 5%, and
445 the percent of row crop land cover rises 14% to 74% (Table 1). The most significant changes occur
446 between the High Plains and the Central Great Plains. These patterns are in contradiction to
447 ecoregion maps (Omernik 1987; Bailey 2015), which hold the difference between the Central Great
448 Plains and the Western Cornbelt Plains as much more fundamental (a Level I division) than that
449 between the High Plains and the Central Great Plains (a Level III division). To the extent that the
450 land use cover in each 400 m route buffer around the ~40 km route reflects on a gross level the land
451 cover of each ecoregion, it seems likely that the heterogeneity within the Plains landscapes due to
452 agriculture and grazing has been reduced.

453 The length of each transition zone is suggestive of soft, rather than the hard boundaries depicted on
454 ecoregion maps (Bailey 1983; Omernik 1987). The long transition from the Cornbelt Plains to the
455 Northern Lakes and Forest, which covered more than 400 kilometres, may be impacted by two
456 factors: First, the final two routes in the Cornbelt Plains occur on the upward sweep of the transect
457 and so are substantially more northern than the other Cornbelt Plains routes. Latitude is known to

458 affect animal communities (Clergeau *et al.* 2006). Second, the first route in the Northern Lakes
459 ecoregion technically falls into a narrow band of the North Central Hardwood Forest. This rapid
460 shifting across three ecoregions is captured by FI as a long transition before the fourth regime
461 begins. Finally, the higher cvFI and thus relative variability of FI in the fourth regime, which falls
462 wholly within the Northern Lakes and Forest ecoregion, is possibly explained by the heterogeneity of
463 the land cover, though it is also possible that further data points would reveal the fourth regime as
464 another transition as the study ends at a geographic rather than ecological border. However,
465 community structure in this ecoregion is likely more variable than in the other regimes because the
466 landscape itself is more variable, as it is a patchy mosaic of water features and forest (Table 1).

467 The zooplankton data tell a similar story to the avian data. Although there is correspondence
468 between zooplankton community structure, large scale oceanic structure, and regime transitions as
469 detected by FI, some boundaries are less defined than *a priori* expectations. Domains thought to
470 contain distinct communities, such as the Bering Sea or Beaufort Sea Shelf (Springer *et al.* 1989;
471 Hopcroft *et al.* 2010; Pomerleau *et al.* 2014), appear to be transition zones between stable
472 communities. The failure of both FI and the nMDS to distinguish between the Canadian Arctic
473 Archipelago and Davis Strait/Labrador Sea may be a function of inconsistent sample coverage.
474 Further work examining how the frequency of sampling affects the power and sensitivity of FI is
475 warranted.

476 The inability of FI to crisply distinguish between the Bering Sea and the Chukchi Sea is consistent
477 with our understanding of the region as a mixing zone where Bering Shelf water mixes with water
478 from the Anadyr current, which enters from the west, and Alaska coastal water, which enters the
479 Bering Strait from the east (Coachman *et al.* 1975). These three water masses are believed to
480 harbour unique zooplankton communities (Springer *et al.* 1989), and as the water masses do not mix
481 until they pass through the Bering Strait into the Chukchi Sea, the zooplankton community contains
482 a mixture of communities that differ from the southern Bering Sea and have high patchiness (Eisner

483 *et al.* 2014; Pomerleau *et al.* 2014). As the transect enters the Beaufort Sea, there is a decline in
484 both Pacific taxa and zooplankton community patchiness associated with the mixing of the three
485 Pacific water masses and Arctic water, corresponding to greater similarity among samples and
486 increasing dynamic order in FI. The expectation was that the Chukchi, understood to be a mixing
487 zone of watermasses, would be identified by FI as a transition zone, while the Beaufort Sea Shelf
488 would be a stable regime. Instead, the northern part of the Bering Sea and the Chukchi had a stable
489 FI value denoting it as a regime, while the Beaufort Sea Shelf underwent a long and significant
490 increase in dynamic order that never flattened sufficiently to qualify as a regime. This means that
491 the variability in zooplankton community structure as the transect traverses the Beaufort Sea was
492 much higher than that of the northern Bering/Chukchi Sea, despite the latter region consisting of a
493 mixing zone of multiple water masses. The FI results suggest that studies on dominant zooplankton
494 species within each domain (Nelson *et al.* 2009; Walkusz *et al.* 2010; Pomerleau *et al.* 2014) may not
495 strictly correlate to bigger picture studies which assess variability in community structure over space,
496 or that zooplankton species compositional data or the way in which they are collected are not a
497 good proxy for spatial regimes.

498 *What Fisher information captures that multivariate analysis does not*

499 The nMDS analysis largely aligned with the *a priori* ecoregion and oceanographic domain
500 expectations, but was not always able to distinguish between ecoregions (the High Plains and
501 Central Plains) or domains (Canadian Arctic and Davis Strait/Labrador Sea), though in the case of the
502 zooplankton data, may be a function of insufficient sampling stations in those domains. Perhaps
503 most importantly, the multivariate analyses are largely visual; ordination methods create their own
504 space, and thus do not tell us about spatial shifts in the location of a community. Routes that were
505 geographically farther away from each other tended to be more dissimilar than routes that were
506 close together. However, this rather crude depiction of community structure does not tell us where
507 the boundaries between communities occur, whether they are hard or soft, or if the soft boundaries
508 are themselves ecotones with stable community structure. Furthermore, the approach does not

509 provide any insight on the spatial extent of the transitions. The ability to assess whether or not a
510 particular community is gaining or losing order over time could allow land use managers to
511 anticipate a potential regime shift within a location, or document if community locations shift in
512 space over time. That said, our ability to detect change using FI may be improved by employing
513 post-hoc tests to assess trends in the index. Researchers have explored approaches such as cut-offs,
514 Mann-Kendall tests, and Bayesian methods to help reduce interpretive uncertainty (Heberling &
515 Hopton 2010; Vance *et al.* 2015; González-Mejía *et al.* 2016), but these methods are still under
516 development.

517 *Idio- or non-idiosyncratic changes in animal community regimes?*

518 To what extent can we expect changes in plant and animal communities to occur in a fashion
519 detectable by monitoring and analytical methods like the one presented here? Our contention is
520 that it will depend on whether or not species' response to anthropogenic change is idiosyncratic
521 within and across taxa. If species' responses are fully idiosyncratic, then the patterns at the
522 community level will become chaotic as a function of independent species' responses as
523 anthropogenic impacts accumulate and intensify. Accordingly, tracking spatial regimes and the
524 location of the transition zones between them would not be a useful activity for managers or
525 scientists. There are, however, constraints on individual response such that pattern identification
526 will remain useful and feasible on shorter timescales, though the possibility of no-analog
527 communities seems highly likely for multi-decadal or longer time scales (Williams & Jackson 2007).
528 In general, we expect to see changes in animal abundances in the short term as a response to
529 climate change and anthropogenic influence, as opposed to changes in presence/absence. Changes
530 may result from range shifts, as there is substantial evidence documenting vagile species recently
531 shifting their ranges to track their climatic niche (Parmesan, 2006; Parmesan & Yohe, 2003; Tingley
532 *et al.*, 2009), but the rate of climate change is such that migration capabilities are unlikely to keep up
533 with the rate of thermal change (Thuiller *et al.* 2008), and the ability to shift ranges is further
534 impeded by habitat fragmentation, which has been shown to reduce range shift (Iverson *et al.* 2004;

535 Thuiller *et al.* 2008). As a result, range contraction due to a lack of suitable habitat and reduced
536 survivorship within their original range is also expected (Davis & Shaw 2001; Parmesan 2006).

537 These issues confound the identification of ecological boundaries and our ability to track changes in
538 boundaries over time. Fisher information can assist researchers and managers in tracking changes in
539 the patterns of community structure associated with habitat types or biogeographical distribution
540 areas, as well as the temporal dissolution of community structure as no-analog communities
541 assemble over time. A substantial benefit to Fisher information is that it circumvents many of the
542 difficulties currently present in defining ecological boundaries, such as problems of non-linear
543 responses across ecotones, landscape fragmentation, and land use change in terrestrial systems, or
544 the ephemeral nature of some oceanographic boundaries, as well as the vast spatial scales involved,
545 all of which can be difficult to capture without exhaustive data collection (Strayer *et al.* 2003; Kent *et al.*
546 *al.* 2006; Danz *et al.* 2012). Other researchers have discussed the challenges of tracking boundary
547 region shifts as a way to monitor climate change, when, for example, little to no native vegetation
548 remains (less than 5% of the original prairie in the United States due to land conversion), and critical
549 structuring processes have been repressed or altered (natural fire regimes suppressed) (Danz *et al.*
550 2012). Fisher information allows for the simultaneous analysis of multiple, disparate variables and
551 provides a synoptic approach that may allow for detection of ecological change and boundary shift
552 without pre-supposing key taxa as bell-weather species of change. However, future studies wishing
553 to estimate more precisely the location of boundaries and how they may shift over time may also
554 need to account for phenological/seasonal detection differences in the taxon under question.

555 We also propose that monitoring animal populations is more likely to reflect currently changing
556 conditions and is easier than detecting variation in plant communities or oceanographic properties.
557 Remotely-sensed data remain challenged to identify physically similar but floristically different
558 species, and ground-truthing large ecological regions is unfeasible. Animal species' responses are
559 likely to occur more rapidly than plants, as there can be a large mismatch between vegetation and

560 climate change, with changes in vegetation lagging substantially behind changes in climate (Beckage
561 *et al.* 2008). Long-lived species such as trees can exhibit ecosystem responses to land use and
562 climate change at century-scales because of the spatial and temporal processes structuring forests
563 (Starfield & Chapin 1996), while terrestrial animal species are more vagile and can act as a leading
564 indicator of vegetation change, or of a change in climatic variables such as temperature.
565 Furthermore, as we demonstrated, there can be significant differences between ecoregion mapping,
566 which is based on potential vegetation as a function of geomorphology and soils, and the location of
567 spatial regimes actually present after decades of land use changes. All of these issues make it critical
568 to identify reliable spatially-explicit tools for mapping the effects of climate and land use change on
569 biodiversity (Mokany & Ferrier 2011), and our research suggests that Fisher information can be one
570 of those tools.

571 **Conclusion**

572 Our analyses confirmed that when using multivariate data, traditional early warning indicators are
573 very difficult to interpret, and integrated indicators such as FI and VI more consistently detect
574 regime shifts. We found that Fisher information provided the clearest, most detailed, and
575 interpretable signal of spatial regime shifts. Although the Variance Index did not provide clear
576 signals as a stand-alone indicator, some congruent trends are found when the results are presented
577 in conjunction with FI. Fisher information has the further benefit of being highly flexible in terms of
578 the choice of variable selection and data input, and is able to detect a clear signal without the need
579 for difficult-to-acquire high resolution data.

580 This research had the further benefit of highlighting the incongruence between terrestrial ecoregion
581 maps, which are focused on ecological potential, and the ecological reality of community regimes
582 given land use and climate change. The method presented would allow researchers to track both
583 the shifting spatial locations of communities over time, as well as the change over time within a

584 location, both of which are critical as the consequences of anthropogenic change manifests in
585 community structure and dynamics over time and space.

586 We appreciate that for both systems analysed, a different taxa could show spatial regimes in
587 different locations. Reptile or mammal community regime location may or may not overlap bird
588 regime location, and the transitions between ecoregions may be more or less steep given the taxa
589 under consideration. Neither mammals nor reptiles tend to be as vagile as birds, and their ability to
590 disperse in response to climate or land use change is accordingly more limited. Further research
591 evaluating the spatial regimes of other taxa and the extent to which they overlap bird and
592 zooplankton species would be useful.

593 Finally, further studies that looked more deeply into community structure within a spatial regime
594 could inform managers as to which subgroups of species are most dominant within each regime,
595 while correlation analysis could identify the subgroups of species responsible for driving the value of
596 Fisher information within each regime, both of which would allow managers to objectively select
597 subgroups of species to monitor as the primary indicators of ecological stability within a community.

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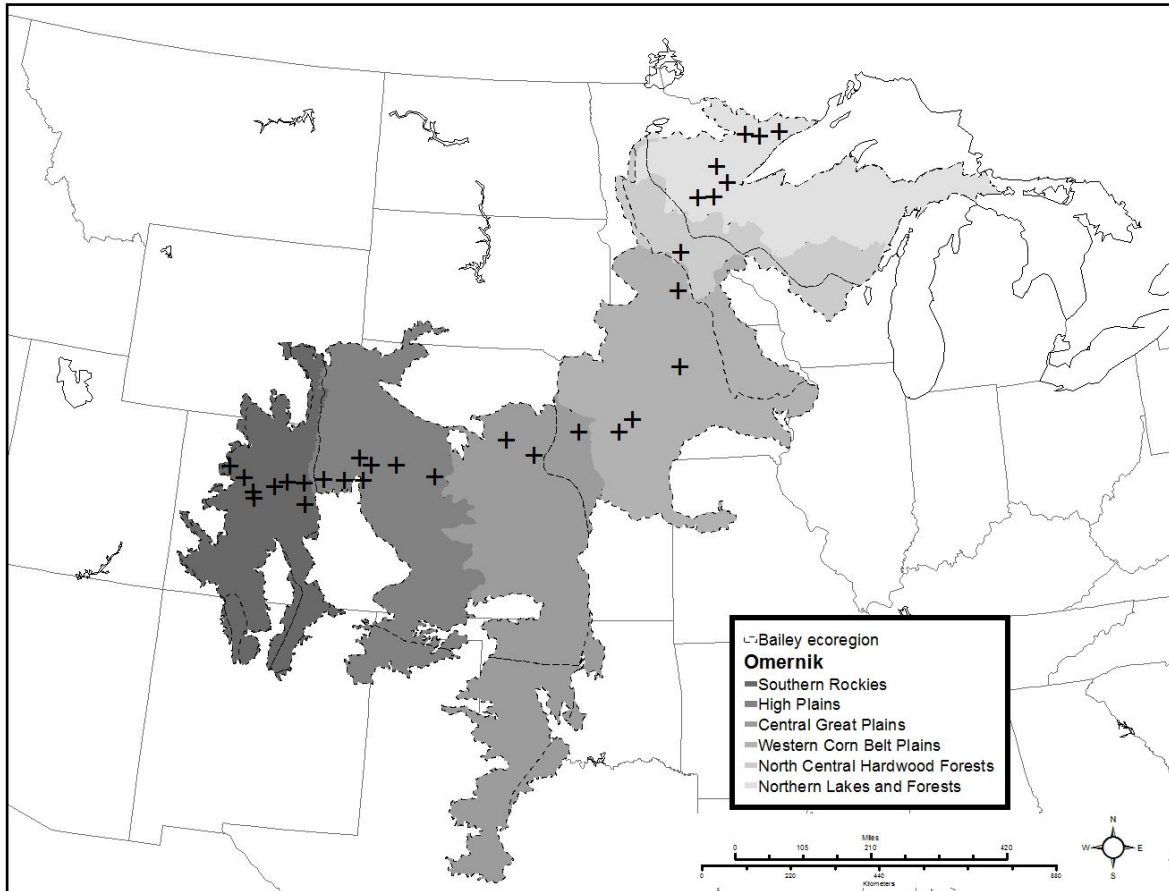
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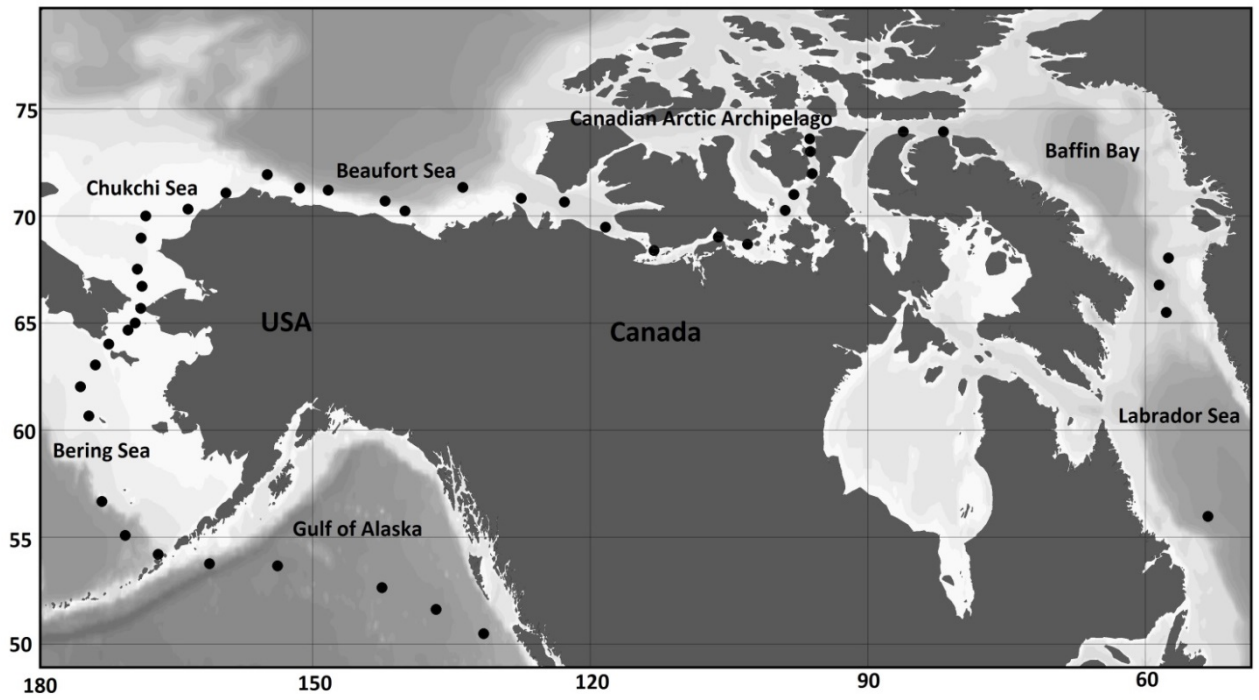
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923 Figure 1A. The USGS Breeding Bird Survey route locations in the central and northern United States.
924 The Omernik Level III ecoregion boundaries are colored in grayscale , while the Bailey Level III
925 ecoregion boundaries are shown using dotted lines.



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928 Figure 1B. Zooplankton data collection locations.



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Figure 2. Fisher information ((FI; bold solid line)) and Variance Index (VI; faint dotted line) for Breeding Bird Survey community data from 30 routes (numbered from 1 to 30 on the x-axis, reflecting the west to east ordering of the routes in geographic space). Regimes identified by FI are shown as shaded boxes around the plotted line. The Omernik ecoregion domains under the x-axis allow comparison as to how well the regimes align with the ecoregions, which represent potential rather than actual vegetation. Because one FI value is produced per window, the first FI value is at route 5.

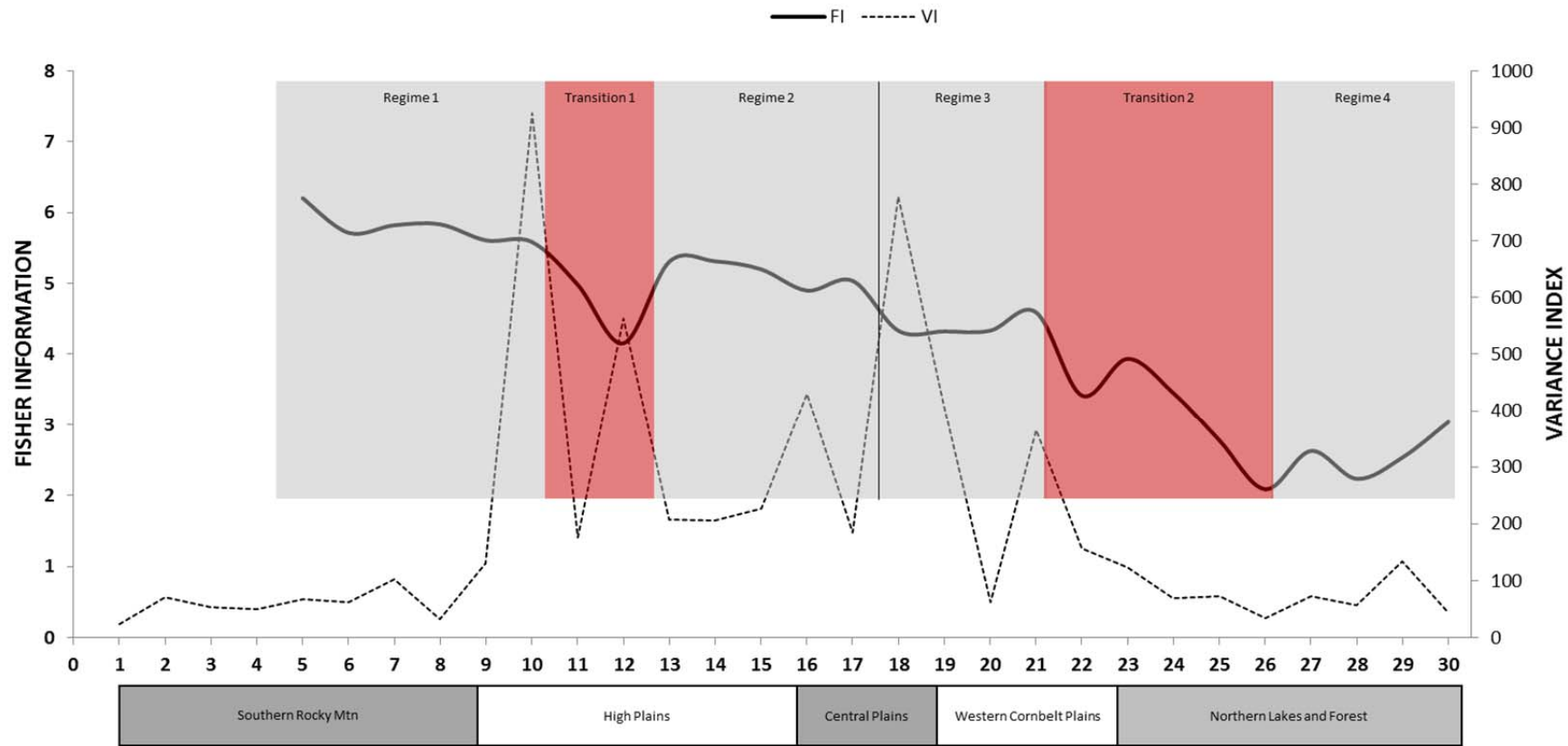


Figure 3. Results for traditional regime shift parameters applied to the BBS avian community data: variance, skewness, kurtosis, and ARI (critical slowing down). The graphs are largely uninterpretable when used on multivariate data such as this.

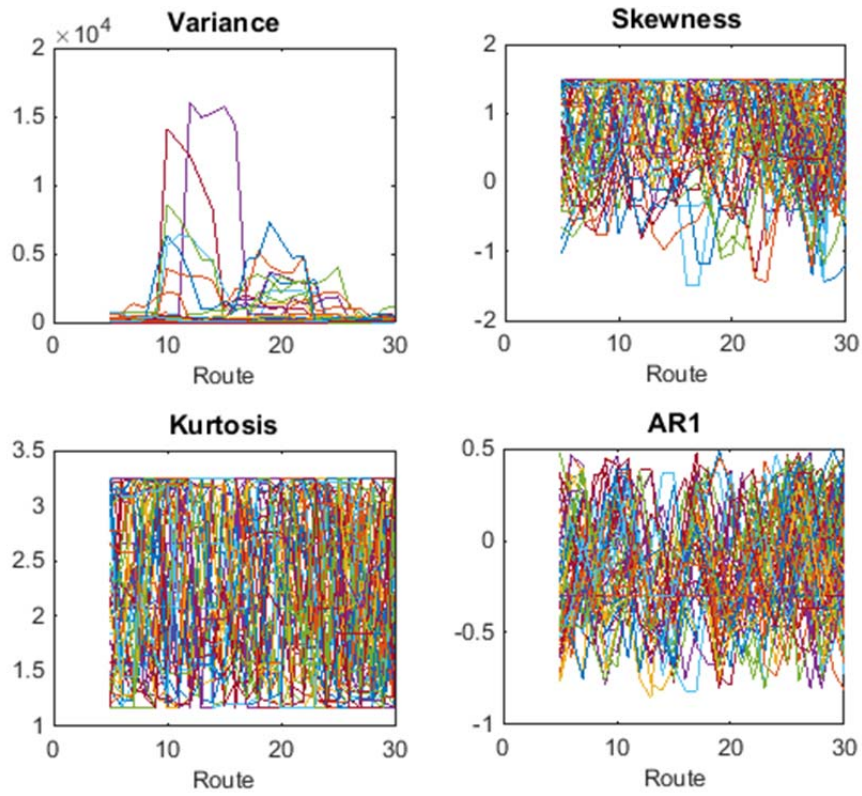
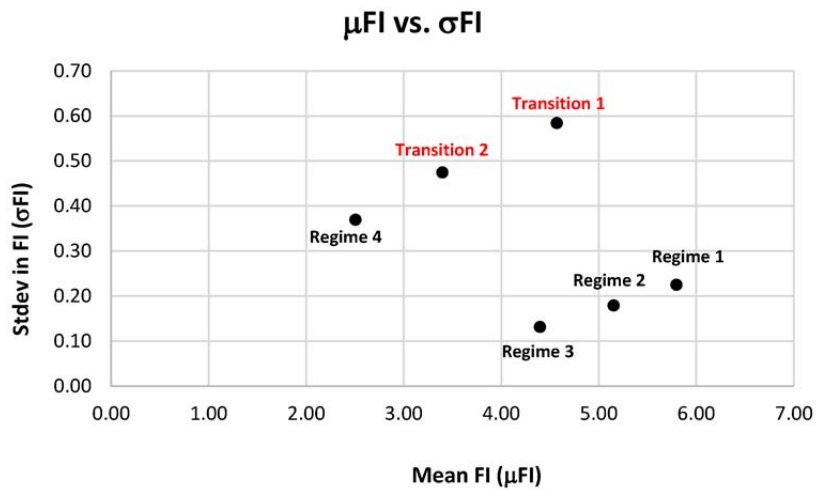


Figure 4. The stability of each terrestrial regime over space, as defined by the mean (μ FI), standard deviation (σ FI), and coefficient of variation (cvFI) of FI. While regimes 1-3 are clustered together and relatively stable with high μ FI, low σ FI and cvFI, Regime 4 was highly variable (low μ FI, high σ FI and cvFI). The transition periods exhibited the least amount of stability.



	Route	μ FI	σ FI	cvFI
Regime 1	5-10	5.79	0.23	0.04
Transition	11-12	4.57	0.58	0.13
Regime 2	13-17	5.15	0.18	0.03
Regime 3	18-21	4.40	0.13	0.03
Transition	22-25	3.40	0.48	0.14
Regime 4	26-30	2.50	0.37	0.15

Figure 5. Ordination plot for the BBS avian community data ($k = 2$, stress = 0.080). The BBS routes are shown with open circles, while the polygons contain all the routes that fall into the ecoregions (Omernik 1987). The overlap between the High Plains and the Central Plains suggests that these two ecoregions do not substantially differ in avian community structure.

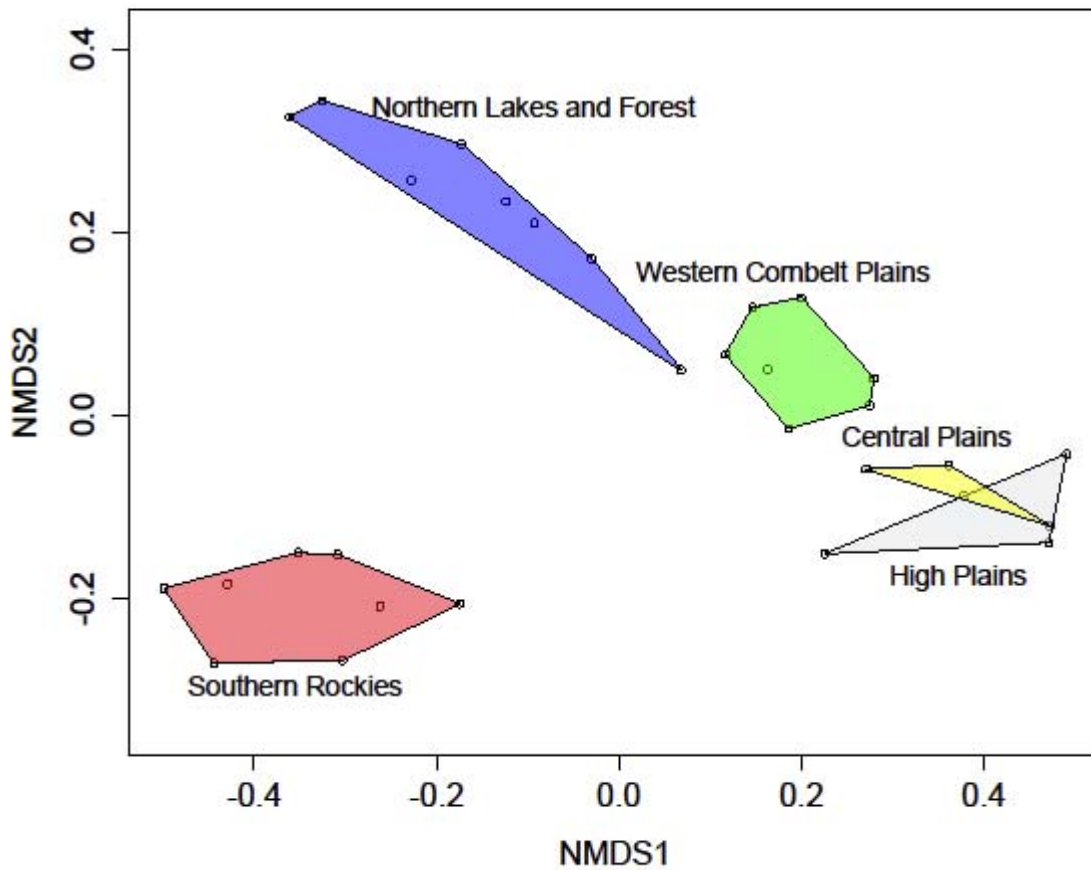


Figure 6. Fisher information (FI; bold solid line) and Variance Index (VI; faint dotted line) for zooplankton community data collected from 44 stations along a transect that begins in the Pacific ocean, traverses the Arctic, and ends in the Labrador Sea (numbered from 1 to 44 and ordered from west to east along the x-axis). Because one FI value is produced per window, the first FI value is at route 5. The regimes and transition zones identified by FI are shown as boxes drawn around the FI plotted line. The *a priori*-defined oceanic domains are under the x-axis, to see how well the location of the regimes identified by FI align with the oceanic domains identified in the literature.

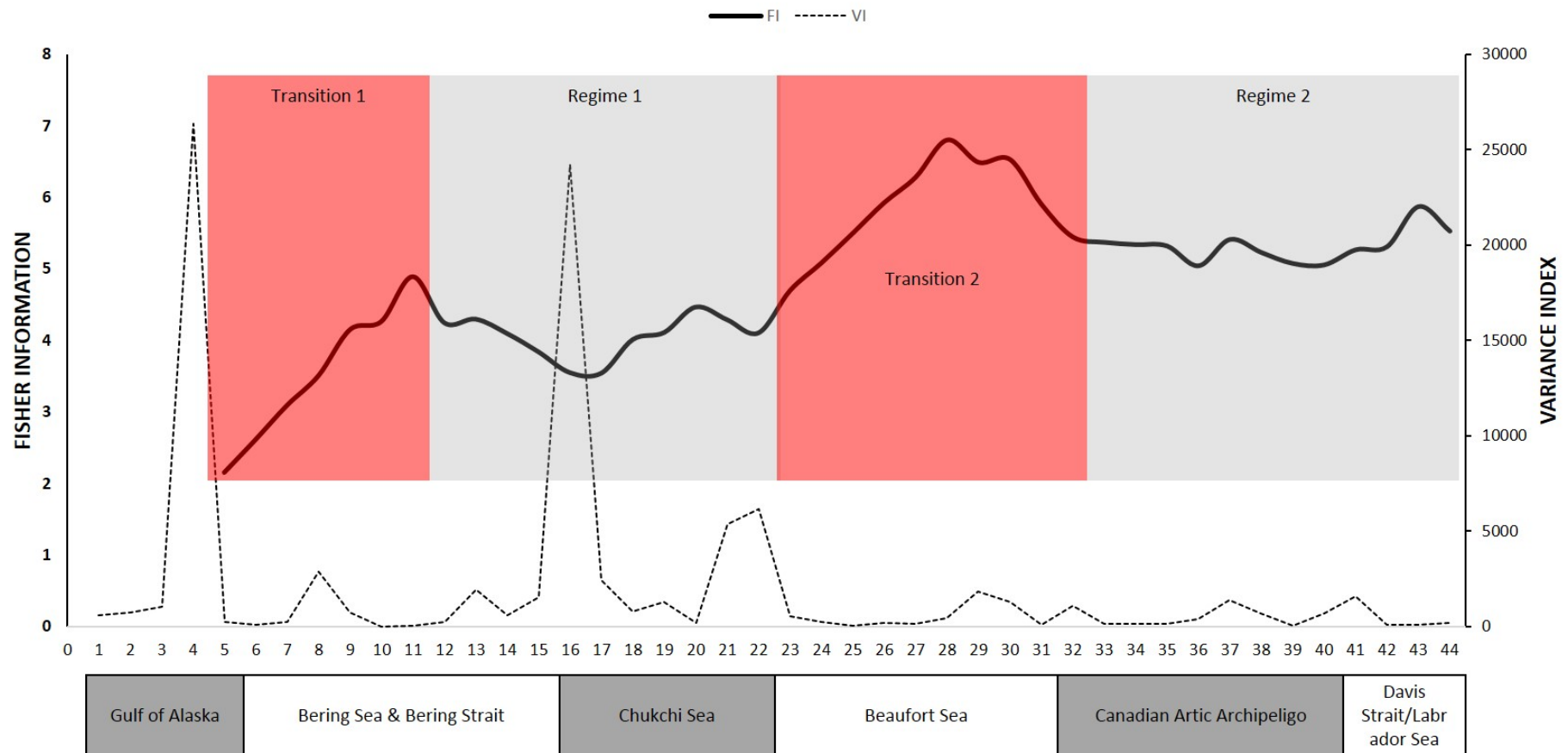
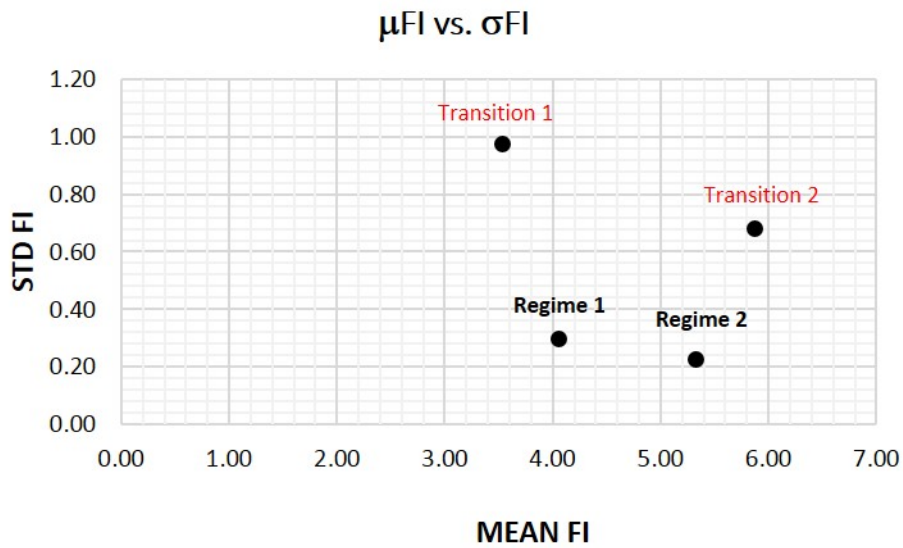


Figure 7. The stability of each marine regime over space, as defined by the mean (μ FI), standard deviation (σ FI) and coefficient of variation of FI (cvFI). While the two regimes are relatively stable with high μ FI, low σ FI and low cvFI, the transition periods exhibited the least stability. Note: Regimes reflect the domains identified by the trend in FI, **not** the regimes *a priori* identified using Carmack et al. (2010)) and Archambault et al. (2010).



	Station ID	μ FI	σ FI	cvFI
Transition 1	5-11	3.53	0.97	0.28
Regime 1	12-22	4.05	0.30	0.07
Transition 2	23-32	5.87	0.68	0.12
Regime 2	33-44	5.32	0.23	0.04

Figure 8. Ordination plot for the zooplankton community data ($k = 3$; stress = 0.121). The sampling stations are shown with open circles. The results of a cluster analysis (pruned to 6 clusters) are shown with black spiders, while the oceanic domains *a priori* identified from the literature are represented by the colored polygons. Both the nMDS and the cluster analysis fail to assign some sampling stations to the 'correct' oceanic domain for all domains except the Gulf of Alaska.

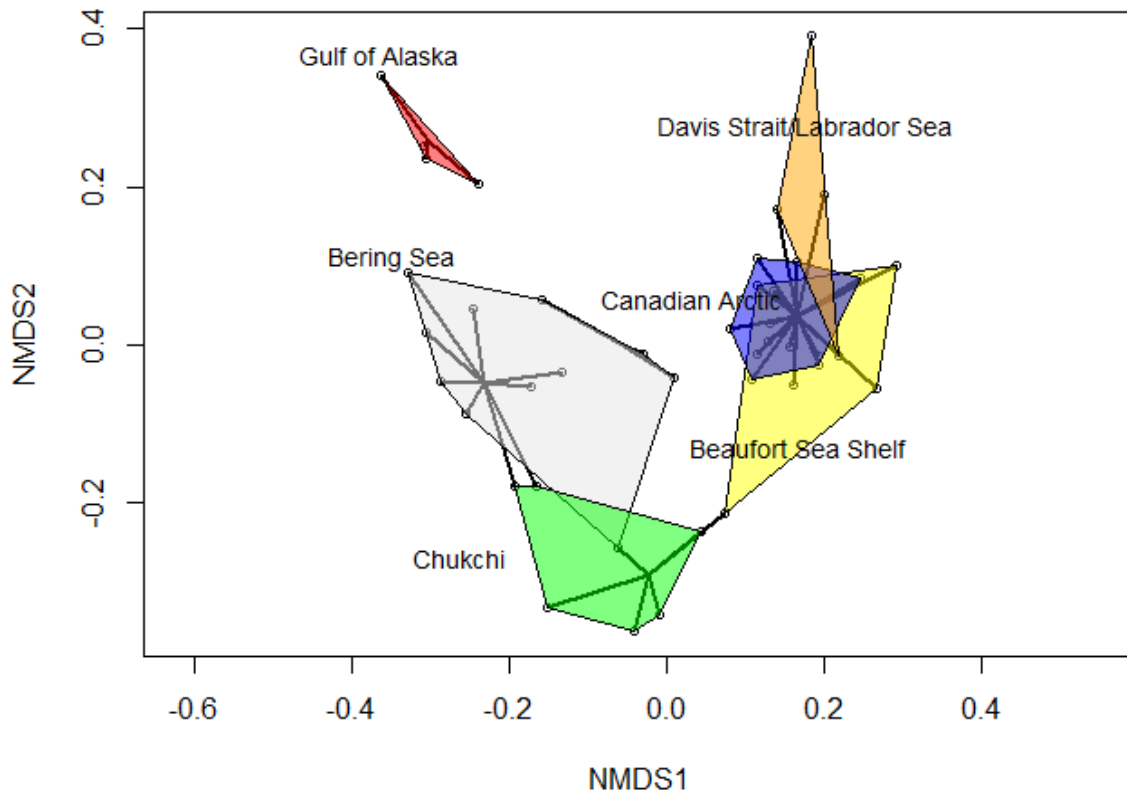


Table 1. Land cover classification for a 400 m buffer around each 41 km BBS route. The dominant land cover type for each ecoregion is in bold. Note that Northern Lakes and Forest is roughly evenly split between Deciduous Forest and Woody Wetlands, evidence for the heterogeneity of the region.

Landcover Type	Southern Rockies	High Plains	Central Plains	Western Cornbelt	Northern Lakes and Forest
Open Water	0.01		0.01	0.01	0.04
Low Intensity Residential				0.02	
Deciduous Forest	0.14		0.02	0.03	0.25
Evergreen Forest	0.47				0.12
Mixed Forest	0.01				0.11
Shrubland	0.15				
Grassland/Herbaceous	0.18	0.61	0.20	0.05	
Pasture/Hay	0.02	0.04	0.08	0.12	0.10
Row Crops		0.14	0.66	0.74	0.03
Small Grains		0.13	0.02	0.01	
Fallow		0.07			
Woody Wetlands					0.28
Emergent Herb Wetland				0.01	0.04

*Only showing those categories for which at least one ecoregion has > 1%