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4 Structural diversity as a habitat indicator for endangered lakeshore flora using an
5 assemblage of common plant species in Atlantic Canada

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20 ABSTRACT

21 Vegetation structure, defined by the height, cover and types of plants, is an important
22 component of habitat suitability for plant species or communities. The identification of
23 potential habitat is a crucial knowledge gap for endangered Atlantic Coastal Plain Flora
24 (ACPF), a group of taxonomically unrelated plants that share common habitat types and
25 are mostly found on lakeshores and wetlands in the Atlantic coastal region of North
26 America. Our objectives were to assess spatial patterns and relationships of ACPF richness
27 and structural diversity indices at different scales and positions along the lakeshore-to-
28 forest gradient. We sampled 16 sites at 7 lakes in southwestern Nova Scotia using
29 contiguous 20 x 20 cm quadrats along 20 m transects, perpendicular to the waterline, and
30 in 5 x 5 m grids, between the lake and the forest edge. We measured the cover of 19 ACPF
31 species and structural elements at different heights and calculated structural diversity
32 indices using the Shannon index. Spatial patterns were assessed using one and two-
33 dimensional wavelet variance and covariance. The edge of the zone of high ACPF richness
34 coincided with greater structural diversity at the lakeshore edge. Herbaceous ACPF
35 richness was positively associated with structural diversity at finer scales and on
36 lakeshores, but negatively associated at coarser scales and farther from the waterline. A
37 strong association of structural diversity with ACPF richness suggests it could be used as
38 a habitat indicator for ACPF on lakeshores, which could help the identification and
39 conservation of potential suitable shorelines for ACPF populations in Nova Scotia.

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43 KEYWORDS

44 Atlantic Coastal Plain Flora; community level; lakeshore-to-forest gradient; spatial
45 pattern; vegetation structure; wavelet analysis

46

47 INTRODUCTION

48 Edges, defined as zones of transition between plant communities, are important
49 parts of landscapes as they control the flow of energy and materials across ecosystems and
50 are characterized by unique abiotic and biotic gradients (Harper et al. 2005). Edges
51 generally support higher levels of structural diversity because of interactions occurring
52 between physical processes and microclimatic conditions (e.g., increased exposure to wind
53 and solar radiation; Fraver 1994; Ploff et al. 1997). Riparian edges are expected to support
54 greater structural diversity because they are shaped by moderate levels of hydrological
55 disturbance (e.g., wave action and ice scouring), encompass vegetation elements from both
56 lakeshore and forest communities, and experience higher tree mortality (Fetherston et al.
57 1995; Pabst and Spies 1998; Komonen 2009). As high levels of structural diversity offer a
58 variety of habitats, vegetation structure is often positively correlated with biodiversity
59 (Tews et al. 2004; McElhinny et al. 2005). Furthermore, riparian zones provide favored
60 habitat for some rare species (Komonen 2009), as hydrological stress, such as deficiencies
61 (e.g., nutrient poor soils) or excesses (e.g., saturated soils) of abiotic factors, allows the
62 displacement of competitive species with stress-tolerant species (Grime 1977).

63 Habitat patches are mostly delimited by vegetation structure (Chen et al. 1996),
64 which represents the physical organization of plants (e.g., height and cover; Noss 1990).
65 Assessing vegetation structure can consequently contribute to the characterization of

66 habitat structure (Pabst and Spies 1998) and be integrated into different indices of structural
67 diversity or richness of structural elements (Dodonov 2015). By synthesizing the spatial
68 distribution, functional diversity and composition of vegetation, structural diversity could
69 be used as a proxy to identify microhabitats and associated habitat characteristics
70 (McElhinny et al. 2005). Structural diversity is increasingly recognized as a surrogate for
71 ecological requirements, but has not normally included other structural components than
72 trees (McElhinny et al. 2005). Incorporating a variety of structural elements at a ground
73 and above ground level would allow to appropriately represent the entire habitat structure
74 complexity. Furthermore, forest edges have usually been disregarded but could have an
75 important effect on riparian plant communities, as decreased pollination activities on
76 lakeshores might result from the degradation of the shrub zone (Environment Canada and
77 Parks Canada Agency 2010).

78 Riparian plant communities offer insight into the variation of species richness at
79 different spatial and temporal scales, as they support complex habitat patches that are
80 created and destroyed by hydrological disturbances, resulting in an annual redistribution of
81 species (Naiman et al. 1988; Naiman and Decamps 1997). The distribution of riparian
82 species is influenced by physical and disturbance features, such as propagule dispersal,
83 seed germination, seedling survival, power and frequency of floods and site specific
84 erosion (Naiman and Decamps 1997). The spatial pattern of plants is defined by the
85 physical arrangement and size of patches with high or low levels of certain vegetation
86 attributes (Dale 1999). As community structure and plant distributions vary with the scale
87 of observation (Dale 1999; Kembel and Dale 2006), scale is a key component of spatial
88 patterns and relationships (Noss 1990; McElhinny et al. 2005). It is increasingly known

89 that ecological understanding must address multiple scales, as species are related to
90 different abiotic and biotic environmental factors occurring at many scales (Bellamy et al.
91 2013). Using fine scale spatial patterns and a community level approach could provide
92 critical information on the specific location of suitable habitat and underlying ecological
93 processes for associated rare, cryptic and ephemeral species (Rawinsky and Price 1994;
94 McIntire and Fajardo 2009).

95 We related spatial patterns of structural diversity to Atlantic Coastal Plain Flora
96 (ACPF), a group of taxonomically unrelated plant species mostly found on lakeshores and
97 wetlands along the Atlantic coastal plain physiographic region of North America (Wisheu
98 and Keddy 1989; Sweeney and Ogilvie 1993). We previously assessed the influence of
99 specific abiotic (i.e., topography, substrate) and biotic (i.e., functional groups of plants)
100 habitat characteristics at local and landscape (i.e., shoreline, lake, watershed) scales on
101 ACPF lakeshore communities (Dazé Querry et al. 2017). Our goal for this paper was to
102 determine if structural diversity can be used as an indicator of suitable habitat for ACPF
103 by using wavelet analysis to assess relationships at different scales and positions along an
104 environmental gradient, as different types of associations could arise. This will help to
105 address some knowledge gaps, such as the identification of key habitat characteristics and
106 potential habitats, which restrict the establishment of strategic conservation plans in Nova
107 Scotia (Environment Canada and Parks Canada Agency 2010). Our first objective was to
108 assess spatial patterns of ACPF richness, individual ACPF species cover, and structural
109 diversity indices along the lakeshore-to-forest gradient. Our second objective was to assess
110 spatial relationships between ACPF richness (and individual ACPF species cover) and

111 structural diversity indices at different scales and positions. For ACPF richness, we used
112 an assemblage of common ACPF species as surrogates for the entire ACPF community.

113

114 METHODS

115 **Study area**

116 Our study was conducted in southwestern Nova Scotia, a disjunct region from
117 ACPF main range, which include some of the most suitable remaining habitats and the last
118 large undisturbed ACPF populations in the world (Francis and Munro 1994; Wisheu et al.
119 1994). Southwestern Nova Scotia is generally characterized by sandy acidic soils with
120 mixed drainage and an inland climate with high humidity (Sweeney and Ogilvie 1993).
121 Mean daily annual temperature ranges from -5 °C in January to 19 °C in July and monthly
122 precipitation ranges from 96 to 165 mm in Bridgewater, Nova Scotia (Climate Canada
123 2015). Lakeshore vegetation consists of a mixture of coniferous and deciduous tree species,
124 such as red maple (*Acer rubrum*), beech (*Fagus grandifolia*), yellow birch (*Betula*
125 *alleghaniensis*), red spruce (*Picea rubens*) and white pine (*Pinus strobus*). Common woody
126 shrub species include sweet gale (*Myrica gale*), witherod (*Viburnum nudum*) and Canada
127 holly (*Ilex verticillata*) (Sweeney and Ogilvie 1993).

128 We chose lakes in the Medway watershed, the second most important site for ACPF
129 in Nova Scotia (Sweeney and Ogilvie 1993), and the Mersey watershed, where important
130 populations of many ACPF species are found (Francis and Munro 1994). We listed species
131 found on each lake using the Mersey Tobeatic Research Institute (2015) ACPF database
132 from 36 high priority lakes. We then selected a subset of 19 ACPF species co-occurring on
133 lakeshores (Table 1) by excluding species that were relatively uncommon, taxonomically

134 questionable, difficult to identify/find or floating/submerged aquatic species. We located
135 one to five sites per lake on seven lakes that supported the highest number of selected
136 species for a total of 16 sites (Figure 1). We used the following criteria for site selection:
137 high ACPF species richness, west or southwest facing shorelines to keep environmental
138 factors consistent (e.g., wave and wind exposure) and site accessibility.

139 As many ACPF are restricted to specific habitats, leading to relatively rare
140 occurrences and scarcity of suitable habitats (Wisheu and Keddy 1989), random sampling
141 methods result in an insufficient number of individuals and are therefore not appropriate
142 (Edwards et al. 2005). Alternative methods include generating sampling strata within
143 suitable habitats (Edwards et al. 2005) and sampling common species from the same plant
144 community (Elith et al. 2006). Accordingly, we selected sites rich in ACPF and a subset of
145 common species to gather enough data on ACPF communities during a growing season
146 limited by low water levels.

147

148 **Sampling design**

149 At each of our 16 sites, we located one 20 m transect perpendicular to the waterline
150 with one hundred 0.2 x 0.2 m contiguous quadrats (Figure 2). We chose contiguous fine
151 scale quadrats to minimize the probability of missing fine scale spatial patterns while
152 allowing for fine and coarse scale pattern assessment (Dale 1999). Between mid-June and
153 mid-July 2015, we established the start of transects where vegetation emerged
154 (approximately 1-2 m in the water at that time of the year) to at least 5 m beyond the forest
155 edge.

156 We also used a two-dimensional sampling approach for exploring the spatial
157 relationship of ACPF richness with structural diversity, as it offers more appropriate and
158 representative insights into ecosystems processes and structures (Hufkens et al. 2009).
159 From mid-August to early September 2015, we centred a 5 x 5 m grid on each of five
160 transects, which were those with the highest ACPF richness and widest shorelines to
161 maximize the number of quadrats with ACPF (Figure 1). Each grid was divided into 625 -
162 0.2 x 0.2 m contiguous quadrats and was positioned between the edge of the vegetation
163 near the waterline at that time of the year and the forest edge (Figure 2).

164 Within each quadrat along transects and in grids, we visually estimated the cover
165 of 19 ACPF species and structural elements using cover classes of < 5%, 6-25%, 26-50%,
166 51-75% and > 76%. Ground elements included plant (leaf and needle litter, roots, seeds)
167 and woody material (twigs, logs, snags, bark), non-vascular plants (bryophytes, lichens)
168 and other elements (algae, fungus, rock). Above ground elements included vascular plants
169 (sundews, horsetails, graminoids, ferns, evergreen and deciduous herbs, vines, deciduous
170 and coniferous woody plants) measured at different heights (every 0.2 m height up to 2 m,
171 2-3 m, 3-5 m, > 5 m).

172

173 **Data analysis**

174 We calculated different indices of structural diversity for each quadrat using the
175 Shannon index with structural elements as pseudo-species (McElhinny et al. 2005) under
176 the Vegan package (Oksanen et al. 2015) in R 3.2.2 (R Core Team 2015). Although the
177 Shannon index has some limitations, such as sensitivity to sample size and difficult
178 interpretation, it is still widely and persistently used (Magurran 2004), and is therefore

179 more comparable. We calculated an overall structural diversity index using the midpoint
180 cover value of each structural element at different heights. We then calculated the Shannon
181 index of the two main categories of structural elements, defined as substrate (i.e., ground)
182 and plant (i.e., above ground) diversity. We also calculated a shrub diversity index with the
183 cover of coniferous and deciduous woody species at every 0.2 m height up to 2 m. ACPF
184 richness was defined as the number of ACPF species in each quadrat.

185 Wavelet analysis quantifies spatial patterns at different scales and positions in one
186 (e.g., transect) or two dimensions (e.g., grid). This spatial analysis has the advantage of not
187 requiring stationarity of the data, meaning that the characteristics (e.g., mean and variance,
188 Brosnoff et al. 1999) of the spatial pattern don't have to be constant across positions
189 (Bradshaw and Spies 1992; Dale and Mah 1998; Rosenberg and Anderson 2011). Wavelet
190 analysis consists of a moving template that assesses the similarity between the template
191 and the data at each position along the transect or grid, and at several scales by increasing
192 the size of the template. The template represents the shape of a spatial structure, such as
193 transitions (Haar template) or patches (Mexican hat template). High wavelet transform
194 indicates a match between the template and the data, and consequently a non-random
195 spatial association, revealing the presence of the spatial structure defined by the template
196 (Dale and Mah 1998; Kembel and Dale 2006; James and Fleming 2010). Then, wavelet
197 variance is used to assess spatial patterns by calculating the average square of the wavelet
198 transform (i.e., similarity between the template and data) at every position for a given scale
199 (Bradshaw and Spies 1992).

200 To assess spatial patterns along the lakeshore-to-forest gradient (transects), we used
201 one-dimensional analysis. For ACPF richness and structural diversity indices (overall,

202 substrate, plant, shrub), we used position variance calculated from wavelet analysis with
203 the Haar template to detect the position of transitions, edges and gradients (Bradshaw and
204 Spies 1992). Wavelet position variance assesses spatial patterns across positions and is
205 mostly used to identify patches or transitions in species composition along transects (Dale
206 and Mah 1998). Wavelet position variance sums wavelet variance across all scales for each
207 position. Peaks/shoulders of the wavelet position variance indicate the locations of the
208 spatial structure (Kembel and Dale 2006). We used wavelet position variance with the
209 Mexican hat wavelet (Dale and Mah 1998) to assess patches of individual herbaceous and
210 shrub ACPF species cover that were present in at least 30 quadrats overall and for sites
211 where the species was present in > 5% of quadrats. We expected a non-random spatial
212 distribution of individual ACPF species in the form of patches along the lakeshore-to-forest
213 gradient due to species zonation, while spatial patterns of ACPF richness and structural
214 diversity indices, which included numerous species or structural elements, would appear
215 in the form of transitions instead of patches.

216 To assess spatial relationships between ACPF richness and structural diversity
217 indices (overall, substrate, plant, shrub) at different scales and positions along the transects,
218 we performed wavelet covariance analysis with the Haar template (Kembel and Dale
219 2006). Wavelet covariance multiplies the wavelet transforms of two variables to assess
220 spatial relationships between two variables at different scales and positions (Kembel and
221 Dale 2006). A positive wavelet covariance implies that the two variables vary in the same
222 direction, whereas a negative value indicates that the variables vary in opposite directions.
223 We focused on the most abundant and diverse ACPF functional group (i.e., herbaceous
224 species), as shrub and graminoid ACPF may not be influenced by structural diversity in

225 the same way. We consequently used overall structural and plant diversity indices that
226 excluded herbaceous species cover to eliminate any possible autocorrelation. We also
227 performed two-dimensional wavelet covariance analysis on the grid data, with the two-
228 dimensional template that is based on the Haar template (i.e., Boater; Rosenberg and
229 Anderson 2011). We assessed covariance at different scales between herbaceous ACPF
230 richness and individual ACPF species cover (in a minimum of 10% of grid's quadrats) and
231 structural diversity indices (overall, substrate, plant). We did not use shrub diversity as
232 shrubs were only present in two grids with low percent cover.

233 For one and two-dimensional analyses, we used a maximum scale of 30% (6 m)
234 and 25% ($1.2 \times 1.2 \text{ m} = 1.44 \text{ m}^2$) as restricted by the Boater template, respectively, and
235 conducted randomization tests using 999 iterations with a 95% confidence interval in
236 PaSSAGE 2.0 (Rosenberg and Anderson 2011). Maximum available scales vary according
237 to the template chosen (Rosenberg and Anderson 2011). For one-dimensional analysis, we
238 chose a maximum scale as coarse as 30% to explore a wide range of scales. Using wavelet
239 analysis with null models (e.g., randomization tests) permits the identification of
240 significant scales and locations of spatial patterns and relationships. Null models represent
241 spatial processes deprived of pattern (e.g., under stochasticity processes) and involve the
242 same analysis but with a random resampling of the data along transects (James and Fleming
243 2010). Scales and positions for which the wavelet variance or covariance value is higher
244 than the value provided by null models (i.e., above the 95% confidence interval) are
245 considered significant. We then calculated the mean of significant wavelet
246 variance/covariance across sites for each scale or position to summarize the results for all
247 transects or grids.

248 RESULTS

249 **Spatial patterns along the lakeshore-to-forest gradient**

250 Significant peaks in wavelet position variance using the Haar template indicate a
251 transition, gradient or boundary in the spatial pattern of a variable, which can be either a
252 positive (increase) or negative (decrease) change (Bradshaw and Spies 1992). First and last
253 transitions could consequently represent the zone of occurrence of that variable. For ACPF
254 richness, almost all transitions were located between 0.2 and 7.6 m from the waterline
255 (Figure 3a). First transitions (closest to the waterline, 0 m) in ACPF richness were more
256 abrupt compared to last transitions, indicated by higher wavelet position variance values.
257 The average last significant transition in ACPF richness (5.5 m, Table 2) was located before
258 the average first significant transition in plant (5.7 m), shrub (6.2 m) and structural diversity
259 (6.8 m).

260 Transitions in structural diversity indices first appeared farther from the waterline
261 and were distributed along the entire lakeshore-to-forest gradient compared to transitions
262 in ACPF richness. All transitions in structural diversity occurred between 2.4 and 19.2 m
263 (Figure 3b) with similar intensities (values of wavelet position variance), and between 0.8
264 and 20.0 m for substrate diversity, with abrupt transitions between 1 and 5 m (Figure 3c).
265 For plant and shrub diversity, all transitions were located between 1.4 and 20.0 m and
266 between 2.4 and 19.8 m, respectively (Figure 3d and e). Numerous transitions in spatial
267 patterns were found for each transect (average number of peaks, Table 2), suggesting
268 different levels ACPF richness and structural diversity indices along the lakeshore-to-forest
269 gradient. Transitions in ACPF richness were more abrupt than transitions in structural
270 diversity indices, as shown by higher wavelet position variance values.

271 Patches of individual herbaceous ACPF species, indicated by significant peaks in
272 wavelet position variance using the Mexican hat template (Dale and Mah 1998), were
273 mainly found at closer distances from the waterline (e.g., lance-leaved violet (*Viola*
274 *lanceolata*): 2.9 to 4.0 m, Figure 3f – l, Table 3). In contrast, patches of shrub species were
275 located at farther distances from the waterline (e.g., northern bayberry (*Morella*
276 *pensylvanica*): 8.4 to 13.1 m, Figure 3m and n, Table 3). It is important to note that some
277 species have small sample sizes ($n < 3$), which severely limits the ability to make broad
278 predictions regarding the position occupied by the species.

279

280 **Spatial relationships at different positions and scales**

281 Along the lakeshore-to-forest gradient, a positive association between herbaceous
282 ACPF richness and structural diversity became negative mostly after 3.2 m from the
283 waterline (Figure 4a). A negative association with substrate and plant diversity mainly
284 arose after 4.0 m and 2.8 m along the transect, respectively (Figure 4b and c). The
285 association between herbaceous ACPF richness and shrub diversity was almost always
286 negative, except between 1.6 and 2.4 m, with a low positive association compared to the
287 other structural diversity indices (Figure 4d).

288 Along the lakeshore-to-forest gradient, herbaceous ACPF richness was positively
289 associated with structural diversity at finer scales (< 2.8 m) and became negatively
290 associated at coarser scales (> 2.8 m up to 6.0 m) (Figure 5a). Similarly, positive
291 associations with herbaceous ACPF richness became negative at a scale of 1.6 m for plant
292 diversity and 1.2 m for substrate and shrub diversity. The highest positive associations
293 occurred with structural, plant, substrate then shrub diversity at a dominant scale of 0.4 m.

294 In the grids, the association between herbaceous ACPF richness and structural or substrate
295 diversity was positive across all scales (Figure 5b). Positive association with plant diversity
296 became negative at a scale of 1.44 m², but was very low and for one site only. The highest
297 positive associations occurred with structural, substrate then plant diversity at a dominant
298 scale of 0.36 m².

299 Individual species associations will only be discussed for species that were present
300 in more than two grids ($n > 2$) for limited results inference. Golden pert (*Gratiola lutea*)
301 and yellow-eyed grass (*Xyris difformis*) showed positive associations with structural
302 diversity across all scales; a negative association occurred at a 0.64 m² scale for redroot
303 (*Lachnanthes caroliniana*) and lance-leaved violet, and at 1.44 m² for slender fragrant
304 goldenrod (*Euthamia caroliniana*) (Figure 6a). Redroot, lance-leaved violet and yellow-
305 eyed grass displayed positive associations with substrate diversity at all scales, whereas a
306 negative association occurred for golden pert at 1.44 m² and between 0.64 and 1 m² for
307 slender fragrant goldenrod (Figure 6b). For associations with plant diversity, golden pert
308 and slender fragrant goldenrod showed positive covariance at all scales, and there was
309 negative covariance at a scale of 0.64 m² for yellow-eyed grass and 1.44 m² for redroot and
310 lance-leaved violet (Figure 6c).

311

312 DISCUSSION

313 **Spatial patterns along the lakeshore-to-forest gradient**

314 The zone of greater ACPF richness (1.0 to 5.5 m) appeared at distances closer to
315 the waterline than the forest, because of their close association with hydrological
316 disturbances (e.g., water level fluctuations, flooding, ice scouring, wave action) that reduce

317 competition on lakeshores (Keddy 1985; Wilson and Keddy 1986; Wisheu and Keddy
318 1989). However, the highest ACPF richness was found at 4-5 m from the waterline. Species
319 richness has been shown to be highest at a moderate level of disturbance (Wilson and
320 Keddy 1986; Schneider 1994; Hill et al. 1998). Flooded conditions and wave exposure may
321 exceed the hydrological tolerance of some species and lead to insufficient nutrient content
322 (Sorrie 1994; Hill et al. 1998), decreasing plant diversity and seed density at lower
323 elevations (Schneider 1994).

324 The edge of the zone of greater ACPF richness (5.5 m) coincided with an increase
325 in structural, plant and shrub diversity, similar to what Schneider (1994) found at the
326 boundary between rare lakeshore plants and forest communities. The occurrence of woody
327 species usually delimits the upper boundary of lakeshore plant communities (Schneider
328 1994), as most shrubs are sensitive to flooding (Keddy and Reznicek 1982; Keddy 1985;
329 Wisheu and Keddy 1989). Even ACPF shrub species occurred at a farther distance from
330 the waterline (> 5 m) and were distributed into the forest, in contrast to ACPF herbaceous
331 species which showed different distributions mostly within 5 m of the waterline.

332 The zone with higher levels of structural diversity along the lakeshore-to-forest
333 gradient (6.8 to 13.2 m) could indicate the presence of the forest edge, as plant communities
334 at natural edges tend to be more diverse and dense (Naiman et al. 1988; Fraver 1994; Ploff
335 et al. 1997). Lakeshore edges are expected to harbor high levels of structural diversity as
336 wave and wind action causes seedling uproot, stem and root breakage, and woody species
337 mortality (Keddy 1982, 1985; Komonen 2009). Canopy gaps from fallen trees at the edge
338 enhance regeneration and allow a greater number of species to coexist, and the resulting

339 woody debris provides microsites for seed establishment and germination (Fetherston et al.
340 1995; Naiman and Decamps 1997; Pabst and Spies 1998; Komonen 2009).

341 The first increase in substrate diversity was located closer to the waterline (3.6 m)
342 compared to other structural diversity indices. Day et al. (1988) used litter removal on
343 lakeshores to quantify the level of disturbance from winter and spring erosion, as wave
344 action washes fine sediments, nutrients, organic matter, seeds, seedlings and plant parts
345 (Keddy 1982, 1985; Day et al. 1988). Therefore, ground structural elements could indicate
346 the limit of current flooding, whereas the occurrence of above ground structural elements,
347 such as woody species, would be determined by longer-term water level fluctuations
348 (Schneider 1994).

349

350 **Spatial relationships at different positions and scales**

351 In theory, two elements have a negative spatial relationship at very fine scales, as
352 they cannot share the same space. However, we found a positive association between
353 herbaceous ACPF richness and structural diversity indices at fine scales and closer to the
354 waterline (< 3.2 m). This indicates that high levels of ACPF richness are associated with
355 high levels of structural diversity. Although lakeshores support relatively low levels of
356 structural diversity compared to the forest edge, ACPF species can be found associated
357 with structural elements that provide more microhabitats within this zone.

358 The hydrological gradient on lakeshores is a complex combination of stress and
359 disturbance from saturated conditions with low fertility and the destruction of biomass,
360 respectively (Wilson and Keddy 1986). Habitat would consequently be suitable only for
361 species that tolerate these conditions (Shipley et al. 1991), such as many lakeshore ACPF

362 species. With decreased flooding and nutrient poor conditions (Pabst and Spies 1998),
363 lakeshore species will be replaced by more dominant competitors such as shrubs, which
364 are more common towards the forest (Shipley et al. 1991). The high competitive ability of
365 woody species explains the negative association between shrub diversity and herbaceous
366 ACPF richness across almost all scales and positions.

367 As intermediate levels of hydrological disturbances lead to increased density of
368 plant communities at lakeshore forest edges, structural diversity increases. Gradient of
369 herbaceous ACPF richness and structural diversity consequently varied in opposite
370 directions (i.e., high herbaceous ACPF richness associated with low levels of structural
371 diversity), resulting in a negative covariance at coarser scales and away from the waterline
372 (> 3.2 m).

373 In comparison with the transects, grids within five meters of the waterline did not
374 usually support high levels of structural diversity. Consequently, herbaceous ACPF
375 richness showed a strong association with structural diversity across all scales, but was
376 more related to substrate diversity than plant diversity. Hydrological disturbances on
377 lakeshores create microsites with heterogeneous substrate and moisture conditions (Pabst
378 and Spies 1998), and woody debris deposition (Komonen 2009). Woody debris offers
379 favorable conditions for plant colonization by influencing seedbank germination and
380 seedling survival (e.g., support and protection; Naiman and Decamp 1997, capture of
381 nutrients; Fetherston et al. 1995), critical processes in lakeshore plant communities (Moore
382 and Keddy 1988). Hydrological disturbances also lead to diverse plant communities, from
383 submerged and emerged aquatic plants to sedges (Naiman et al. 1988) and carnivorous
384 species (e.g., sundews; Wilson and Keddy 1986; Wisheu and Keddy 1989). However, too

385 high diversity of plants on lakeshores would lead to increased competition for light and
386 nutrients, resulting in a lower positive association with herbaceous ACPF richness and even
387 a negative association at coarser scales.

388 Redroot (*Lachnanthes caroliniana*), lance-leaved violet (*Viola lanceolata*) and
389 slender fragrant goldenrod (*Euthamia caroliniana*) were all negatively correlated with
390 shrub cover (Dazé Querry et al. 2017), which could explain why only those species had a
391 negative association with structural diversity at coarse scales, as compared to golden pert
392 (*Gratiola lutea*) and yellow-eyed grass (*Xyris difformis*). Opposing spatial relationships
393 with ACPF species were found between plant and substrate diversity, suggesting that
394 individual species would have habitat preferences for either ground (redroot, lance-leaved
395 violet and yellow-eyed grass) or above ground (golden pert, slender fragrant goldenrod)
396 structural elements at coarse scales. Species that were positively associated with substrate
397 diversity across all scales were the same species that were positively correlated with
398 different substrate types (e.g., gravel, cobble, organic; Dazé Querry et al. 2017).

399 Although the specific inferences of our results might be limited to rich ACPF sites
400 and our subset of species, ACPF species form a whole plant community by sharing similar
401 habitat types and specific ecological requirements (Wisheu et al. 1994). Some ACPF
402 species can also show irregular occurrences due to their high reliability on variable
403 hydrological disturbances (Rawinski and Price 1994), which could interfere with the
404 distinction between suitable occupied habitat from suitable but unoccupied habitat. ACPF
405 species composition varies greatly between growing seasons (Sorrie 1994; Hill et al. 1998),
406 where some species may not even be present every year (Rawinsky and Price 1994). Such
407 false absences could bias results applications (Rebelo and Jones 2010). Consequently,

408 subjective sampling methods are still valuable, especially for rare species, as they can
409 provide relative indices of habitat suitability (Elith et al. 2006), characterize environmental
410 conditions associated with species presence (Pearce and Boyle 2006) and allow the
411 ecological understanding of associated cryptic, ephemeral or poorly understood species
412 (Rawinski and Price 1994).

413

414 CONCLUSION

415 We conclude that herbaceous Atlantic Coastal Plain Flora (ACPF) richness was
416 associated with overall low levels of structural diversity along the lakeshore-to-forest
417 gradient, but high structural diversity within lakeshore zones. Structural diversity could be
418 used as a tool to facilitate the identification and management of suitable ACPF habitats
419 along lakeshores, which are mostly privately owned in southwestern Nova Scotia. Habitat
420 conservation should prioritize the protection of shorelines that support small plants and
421 ground materials, and disregard bare or densely vegetated shorelines. For the restoration
422 and maintenance of known ACPF habitats, increasing the level of structural diversity on
423 bare shorelines or reducing the level of structure on densely vegetated shorelines could
424 help ACPF to persist by colonizing new shorelines. Furthermore, the level of structural
425 diversity could potentially serve as a surrogate for the intensity of hydrological
426 disturbances and the level of competition, which determines the suitability of habitat for
427 many stress-tolerant species found on lakeshores. Disturbed and poor nutrient shorelines
428 would support low biomass compared to densely vegetated undisturbed nutrient rich
429 shorelines.

430 By conducting spatial pattern analysis, important breaks in lakeshore species
431 distribution can be located and habitat associations can be defined at different scales and
432 positions along the lakeshore-to-forest gradient. Vegetation structure is an important
433 component of habitat variability (Chen et al. 1996), underscoring the importance of
434 improved knowledge on structural diversity and its role in the development of more
435 appropriate conservation measures (Pabst and Spies 1998). Our study provides insights on
436 how to characterize structural diversity and relate it to plant communities along an
437 environmental gradient, with the aim of using structural diversity as an indicator of suitable
438 habitat, which can be applied to endangered or poorly understood species.

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618 Species in Nova Scotia: Distribution, habitat and conservation priorities. *Biol Conserv*
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620

621 Table 1. Description of the Atlantic Coastal Plain Flora species examined in this study,
 622 including the functional group (shrub, herb, graminoid), the scientific and common name,
 623 and the Nova Scotia general conservation status (and one Species At Risk Act (SARA)
 624 status) (Crowley and Beals 2011)
 625

Functional group	Scientific name	Common name	NS general status	
Shrub	<i>Cephalanthus occidentalis</i>	(Common) Buttonbush	Sensitive	
	<i>Ilex glabra</i>	Inkberry	Secure	
	<i>Morella pensylvanica</i>	Northern bayberry	Secure	
	<i>Rosa palustris</i>	Swamp rose	Secure	
	<i>Smilax rotundifolia</i>	Round-leaved greenbrier	Secure	
	<i>Toxicodendron radicans</i> var. <i>radicans</i>	(Eastern) Poison ivy	Secure	
	Herb	<i>Bartonia paniculata</i> var. <i>iodandra</i>	Branched bartonia (Screwstem)	Secure
<i>Euthamia caroliniana</i>		Slender (Carolina) fragrant goldenrod	Secure	
<i>Gratiola lutea</i>		Golden pert	Secure	
<i>Hypericum virginicum</i>		Virginia (Marsh) St. John's-Wort	Secure	
<i>Lachnanthes caroliniana</i>		Redroot	At risk (SARA: Special concern)	
<i>Lycopodiella appressa</i>		Southern bog clubmoss	Secure	
<i>Rhexia virginica</i>		Virginia meadow-beauty	Secure	
<i>Sisyrinchium atlanticum</i> and <i>angustifolium</i>		Eastern and pointed blue-eyed grass	Secure	
<i>Viola lanceolata</i>		Lance-leaved violet	Secure	
<i>Xyris difformis</i>		Lakeshore yellow-eyed grass	Sensitive	
Fern		<i>Woodwardia virginica</i>	Virginia chain fern	Secure
Graminoid		<i>Cyperus dentatus</i>	Toothed flat-sedge	Secure
		<i>Panicum virgatum</i>	Old switch panic grass	Secure

626

627 Table 2. Average (with standard deviation) distance of first and last significant peaks and
 628 number of significant peaks of ACPF richness (number of species), structural diversity (all
 629 structural elements), substrate diversity (ground elements), plant diversity (above ground
 630 elements) and shrub diversity (shrub cover at different heights) along the transects (n = 16)
 631 using wavelet position variance with the Haar template
 632

Indices	Average distance of first peak (m)	Average distance of last peak (m)	Average number of peaks
ACPF richness	1.0 ± 0.6	5.5 ± 4.3	3.3 ± 1.2
Structural diversity	6.8 ± 3.5	13.2 ± 4.3	2.5 ± 1.2
Substrate diversity	3.6 ± 2.3	14.1 ± 5.1	3.8 ± 1.1
Plant diversity	5.7 ± 2.6	14.3 ± 4.7	3.1 ± 1.2
Shrub diversity	6.2 ± 2.9	12.6 ± 5.8	3.0 ± 1.6

633

634 Table 3. Average (with standard deviation) distance and standard deviation of the start and
 635 end of significant peaks and number of significant peaks for individual ACPF species along
 636 the transects (for sites with a frequency of > 5% quadrats (n = # transects)) using wavelet
 637 position variance with the Mexican hat template
 638

Functional group	Species	Average distance of peak start	Average distance of peak end	Average number of peaks
Herb	Virginia meadow-beauty (n = 3*)	0.6	0.8	1.0
	Golden pert (n = 7)	1.1 ± 0.8	1.2 ± 0.7	1.3 ± 0.5
	Lakeshore yellow-eyed grass (n = 7)	1.8 ± 0.9	2.9 ± 1.4	1.7 ± 0.8
	Redroot (n = 5)	1.4 ± 0.9	1.9 ± 0.8	1.3 ± 0.6
	Lance-leaved violet (n = 10)	2.9 ± 1.4	4.0 ± 1.2	1.7 ± 0.8
	Slender fragrant goldenrod (n = 6)	1.9 ± 0.9	3.0 ± 1.1	1.4 ± 0.6
	Southern bog clubmoss (n = 2*)	2.0	2.4	1.0
Shrub	Northern bayberry (n = 5)	8.4 ± 5.9	13.1 ± 4.7	1.8 ± 0.8
	Inkberry (n = 2)	6.2 ± 2.8	9.3 ± 5.5	2.0 ± 0

639
 640 * Only one site had significant wavelet variance values (i.e., above the confidence interval
 641 determined by randomization tests).

642 FIGURE CAPTIONS

643

644 **Fig.1** Location of sites (n = 16) on seven lakes: Molega (Mo, n = 5), Kejimkujik (Ke, n =
645 1), Ponhook (Po, n = 4), Seven mile (Se, n = 1), First Christopher (Fc, = 1), Cameron (Ca,
646 n = 2) and Hog (Ho, n = 2). Sites for grids (n = 5) are Ca2, Ke1, Se1, Ho2 and Po3. The
647 inset map shows the range of high priority Atlantic Coastal Plain Flora species (darker grey
648 shading) in southwestern Nova Scotia (Environment Canada and Parks Canada Agency
649 2015, based on data from Atlantic Canada Conservation Data Centre) (maps are powered
650 by Esri, HERE, DeLorme, NGA, USGS, NRCan)

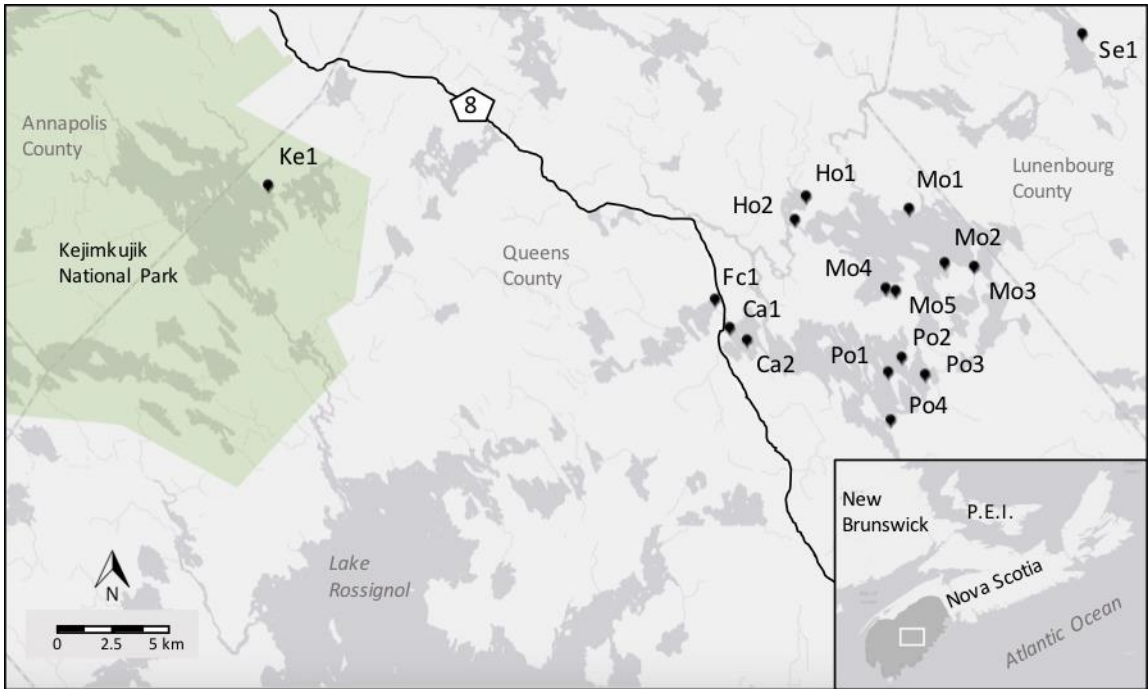
651 **Fig.2** Diagram showing the locations of a transect (a) and a grid (b) with respect to the
652 waterline and the forest edge (trees) with contiguous quadrats of 0.2 x 0.2 m

653 **Fig.3** Average significant wavelet position variance of herbaceous ACPF richness (a,
654 number of species), structural diversity (b, all structural elements), substrate diversity (c,
655 ground elements), plant diversity (d, above ground elements), shrub diversity (e, shrub
656 cover at different heights) and individual species across sites along the transects (n = 16
657 unless otherwise indicated). The Haar template was used for richness and structural
658 diversity indices, and the Mexican hat template was used for individual species (f-n, for
659 transects with a frequency of > 5% quadrats)

660 **Fig.4** Average significant wavelet position covariance between herbaceous ACPF richness
661 and structural diversity (a, all structural elements), substrate diversity (b, ground elements),
662 plant diversity (c, above ground elements) and shrub diversity (d, shrub cover at different
663 heights) across sites along the transects (n = 16) with the Haar template

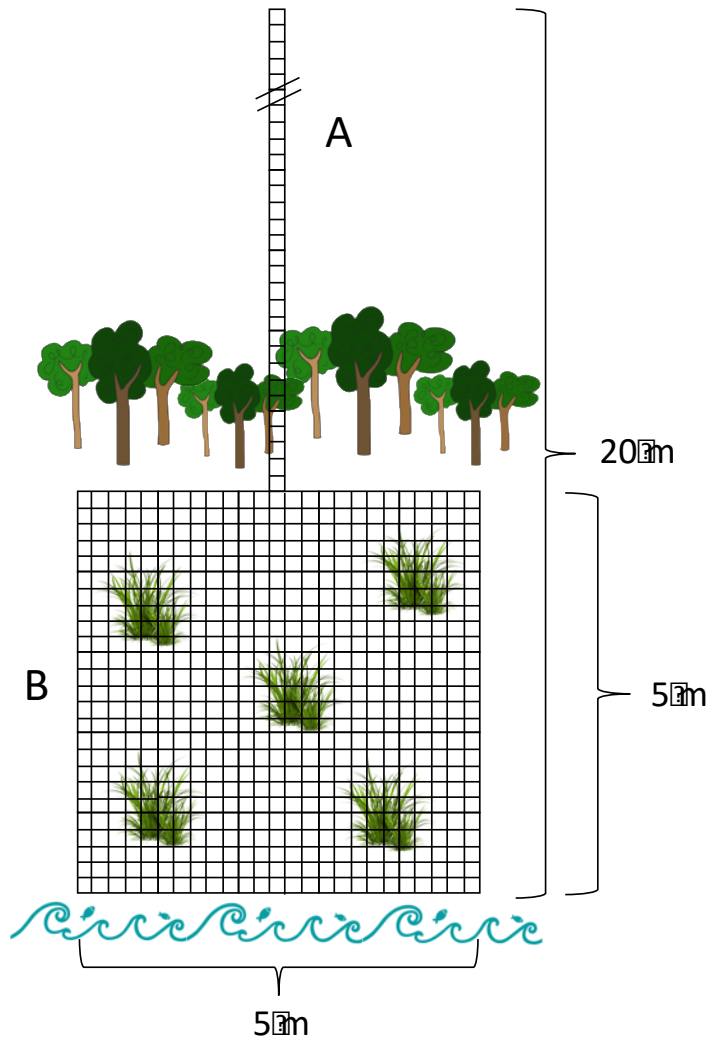
664 **Fig.5** Average significant wavelet covariance between herbaceous ACPF richness and
665 structural diversity (all structural elements), substrate diversity (ground elements), plant
666 diversity (above ground elements) and shrub diversity (shrub cover at different heights)
667 across sites for each scale along the transects (a) and within the grids (b). The Haar
668 template with a maximum scale of 30% (6 m) was used for the transects, and the Boater
669 template with a maximum scale of 25% (1.44 m²) for the grids
670

671 **Fig.6** Average significant wavelet covariance between individual ACPF species (present
672 in > 10% of quadrats and if > 2 grids) and structural diversity (a, all structural elements),
673 substrate diversity (b, ground elements), plant diversity (c, above ground elements) with
674 the Boater template and a maximum scale of 25% (1.44 m²)



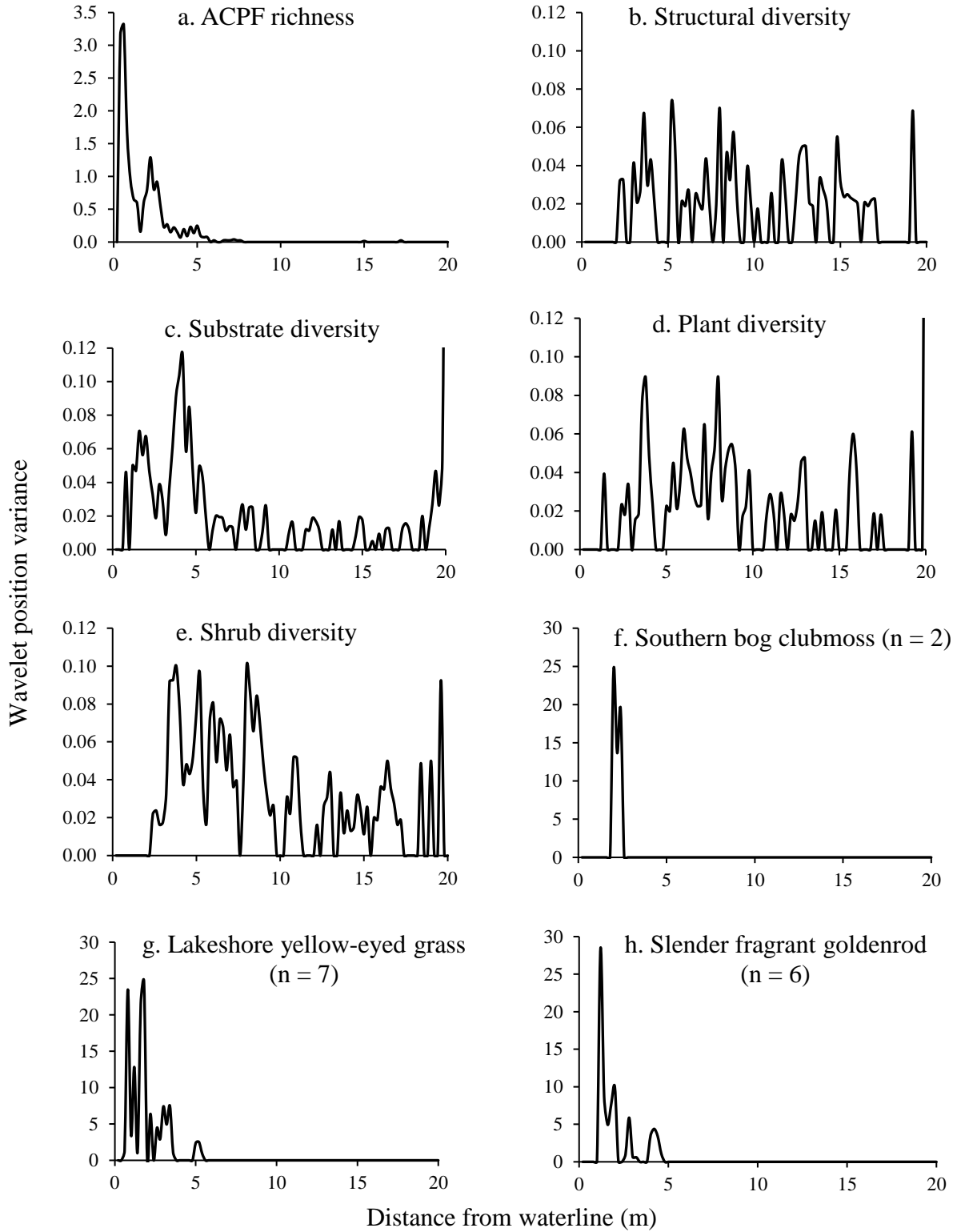
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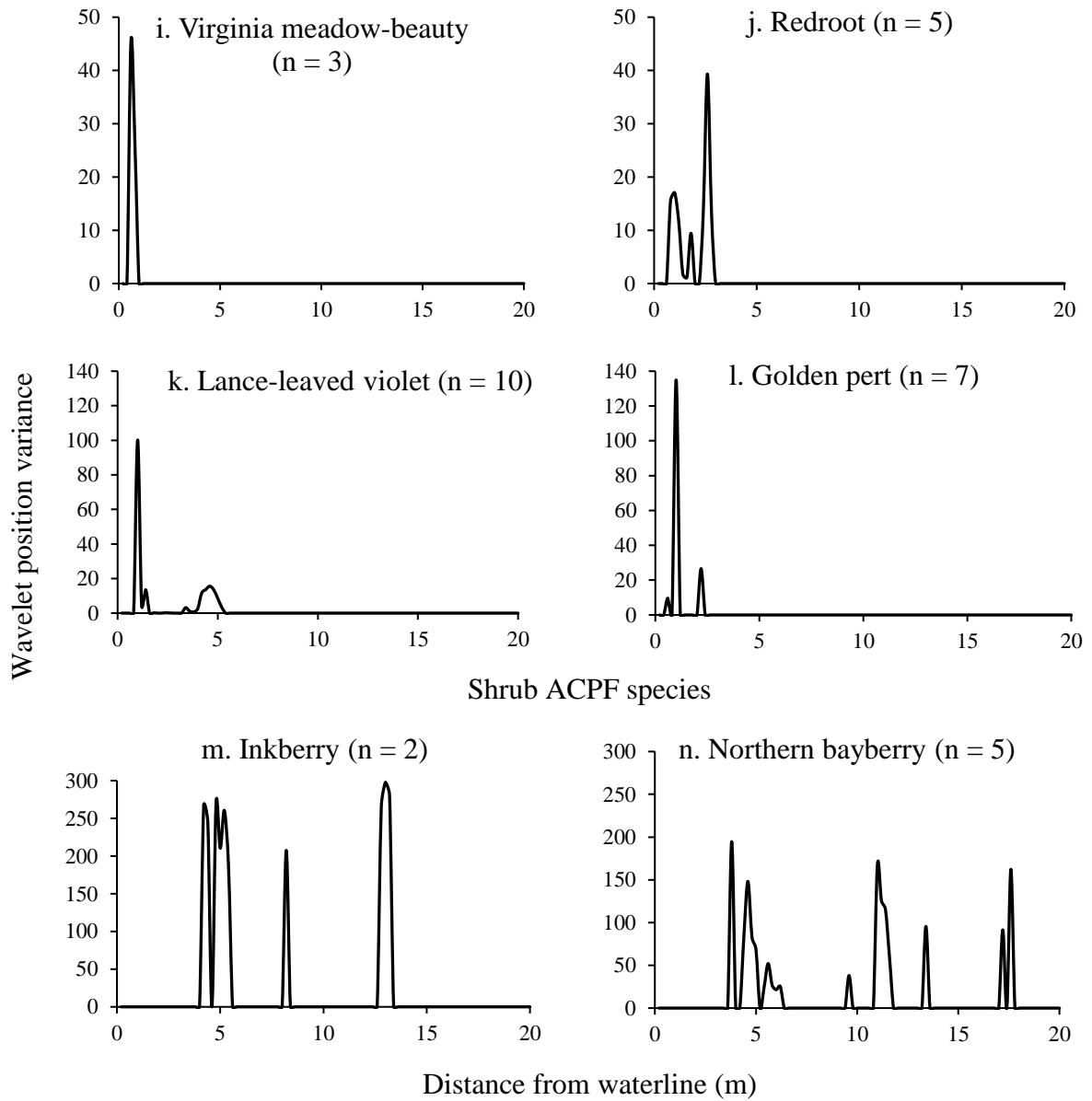
676 Fig.1



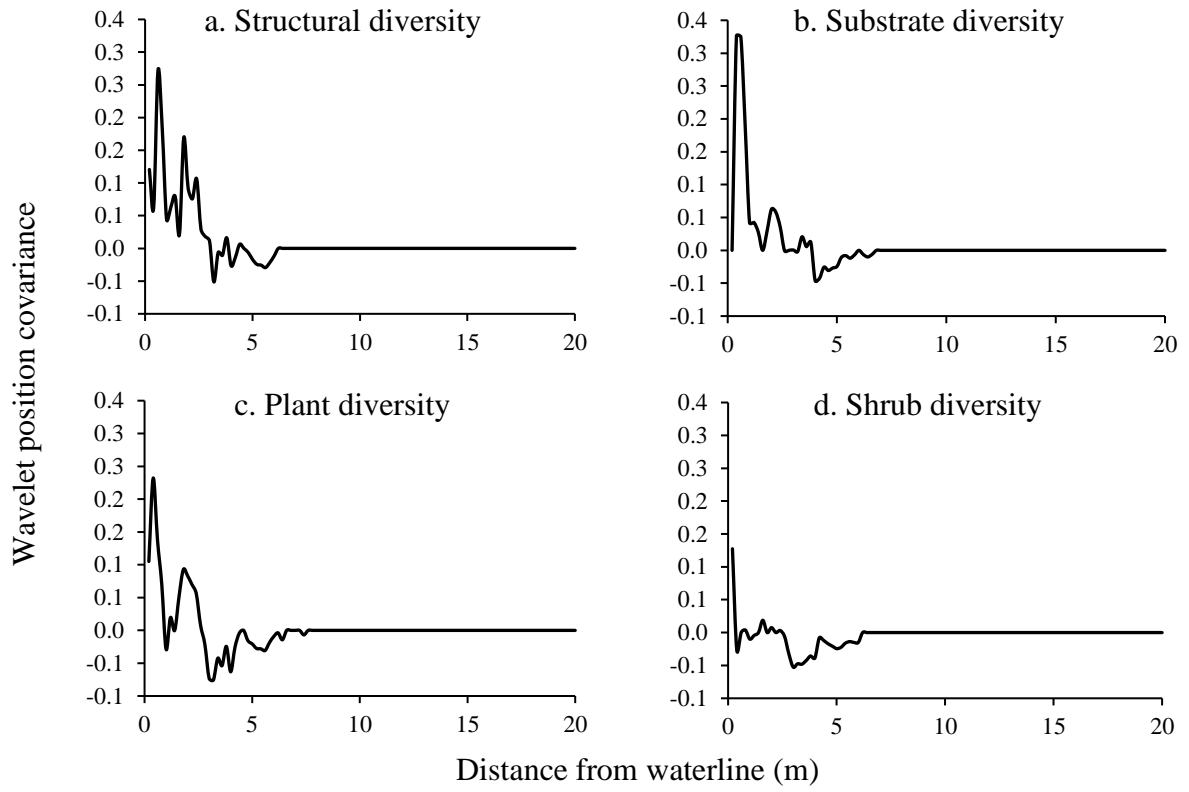
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678 Fig.2

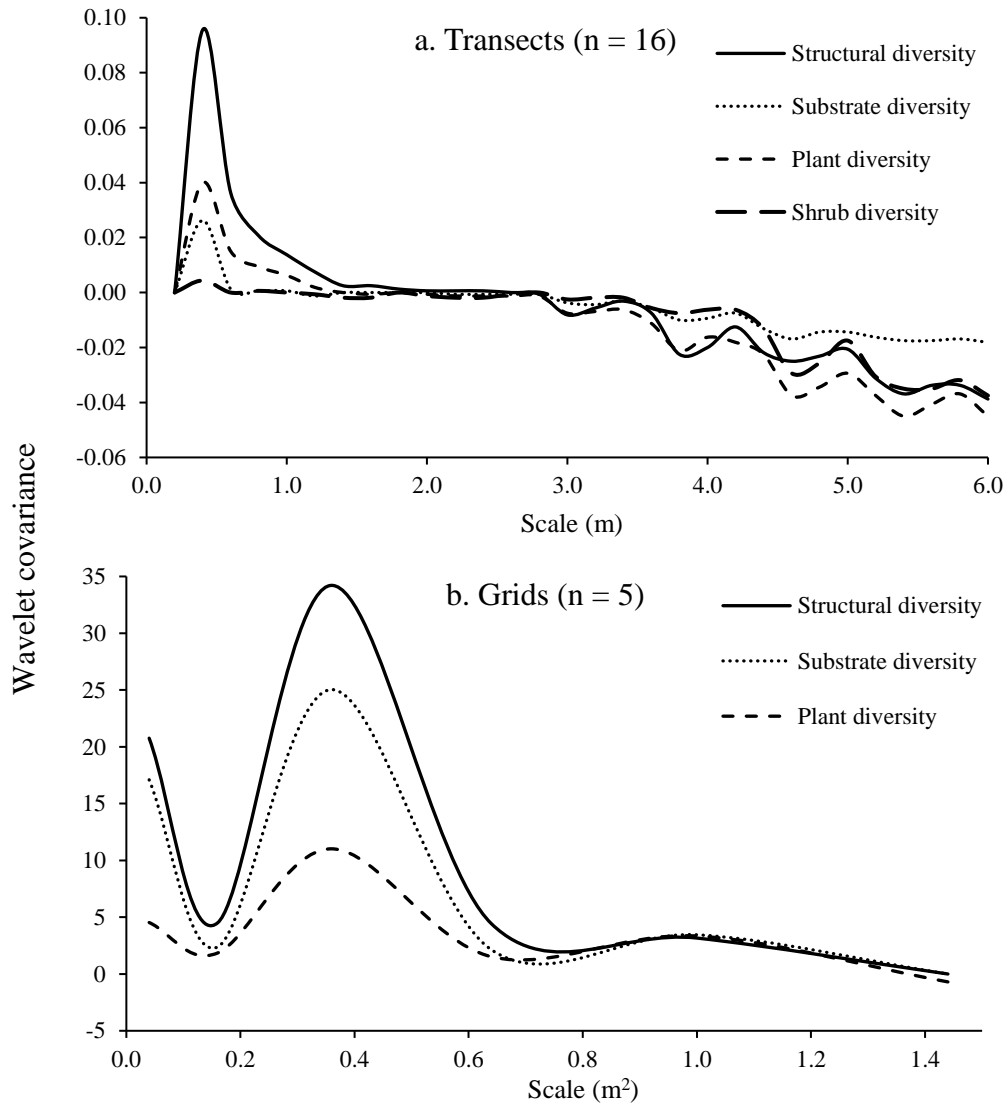




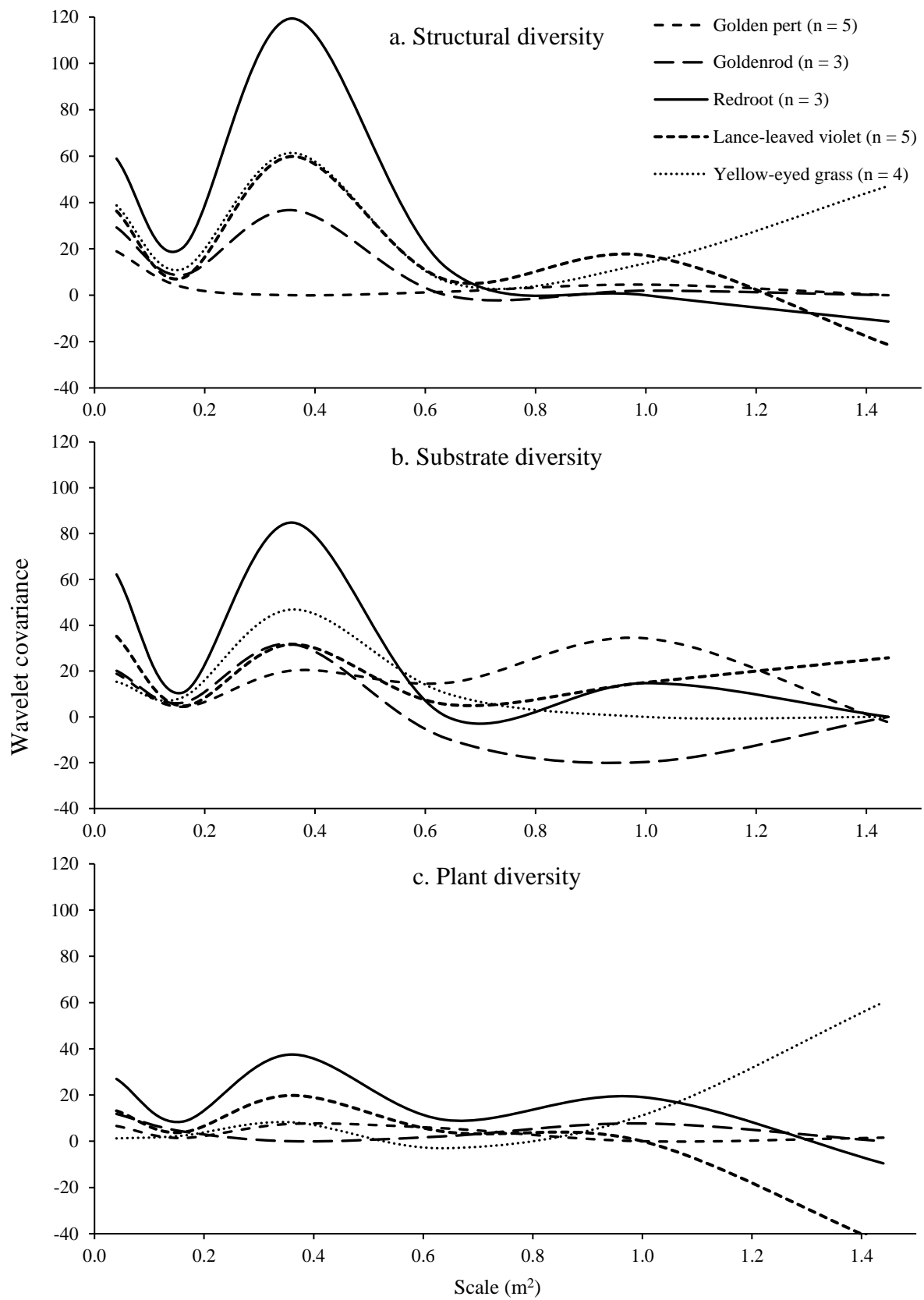
679 Fig.3



680 Fig.4



681 Fig.5



682 Fig.6