

A community analysis approach to parasite transmission in multi-host systems: Assemblages of small mammal prey and Echinococcus multilocularis in an urban area in North America

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21 **ABSTRACT**

22 **Background:** *Echinococcus multilocularis* (*Em*) is a parasite with a complex life cycle whose 23 transmission involves a predator-prey interaction. Accidental ingestion of *Em* eggs by humans 24 may cause alveolar echinococcosis, a potentially fatal disease. Although previous research 25 suggested that the composition of the assemblage of prey species may play a key role in the 26 transmission, the relation between *Em* presence and the prey assemblages has never been 27 analyzed. Herein, we propose a community analysis approach, based on assemblage similarity 28 statistics, clustering, non-metric dimensional scaling and GLM modelling to analyze the 29 relationships between small mammal assemblages, environmental variables, and the prevalence 30 of *Em* in intermediate and definitive hosts in an urban area.

31 **Results:** In our study areas within the City of Calgary, Alberta (Canada), we identified three 32 main small mammal assemblages associated with different prevalence of *Em*, characterized by a 33 different proportion of species known to be good intermediate hosts for *Em*. As expected, 34 assemblages with higher proportion of species susceptible to *Em* were observed with higher 35 prevalence of parasite, whereas the total abundance *per se* of small mammals was not a predictor 36 of transmission likely due to dilution effect. Furthermore, these assemblages were also predicted 37 by simple environmental proxies such as land cover and terrain.

38 **Conclusions:** Our results indicated that the use of a community analysis approach allows for 39 robust characterization of these complex and multivariate relationships, and may offer a 40 promising tool for further understanding of parasite epidemiology in complex multi-host 41 systems. In addition, this analysis indicates that it is possible to predict potential foci of disease 42 risk within urban areas using environmental data commonly available to city planners and land 43 managers.

- *Keywords*: Epidemiology, *Echinococcus multilocularis*, community ecology, community
- 46 analysis, urban parks, trophically transmitted parasite with complex life cycle, small mammals

48 **1. BACKGROUND**

49 *Echinococcus multilocularis* (*Em*) is a parasitic tapeworm that can cause human alveolar 50 echinococcosis (AE), currently considered among the most serious zoonotic diseases outside of 51 the tropics (Massolo et al., 2014). The parasite is endemic across the northern hemisphere, and 52 its distribution is expanding (Davidson et al., 2012; Massolo et al., 2014). The disease has high 53 fatality rate (i.e. > 90%) if not treated, and often requires life-long treatments (Craig, 2003). In 54 2010, it was estimated that globally there were 18,235 human cases of AE annually (Torgerson 55 et al., 2010) with an increasing trend. Only few cases were reported in North America outside of 56 Alaska, but there are indications that the risk of AE may be increasing (Massolo et al., 2014). 57 *Echinococcus multilocularis* is a trophically transmitted parasite with a complex life cycle that 58 involves two different hosts and a free-living stage. The parasite typically infects canid predators 59 such as foxes *Vulpes* spp. and coyotes *Canis latrans* (but also domestic dogs) as definitive hosts 60 (DH). The adult parasite, in the DH intestine, produces embryonated eggs which are released in 61 the environment with feces. More than 40 small mammal species (usually rodents) act as 62 intermediate hosts (IHs) by accidentally ingesting these eggs (Liccioli et al., 2013; Vuitton et al., 63 2003) and developing the final infectious larval stage in the target organ (often the liver). The 64 life cycle is completed when infectious IHs are predated by DHs. Although climate conditions 65 likely determine the limit of the parasite distribution at the global scale, at more local scales the 66 presence and relative abundance of the IH species plays a key role in the parasite distribution and 67 transmission intensity (Giraudoux et al., 2004; Liccioli et al., 2013; Romig et al., 2017). In the 68 southern edge of its European distribution, for example, *Em* spread was deemed to be limited by 69 the presence of single species of small mammal IH (Guerra et al., 2014). Landscape and 70 environmental characteristics that define the distribution of small mammals (e.g., the proportion

71 of the landscape composed by optimal habitat for the susceptible small mammal species) can be 72 important predictors of where the intensity of the parasite transmission is high (Giraudoux et al., 73 2004; Raoul et al., 2015).

74 However, the influence of susceptible small mammal species on the transmission of *Em* is made 75 complex by interactions among small mammal species and between predator and prey. Higher 76 population density of DH is expected to increase the transmission rate (Raoul et al., 2015). Even 77 in an area inhabited by susceptible small mammal species, parasite transmission is unlikely if 78 their relative abundance within the prey ensemble is low. The presence of other species that are 79 not susceptible to the parasite but preferred as prey by DHs will reduce the probability of *Em* 80 transmission (Baudrot et al., 2016; Guerra et al., 2014). Our previous research on the distribution 81 of small mammals and *Em* in the City of Calgary suggested that the proportion of susceptible 82 species within the small mammal community may be a key factor in determining the prevalence 83 of the parasite (Liccioli et al., 2014).

84 Despite these recent findings, so far researchers have only analyzed the effects of single 85 intermediate species variations on transmission of *Em*, and speculated on or modelled the effects 86 of the small mammal assemblages as a whole. Following up on our previous study (Liccioli et 87 al., 2014), we wanted to explore in more detail the association between small mammal 88 assemblages and *Em* transmission using an analytical approach typical of community ecology. In 89 addition, we analyzed environmental features associated with the prevalence of the parasite, 90 which may allow us to predict areas of high risks.

91 In particular, we aimed to

92 A. characterize the composition and structure of the various types of small mammal prey 93 assemblages in the study area;

- 94 B. explore the association between the various types of prey assemblages and *Em* infection 95 in both definitive and intermediate hosts;
- 96 C. identify the environmental proxies that are associated with the various assemblages, and 97 the environment where *Em* transmission is more likely to occur, using geographical data 98 commonly available for city planners.
- 99

100 **2. METHODS**

101 *2.1 Study area and data description*

102 The samples were collected in the City of Calgary (AB, Canada; $51^{\circ}5'N$, $114^{\circ}5'W$; Figure 1), 103 located in the southeastern region of Alberta in the foothills of the Canadian Rocky Mountains, 104 from June 2012 to July 2013. The city encompasses an area of 848 km^2 and has a population of 105 1,235,171 (The City of Calgary, 2016). The city ranges in elevation from 965 to 1304 meters 106 a.s.l., and encompasses many streams and water bodies with riparian habitats that are often 107 designated as parks and natural areas. The climate is relatively dry (annual precipitation of 412.6 108 mm) and cold, with an average annual high temperature of 10.5 $^{\circ}$ C and low temperature of -2.4 ^oC (Statistics Canada, 2017). Common habitats in parks and natural areas are grasslands in dry 110 areas, aspen forests in moderately well-drained areas, and willow shrublands in imperfectly 111 drained areas (The City of Calgary, 2014). 112 Common mammals in the city area are snowshoe hares (*Lepus americanus*), white-tailed jack 113 rabbit (*Lepus townsendii*), Richardson's ground squirrels (*Urocitellus richardsonii*), gray 114 squirrels (*Sciurus carolinensis*), southern red-backed and meadow vole (*Myodes gapperi*;

- 115 *Microtus pennsylvanicus*), deer mouse (*Peromyscus maniculatus*), muskrat (*Ondatra zibethicus*),
- 116 coyote, beaver (*Castor canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer

117 (*Odocoileus virginianus*), and less commonly red fox (*Vulpes vulpes*; The City of Calgary,

118 2014). Of these, only southern red-backed vole, meadow vole, deer mouse, beaver and muskrat

119 are currently described as IHs for *Em* (Liccioli et al., 2013), but beaver and muskrats were rarely

120 reported in the diet of urban coyotes in the City of Calgary (Liccioli et al., 2015).

121 We used data on small mammal relative abundance per site collected for the study of Liccioli et 122 al. (2014) between June 2012 and July 2013 in sites within Calgary urban parks and natural 123 areas. Specifically, these sites were located in Nose Hill Park (site NHP1 ~ NHP3), Bowmont 124 (BM1 ~ BM3), Weaselhead (WSH1 ~ WSH3), Southland lowland (SL1 & SL2), and Fish Creek 125 Provincial Park (FCPP1 ~ FCPP3; Figure 1). Samples collected in June and July 2013 were not 126 used in the study by Liccioli et al. (2014) because of their interest in seasonal pattern, but were 127 included in this study in order to increase the sample size, whereas the first trapping session in 128 June 2012 included in Liccioli et al. (2014) was removed from this study because it was 129 conducted with a different protocol (i.e. trappings were conducted for 4 nights in row instead of 130 3 due to weather condition causing most traps to misfire on the first night). The small mammals 131 sampled within these sessions totaled 1223 small mammals of 9 different species (Liccioli et al., 132 2014).

133 We used DH prevalence estimated from 385 coyote feces collected by Liccioli et al. (2014) in 134 the same five areas between May 2012 and July 2013 (Table 1: Liccioli et al., 2014). For more 135 details on the small mammal and fecal collection methods and data analysis methods, see 136 Liccioli et al. (2014).

137

138 *2.2 Assemblage analysis*

139 The trap catch-rate of small mammals caught at each site were standardized by aggregating all 140 captures for each site and then divided by number of trap-nights, not counting misfires and traps 141 that caught other species (e.g. a trap that caught a deer mouse could not have caught a meadow 142 vole that same night) to represent the relative abundances of each species (Table 1). Differences 143 between species composition at each trap site were measured using the Bray-Curtis statistic 144 (Bray and Curtis, 1957), treating each trap site as statistical unit and the relative abundance for 145 each species as variable. The relative abundances were log-transformed $(log(x+1))$ before 146 calculation of the similarity matrix (Beals, 1984). 147 The Bray-Curtis similarity was visualized through hierarchical agglomerative clustering 148 dendrogram, using group average algorithm to calculate the distance between clusters (Field et 149 al., 1982). To test the robustness of the cluster structures, clustering with single-linkage and 150 complete-linkage algorithms were also performed. In addition, hierarchical agglomerative

151 clustering was performed on data transformed to percentage of each species before calculation of

152 Bray-Curtis similarity, again using group average, single-linkage, and complete-linkage.

153 Resulting cluster structures were compared for consistency. Significance of the clusters were

154 tested using similarity profile (SIMPROF) tests (Clarke et al., 2008). The association between

155 clusters and presence of *Em* infected small mammals were statistically tested using Fisher's

156 exact test (Sokal and Rohlf, 1995).

157 To identify the general characteristics of each cluster type, we performed Canonical Correlation

158 Analysis on the principal coordinates (CAP) procedure (Anderson and Willis, 2003). This

159 procedure displays cloud of multivariate points with reference to a hypothesis set a priori by

160 finding axes that maximize the difference among groups. The procedure also tests the

161 significance in the difference among groups using permutation tests and "trace" statistics,

162 equivalent to Pillai's trace statistics in traditional multivariate analysis of variance test. Pearson 163 correlation coefficients between the abundance and proportion of each species to the CAP axes 164 were calculated and their vectors overlaid on the plot.

165 A pooled *Em* prevalence was calculated for each small mammal assemblage for each site as the 166 number of infected animals divided by the total number of small mammals caught. This pooled 167 prevalence was a simple estimate of the likelihood for a coyote to become infected by preying on 168 a specific assemblage.

169 We associated the DH prevalence estimates for the five areas to the trap sites in each area, which 170 is a reasonable assumption considering the distance between each area and territoriality of 171 coyotes. The possible exception was the FCPP3 site which was close to SL. However, because 172 SL and FCPP had similar estimate of DH prevalence, FCPP3 could be either associated with DH 173 of FCPP or SL with little difference.

174

175 *2.3 Environmental analysis*

176 The environmental proxies surrounding each trap site were identified using ArcGIS Desktop 177 (Release 11. Redlands, CA: Environmental Systems Research Institute). We hypothesized that 178 combination of land cover types, distance to water, and terrain features would allow us to 179 identify habitats associated with small mammal assemblages. Land cover types and distance to 180 water were obtained from a Land Cover map (updated at 2014) with 5 meter resolution (Fiera 181 Biological Consulting Ltd., 2014). Terrain features (the average aspect, slope, and "ruggedness" 182 or the standard deviation of the slope) of each trap site were calculated from a digital elevation 183 model with resolution of 0.75 arc-second, or approximately 18 meters (Natural Resources 184 Canada, 2012).

185 A multinomial logistic regression (MLR) model (Fox, 2008; Hosmer et al., 2013) associating the 186 environmental variables to assemblage types was developed. We built a set of alternative models 187 based on what we considered biologically relevant combinations, such as land cover types of 188 forest, grassland, and shrub lands and terrain features. We used focal statistics with circle of 200 189 meter radius to standardize the way we measure surrounding environment, assuming that areas 190 within 200 meter were sufficient for identifying the habitats influencing the small mammals 191 based on their home ranges while also approximating the areas covered by trap grids (Madison, 192 1980; Madison et al., 1984). We used total numbers of raster cells within 200 meter radius for 193 each land cover type as predictor variables. We used the mean value of the cells within 200 194 meter radius for the terrain variables after resampling each terrain raster to 5 meter resolution. 195 The models were then compared using the corrected AICc scores and weights (Burnham and 196 Anderson, 2002). The best performing MLR model was then applied to develop a predicted 197 distribution map of the small mammal assemblage for the entire area of the City. Because we did 198 not sample small mammals from agricultural areas, and because the agricultural areas were at the 199 periphery of the city, we removed agricultural areas from the final map. Similarly, because small 200 mammals are known to avoid mowed grass (Bowers and Dooley, 1993), and because in one 201 experimental trapping we found no small mammal in a field of mowed grass adjacent to a 202 naturally wooded area, we also removed areas classified as manicured grass. Final map was 203 resampled to 50 meters resolution to be used for an agent-based simulation of the transmission of 204 *Em* in future study. 205 All the statistical analysis, except for the MLR were performed using software Primer ver.6 with 206 PERMANOVA+ add-on (Anderson et al., 2008). MLR was performed using SPSS ver.24 (IBM

207 Corps. 2016).

208

209 **3. RESULTS**

210 *3.1Assemblage analysis*

211 To reduce the noise on the community analysis, least chipmunk, northern pocket gopher, and 212 house mice were removed from relative abundance data prior to the calculation of the Bray-213 Curtis similarity matrix because of their minimal abundance in the data. The hierarchical 214 clustering of the small mammal assemblage identified three major assemblage types using an 215 arbitrary cut-off line of 45% similarity, although SIMPROF test failed to detect significance 216 (p=0.678, Figure 2a).

217 Cluster 1 consisted of three BM sites, where Liccioli et al. (2014) found two IHs positive for *Em*, 218 and estimated highest prevalence among DH. Cluster 2 consisted of three NHP sites, FCPP1, 219 SL1, WSH2 and WSH3. Liccioli et al. (2014) found positive IHs in three sites and estimated 220 moderately high prevalence among DH in NHP. The remaining sites WSH1, SL2, FCPP2, and 221 FCPP3 constituted cluster 3. Liccioli et al. (2014) found no positive IH in these sites and 222 estimated low prevalence of DH in these areas (Table 1). Fisher's exact test on the *Em* positive 223 cases of small mammals and the three clusters could not detect any significant difference ($p =$ 224 0.136).

225 Clustering with complete-linkage algorithm also grouped trap sites into the same three clusters (p $226 = 0.695$. Figure 2b). The same pattern was not observed with single-linkage, where trap sites 227 successively joined groups instead of grouping into distinct clusters (not shown, $p = 0.718$). 228 Similar, but slightly different cluster patterns were observed when group-average and complete-229 linkage clustering algorithms were performed on percentage of species ($p = 0.144$ and 0.136 230 respectively, result of group-average shown in Figure 2c). With percentage of species, cluster 3

231 was smaller and consisted of only two sites, but BM still formed a single cluster. Clustering 232 percentage data with single-linkage algorithm showed less distinct a pattern, but BM sites still 233 grouped into a single cluster ($p = 0.127$). All the following analyses are based on relative-234 abundance data and clusters based on group-average algorithm. 235 Conversely, CAP procedure of the small mammal assemblages, using the three clusters identified 236 as grouping factors (Figure 3), highlighted the significant difference between the three clusters 237 (trace statistics 1.6536, $p = 0.001$). Vectors representing the correlation between the CAP axes 238 and the abundances of each species overlaid in Figure 3a indicated that all the species were more 239 abundant in cluster 2. Vectors indicating the correlation of the CAP axes to the proportion of 240 each species and (Figure 3b) indicated that cluster 1 assemblages (particularly BM 1 and BM2) 241 were dominated by deer mice, whereas cluster 3 sites (SL2 and FCPP2) were characterized by 242 shrews.

243

244 *3.2 Environmental proxies for assemblages*

245 The best MLR model selected by AICc used north-south aspect and ruggedness as predictor 246 variables, with AICc of 18.722 and classified 13 out of 14 trap sites correctly (Table 2).When 247 this model was applied to the natural areas of the City of Calgary, 1209 ha (6.96%) were 248 predicted to be habitat for cluster 1, 8164 ha (47.02%) for cluster 2, and 7991 ha (46.02%) for 249 cluster 3 (Figure 4; see supplementary material for parameter estimates).

250

251 **4. DISCUSSION**

252 Using a community ecology analytical approach, we identified three assemblage types of small

253 preys of coyotes, the main carnivore species in urban settings in Calgary, Alberta (Canada).

254 More importantly, we highlighted an association between these assemblages and the presence of 255 *Echinococcus multilocularis* in wild hosts. Finally, we identified potential environmental proxies 256 calculated from land use data readily available for urban settings that could be associated with 257 parasite within this sylvatic cycle. Our results provided evidence to support recent theoretical 258 models that emphasized the role of complexity of host community in transmission of trophically 259 transmitted parasites (Baudrot et al., 2016).

260

261 *4.1 Small prey assemblages and Echinococcus multilocularis*

262 Our clustering analysis using Bray-Curtis similarity identified three clusters. Although the 263 clusters structures were not statistically significant by SIMPROF test possibly due to small 264 sample size, similar structure were observed in both relative abundances and percentage of 265 species, and with different clustering algorithms, providing some confidence in classifying the 266 small mammal assemblages to the three assemblage types. Assemblage 1 consisting of BM sites 267 seemed to be highly susceptible to the transmission of *Em*, while assemblage 3 seemed to be 268 least susceptible to *Em* transmission.

269 In our study area, the three small mammal species of most interest due to their known

270 susceptibility to *Em* are deer mice, meadow voles, and southern red-backed voles (Liccioli et al.,

271 2013a). Particularly interesting was the correlation of proportion of deer mice to assemblage 1,

272 where the prevalence among DH was high (Figure 3b). This is consistent with conclusions drawn

273 by Liccioli et al. (2014) that proportion of susceptible species is the key factor in the

- 274 transmission of the parasite. However, even though assemblage 1 and 2 had about same
- 275 proportion of susceptible species, assemblage 1 was associated with higher prevalence in both

276 DH and IH. Compared to assemblage 1, assemblage 2 had higher abundance of most species of 277 small mammals (Figure 3a). Therefore we suspect that higher abundance of small mammals in 278 general, both susceptible and non-susceptible, led to dilution of exposure and reduced 279 transmission (Baudrot et al., 2016). 280 Any inference drawn from this cluster analysis is limited by the samples size - an issue 281 associated with the low prevalence at which the parasite occurs in intermediate hosts, which 282 likely caused the lack of statistical significance for the Fisher's exact test on the assemblage 283 types and the presence of positive IHs. However, the patterns observed were in agreement with 284 the theoretical studies (Baudrot et al., 2016; Raoul et al., 2015). 285 286 *4.2 The urban small mammal assemblages and their landscape proxies* 287 In our study, the terrain features (north-facing aspect and ruggedness) turned out to be better 288 predictors of assemblage types than land cover types and were selected for the best MLR model. 289 This was probably because the land cover classification was too coarse for the habitats of small 290 mammals. While land cover types were good indicator of where the natural land covers were 291 (because we collected samples only from natural areas), terrain features were probably better 292 indicators of subtle differences in habitats (Franklin, 1995). For example, assemblage 2 seemed 293 to be associated positively with north-facing aspect and negatively with ruggedness 294 (supplementary Table). These terrain features may be better predictors of vegetation types that 295 prefer moist environment. Distance to water was not selected in the model, probably because 296 most sites were close to water, and the only site that differed for this variable (NHP3) had

297 species composition resembling other sites.

298 Interestingly, the predicted distribution of the small mammal assemblage type 1 was

299 characterizing most of BM and a fair portion of NHP (Figure 4). The prevalence of *Em* in these 300 two areas were higher than the other three areas (Liccioli et al., 2014) and in agreement with our 301 inference that assemblage 1 contributed most to the transmission of the parasite, and possibly 302 explains why NHP had higher prevalence even though all three NHP sites were in assemblage 2. 303 However, the predicted distribution of assemblage 1 also covered large area of FCPP, where the 304 prevalence of *Em* was estimated to be low, both in DH and IH (Liccioli et al., 2014).

305 Another possible explanation for the observed pattern of *Em* prevalence would be the availability 306 to coyotes of food sources other than small mammals, which was not quantified in our study. 307 Coyote diet in our study area includes deer and lagomorphs, fruits and vegetable matters, and 308 anthropogenic food sources (Liccioli et al., 2015). Abundance of deer in the area is expected to 309 be particularly important in winter, when they are more frequently consumed and the parasite 310 prevalence in IH is highest (Liccioli et al., 2015; Liccioli et al., 2014). Large and/or connected 311 parks such as NHP, FCPP, and WSH would likely be used by deer more frequently than smaller, 312 less connected parks such as BM and SL.

313 The feeding and marking behavior of coyotes (i.e., DHs) can also be important for the 314 transmission of the parasite. Although the small mammal assemblages and environmental 315 proxies in and around each site may provide some clues on the parasite transmission, coyotes are 316 known to have wide home ranges and readily travel through urban areas (Gehrt, 2007; Lamy, 317 2015). To estimate transmission of parasites and their spatial patterns, analysis of small mammal 318 assemblages alone is not sufficient. Studies on spatial behavior of coyotes, using simulations 319 such as agent-based models, would provide further understanding of the spatial patterns of *Em*

320 transmission. Such studies would also allow testing if changes in small mammal assemblages 321 could exert significant effects on parasite transmission.

322

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414 **LIST OF TABLES**

415 Table 1. This table summarizes the data on small mammal assemblages composition extracted 416 from (Liccioli et al., 2014) collected in 2012-2013 in city parks and natural areas in the 417 City of Calgary (Alberta, Canada). In table are reported the catch rate for each species 418 (indicated by genus names) for every hundred trap-nights, the presence of *Echinococcus* 419 *multilocularis* (1= present, 0 = absent) and prevalence (%) among intermediate hosts (IH), 420 and prevalence among definitive hosts (DH) at each site. The species of small mammals 421 are: Deer mouse (*Peromyscus maniculatus*), Meadow vole (*Microtus pennsylvanicus*), 422 Shrews (*Sorex* sp.), Southern red-backed vole (*Myodes gapperi*), Western jumping mouse 423 (*Zapus princeps*), Thirteen-lined ground squirrel (*Spermophilustri decemlineatus*), Least 424 chipmunk (*Tamias minimus*), Northern pocket gopher (*Thomomys talpoides*), and House 425 mouse (*Mus musculus*). 426

427 Table 2. Comparison of multinomial logistic regression models predicting various types of 428 assemblages of small mammals developed from data collected in 2012-2013 in city parks 429 and natural areas in the City of Calgary, (Alberta, Canada). The values k, Δ_i , and w_i 430 indicate number of parameters estimated, difference in AICc, and relative weights of AICc, 431 respectively. Although the model with north-south aspect and ruggedness performed best 432 in terms of AICc, N-S aspect and slope model, N-S aspect, slope, and ruggedness model 433 performed comparably well.

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436 **LIST OF FIGURES**

437 Figure 1. Study sites for the characterization of the small mammal assemblages in urban Calgary, 438 AB, Canada in 2012-2013, showing the location of five areas in Urban Calgary and 439 detailed map of Bowmont, Southland Lowlands, and Weaselhead. Bowmont (BM), 440 Fishcreek Provincial Park (FCPP), Nose Hill Park (NHP), Southland Lowlands (SL), and 441 Weaselhead (WSH).

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454 Figure 3. Plot of the Canonical Correlation Analysis on the principal coordinates (CAP) of small 455 mammal assemblages in five parks and natural areas in urban Calgary, AB, Canada, 2012- 456 2013, using the cluster as a grouping factor. The cluster 1 is on the lower right corner, 457 cluster 2 is on the lower left corner, and cluster 3 is on the center to the top of the plot. The

466 predicted for the City of Calgary area by a multinomial logistic regression (MLR) model 467 associating the environmental variables to assemblage types, developed from data collected 468 in 2012 and 2013 (Liccioli et al., 2014). Note how large portion of BWM and NHP were 469 classified as assemblage 1 as expected, but also large portion of FCPP, where it was not 470 expected.

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Table 1. 472 Table 1.

Table 2. 476 Table 2.

