

Trzcinski et al.: Local interactions in pitcher plant communities

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**Local interactions in pitcher plant communities scale-up to regional patterns
in distribution and abundance**

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1 Abstract

2 We used the aquatic communities living in the purple pitcher plant (*Sarracenia purpurea* L.,
3 Sarraceniaceae) to determine if patterns produced by trophic interactions at the local scale can be
4 detected at larger spatial scales. Mosquitoes (*Wyeomyia smithii* Coq., Diptera: Culicidae) are
5 known to have a negative effect on the aquatic microfauna within leaves. We compared the
6 abundance of two microfaunal taxa, *Bodo* (Kinetoplastea: Bodonidae), and *Habrotrocha rosa*
7 Donner (Rotifera: Bdelloidea), in bogs with and without pitcher-plant mosquitoes. Bogs
8 containing pitcher plant mosquitoes had lower densities of bacteria through the study period.
9 However, within these bogs, leaves with mosquitoes did not have lower bacterial densities. We
10 found that the pattern for *Bodo* was similar at the leaf and bog spatial scales. Abundance of *Bodo*
11 was closely linked to bacterial densities and the presence of mosquitoes strengthened that
12 relationship, due to greater predator impacts when bacteria were scarce. In contrast, different
13 patterns emerged at the two scales for *H. rosa*. At the leaf scale, a predator effect was seen only
14 for low bacterial densities (as for *Bodo*), but at the bog scale, *H. rosa* was less abundant in
15 mosquito bogs, and abundance was not associated with bacterial levels. We suggest that
16 differences in life history characteristics (population growth rate and average abundance) may
17 influence the relative influence of local interactions and regional processes such as colonization.

18

19 Keywords: spatial scaling, pitcher plant, aquatic microfauna, flagellate, rotifer, *Wyeomyia*
20 *smithii*, spatial population dynamics.

21 Introduction

22 The degree to which broad scale patterns in community structure are due to local processes
23 versus regional processes is poorly understood for most communities. One possibility is that
24 strong interactions at the local scale may ‘scale-up’ to produce regional patterns in abundance
25 and diversity (Wootton 2001). In these cases, models of local interactions accurately predict
26 regional patterns in distribution and abundance. A competing hypothesis is that local interactions
27 do not scale-up directly without the incorporation of spatial patterns in dispersal, productivity
28 and mortality (Maron and Harrison 1997, Cronin et al. 2000). When this is the case, there
29 typically are temporal or spatial discontinuities between the distribution and abundance of the
30 predator and its prey, and models based only on local interactions are incapable of reproducing
31 regional patterns.

32 The local dynamics of the microfaunal populations living in the purple pitcher plant
33 (*Sarracenia purpurea* L., Sarraceniaceae) are strongly influenced by predation. Predation by
34 mosquito larvae (*Wyeomyia smithii* Coq., Diptera: Culicidae) causes shifts in the relative
35 abundances of the various members of the microfaunal community by direct consumption, and
36 by altering bacterial density and composition (e.g. Addicott 1974, Cochran-Stafira and von Ende
37 1998, Kneitel and Miller 2002, Trzcinski et al. 2005). In addition, mosquito predators decrease
38 the probability of establishment, increase temporal variability and decrease persistence time for
39 some taxa (Miller et al. 2002, Trzcinski et al. 2005). As a consequence, mosquitoes can cause an
40 overall reduction in microfaunal diversity (Addicott 1974, Kneitel and Miller 2003).

41 If local interactions directly scale-up in pitcher plant communities, then regional patterns in
42 the abundance of the aquatic microfauna may simply reflect the distribution and abundance of

43 mosquitoes. There is some support for this hypothesis at the very largest spatial scale, where the
44 species richness of protozoa and bacteria within pitcher plants increases with latitude as
45 mosquito abundance decreases (Buckley et al. 2003). At regional scales (among bogs), mosquito
46 distribution has been linked to factors such as microclimate, and landscape features (e.g.
47 proximity to forest edges, bog isolation) (Heard 1994a, Miner and Taylor 2002, Krawchuk and
48 Taylor 2003), as well as finer features within a bog (Trzcinski et al. 2003) and protozoa
49 abundance and distribution may follow similar patterns.

50 A simple empirical method for determining the contribution of local trophic interactions to
51 regional patterns in abundance, short of parameterizing complex spatial models, is to compare
52 statistical models that differ only in one parameter - the spatial scale at which the trophic
53 interaction is tested. If the similar effects of predation are observed at the broader spatial scale,
54 then there is some evidence for direct scaling-up. If not, then either other local processes
55 predominate or broad scale processes such as predator and prey dispersal or spatial patterns in
56 productivity or survival need to be incorporated.

57 In this study we wanted to determine if the effect of mosquitoes on the population abundance
58 of microfauna observed at the scale of individual pitcher plant leaves can be detected at the
59 spatial scale of a bog. Toward the northern extreme of the range of pitcher plant communities,
60 mosquitoes are absent from some bogs. We measured the abundance of two microfaunal taxa
61 commonly found in pitcher plants, the flagellate *Bodo* (Kinetoplastea: Bodonidae), and the
62 rotifer *Habrotrocha rosa* Donner (Rotifera: Bdelloidea), and determined whether differences in
63 abundance are associated with the presence of mosquitoes at both leaf and bog spatial scales.

64

65 Methods

66 Protozoan samples were collected from six bogs in western Newfoundland (Fig. 1) in August
67 2000 (a subset of the bogs used in Miner and Taylor (2002)). Three were known not to contain
68 pitcher plant mosquitoes. The bogs varied in size from small (10 - 200 m in diameter) to large
69 (500 – 2000 m in diameter), and were separated by distances of 0.5 to 12 km. All were within 1
70 km of the coast, and had the same orientation to the coastline.

71 We randomly located 20 plants in each bog, selected the first leaf produced from each plant,
72 and collected microfaunal samples on 20th, 25th and 30th of August. For each leaf, we measured
73 water depth, pipetted 3 samples (170 μ L) from mid-depth, touching the edge of the leaf, and then
74 replaced the liquid with distilled water. Samples were preserved with 10 μ L HgCl₂ (saturated),
75 and refrigerated until analyzed. We reduced sampling effort when water level was low: depth < 5
76 mm: no sample, 5 – 10 mm: 1 sample, 11 – 20 mm: 2 samples. A total of 1162 water samples
77 were collected from 118 leaves.

78 We focused on the flagellate, *Bodo*, and the rotifer, *H. rosa*, because they were common and
79 easy to identify, and because they have been the focus of other recent studies (Cochran-Stafira
80 and von Ende 1998, Bledzki and Ellison 1998, Kneitel and Miller 2002). Since densities were
81 frequently low, we concentrated samples prior to counting, centrifuging lightly (500 g for 10
82 minutes), and removing the top 145 μ L (80%). We re-suspended the remaining 35 μ L, and
83 loaded a hemocytometer with two 10 μ L drops. For each drop, we scanned 0.016 μ L at 400 \times for
84 *Bodo*, and 0.9 μ L at 100 \times for *H. rosa*, producing detection limits of 343 per mL (*Bodo*) and 3.3
85 per mL (*H. rosa*) of unconcentrated fluid. We used a regression model to estimate water volume
86 and multiplied densities by water volume to obtain an estimate of total abundance in each leaf

87 (Trzcinski et al. 2005). We classified bacterial densities (viewed at 400×) into five categories:
88 none, low, medium, high, and extremely high (0, 1-5, 6-99, 100-500, >500 cells per 0.004 μL of
89 concentrated fluid).

90 On the last date, we collected and measured the leaves, (length, maximum diameter); two
91 leaves were lost or damaged reducing our sample size to 118 leaves. We filtered leaf contents
92 (85 μm mesh) and counted mosquitoes, midges (*Metriocnemus knabi* Coq., Diptera:
93 Chironomidae), mites (*Sarraceniopus gibsoni* Nesbitt, Acari: Histiostomatidae), and the head
94 capsules of other arthropods retained on the mesh (at 25× power). Mites were found in most
95 leaves (114/118), but were uncorrelated with any of the microfauna and were excluded from
96 further analyses. A sarcophagid fly (*Fletcherimyia fletcheri* Aldrich, Diptera: Sarcophagidae)
97 pupates during mid-summer and larvae were not present in the leaves at the time of collection.

98 We were principally interested in comparing microfaunal abundance in bogs with and
99 without mosquitoes. We tested for the effect of mosquitoes within a bog on the abundance of
100 *Bodo* and *H. rosa*, and bacteria over our study period using a generalized linear mixed effects
101 model (glmmPQL in S-plus 6.2), similar to the methods presented in Trzcinski et al. (2003).As
102 midges also affect bacterial and protozoan abundance (Heard 1994b, Trzcinski et al. 2005), we
103 included midge abundance and bacterial density as covariates in our models of *Bodo* and *H. rosa*
104 abundance. We assumed a Poisson error distribution for *Bodo* and *H. rosa* abundance
105 (untransformed data), and a Gaussian error distribution for bacterial densities. We treated bog,
106 leaf within bog, and repeated samples of a leaf on a given date as random effects. We removed
107 the sampling variability within date (random effect), and tested for linear trends over time (fixed
108 effect). The bogs in this study are treated as replicates of bogs of two types - with or without

109 mosquitoes (fixed effect). We tested for the fixed effects of bog type (presence of mosquitoes),
110 abundance of midges, changes in abundance over our study period (linear), and all two-way
111 interactions with bog type. Entering bog type first or after our covariates had no effect on any of
112 our conclusions. Models with the same structure were used to test the effect of mosquito
113 presence within a leaf in bogs containing *Wyeomyia smithii*. We examined residuals plots to
114 assess model fit, and interpreted our results based on coefficients, standard errors and the
115 proportion of deviance explained (F-tests on deviances, scaled by their degrees of freedom:
116 Venables and Ripley (1999)). We also tested for differences in leaf length, number of head
117 capsules, and midge density between mosquito and no-mosquito bogs. In these tests, parameters
118 were estimated using separate one-way generalized mixed effects models where only a bog level
119 random effect was estimated.

120

121 Results

122 In bogs with mosquitoes, 22.4% of the leaves were occupied by mosquitoes at the time of
123 collection, and abundance ranged from 1 to 3 larvae per leaf. No mosquitoes were found in
124 leaves from bogs thought to be free of mosquitoes, confirming results from previous censuses
125 (Miner and Taylor 2002).

126 Most of the variation in *Bodo* abundance at both the leaf and bog scale was explained by the
127 presence/absence of mosquitoes, variation in bacterial densities, temporal changes in abundance
128 and their interactions (Tables 1 and 2). The strongest relationships, at both the leaf and bog scale,
129 involved bacterial densities. At both scales, higher numbers of *Bodo* were found in pitchers with
130 high bacterial densities, and at both spatial scales the steepness of the relationship was higher in

131 the presence of mosquitoes (Mosquito X Bacteria interactions, Tables 1 and 2). In addition,
132 average *Bodo* abundance was lower in bogs with mosquitoes throughout the study period (Fig. 2,
133 Table 1).

134 Most of the variation in *H. rosa* populations at the bog scale was associated with time, at
135 both the leaf and bog scales (Tables 1 and 2). There was a positive relationship between *H. rosa*
136 abundance and bacterial densities, but only in the presence of mosquitoes, and only at the leaf
137 scale (Table 2). Average abundance of *H. rosa* was lower in bogs with mosquitoes initially, but
138 the effect was no longer present on the last sampling date (Fig. 2).

139 The presence of mosquitoes in a bog also affected the relationship between midges and the
140 microfaunal taxa (Table 1). In bogs with mosquitoes, the abundances of both *Bodo* and *H. rosa*
141 declined with midges. Without mosquitoes, however, *Bodo* increased with midge abundance and
142 there was no relationship between *H. rosa* and midges. Bacterial densities were lower in bogs
143 containing pitcher plant mosquitoes through the study period (Table 1). However, within these
144 bogs, leaves with mosquitoes did not have lower bacterial densities (Table 2).

145 The variance components analysis (variance estimates of random effects) showed that there
146 was more variation in *Bodo*, and *H. rosa* abundance and bacterial density among plants (one leaf
147 sampled per plant) than among bogs (Table 3). Among bog variation in *H. rosa* abundance was
148 more than twice as large as *Bodo* abundance. Bogs without mosquitoes tended to have shorter
149 leaves ($p = 0.07$), but were similar to bogs containing mosquitoes in resource capture rates and
150 midge abundance (Table 4).

151

152 Discussion

153 Local interactions (mosquito predation, midge shredding, competition) are known to affect
154 the local population dynamics of the aquatic microfauna living in pitcher plant leaves (Addicott
155 1974, Heard 1994b, Cochran-Stafira and von Ende 1998, Kneitel and Miller 2002, Trzcinski et
156 al. 2005). Here we demonstrate that the population sizes of *Bodo* and *H. rosa* differed between
157 leaves and bogs with and without mosquitoes. The similarity in our models of *Bodo* abundance at
158 the two spatial scales suggests that the major trophic interactions scale-up, producing similar
159 patterns of regional *Bodo* abundance. *Bodo* numbers were closely linked to bacterial densities at
160 the leaf scale, suggesting resource limitation. This relationship was steeper for leaves with
161 mosquitoes, with *Bodo* abundance lower than expected at low bacterial densities. Mosquitoes
162 could have lowered *Bodo* numbers directly through consumption or via competition for the
163 scarce bacterial resources. Consumption seems the more likely mechanism, as there was no
164 evidence that mosquitoes depressed bacterial numbers at the leaf scale. The similarity of the
165 patterns at the bog scale suggest that resource (bacterial) density remains a key determinant of
166 *Bodo* abundance at larger scales, and that mosquitoes modify the relationship in a similar
167 manner, depressing *Bodo* densities where resources are scarce.

168 In contrast, patterns at the bog scale do not closely reflect those at the leaf scale for *H. rosa*
169 populations. The pattern for *H. rosa* at the leaf scale was similar to that seen for *Bodo*; *H. rosa*
170 abundance also increased with bacterial density, and the relationship was stronger for leaves with
171 mosquitoes. At the bog level, however, *H. rosa* and bacterial densities were unrelated, regardless
172 of the presence of mosquitoes. At this scale, therefore, some other factor(s) were the prime
173 determinants of *H. rosa* abundance. Bacterial levels in bogs without mosquitoes may have been
174 sufficiently high that *H. rosa* numbers were limited by factors such as dispersal rather than by

175 resources. At the bog scale, mosquitoes may have depressed *H. rosa* numbers sufficiently, at
176 least over the earlier sampling dates, that no relationship with bacteria was observed. The shift in
177 relationships between *H. rosa*, mosquitoes and bacteria across scales suggests that regional
178 factors (e.g. dispersal, environmental heterogeneity) may play a greater role in determining
179 regional patterns of abundance for *H. rosa* than for *Bodo*. In sum, mosquitoes appear to reduce
180 *Bodo* densities only at low bacterial densities at both leaf and bog scales. Mosquitoes influence
181 *H. rosa* in a similar manner at the leaf scale, but reduce abundance across bacterial densities at
182 the bog scale, at least for part of the season.

183 *Bodo*, a microflagellate, and *H. rosa*, a rotifer, differ in ways that likely affect their
184 vulnerability to mosquitoes, and perhaps their relationship to bacterial abundance. Mosquito
185 larvae filter feed just below the water surface. Larvae will dive when disturbed, but do not
186 normally feed at lower depths. Lifestyle comparisons seem to suggest that *Bodo* should be more
187 vulnerable to mosquito predation, due to its small size, and planktonic swimming and feeding
188 habits. *H. rosa* is much larger (approx. 15 times) and filter feeds in the water column or while
189 attached to substrate (leaf edge, detritus). While on these substrates, *H. rosa* is less susceptible to
190 mosquitoes, and it has been suggested that the rotifer's persistence under natural conditions is
191 linked to use of such refugia (Bledzki and Ellison 1998). However, previous work suggests that
192 mosquitoes have a greater effect on the abundance and persistence of *H. rosa* than *Bodo*
193 populations (Trzcinski 2005). A likely explanation is the higher potential growth rate of *Bodo*.
194 *Bodo* populations can double every 5 hours, and thus can both closely track resource levels and
195 compensate for losses due to predation. Estimated doubling time for *H. rosa* is 14 hours, and
196 thus predation can more easily decouple the consumer – resource relationship. Larger body size

197 and lower overall population size for *H. rosa* also means that colonization by passive means such
198 as wind dispersal are more likely to be limiting for the rotifer.

199 We have interpreted the differences in microfaunal abundance among bogs in terms of
200 presence/absence of mosquitoes. It is, of course, possible that the differences between bogs with
201 and without mosquitoes were caused by other factors that co-varied with mosquito distribution.
202 However, none of the obvious factors seem likely to have produced the patterns. Midge
203 abundance, resource levels and water levels were similar. Average leaf size did differ, but the
204 difference (smaller in no mosquito bogs) should have led to fewer rather than more *Bodo* and *H.*
205 *rosa* in these bogs. Thus, though this type of study cannot eliminate the possibility that some
206 unmeasured factor caused the patterns, the presence of mosquitoes seems to be the most likely
207 cause. The pitcher plant community is highly dynamic over time (Addicott 1974, Kneitel and
208 Miller 2003, Trzcinski et al. 2005), and temporal changes in community structure may affect
209 when trophic interactions do or do not scale-up. Thus it also remains possible that trophic
210 interactions involving *H. rosa* may scale-up more strongly at other times of the year.

211 We found greater variability in the abundance of *Bodo* and *H. rosa* among plants (leaves
212 were collected from separate plants) than among bogs. To our knowledge, this is the first study
213 to report variance components across spatial scales for the pitcher plant microfauna. The pattern
214 is similar to that seen for mosquito and midge abundance from these bogs, where among-bog
215 variation was important, but among-leaf and among-plant variation was greater (Miner and
216 Taylor 2002, Krawchuk and Taylor 2003). A contrasting pattern was seen in the southern part of
217 the range for pitcher plant communities, where mosquitoes are more abundant. Similar amounts
218 of variability were found at bog, sub-population within bog and plant scales for the mosquito,

219 while the greatest variability in midge abundance was among bogs (Harvey and Miller 1996). If
220 mosquitoes also structure pitcher plant communities in the south, we would expect the variance
221 components of the microfauna to mirror that of mosquitoes. Pitcher plant mosquitoes are clearly
222 a key species in this community, making decisions at several spatial scales when choosing where
223 to oviposit (Trzcinski et al. 2003, Krawchuk and Taylor 2003); these decisions then affect
224 microfaunal population dynamics (Addicott 1974, Cochran-Stafira and von Ende 1998, Kneitel
225 and Miller 2002, Trzcinski et al. 2005), and ultimately influence the pitcher plant's supply of
226 nitrogen and phosphorus (Bledzki and Ellison 1998, Ellison and Gotelli 2002).

227 Midges are expected to have a positive effect on microfaunal abundances because they
228 increase the decomposition rate in pitcher plant leaves, and thus the abundance of bacteria
229 (Heard 1994b, Trzcinski et al. 2005). Positive associations between midges and *Bodo* abundance
230 were seen in previous work 710 km to the southwest (Trzcinski et al. 2005). In this study,
231 however, *Bodo* increased with midges only in bogs without mosquitoes, and in mosquito bogs,
232 there was actually a negative association between midges and both *Bodo* and *H. rosa*. It seems
233 unlikely that midges were competing with, or harming *Bodo* or *H. rosa* directly, and thus the
234 association is likely due to the fact that leaves with high numbers of midges were more likely to
235 also contain mosquitoes (Heard 1994b). The pattern does suggest, however, that any enhanced
236 resource availability due to shredding by midges was not enough to offset negative effects on
237 abundance by mosquitoes.

238 Mosquitoes have been found in all parts of the pitcher plant's range and were present in all
239 the samples collected by Buckely et al. (2003). So why are mosquitoes absent from some bogs in
240 Newfoundland? Possible explanations are: (1) dispersal is low and therefore mosquitoes have

241 never colonized, or (2) microclimate conditions are such that mosquitoes frequently or
242 occasionally go extinct in some bogs, and recolonization has not yet occurred. It seems unlikely
243 that some bogs have never been colonized, while relatively nearby locations have mosquitoes.
244 However, colonization rates are probably low, as these mosquitoes are reported to be weak flyers
245 (Istock and Weisburg 1987, Heard 1994a, Krawchuk and Taylor 2003), and genetic work
246 indicates that between bog movements are infrequent (Istock and Weisburg 1987, Ambruster et
247 al. 1998). Features such as bog size and exposure will also affect the probability that particular
248 bogs are colonized (Miner and Taylor 2002). Occasional or even frequent extinctions may well
249 occur in some bogs, as the study area is at the northern limit of the distribution of the pitcher
250 plant mosquito, with presumably correspondingly low survival rates. Heard (1994a) suggested
251 that low temperatures cause extinctions in wind swept bogs because of the absence of insulating
252 snow. It is also possible that higher rates of desiccation in exposed bogs may contribute to or
253 cause extinctions (Miner and Taylor 2002).

254 There is tension in spatial ecology between those that favour explaining spatial patterns in
255 communities as a function of local processes that ‘scale up’, and those that interpret patterns in
256 terms of regional processes (e.g. movement, community assembly, disturbance) (Tilman and
257 Kareiva 1997). In general, local effects do not scale up directly to larger spatial scales when site
258 or regional abundance is significantly modified by dispersal and/or environmental heterogeneity.
259 For example, regional patterns cannot be understood without considering dispersal in tussock
260 moths and their parasitoids (Maron and Harrison 1997, Wilson et al. 1999), or bark beetles and
261 their predators (Cronin et al. 2000, Turchin 2003). In a similar manner, environmental
262 heterogeneity must be included to explain regional patterns in the intertidal; the consequences of

263 local competitive and predatory interactions for large scale patterns of abundance depend on
264 spatial variation in waves and oceanic conditions (Thrush et al. 2000, Wootton 2001, Guichard et
265 al. 2003). In pitcher plant microfaunal communities, local interactions scaled-up for one taxon,
266 *Bodo*; predators strengthen the relationship between *Bodo* and bacterial densities at both local
267 and regional scales. In contrast, the effect of predators on *H. rosa* changes across scales,
268 suggesting that regional processes come into play at larger scales. Dispersal and/or
269 environmental heterogeneity set the limit to the scaling-up; factors affecting mosquito
270 distribution determine where microfaunal communities are structured by predation and where
271 other factors (resource levels and competition) probably play a greater role.
272

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278

279 References Cited

- 280 **Addicott, J. F. 1974.** Predation and prey community structure: an experimental study of the
281 effects of mosquito larvae on the protozoan communities of pitcher plants. *Ecology* 55: 475-
282 492.
- 283 **Ambruster, P., W. E. Bradshaw, and C. M. Holzapel. 1998.** Effects of postglacial range
284 expansion on allozyme and quantitative genetic variation of the pitcher-plant mosquito,
285 *Wyeomyia smithii*. *Evolution* 52: 1697-1704.
- 286 **Bledzki, L. A., and A. M. Ellison. 1998.** Population growth and production of *Habrotrocha*
287 *rosa* Donner Rotifera: Bdelloidea and its contribution to the nutrient supply of its host, the
288 northern pitcher plant, *Sarracenia purpurea* L. Sarraceniaceae. *Hydrobiologia* 385: 193-200.
- 289 **Buckley, H. L., T. E. Miller, A. M. Ellison, and N. J. Gotelli. 2003.** Reverse latitudinal trends
290 in species richness of pitcher-plant food webs. *Ecol. Lett.* 6: 825-829.
- 291 **Cochran-Stafira, D. L., and C. N. von Ende. 1998.** Integrating bacteria into food webs: studies
292 with *Sarracenia purpurea* inquilines. *Ecology* 79: 880-898.
- 293 **Cronin, J. T., J. D. Reeve, R. Wilkens, and P. Turchin. 2000.** The pattern and range of
294 movement of a checkered beetle predator relative to its bark beetle prey. *Oikos* 90: 127-138.
- 295 **Ellison, A. M., and N. J. Gotelli. 2002.** Nitrogen availability alters the expression of carnivory
296 in the northern pitcher plant, *Sarracenia purpurea*. *Proceedings of the National Academy of*
297 *Sciences* 99: 4409-4412.
- 298 **Guichard, F., P. M. Halpin, G. W. Allison, J. Lubchenco, and B. A. Menge. 2003.** Mussel
299 disturbance dynamics: signatures of oceanographic forcing from local interactions. *Am. Nat.*
300 161: 889-904.

- 301 **Heard, S. B. 1994a.** Wind exposure and distribution of pitcher plant mosquito Diptera: Culicidae.
302 Environmental Entomology 23: 1250-1253.
- 303 **Harvey, E., and T. E. Miller. 1996.** Variance in composition of inquiline communities in leaves
304 of *Sarracenia purpurea* L. on multiple spatial scales. Oecologia 108: 562-566.
- 305 **Heard, S. B. 1994b.** Pitcher plant midges and mosquitoes: a processing chain commensalism.
306 Ecology 75: 1647-1660.
- 307 **Istock, C. A., and W. G. Weisburg. 1987.** Strong habitat selection and the development of
308 population structure in a mosquito. Evolutionary Ecology 1: 348-362.
- 309 **Kneitel, J. M., and T. E. Miller. 2002.** Resource and top-predator regulation in the pitcher plant
310 *Sarracenia purpurea* inquiline community. Ecology 83: 680-688.
- 311 **Kneitel, J. M., and T. E. Miller. 2003.** Dispersal rates affect species composition in
312 metacommunities of *Sarracenia purpurea* inquilines. Am. Nat. 162: 165-171.
- 313 **Krawchuk, M. A., and P. D. Taylor. 2003.** Changing importance of habitat structure across
314 multiple spatial scales for three species of insects. Oikos 103: 153-161.
- 315 **Maron, J. L., and S. Harrison. 1997.** Stable pattern formation in an insect host-parasitoid
316 system. Science 278: 1619-1621.
- 317 **Miller, T. E., J. M. Kneitel, and J. H. Burns. 2002.** Effect of community structure on invasion
318 success and rate. Ecology 83: 898-905.
- 319 **Miner, J. A. and P. D. Taylor. 2002.** Effects of peatland size and exposure on two species of
320 Diptera inhabiting the pitcher plant *Sarracenia purpurea* L. Ecoscience 9: 347-354.

321 **Thrush, S. F., J. E. Hewitt, V. J. Cummings, M. O. Green, G. A. Gunnell, and M. R.**
322 **Wilkinson. 2000.** The generality of field experiments: interactions between local and broad-
323 scale processes. *Ecology* 81: 399-415.

324 **Tilman, D. and P. Kareiva. 1997.** Spatial ecology. The role of space in population dynamics
325 and interspecific interactions. Princeton University Press, Princeton, New Jersey.

326 **Trzcinski, M. K., S. J. Walde, and P. D. Taylor. 2003.** Colonisation of pitcher plant leaves at
327 several spatial scales. *Ecological Entomology* 28: 482-489.

328 **Trzcinski, M. K., S. J. Walde, and P. D. Taylor. 2005.** Stability of pitcher-plant microfaunal
329 populations depends on food web structure. *Oikos* 110: 146-154.

330 **Turchin, P. 2003.** Complex population dynamics. A theoretical / empirical synthesis.
331 Princeton University Press, Princeton, New Jersey.

332 **Venables, W.N., and B. D. Ripley. 1999.** Modern applied statistics with S-Plus, third edition. -
333 Springer-Verlag, New York.

334 **Wilson, W. G., S. P. Harrison, A. Hastings, and K. McCann. 1999.** Exploring stable pattern
335 formation in models of tussock moth populations. *J. Animl. Ecol.* 68: 94-107.

336 **Wootton, J. T. 2001.** Local interactions predict large-scale pattern in empirically derived cellular
337 automata. *Nature* 413: 841-844.

338 **Table 1. Effects of the presence of mosquitoes in a bog (Type), the density of bacteria and the number of midges on the**
 339 **abundance of *Bodo* and *H. rosa* populations and the density of bacteria in 118 leaves over 15 days (1162 samples). NA = not**
 340 **applicable.**

	<i>Bodo</i>					<i>H. rosa</i>				Bacteria			
	Df	Coeff.	S.E.	F-value	Pr(F)	Coeff.	S.E.	F-value	Pr(F)	Coeff.	S.E.	F-value	Pr(F)
Intercept	1	-1.320	0.45			-1.850	0.68			3.02	0.18		
Type	1	-2.428	0.71	11.05	0.03	-1.745	1.02	0.71	0.44	-1.14	0.26	18.04	0.01
Bacteria	1	0.183	0.06	23.81	<.0001	-0.124	0.10	0.63	0.43	NA	NA	NA	NA
Midge	1	0.026	0.02	0.10	0.75	0.014	0.02	0.61	0.44	-0.003	0.01	1.57	0.21
Time	1	0.107	0.04	25.88	<.0001	-0.025	0.04	7.63	0.006	-0.021	0.02	1.56	0.21
Type * Bacteria	1	0.553	0.14	13.59	0.0003	0.179	0.18	0.95	0.33	NA	NA	NA	NA
Type * Midge	1	-0.071	0.02	7.51	0.007	-0.091	0.04	5.28	0.02	0.020	0.01	2.60	0.11
Type * Time	1	0.111	0.06	3.36	0.07	0.255	0.06	16.50	0.0001	0.015	0.02	0.51	0.47

341

342 **Table 2. Effects of the presence of mosquitoes within a leaf (Mosq), the density of bacteria and the number of midges on the**
 343 **abundance of *Bodo* and *H. rosa* populations and the density of bacteria in 58 leaves over 15 days (586 samples). Only leaves in**
 344 **bogs with mosquitoes were included. NA = not applicable.**

	<i>Bodo</i>					<i>H. rosa</i>				Bacteria			
	Df	Coeff.	S.E.	F-value	Pr(F)	Coeff.	S.E.	F-value	Pr(F)	Coeff.	S.E.	F-value	Pr(F)
Intercept	1	-3.96	0.51			-3.78	0.89			2.06	0.32		
Mosq	1	-3.38	1.52	0.01	0.92	-6.46	2.87	0.006	0.94	-0.20	0.53	0.02	0.89
Bacteria	1	0.57	0.10	41.59	<.0001	-0.20	0.14	0.74	0.39	NA	NA	NA	NA
Midge	1	-0.05	0.02	7.04	0.01	-0.07	0.04	3.68	0.06	-0.001	0.01	0.37	0.55
Time	1	0.23	0.06	18.77	<.0001	0.26	0.06	20.80	<.0001	0.004	0.02	0.19	0.66
Mosq * Bacteria	1	1.51	0.42	12.49	0.0005	2.01	0.73	7.05	0.008	NA	NA	NA	NA
Mosq * Midge	1	-0.02	0.04	0.28	0.60	-0.02	0.08	0.03	0.87	0.02	0.02	1.07	0.31
Mosq * Time	1	0.03	0.13	0.06	0.80	0.18	0.20	0.80	0.37	-0.05	0.03	2.00	0.16

345 **Table 3. Variance components for random effects corresponding to the models in Table 1.**
 346 **Results are expressed as a proportion of the total variance explained by random effects and**
 347 **residual variance. Only the first leaf produced by the plant was sampled.**

Random effect	Taxa		
	<i>Bodo</i>	<i>H. rosa</i>	Bacteria
Bog	0.07	0.20	0.002
Plant	0.43	0.38	0.80
Time	0.46	0.26	0.43
Sample	0.18	0.32	0.17

348

349 **Table 4. Means (S.E.) of leaf length, number of insects captured (Capture), and abundance**
 350 **of midges for 118 leaves in mosquito and no-mosquito bogs. Parameters were estimated**
 351 **using separate one-way generalized mixed effects models where only a bog level random**
 352 **effect was estimated.**

Factor	Mosquitoes		Pr(F)
	Absent	Present	
Leaf length (mm)	92.52	116.18	0.07
(S.E.)	(6.68)	(9.47)	
Capture	11.23	16.87	0.16
(S.E.)	(2.27)	(3.23)	
Midges	9.08	13.89	0.61
(S.E.)	(6.06)	(8.57)	

353 Figures

354

355 **Fig. 1.** The location of six bogs used in this study in western Newfoundland. 1 = *Wyeomyia*
356 *smithii* present, 0 = *Wyeomyia smithii* absent.

357

358 **Fig. 2.** The dynamics of *Bodo* and *Habrotricha rosa* populations and trends in bacterial density
359 in 118 leaves located in three bogs without mosquitoes (solid line), and three bogs with
360 mosquitoes (dashed line). Error bars are \pm SE. Bacterial densities were classified into 5
361 categories: none, low, medium, high, and extremely high (see Methods).

362



