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Indirect and direct controls of macroinvertebrates and small fish by abiotic factors and trophic interactions in the Florida Everglades

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6   **Indirect and direct controls of macroinvertebrates and small fish by abiotic factors**

7   **and trophic interactions in the Florida Everglades**

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25   **Abbreviated title:** Indirect and direct controls of Everglades consumers

26   **Key words:** indirect effects, bottom-up and top-down control, hydrological disturbance,

27   phosphorus, Florida Everglades

28

29   **Summary**

30   1. The roles of nutrients, disturbance and predation in regulating consumer densities

31   have long been of interest, but their indirect effects have rarely been quantified in

32   wetland ecosystems. The Florida Everglades contains gradients of hydrological

33   disturbance (marsh drying) and nutrient enrichment (phosphorus), often correlated with

34   densities of macroinvertebrate infauna (macroinvertebrates inhabiting periphyton), small

35   fish and larger invertebrates, such as snails, grass shrimp, insects and crayfish. However,

36   most causal relationships have yet to be quantified.

37   2. We sampled periphyton (content and community structure) and consumer (small

38   omnivores, carnivores and herbivores, and infaunal macroinvertebrates inhabiting

39   periphyton) density at 28 sites spanning a range of hydrological and nutrient conditions

40   and compared our data to seven *a priori* structural equation models.

41   3. The best model included bottom-up and top-down effects among trophic groups and

42   supported top-down control of infauna by omnivores and predators that cascaded to

43   periphyton biomass. The next best model included bottom-up paths only and allowed

44   direct effects of periphyton on omnivore density. Both models suggested a positive

45   relationship between small herbivores and small omnivores, indicating that predation was

46   unable to limit herbivore numbers. Total effects of time following flooding were

47   negative for all three consumer groups even when both preferred models suggested

48   positive direct effects for some groups. Total effects of nutrient levels (phosphorus) were

49   positive for consumers and generally larger than those of hydrological disturbance, and

50   were mediated by changes in periphyton content.

51 4. Our findings provide quantitative support for indirect effects of nutrient enrichment on

52 consumers, and the importance of both algal community structure and periphyton

53 biomass to Everglades food webs. Evidence for top-down control of infauna by

54 omnivores was noted, though without substantially greater support than a competing

55 bottom-up only model.

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74   **Introduction**

75   How abiotic and biotic factors influence populations and communities has long

76   been a central question in community ecology (e.g., Menge & Sutherland, 1987; Pace *et*

77   *al.*, 1999), but understanding their interactions and indirect effects as mediated by species

78   interactions remains a critical step to developing predictive models of how populations

79   are controlled and respond to environmental change (Wootton, Parker, & Power, 1996;

80   Kneitel & Chase, 2004; Gotelli & Ellison, 2006). To identify the mechanisms by which

81   environmental gradients influence communities, they must be examined in the context of

82   food webs and using methods that can explore their interactions and community-level

83   effects. We used structural equation modeling, a multivariate technique that explicitly

84   examines indirect and direct effects, to determine how hydrological disturbance, nutrients

85   and trophic interactions influence primary production and densities of small consumers

86   (predominantly invertebrates and small fish) in the Florida Everglades.

87   Studies of aquatic systems have revealed diverse effects of disturbance,

88   productivity and predation on food webs, densities and community structure (e.g., Power,

89   Parker, & Wootton, 1996; Shurin *et al.*, 2002; Chase, 2003). In pond and wetland

90   ecosystems, hydrological disturbance is expected to shape community structure by

91   permanently limiting or periodically reducing biota, especially larger organisms

92   (Wellborn, Skelly, & Werner, 1996). Disturbance in the form of drought can decrease

93   macroinvertebrate and fish densities through direct mortality or reduction of food

94   biomass. In habitats where larger organisms are more susceptible to drying conditions,

95   droughts may actually increase macroinvertebrate densities by removing predatory fish

96   (Corti, Kohler, & Sparks, 1997; Liston, 2006; Dorn, 2008). The effects of nutrient

97   enrichment on fish and invertebrate densities can depend on disturbance, the strength of

98   trophic interactions, and the degree to which predators can reduce prey populations. For

99   example, while fish biomass generally increases with nutrients, similar increases in

100   invertebrate biomass may hinge on whether fish are present and limit invertebrate

101   densities (Wootton & Power, 1993; Marks, Power, & Parker, 2000; Liston, 2006).

102   Increasing nutrients can also encourage successional changes toward well-defended but

103   competitively inferior invertebrates and thereby reduce the strength of trophic cascades

104   by fish (Chase, 2003). Relatively few studies have addressed these interactive effects and

105   indirect relationships in wetlands, leaving such questions unanswered for many systems.

106   The Florida Everglades is a highly oligotrophic marsh ecosystem with gradients

107   of anthropogenic nutrient (phosphorus) enrichment and hydrological disturbance (drying

108   of the marsh) (Gunderson & Loftus, 1993; Davis, 1994). Drying events cause direct

109   mortality of fish and invertebrates as well as movements toward deeper refuges, and thus

110   community trajectories in the Everglades reveal shifts from abiotic to biotic control as a

111   function of time following a disturbance (Trexler, Loftus, & Perry, 2005), similar to

112   patterns in floodplain habitats (Winemiller, 1996). The density of small fish typically

113   increases with time following a drying event (Trexler *et al.*, 2002, 2005; Dorn, 2008) and

114   often with nutrient levels (Turner *et al.*, 1999; Trexler *et al.*, 2002; Gaiser *et al.*, 2005).

115   Similarly, invertebrates often increase coincident with hydroperiod and nutrients,

116   although this pattern varies with taxa, sampling method, microhabitat and nutrient level

117   (Rader & Richardson, 1994; McCormick, Shuford, & Rawlik, 2004; Liston, 2006; King

118   & Richardson, 2007; Liston, Newman, & Trexler, 2008). It is generally presumed that

119   nutrients amplify fish and macroinvertebrate densities indirectly via stimulation of

120   periphyton production (aggregations of benthic algae, detritus, fungi and bacteria), a

121   major source of primary production for the food web and habitat for invertebrates.

122   Nutrient enrichment, localized around areas of water inflow, alters algal community

123   composition and consequently changes the periphyton physical structure and constitution

124   (e.g., from floating calcareous mats to epiphytic filamentous green algae aggregates)

125   (McCormick *et al.*, 1996; Gaiser *et al.*, 2005, 2006). Hydrology may also shape

126   periphyton community structure (Gottlieb, Richards, & Gaiser, 2006; Thomas *et al.*,

127   2006). The maintenance of large expanses of periphyton and apparent limits on

128   macroinvertebrate densities suggest that fish predation on invertebrates may generate a

129   trophic cascade (Turner *et al.*, 1999; Liston, 2006).

130   While these general trends in Everglades communities have been identified,

131   indirect and direct effects and food-web interactions have not yet been explicitly

132   quantified in natural contexts and at large spatial scales. Anthropogenic activities have

133   modified the Everglades through nutrient enrichment and alteration of hydrological

134   patterns (Davis, 1994), and the Everglades is now the subject of a large-scale restoration

135   project (Davis & Ogden, 1994). Using structural equation modeling (path analysis) and a

136   model comparison approach, we identified possible causal models quantifying the

137   indirect, direct and total effects of drought, nutrient enrichment and trophic interactions

138   on small aquatic consumers in the Everglades. This analysis provides greater insight into

139   possible mechanistic models describing how basal consumer densities are controlled in

140   this ecosystem, informing restoration policies and practices.

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143   **Methods**

144   *Field Sampling and Sample Processing*

145   In November and December 2005, we sampled fish, amphibian and aquatic invertebrate

146   communities in 28 sites across the Florida Everglades (Everglades National Park, Water

147   Conservation Areas, and Loxahatchee National Refuge; approximately 25°19'N,

148   80°56'W) (Fig. 1). Sampling sites were selected from a larger set of possible study sites

149   identified by a Generalized Random Tessellation Stratified (GRTS) survey design

150   (Stevens and Olsen 2003) applied to the Greater Everglades ecosystem (Scheidt and

151   Kalla 2007). The GRTS design provides a specially balanced sample of the ecosystem;

152   sites were selected for this study because they were located in wet-prairie slough habitats

153   that are the focus of management concern because of their role as foraging habitats for

154   wading birds (Trexler and Goss 2009); wet prairie sloughs are characterized by

155   spikerush-dominated (*Eleocharis cellulosa* Torr.) emergent vascular plants (Gunderson

156   1994) and large standing stocks of periphyton mats formed by benthic algae, detritus,

157   fungi and bacteria (Turner *et al*. 1999). Sargeant et al. (2010) and Table 1 provide further

158   description of the conditions at these sites.

159   We sampled small fish and amphibians (<8 cm) and large invertebrates (snails,

160   crayfish, grass shrimp, and large insects, >5 mm) using a standardized throw-trap

161   sampling protocol (Jordan, Coyne, & Trexler, 1997) with 1-m^2 throw traps enclosed by 2-

162   mm mesh. Traps were cleared using a bar seine (2-mm mesh) and dip nets (1- and 5-mm

163   mesh), and vertebrates were euthanized by immersion in an MS-222 (tricaine

164   methanesulfonate) bath. Three throw-trap samples were collected per site. To sample

165   macroinvertebrate infauna (including nematodes, copepods, and cladocerans, inhabiting

166   periphyton mats, typically 0.25-8mm long), periphyton mat samples (6-cm diameter

167   cores from top to bottom of the mats, typically 2.5 cm deep) were collected from within

168   each throw trap (Liston and Trexler 2005). All animals captured were kept on ice in the

169   field, and then frozen for storage before identification and enumeration in the lab. The

170   densities (number·m^{-2}) of small primary and secondary consumers were determined for

171   each site by calculating the mean of the counts from the three throw-trap samples.

172   Herbivores included herbivorous fish, tadpoles, beetles, mayfly larvae and snails. Small

173   fish, newts, sirens, beetle larvae, odonate larvae, insects, crayfish and shrimp were

174   considered secondary consumers and are omnivorous or carnivorous in the Everglades.

175   Periphyton subsamples (15-30 mL) were haphazardly selected from thawed cores and

176   two different workers identified macroinvertebrates under a light microscope. Periphyton

177   macroinvertebrate density (number·m^{-2}) (Liston, 2006) was determined for each site

178   using the means of the three periphyton core samples. Details on species collected, their

179   densities and frequency of occurrence at sites, and their trophic classification (for throw-

180   trap organisms) are available in Table S1 of Supporting Information Appendix S1. All

181   trophic assignments were based on published and unpublished studies reporting gut

182   content (Gunderson and Loftus, 1993; Loftus 1999), stable isotopic (Loftus 1999;

183   Williams and Trexler 2006; Sargeant et al. 2010) and fatty acid profile (LL Belicka,

184   personal communication) analyses of specimens collected from the Everglades. Feeding

185   relationships of Everglades aquatic animals are complex, with widespread omnivory and

186   intraguild predation; a small fraction of animals sampled for this study are exclusively

187   carnivores (e.g., dragonfly naiads) feeding on other omnivores and herbivores. For

188   simplicity sake, we have lumped these animals as 'omnivores' for this study, consistent

189 with Morin's (1999) definition that omnivores are species that feed at more than one

190 trophic level.

191   We determined phosphorus levels, periphyton composition and hydrological

192 disturbance estimates corresponding to each of our sites. Periphyton volume (ml) was

193 estimated in the field by placing periphyton in graduated cylinders, and periphyton aerial

194 cover (%) was measured as the estimated percentage of the surface area enclosed by the

195 throw trap that was covered by periphyton. Separate periphyton samples (3 samples per

196 site, corresponding to locations of throw-trap samples) were obtained to determine total

197 phosphorus content (TP) (μg·g dry^{-1}), ash-free dry mass (AFDM) (g·m^{-2}) as an estimate

198 of biomass, percent nitrogen and organic content, chlorophyll *a* concentration (μg·g dry^{-1})

199 and density (μg·m^{-2}) and algal species composition as described by Gaiser *et al.* (2006;

200 see also Stevenson et al. 2002). Total phosphorus from periphyton is a valuable indicator

201 of nutrient enrichment because phosphorus is quickly absorbed by biota and does not

202 remain in the water column (Gaiser *et al.*, 2006). Algal species were categorized as green

203 algae, diatoms, non-filamentous bluegreen algae (cyanobacteria), filamentous blugreen

204 algae, and the combined relative abundance of diatoms and green algae was used in

205 analyses because those species are thought to be more palatable to consumers (Geddes &

206 Trexler, 2003). Using the Everglades Depth Estimation Network (EDEN) hydrological

207 estimation tool (http://sofia.usgs.gov/eden/stationlist.php), we calculated time since

208 flooding as the number of days since flooding after the most recent drying event (water

209 levels <5 cm). Using this as a measure of time to recover following a drought,

210 hydrological disturbance is inversely related to time since flooding. Sampling occurred

211   in the late wet season when marshes were near peak water depths following summer

212   rains.

213

214   *Data Analysis*

215   To examine complex interactions between these variables in a food-web context,

216   we used structural equation modeling to identify relationships between TP levels, time

217   since flooding, periphyton AFDM, the relative abundance of green algae and diatoms, the

218   density of periphyton macroinvertebrate infauna and the densities of small consumers

219   (fish and large invertebrates from throw-trap samples). Structural equation modeling

220   enables analysis of systems involving multiple simultaneous cause-effect relationships, in

221   contrast to reductionist approaches that examine these relationships singly, with the

222   potential to improve understanding of interaction networks typical of ecological

223   communities (Grace, 2006). For example, it can be used to identify species interactions

224   and their direct, indirect and total effects (Johnson, Huggins, & DeNoyelles, 1991;

225   Wootton, 1994a,b). This method can be applied to experiments (e.g., Johnson *et al.*,

226   1991; Wootton, 1994a,b) or observational data recorded along gradients of natural

227   variability (e.g., Elmhagen & Rushton, 2007; Riginos & Grace, 2008).

228   We developed seven *a priori* models describing hypothesized causal mechanisms

229   for how disturbance, productivity and trophic interactions may determine the densities of

230   small consumers via direct and indirect pathways, based on results of previous studies

231   and theoretical expectations (see Supporting Information Appendix S2 for detailed

232   descriptions of each model and rationale). Models were based on bottom-up control only

233   or reciprocal relationships (both bottom-up and top-down controls) between consumers

234   and prey. Specifically, top-down control was proposed between 1) omnivores and

235   infauna, 2) infauna and periphyton biomass, 3) herbivores and periphyton biomass, and

236   4) omnivores and periphyton biomass. The relationship between herbivores and

237   omnivores was evaluated by comparing models that contained a causal path from

238   herbivores to omnivores to models that assumed no causal link between them. We were

239   unable to include a possible top-down relationship between omnivore density and

240   herbivore density due to empirical underidentification. A model is considered identified

241   if unique estimates can be determined for all of its parameters, which requires a sufficient

242   number of observed variables given the number of parameters to solve (Grace, 2006). In

243   some cases, a model can be theoretically identified but empirically underidentified

244   because of correlations inherent in the data that effectively reduce the number of

245   observations (Kline, 2005; Grace, 2006). However, the small omnivores in question may

246   be unlikely to limit herbivores of similar size.

247   Structural equation modeling (path analysis) was conducted using AMOS 7.0

248   (Amos Development Corporation, Spring House, PA, USA). The site was considered the

249   unit of observation (n=28), with the periphyton, hydrological and consumer variables

250   calculated for each site. All variables were $\log_{10}(y + 1)$ transformed to improve

251   univariate normality and reduce nonlinearities in relationships. Despite transformations,

252   the data continued to show signs of deviation from normality (as indicated by univariate

253   analyses, Mardia's coefficient for multivariate kurtosis, and Mahalanobis d), so we used

254   bootstrapping (based on 2000 bootstrap samples) to test absolute model fit using the

255   Bollen-Stine chi-square test. When data are highly non-normal, traditional chi-square

256   tests of model fit can be overly conservative and the Bollen-Stine chi-square test, which

257   uses bootstrapping to determine the probability of model fit, is recommended as an

258   alternative (Byrne, 2000; Grace, 2006). Models were compared using the Bayesian

259   Information Criterion (BIC) (lower BIC values indicate better fit), which weighs

260   improvement in model fit against model complexity (Claeskens & Hjort, 2008). We

261   report BIC instead of the more common Akaike's Information Criterion (AIC) because

262   BIC provides more consistent model selection as model complexity increases; BIC

263   applies a higher penalty than AIC for adding parameters (Claeskens & Hjort, 2008:

264   Chapter 4) and is more conservative than AIC in the presence of model uncertainty

265   (Burnham and Anderson 2010: pp 271-273). Because we used a model-comparison

266   approach, path coefficients are presented, but were not tested for statistical significance

267   (e.g., Gotelli & Ellison, 2006). We present the unstandardized and standardized path

268   coefficients fitted by maximum likelihood for each direct causal path in the final models.

269   Path coefficients in the model represent partial regression coefficients. Reported total

270   effects of environmental gradients are the sum of direct and indirect causal paths. Our

271   approach should be viewed as exploratory and hypothesis-generating rather than

272   confirmatory given our limited trophic specification made necessary by high sample-size

273   requirements of our model fitting and comparison approach.

274

275   **Results**

276   Samples contained many of the small aquatic fauna common to the Everglades

277   (see Table S1 of Supporting Information Appendix S1). Throw-trap samples were

278   dominated by small fish, grass shrimp, crayfish and dragonfly larvae. Of these, grass

279   shrimp (*Palaemonetes paludosus*, Gibbes) had the largest mean density across all the

280   sites of the omnivorous species and was present in more than 70% of the sites. Least

281   killifish (*Heterandria formosa*, Girard), mosquitofish (*Gambusia holbrooki*, Girard) and

282   bluefin killifish (*Lucania goodei*, Jordan) were also very common and thus typically

283   contributed notably to omnivore density. Herbivorous fish and large invertebrates were

284   lower in density, dominated by planorbid snails (*Planorbella* spp.) with the highest mean

285   density, and flagfish (*Jordanella floridae*, Goode and Bean) at the largest number of sites.

286   Cladocerans, nematodes, copepods, water mites, ostracods, amphipods and dipteran

287   larvae comprised the largest numbers of infaunal macroinvertebrates inhabiting

288   periphyton. Larger beetles, dragonfly larvae and snails were less numerous in periphyton

289   and found at fewer sites.

290   Sites spanned a wide range of hydrological and nutrient levels (Table 1), and time

291   since flooding was positively correlated with periphyton TP (Spearman correlation: $r_s =$

292   0.68). Consistent with several other studies in the Everglades, many attributes of

293   periphyton were associated with time since flooding and/or periphyton TP (Table 2).

294   Increases in nutrient levels and time since flooding were correlated with decreases in

295   periphyton biomass, periphyton volume and the relative abundances of bluegreen and

296   filamentous bluegreen algae, but also with increases in organic content, chlorophyll *a*

297   concentration, and the relative abundances of green algae and diatoms. The density of

298   omnivores increased coincident with nutrient levels and (to a lesser extent) recovery time

299   following drought, while infaunal and herbivore densities did not exhibit strong

300   correlations with either variable (Table 2; Figs. 2 and 3).

301   A comparison of model BIC values indicated that one model (Model 6 in

302   Supporting Information Appendix S2) was preferred to the others (the difference between

303   the BIC of this model and the next best model was >2) (Table 3). Two other models

304   (Model 1 and Model 7 in Supporting Information Appendix S2) had slightly higher BIC

305   values, but only Model 6 and Model 1 showed adequate absolute fit to the data (Bollen-

306   Stine chi-square tests were not statistically significant at the 0.05 level; Table 3).

307   In Model 6 (Fig. 4), changes in periphyton biomass and community structure,

308   driven by increasing phosphorus, are transmitted to omnivores indirectly. Increases in

309   the relative abundance of diatoms and green algae, and increases in periphyton biomass,

310   increased infauna density, which in turn had a positive effect on omnivore density.

311   Omnivores had a negative top-down effect on infauna, and infauna had a small but

312   negative effect on periphyton biomass. Both periphyton biomass and the relative

313   abundance of diatoms and green algae were negatively related to herbivore density, while

314   increasing herbivores increased omnivore density with no reciprocal top-down effect.

315   Model 1 (Fig. 5) included only bottom-up effects and incorporated direct effects

316   of periphyton biomass and relative abundance of diatoms and green algae on omnivore

317   density. Direct effects of time since flooding and periphyton TP were generally similar

318   to those in Model 6. Relationships between trophic groups were bottom-up and mostly

319   positive (increases in prey resulted in increases in consumers) or weak, with the

320   exception of herbivores.

321   Some patterns were shared by Model 6 and Model 1. Herbivore density was

322   negatively related to periphyton biomass and the relative abundance of diatoms and green

323   algae in both models. The total effect of periphyton TP was positive for omnivores and

324   herbivores, but was nearly zero for infauna (Table 4). In Model 1 this resulted only from

325   phosphorus's effect on periphyton community structure and biomass, but in Model 6 the

326   negligible total effect of phosphorus was largely driven by top-down effects. Time since

327   flooding increased infauna density and omnivore density directly, but decreased

328   herbivore density directly in both models. However, time since flooding increased

329   periphyton biomass and decreased the relative abundance of diatoms and green algae,

330   making the total effect of hydrological disturbance negative for infauna and omnivores

331   (Table 4). The effect of time since flooding was more complex for herbivores. In Model

332   6, the negative effect was caused by a strong direct path and multiple indirect effects. In

333   Model 1, the total effect was weaker, and the negative direct effect was moderated by

334   positive indirect effects through periphyton. The total effects of periphyton TP on

335   periphyton and consumers were larger than those of time since flooding in both models

336   (Table 4), with the exception of infauna density.

337

338

339   **Discussion**

340   Using structural equation modeling, we identified two possible mechanistic

341   models describing the effects of nutrient enrichment, disturbance and food-web

342   interactions on small consumers in the Florida Everglades. The best-supported model

343   (Model 6) showed evidence for top-down control of periphyton infauna densities, and

344   suggested that trophic cascades may help maintain periphyton biomass against herbivory

345   in the Everglades. However, the BIC value of Model 1 (a model allowing bottom-up

346   effects only and including omnivory) was only slightly higher, indicating that it also

347   deserves consideration. While other studies have illustrated the importance of

348   hydrological disturbance in shaping temporal trends in Everglades aquatic communities,

349 our findings emphasize a greater role of nutrient gradients in contributing to consumer

350 densities across large spatial scales in the late wet season, when direct effects of previous

351 drying were relatively weak. Further, the structural equation models identified the effects

352 of food quality (indicated by algal community structure) and food or habitat quantity

353 (indicated by periphyton biomass), allowed effects of nutrient enrichment and hydrology

354 to be disentangled, and provided insight into direct versus indirect effects in this system.

355 Both models incorporated bottom-up effects initiated by increases in nutrients

356 (measured by total phosphorus levels in periphyton). Increasing phosphorus appeared to

357 drive compositional changes in periphyton, including shifts in the dominant algal species,

358 the proportion of organic content and the overall biomass and volume of periphyton.

359 These findings mirror those of several other studies correlating phosphorus addition with

360 increases in the relative abundance of diatoms and green algae and organic content, but

361 decreases in the relative abundance of filamentous bluegreen algae and biomass of

362 bluegreen algae and periphyton (McCormick *et al.*, 1996; Gaiser *et al.*, 2005, 2006). The

363 proportion of periphyton comprised of organic material, diatoms and green algae may

364 reflect food quality since these components are probably more palatable than inorganic

365 components, bluegreen algae or filamentous bluegreen algae (Geddes & Trexler, 2003).

366 Phosphorus addition increases these palatable elements, but decreases the total organic

367 biomass of periphyton (e.g., food quantity and habitat for infauna).

368 These changes in periphyton quality and quantity appear to be the indirect link

369 between phosphorus enrichment and consumer densities. In both models, infaunal

370 density directly increased with periphyton biomass and the proportion of green algae and

371 diatoms. In Model 1, where primary production was directly linked to omnivore density,

372   omnivores responded positively to the relative abundance of diatoms and green algae,

373   and negatively to periphyton biomass (although this latter relationship was quite weak in

374   magnitude). This is in contrast to Model 6, in which changes in food are transmitted to

375   omnivores indirectly through infauna and herbivores. Interestingly, periphyton biomass

376   and the relative abundance of diatoms and green algae had strong negative direct effects

377   on herbivore density in both models, generally contrasting with their effects on infauna

378   and omnivores. A possible explanation may be found in the composition of the herbivore

379   community; flagfish comprised a significant portion of the herbivores in our samples and

380   they may be poor competitors (Trexler *et al.*, 2005). Nonetheless, herbivore density

381   actually increased with nutrient enrichment (i.e., the total effect of periphyton TP) due to

382   the indirect pathways via periphyton biomass. Both models indicate that the quality of

383   periphyton is as important as total food biomass, consistent with previous work

384   demonstrating an increased ability of some consumers to feed on palatable elements

385   following a physical break-up in the periphyton mat (Geddes & Trexler, 2003).

386   In the Everglades, the maintenance of large expanses of periphyton mats and

387   apparent limits on infaunal density even in the face of nutrient enrichment may be

388   evidence for a trophic cascade (Turner *et al.*, 1999; Liston, 2006). Trophic cascades are

389   widespread in aquatic systems (Shurin *et al.*, 2002), often driven by predation of

390   macroinvertebrates by fish (e.g., Wootton & Power, 1993). Few studies of top-down

391   effects have been conducted in wetlands, but some show that small fish and insect

392   predators can reduce invertebrate numbers (Batzer, 1998; Peck & Walton, 2008), while

393   others have not found effects of small predators (Corti *et al.*, 1997). Empirical support

394   for trophic cascades in the Everglades has been lacking (Dorn, Trexler, & Gaiser, 2006;

395   Chick, Geddes, & Trexler, 2008). In the current study, small fish and invertebrates, but

396   not infauna, increased with nutrients, a pattern potentially consistent with a trophic

397   cascade based on predictions from food web theory (Power, 1992). The relative strength

398   of Model 6 suggests that both bottom-up and top-down forces are important in shaping

399   the densities of basal consumers in the Everglades. Like all the models considered,

400   Model 6 includes bottom-up relationships between primary production (periphyton) and

401   higher trophic levels. Increases in phosphorus levels drive changes in periphyton

402   community structure, increasing the proportion of highly palatable algal species while

403   simultaneously reducing the total organic biomass of periphyton. Model 6 assumes that

404   these changes in primary production are transmitted indirectly, through primary

405   consumers (infaunal macroinvertebrates and herbivorous fish, invertebrates, and

406   tadpoles), to omnivorous fish and invertebrates. Omnivores, in turn, limit infauna

407   density, and infauna density has a negative effect on periphyton biomass. These

408   relationships are likely to underpin the pattern of increasing omnivore density, but not

409   infauna density, with nutrient enrichment (e.g., Fig. 3). The positive effect of omnivores

410   (through macroinvertebrate infauna) on periphyton biomass implies that a trophic cascade

411   helps maintain periphyton mats, but herbivores may simultaneously act to stimulate

412   periphyton growth (see below), indicating that multiple factors are important in

413   controlling periphyton biomass.

414   This contrasts with the exclusively bottom-up structure of Model 1. The fact that

415   two very different models had similar support may be explained by the role of omnivory.

416   Model 1 allows for omnivores to feed directly on periphyton, and this may result in

417   similar net effects of periphyton TP as are found in Model 6 in which omnivory is

418   removed. Trophic cascades are generally thought to be limited by omnivory (Polis &

419   Strong, 1996), and could also be restricted in the Everglades by the associative resistance

420   afforded palatable algae by the physical or algal composition of periphyton mats (Geddes

421   & Trexler, 2003; Chick *et al.*, 2008). However, past studies have not found support that

422   omnivorous fishes and invertebrates assimilate more periphyton as nutrients increase

423   (Williams & Trexler, 2006).

424   Herbivorous small fish and invertebrates played a different role than other

425   consumer groups in both models. Herbivore density had a positive effect on omnivore

426   density, presumably via predation where predators were unable to limit prey numbers.

427   The similar size of individuals in the omnivore and herbivore groups may have prevented

428   top-down control; some of the herbivores may have been too large or well-defended for

429   the small omnivores to consume them. In Model 6, herbivores had a positive top-down

430   effect on periphyton biomass, seemingly inconsistent with an expected predator-prey

431   relationship. While a negative effect of predation may be more expected, positive effects

432   could occur through nutrient regeneration (Geddes & Trexler, 2003).

433   Previous studies of Everglades fauna have frequently found negative correlations

434   between small fish and/or macroinvertebrate densities and measures of disturbance

435   (Trexler *et al.*, 2002, 2005; Liston, 2006). The direct effect of time since flooding was

436   positive for infauna and omnivore density in both models, suggesting their numbers

437   increased with recovery time following droughts. However, the opposite pattern was

438   found for herbivores, probably stemming from dominance of flagfish, which tend to

439   decrease with time following droughts (Trexler *et al.*, 2005). Time since flooding was

440   important in contributing to algal community structure, reducing the proportion of

441   diatoms and green algae. Our results are potentially inconsistent with a previous study

442   (Gottlieb *et al.*, 2006) reporting higher relative abundance of diatoms in long-hydroperiod

443   sites, but that study did not separate effects of phosphorus from those of hydrology,

444   which tend to be correlated. Despite a negative direct effect, the overall correlation

445   between time since flooding and the relative abundance of green algae and diatoms was

446   positive, possibly explaining the differences in results between studies. Effects of

447   hydrological disturbance were somewhat weaker than the effects of nutrient enrichment,

448   and the total effect of time since flooding was negative for all three consumer groups as a

449   result of numerous indirect effects. Reduced effects of hydrology relative to nutrients in

450   this study may have resulted from focusing on spatial, rather than temporal, variability

451   and by sampling at the end of the wet season when few sites had been recently dry. This

452   study also used partial regression coefficients to estimate effects of hydrology and

453   nutrients, possibly resulting in different findings than studies relying on correlation alone.

454   Structural equation models can provide important advances in understanding

455   Everglades food webs. However, there are some shortcomings of our study. As is the

456   case for all studies examining open, natural food webs, a limitation of our analysis is that

457   models were necessary simplifications of the true food web. We were unable to include

458   the effects of larger predators, which may have exerted further top-down control on

459   consumers, and detritus-based components of the food web. Effects of predatory fish,

460   such as gar, may actually be included in direct effects of time since flooding, since they

461   are limited to deeper refugia when water levels are low (Chick, Ruetz, & Trexler, 2004).

462   In addition, although we gained some resolution by categorizing consumers into three

463   groups based on size and diet, individual species may exhibit unique and contrasting

464   patterns not fully described by this analysis. For example, Liston (2006) identified

465   effects of hydrology and/or nutrient levels on certain infaunal groups that were

466   sometimes at odds with patterns observed for infauna as a whole. Finally, our study did

467   not incorporate sites with phosphorus levels greatern than 760 μg g^{-1} dry periphyton

468   tissue; at higher levels periphyton mats can completely disappear and densities of fish

469   and macroinvertebrates can be reduced (King & Richardson, 2007; Liston *et al.,* 2008;

470   Rejmánková, Macek, & Epps, 2008). Future research should address food-web structure

471   at artificially high nutrient levels, and ideally incorporate larger predatory fishes and

472   wading birds as a fourth trophic level.

473   By using a multi-model, structural equation modeling approach (Grace, 2006),

474   this study provides insight into direct and indirect effects and the apparently limited role

475   of top-down control in shaping consumer densities. To our knowledge, this is the first

476   such analysis of a natural wetlands food web incorporating multiple trophic levels. Our

477   results should guide future research to on the mechanisms underlying our proposed causal

478   pathways.

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480

481   **Acknowledgments**

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499 **References**

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Table 1 Descriptive statistics for environmental gradients and consumer densities ($n = 28$)

Variables	Minimum Value	Maximum Value	Mean ± SE
Periphyton TP (µg·g dry^{-1})	53	760	272 ± 39
Time since flooding (days)	160	2164	611 ± 134
Periphyton biomass (AFDM) (g·m^{-2})	4	540	107 ± 29
Small omnivore density (number·m^{-2})	1	318	35 ± 11
Small herbivore density (number·m^{-2})	0.0	9.7	1.5 ± 0.41
Periphyton infauna density (number·m^{-2})	409	105,123	37,562 ± 5,622

Table 2 Spearman correlations between major environmental gradients (time since

flooding and periphtyon total phosphorus [TP]) and periphyton characteristics and

consumer densities ($n = 28$)

	Time since flooding, r_s	Periphtyon TP, r_s
Total periphyton volume (ml)	-0.59	-0.88
Total periphyton aerial cover (%)	-0.67	-0.87
Periphyton biomass (AFDM) (g·m^{-2})	-0.68	-0.92
Percent organic content (%)	+0.64	+0.82
Percent carbon (%)	+0.66	+0.84
Percent nitrogen (%)	+0.64	+0.86
Chlorophyll *a* concentration (µg·g dry^{-1})	+0.57	+0.78
Chlorophyll *a* density (µg·m^{-2})	-0.65	-0.88
Relative abundance of non-filamentous bluegreen algae	-0.42	-0.53
Relative abundance of filamentous bluegreen algae	-0.43	-0.80
Relative abundance of green algae	+0.51	+0.61
Relative abundance of diatoms	+0.30	+0.50
Small omnivore density (number·m^{-2})	+0.31	+0.65
Small herbivore density (number·m^{-2})	+0.20	+0.29
Periphyton infauna density (number·m^{-2})	-0.02	+0.03

Table 3 Comparison of structural equation models (see also detailed descriptions in Supporting Information Appendix S2). The BIC and Bollen-Stine chi-square p-values of the best models are in *bold*

Model	Infauna - Periphyton	Herbivores - Periphyton	Omnivores - Periphyton	Omnivores - Infauna	Omnivores - Herbivores	k^1	BIC	Bollen-Stine X^2 *P*-value
1	Bottom-up	Bottom-up	Bottom-up	Bottom-up	Bottom-up	23	**95.197**	**0.15**
2	Bottom-up	Bottom-up		Bottom-up	Bottom-up	21	104.248	0.025
3	Bottom-up	Bottom-up		Bottom-up		20	117.951	0.004
4	Bottom-up	Bottom-up	Bottom-up	Bottom-up		22	106.133	0.027
5	Bottom-up & Top-down	Bottom-up & Top-down		Bottom-up & Top-down		23	108.390	0.004
6	Bottom-up & Top-down	Bottom-up & Top-down		Bottom-up & Top-down	Bottom-up	24	**92.234**	**0.12**
7	Bottom-up & Top-down	Bottom-up & Top-down	Bottom-up & Top-down	Bottom-up & Top-down	Bottom-up	27	95.781	0.033

[1]number of parameters

Table 4 Indirect, direct and total effects of phosphorus enrichment (periphyton TP) and time since flooding for Models 6 and 1

	Log Periphyton TP			Log Time Since Flooding		
	Direct	**Indirect**	**Total**	**Direct**	**Indirect**	**Total**
Model 6						
Log Periphyton Biomass	-1.95 (-1.02)	+0.21 (+0.11)	-1.74 (-0.91)	+0.04 (+0.02)	-0.06 (-0.04)	-0.02 (-0.01)
Log Relative Abundance of Diatoms + Green Algae	+0.66 (+0.90)	0	+0.66 (+0.90)	-0.20 (-0.32)	0	-0.20 (-0.32)
Log Infauna Density	0	+0.05 (+0.03)	+0.05 (+0.03)	+0.18 +(0.12)	-0.30 (-0.21)	-0.12 (-0.09)
Log Herbivore Density	0	+0.48 (+0.57)	+0.48 (+0.57)	-0.37 (-0.51)	+0.20 (+0.27)	-0.17 (-0.24)
Log Omnivore Density	0	+0.83 (+0.68)	+0.83 (+0.68)	+0.17 (+0.16)	-0.37 (-0.36)	-0.21 (-0.20)
Model 1						
Log Periphyton Biomass	-1.77 (-0.92)	0	-1.77 (-0.92)	-0.003 (-0.002)	0	-0.003 (-0.002)
Log Relative Abundance of Diatoms + Green Algae	+0.66 (+0.90)	0	+0.66 (+0.90)	-0.20 (-0.32)	0	-0.20 (-0.32)
Log Infauna Density	0	+0.06 (+0.03)	+0.06 (+0.03)	+0.20 (+0.14)	-0.33 (-0.23)	-0.13 (-0.09)
Log Herbivore Density	0	+0.29 (+0.36)	+0.29 (+0.36)	-0.12 (-0.18)	+0.05 (+0.07)	-0.08 (-0.11)
Log Omnivore Density	0	+0.88 (+0.71)	+0.88 (+0.71)	+0.01 +(0.01)	-0.23 (-0.22)	-0.24 (-0.22)

Standardized coefficients are shown in parentheses.

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3   **Figure Legends**
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8   **Fig. 1** Map of the study area with the location of sampling sites in the Florida Everglades
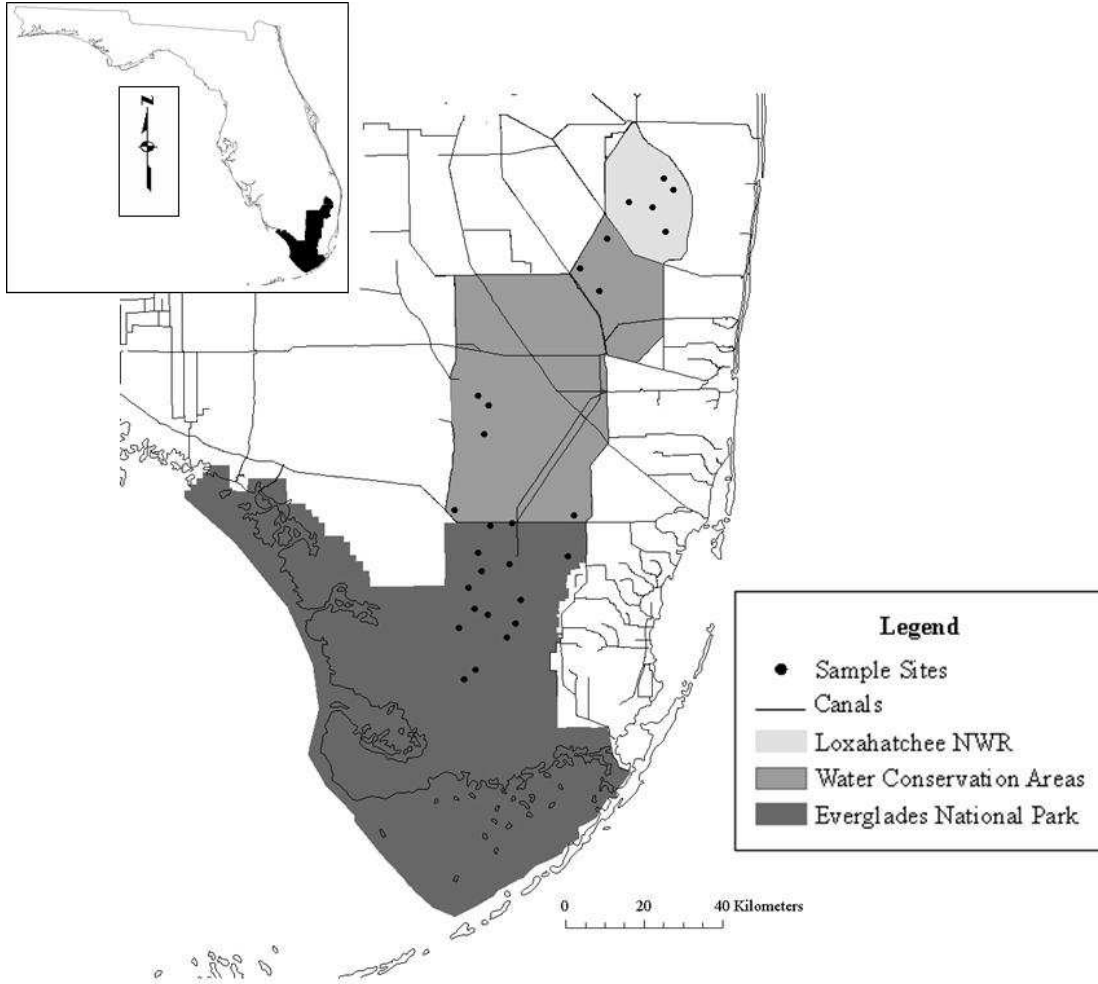9
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13   **Fig. 2** Relationships between consumer densities and time since flooding
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18   **Fig. 3** Relationships between consumer densities and periphyton total phosphorus (TP)
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20   levels
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25   **Fig. 4** Model with the lowest BIC value (Model 6), incorporating bottom-up and top-
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27   down effects and no omnivory. All variables were log-transformed. Unstandardized and
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29   standardized (in parentheses) path coefficients are shown, along with squared multiple
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31   correlation coefficients (R^2) at the upper right corner of each endogenous variable. The
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33   bidirectional arrow between periphyton total phosphorus and time since flooding
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35   represents their non-causal bivariate covariance (correlation if standardized)
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41   **Fig. 5** Model with the second lowest BIC value (Model 1), incorporating bottom-up
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43   effects only and omnivory. All variables were log-transformed. Unstandardized and
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45   standardized (in parentheses) path coefficients are shown, along with squared multiple
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47   correlation coefficients (R^2) at the upper right corner of each endogenous variable. The
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49   bidirectional arrow between periphyton total phosphorus and time since flooding
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51   represents their non-causal bivariate covariance (correlation if standardized)
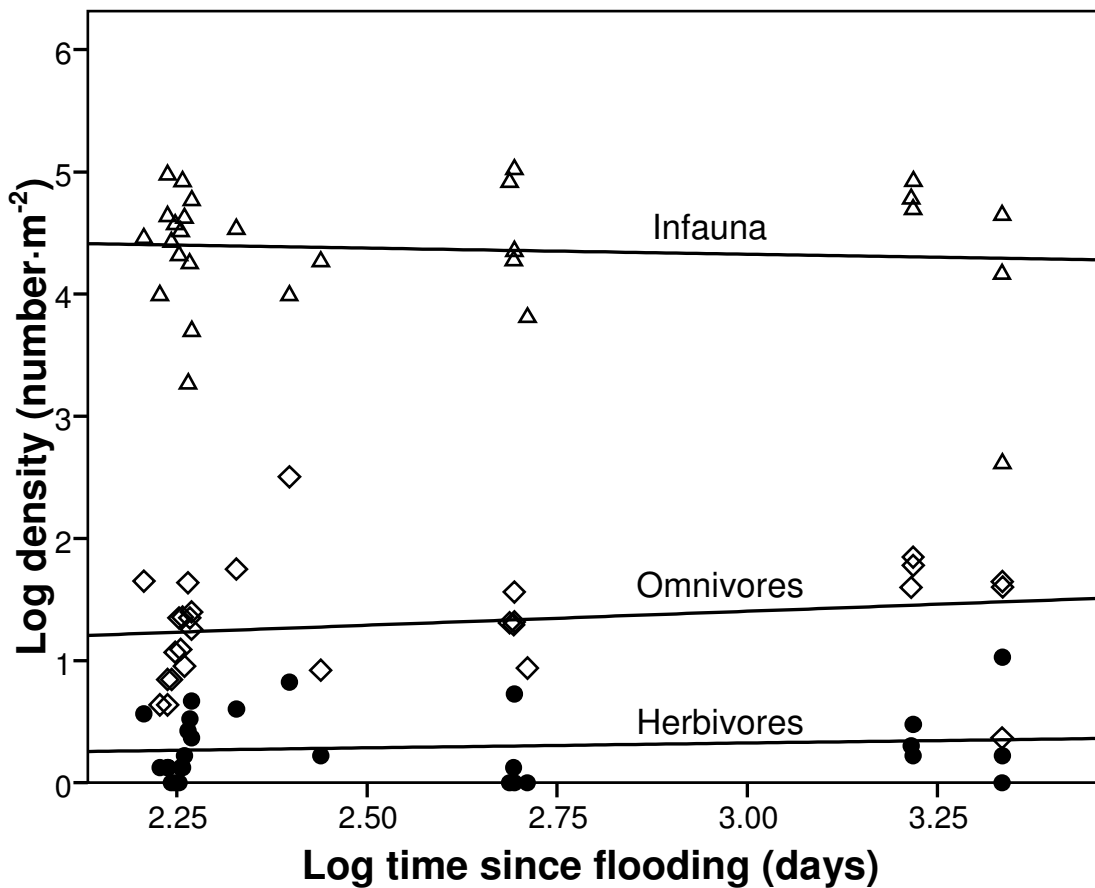52
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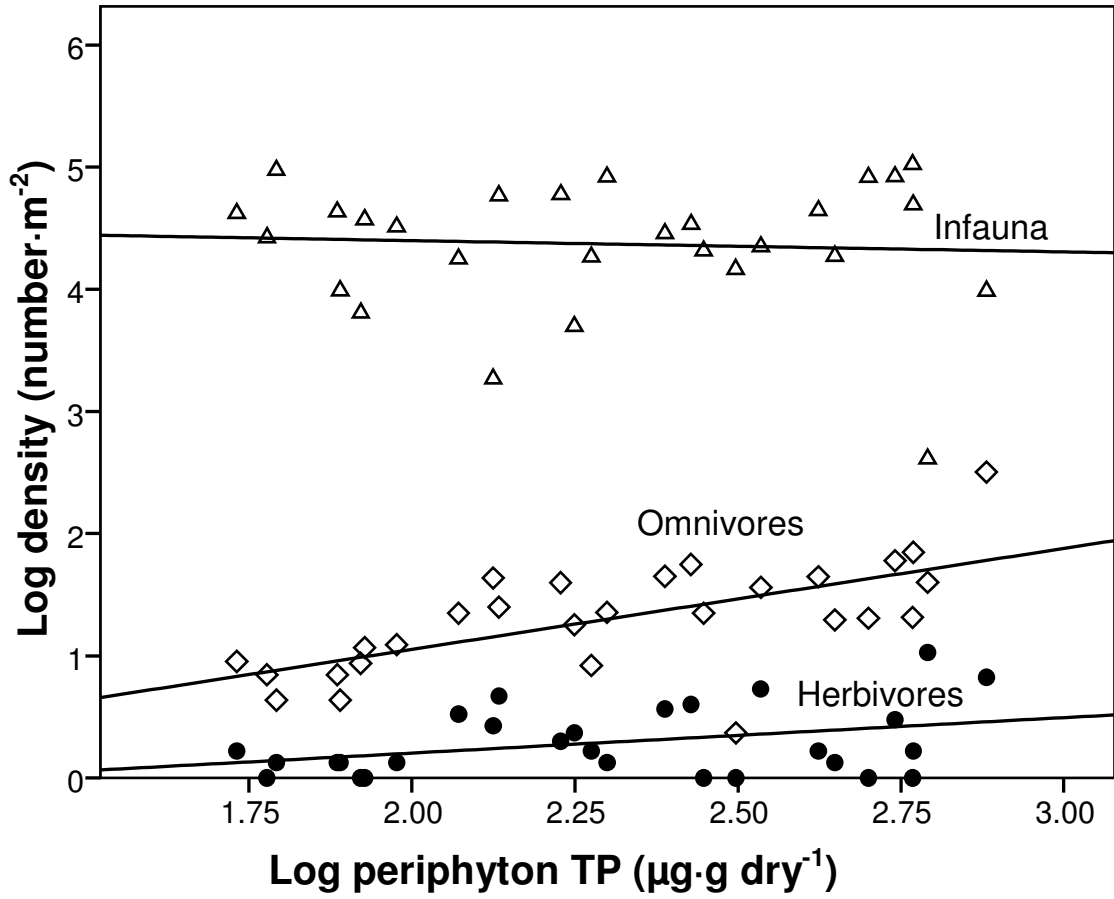58
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Fig. 1

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Fig. 4

Fig. 5

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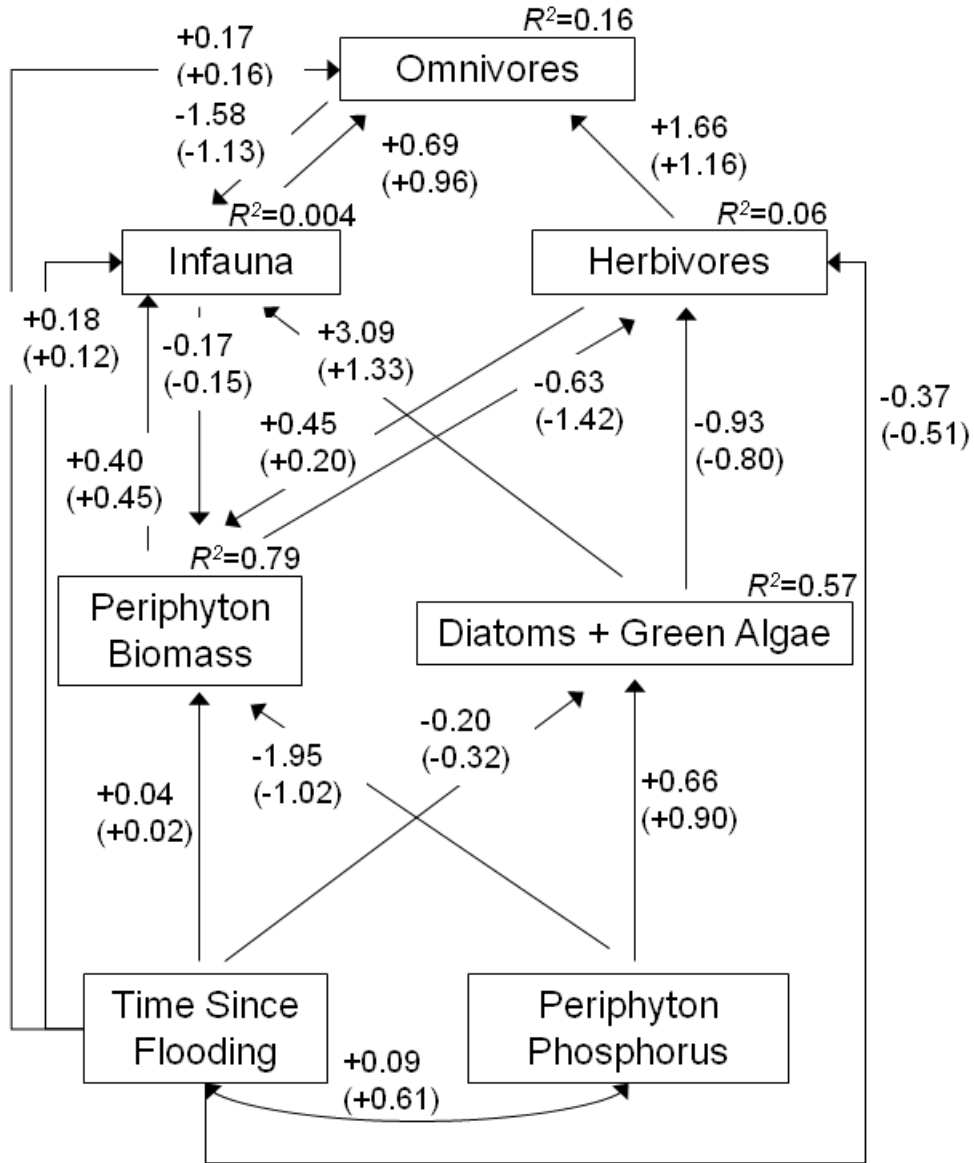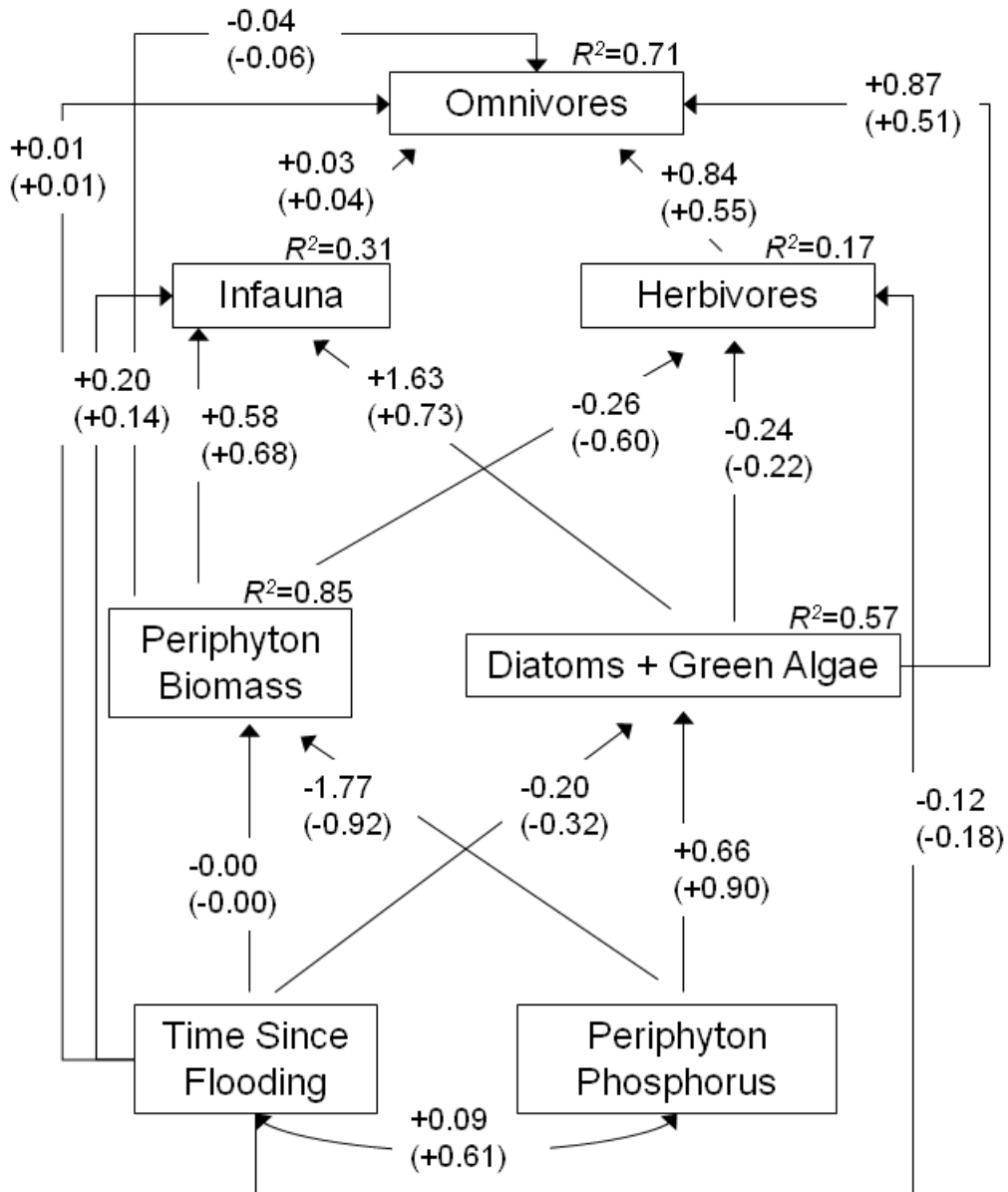42
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Supporting Information, Appendix S1

Table S1 Density and frequency of occurrence of taxonomic groups contributing to

trophic categories. We define omnivores as species feeding at more than one trophic level

and include several taxa that are carnivores acting as intraguild predators, as well as

potentially feeding on herbivores.

Taxonomic group	Common name	Mean density $(\# \ m^{-2})$ (SE)	Number of sites
Throw-trap omnivores			
Palaemonetes paludosus	Grass shrimp	13 (5.4)	20
Heterandria formosa	Least killifish	7 (2.5)	21
Gambusia holbrooki	Mosquitofish	5 (1.5)	23
Lucania goodei	Bluefin killifish	2.4 (0.70)	20
Procambarus fallax	Slough crayfish	1.7 (0.89)	14
Celithemis eponina (larva)	Halloween pennant dragonfly	1.0 (0.25)	18
Procambarus alleni	Everglades crayfish	1.0 (0.39)	9
Fundulus chrysotus	Golden topminnow	0.8 (0.15)	24
Coenagrionidae (larva)	Damselfly	0.6 (0.26)	16
Pelocoris femoratus	Alligator flea	0.5 (0.18)	14
Elassoma evergladei	Everglades pygmy sunfish	0.4 (0.14)	9
Lepomis marginatus	Dollar sunfish	0.4 (0.11)	13
Libellula needhami (larva)	Needham's skimmer dragonfly	0.3 (0.10)	13
Procambarus spp.	Unknown procambarid crayfish	0.3 (0.14)	9
Fundulus confluentus	Marsh killifish	0.16 (0.063)	7
Erythemis simplicicollis (larva)	Eastern pondhawk dragonfly	0.1 (0.11)	2
Belostoma spp.	Giant water bug	0.10 (0.041)	6
Brachymesia gravida (larva)	Four-spotted pennant dragonfly	0.10 (0.084)	2
Enneacanthus gloriosus	Bluespotted sunfish	0.08 (0.053)	3
Coryphaeschna ingens (larva)	Regal darner dragonfly	0.04 (0.020)	3
Cyprinodon variegatus	Sheepshead minnow	0.02 (0.024)	1
Lepomis punctatus	Spotted sunfish	0.02 (0.017)	2
Notophthalmus viridescens	Peninsula newt	0.02 (0.024)	1

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Taxonomic group	Common name	Mean density ($\# \, m^{-2}$) (SE)	Number of sites
Noturus gyrinus	Tadpole madtom	0.01 (0.012)	1
Cybister spp. (larva)	Water beetle	0.01 (0.012)	1
Pseudobranchus axanthus	Dwarf siren	0.01 (0.012)	1
Throw-trap herbviores			
Planorbella spp.	Planorbid snail	0.6 (0.36)	7
Jordanella floridae	Flagfish	0.4 (0.12)	17
Poecilia latipinna	Sailfin molly	0.18 (0.079)	5
Rana spp. (tadpole)	Ranid frog	0.12 (0.075)	3
Coleoptera (adult)	Aquatic beetle	0.07 (0.040)	4
Ephemeroptera (larvae)	Mayfly	0.06 (0.030)	4
Haitia spp.	Unidentified physid snail	0.06 (0.049)	2
Pomacea paludosa	Apple snail	0.01 (0.012)	1
Periphyton infauna			
Cladocera	Cladoceran; water flea	9000 (1700)	27
Nematoda	Nematode; roundworms	6000 (1100)	27
Chironomidae (larva) (excluding Tanypodinae)	Chironomid; non-biting midge	5100 (960)	28
Harpacticoida	Harpacticoid copepod	5000 (2200)	21
Acari	Water mite	5000 (1800)	28
Ostracoda	Ostracod	4000 (900)	28
Amphipoda	Amphipod	900 (220)	26
Tanypodinae (larva)	Chironomid; non-biting midge	800 (150)	27
Dasyhelea spp. (larva)	Biting midge	600 (140)	27
Bezzia spp. (larva)	Biting midge	500 (140)	20
Cyclopoida	Cyclopoid copepod	220 (62)	23
Haitia spp.	Unidentified physid snail	120 (29)	17
Calanoida	Calanoid copepod	120 (55)	17
Copepoda	Unidentified copepod	100 (28)	16
Dryopidae (larva)	Long-toed water beetle	90 (44)	5
Ephemeroptera (larva)	Mayfly	70 (24)	14
Diptera (pupa)	Unidentified fly pupa	60 (14)	20
Heteroptera	Aquatic bug	40 (12)	13
Diptera (larva)	Unidentified fly	43 (9.9)	16
Trichoptera (larva)	Caddis fly	40 (18)	13
Ceratopogonidae (larva)	Biting midge	40 (21)	9
Tipulidae (larva)	Crane fly	21 (10)	6

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Taxonomic group	Common name	Mean density (# m^{-2}) (SE)	Number of sites
Stratiomyidae (larva)	Soldier fly	19 (9.4)	7
Pelocoris femoratus	Alligator flea	18 (6.9)	9
Collembola	Springtail	16 (7.4)	7
Coenagrionidae (larva)	Damselfly	15 (5.5)	11
Planorbella spp.	Planorbid snail	15 (8.6)	8
Coleoptera (adult)	Aquatic beetle	13 (6.1)	6
Berosus spp. (larva)	Aquatic beetle	13 (9.0)	3
Gastropoda	Unidentified snail	5 (4.4)	2
Enochrus spp. (larva)	Aquatic beetle	4 (2.7)	3
Dolichopodidae (larva)	Long-legged fly	3 (3.4)	1
Coleoptera (larva)	Aquatic beetle	3 (2.0)	3
Littoridinops monroensis	Cockscomb hydrobe	3 (2.1)	2
Anisoptera (larva)	Unidentified dragonfly	2 (1.9)	2
Erythemis simplicicollis (larva)	Eastern pondhawk dragonfly	0.7 (0.69)	1
Palaemonetes paludosus	Grass shrimp	0.4 (0.40)	1
Brachymesia gravida (larva)	Four-spotted pennant dragonfly	0.1 (0.12)	1

1   **Supporting Information, Appendix S2**

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3   **Candidate Models**

4   *Model Development*

5   We developed seven *a priori* structural equation models based on previous studies

6   and theoretical expectations. All models contained: 1) variables representing time since

7   flooding, periphyton total phosphorus, periphyton biomass (ash-free dry mass), the

8   combined relative abundance of diatoms and green algae, infauna density (from

9   periphyton core samples), herbivore density (from throw-trap samples), and omnivore

10   density (from throw-trap samples); 2) a covariance between time since flooding and

11   periphyton phosphorus; 3) direct effects of time since flooding on all variables except

12   periphyton phosphorus; and 4) direct effects of periphyton phosphorus on periphyton

13   biomass and the combined relative abundance of diatoms and green algae. Direct effects

14   of phosphorus enrichment on periphyton biomass and algal community structure have

15   been demonstrated previously (e.g., McCormick *et al.*, 1996; Gaiser *et al.*, 2005, 2006).

16   Hydrological impacts on consumer densities, periphyton biomass, and algal community

17   structure have been suggested by several studies (e.g., Trexler, Loftus, & Perry, 2005;

18   Gottlieb, Richards, & Gaiser, 2006; Liston, 2006). Thus, these elements were included in

19   all structural equation models. Models varied in their effects of variables representing

20   infaunal density, herbivore density, and omnivore density, based on models of food webs

21   and trophic interactions (e.g., Power, 1992). Models 1-4 included bottom-up effects (e.g.,

22   effect of infauna density on omnivore density) only, and differed in their inclusion of

23   omnivory (direct effect of periphyton biomass on omnivore density) and effects of

24   herbivores on omnivores. Models 5-7 included both bottom up effects and reciprocal

25   top-down effects (e.g., effect of omnivore density on infauna density), and also differed

26   in their inclusion of omnivory and relationships between herbivores and omnivores. We

27   were unable to test models containing reciprocal relationships between omnivore density

28   and herbivore density due to empirical underidentification.

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30   *Model 1: Bottom-up control, omnivory present*

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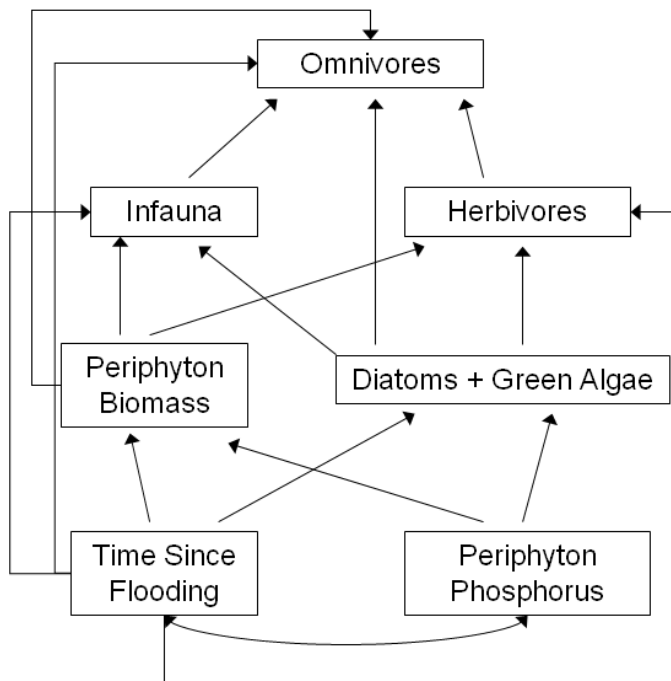
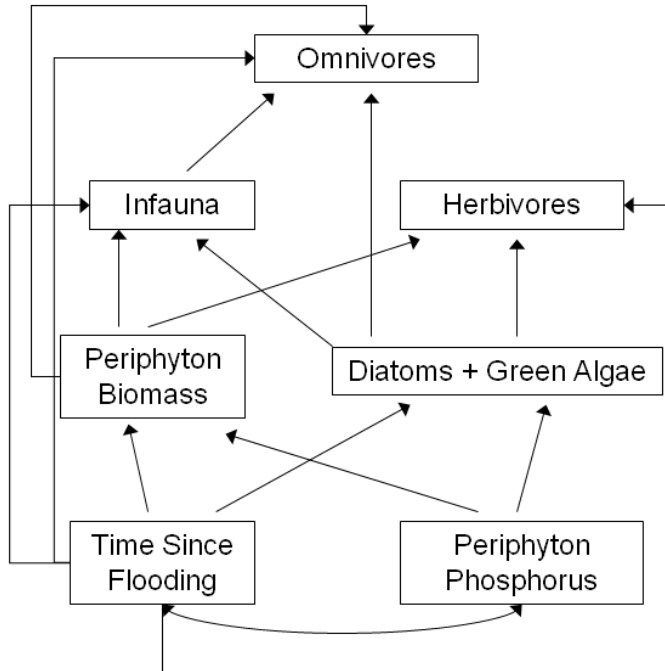38   *Model 2: Bottom-up control, omnivory absent*
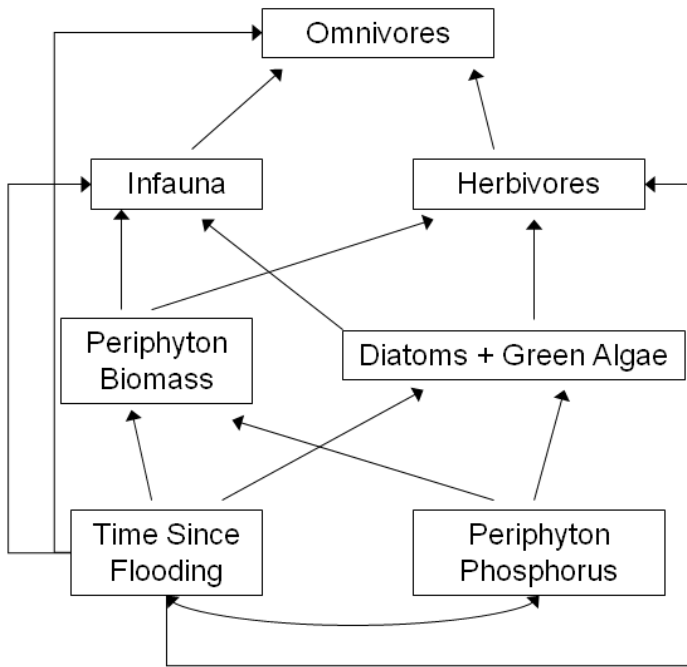
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40   *Model 3: Bottom-up control, omnivory absent, no path between herbivores and*

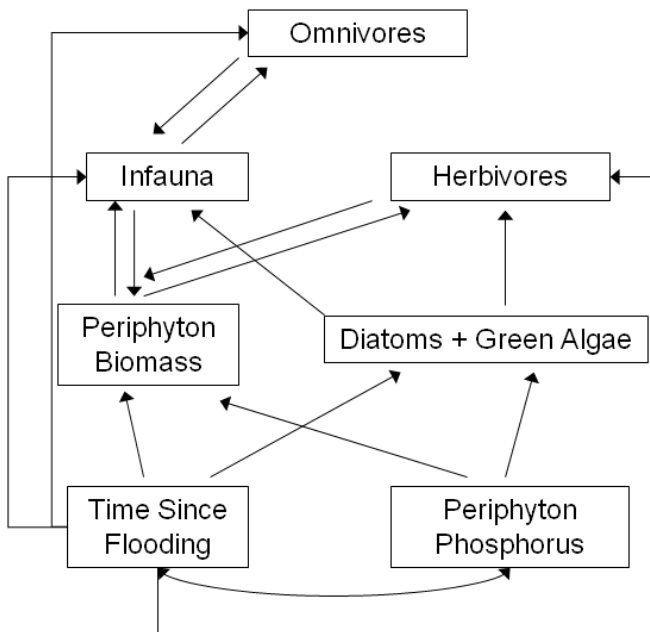41   *omnivores*
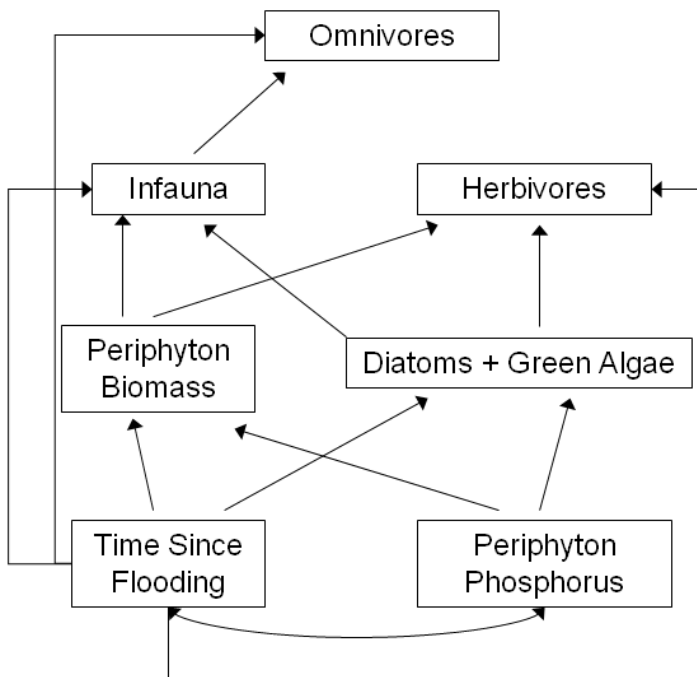
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43   *Model 4: Bottom-up control, omnivory present, no path between herbivores and*
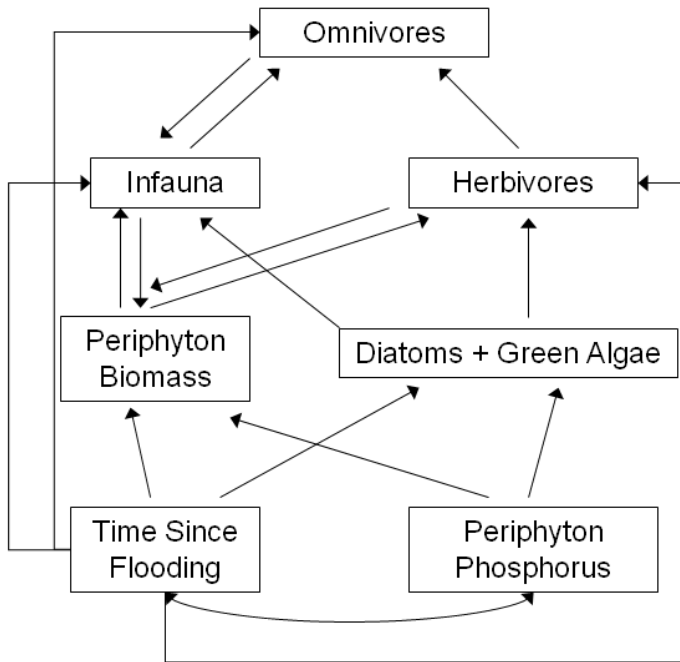
44   *omnivores*

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46   *Model 5: Bottom-up and top-down control, omnivory absent, no path between herbivores*
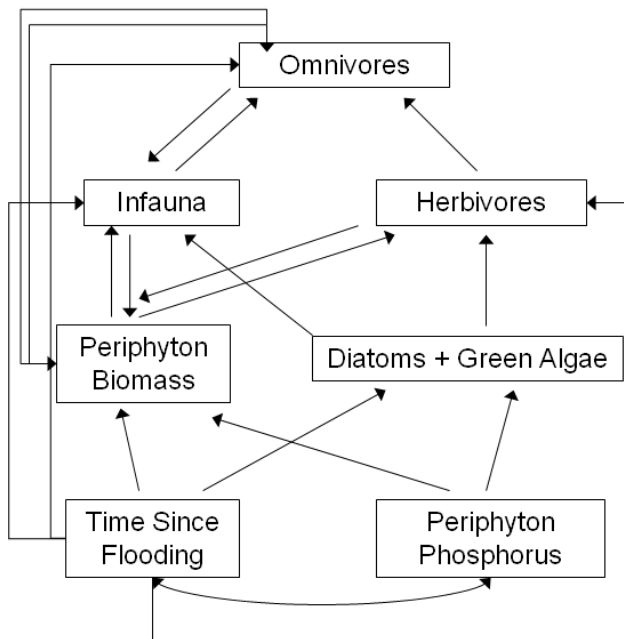
47   *and omnivores*

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49   *Model 6: Bottom-up and top-down control, omnivory absent, only bottom-up control*

50   *between herbivores and omnivores*

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52   *Model 7: Bottom-up and top-down control, omnivory present, only bottom-up control*

53   *between herbivores and omnivores*

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