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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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15 6 **Indirect and direct controls of macroinvertebrates and small fish by abiotic factors**
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18 7 **and trophic interactions in the Florida Everglades**

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48
49 25 **Abbreviated title:** Indirect and direct controls of Everglades consumers

50
51 26 **Key words:** indirect effects, bottom-up and top-down control, hydrological disturbance,
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53 27 phosphorus, Florida Everglades
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3 29 **Summary**
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- 5 30 1. The roles of nutrients, disturbance and predation in regulating consumer densities
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7
8 31 have long been of interest, but their indirect effects have rarely been quantified in
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10 32 wetland ecosystems. The Florida Everglades contains gradients of hydrological
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12 33 disturbance (marsh drying) and nutrient enrichment (phosphorus), often correlated with
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14 34 densities of macroinvertebrate infauna (macroinvertebrates inhabiting periphyton), small
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17 35 fish and larger invertebrates, such as snails, grass shrimp, insects and crayfish. However,
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20 36 most causal relationships have yet to be quantified.
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- 22 37 2. We sampled periphyton (content and community structure) and consumer (small
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24 38 omnivores, carnivores and herbivores, and infaunal macroinvertebrates inhabiting
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27 39 periphyton) density at 28 sites spanning a range of hydrological and nutrient conditions
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29 40 and compared our data to seven *a priori* structural equation models.
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- 32 41 3. The best model included bottom-up and top-down effects among trophic groups and
33
34 42 supported top-down control of infauna by omnivores and predators that cascaded to
35
36 43 periphyton biomass. The next best model included bottom-up paths only and allowed
37
38 44 direct effects of periphyton on omnivore density. Both models suggested a positive
39
40 45 relationship between small herbivores and small omnivores, indicating that predation was
41
42 46 unable to limit herbivore numbers. Total effects of time following flooding were
43
44 47 negative for all three consumer groups even when both preferred models suggested
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46 48 positive direct effects for some groups. Total effects of nutrient levels (phosphorus) were
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48 49 positive for consumers and generally larger than those of hydrological disturbance, and
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50 50 were mediated by changes in periphyton content.
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3 51 4. Our findings provide quantitative support for indirect effects of nutrient enrichment on
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5 52 consumers, and the importance of both algal community structure and periphyton
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8 53 biomass to Everglades food webs. Evidence for top-down control of infauna by
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10 54 omnivores was noted, though without substantially greater support than a competing
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12 55 bottom-up only model.
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Copy for Review

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

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3 97 enrichment on fish and invertebrate densities can depend on disturbance, the strength of
4
5 98 trophic interactions, and the degree to which predators can reduce prey populations. For
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8 99 example, while fish biomass generally increases with nutrients, similar increases in
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11 100 invertebrate biomass may hinge on whether fish are present and limit invertebrate
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13 101 densities (Wootton & Power, 1993; Marks, Power, & Parker, 2000; Liston, 2006).
14
15 102 Increasing nutrients can also encourage successional changes toward well-defended but
16
17 103 competitively inferior invertebrates and thereby reduce the strength of trophic cascades
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19
20 104 by fish (Chase, 2003). Relatively few studies have addressed these interactive effects and
21
22 105 indirect relationships in wetlands, leaving such questions unanswered for many systems.
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24
25 106 The Florida Everglades is a highly oligotrophic marsh ecosystem with gradients
26
27 107 of anthropogenic nutrient (phosphorus) enrichment and hydrological disturbance (drying
28
29 108 of the marsh) (Gunderson & Loftus, 1993; Davis, 1994). Drying events cause direct
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31 109 mortality of fish and invertebrates as well as movements toward deeper refuges, and thus
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34 110 community trajectories in the Everglades reveal shifts from abiotic to biotic control as a
35
36 111 function of time following a disturbance (Trexler, Loftus, & Perry, 2005), similar to
37
38 112 patterns in floodplain habitats (Winemiller, 1996). The density of small fish typically
39
40 113 increases with time following a drying event (Trexler *et al.*, 2002, 2005; Dorn, 2008) and
41
42 114 often with nutrient levels (Turner *et al.*, 1999; Trexler *et al.*, 2002; Gaiser *et al.*, 2005).
43
44 115 Similarly, invertebrates often increase coincident with hydroperiod and nutrients,
45
46 116 although this pattern varies with taxa, sampling method, microhabitat and nutrient level
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48 117 (Rader & Richardson, 1994; McCormick, Shuford, & Rawlik, 2004; Liston, 2006; King
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50 118 & Richardson, 2007; Liston, Newman, & Trexler, 2008). It is generally presumed that
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52 119 nutrients amplify fish and macroinvertebrate densities indirectly via stimulation of
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3 120 periphyton production (aggregations of benthic algae, detritus, fungi and bacteria), a
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5
6 121 major source of primary production for the food web and habitat for invertebrates.
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8 122 Nutrient enrichment, localized around areas of water inflow, alters algal community
9
10 123 composition and consequently changes the periphyton physical structure and constitution
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12 124 (e.g., from floating calcareous mats to epiphytic filamentous green algae aggregates)
13
14 125 (McCormick *et al.*, 1996; Gaiser *et al.*, 2005, 2006). Hydrology may also shape
15
16 126 periphyton community structure (Gottlieb, Richards, & Gaiser, 2006; Thomas *et al.*,
17
18 127 2006). The maintenance of large expanses of periphyton and apparent limits on
19
20 128 macroinvertebrate densities suggest that fish predation on invertebrates may generate a
21
22 129 trophic cascade (Turner *et al.*, 1999; Liston, 2006).

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27 130 While these general trends in Everglades communities have been identified,
28
29 131 indirect and direct effects and food-web interactions have not yet been explicitly
30
31 132 quantified in natural contexts and at large spatial scales. Anthropogenic activities have
32
33 133 modified the Everglades through nutrient enrichment and alteration of hydrological
34
35 134 patterns (Davis, 1994), and the Everglades is now the subject of a large-scale restoration
36
37 135 project (Davis & Ogden, 1994). Using structural equation modeling (path analysis) and a
38
39 136 model comparison approach, we identified possible causal models quantifying the
40
41 137 indirect, direct and total effects of drought, nutrient enrichment and trophic interactions
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43 138 on small aquatic consumers in the Everglades. This analysis provides greater insight into
44
45 139 possible mechanistic models describing how basal consumer densities are controlled in
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47 140 this ecosystem, informing restoration policies and practices.

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3 143 **Methods**

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5 144 *Field Sampling and Sample Processing*

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8 145 In November and December 2005, we sampled fish, amphibian and aquatic invertebrate
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10 146 communities in 28 sites across the Florida Everglades (Everglades National Park, Water
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12 147 Conservation Areas, and Loxahatchee National Refuge; approximately 25°19'N,
13
14 148 80°56'W) (Fig. 1). Sampling sites were selected from a larger set of possible study sites
15
16 149 identified by a Generalized Random Tessellation Stratified (GRTS) survey design
17
18 150 (Stevens and Olsen 2003) applied to the Greater Everglades ecosystem (Scheidt and
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20 151 Kalla 2007). The GRTS design provides a specially balanced sample of the ecosystem;
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22 152 sites were selected for this study because they were located in wet-prairie slough habitats
23
24 153 that are the focus of management concern because of their role as foraging habitats for
25
26 154 wading birds (Trexler and Goss 2009); wet prairie sloughs are characterized by
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28 155 spikerush-dominated (*Eleocharis cellulosa* Torr.) emergent vascular plants (Gunderson
29
30 156 1994) and large standing stocks of periphyton mats formed by benthic algae, detritus,
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32 157 fungi and bacteria (Turner *et al.* 1999). Sargeant et al. (2010) and Table 1 provide further
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34 158 description of the conditions at these sites.

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40 159 We sampled small fish and amphibians (<8 cm) and large invertebrates (snails,
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42 160 crayfish, grass shrimp, and large insects, >5 mm) using a standardized throw-trap
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44 161 sampling protocol (Jordan, Coyne, & Trexler, 1997) with 1-m² throw traps enclosed by 2-
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46 162 mm mesh. Traps were cleared using a bar seine (2-mm mesh) and dip nets (1- and 5-mm
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48 163 mesh), and vertebrates were euthanized by immersion in an MS-222 (tricaine
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50 164 methanesulfonate) bath. Three throw-trap samples were collected per site. To sample
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52 165 macroinvertebrate infauna (including nematodes, copepods, and cladocerans, inhabiting
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3 166 periphyton mats, typically 0.25-8mm long), periphyton mat samples (6-cm diameter
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6 167 cores from top to bottom of the mats, typically 2.5 cm deep) were collected from within
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8 168 each throw trap (Liston and Trexler 2005). All animals captured were kept on ice in the
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10 169 field, and then frozen for storage before identification and enumeration in the lab. The
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12 170 densities (number·m⁻²) of small primary and secondary consumers were determined for
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14 171 each site by calculating the mean of the counts from the three throw-trap samples.
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17 172 Herbivores included herbivorous fish, tadpoles, beetles, mayfly larvae and snails. Small
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19 173 fish, newts, sirens, beetle larvae, odonate larvae, insects, crayfish and shrimp were
20
21 174 considered secondary consumers and are omnivorous or carnivorous in the Everglades.
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23 175 Periphyton subsamples (15-30 mL) were haphazardly selected from thawed cores and
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25 176 two different workers identified macroinvertebrates under a light microscope. Periphyton
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27 177 macroinvertebrate density (number·m⁻²) (Liston, 2006) was determined for each site
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29 178 using the means of the three periphyton core samples. Details on species collected, their
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31 179 densities and frequency of occurrence at sites, and their trophic classification (for throw-
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33 180 trap organisms) are available in Table S1 of Supporting Information Appendix S1. All
34
35 181 trophic assignments were based on published and unpublished studies reporting gut
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37 182 content (Gunderson and Loftus, 1993; Loftus 1999), stable isotopic (Loftus 1999;
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39 183 Williams and Trexler 2006; Sargeant et al. 2010) and fatty acid profile (LL Belicka,
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41 184 personal communication) analyses of specimens collected from the Everglades. Feeding
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43 185 relationships of Everglades aquatic animals are complex, with widespread omnivory and
44
45 186 intraguild predation; a small fraction of animals sampled for this study are exclusively
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47 187 carnivores (e.g., dragonfly naiads) feeding on other omnivores and herbivores. For
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49 188 simplicity sake, we have lumped these animals as ‘omnivores’ for this study, consistent
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3 189 with Morin's (1999) definition that omnivores are species that feed at more than one
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5 190 trophic level.
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8 191 We determined phosphorus levels, periphyton composition and hydrological
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10 192 disturbance estimates corresponding to each of our sites. Periphyton volume (ml) was
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12 193 estimated in the field by placing periphyton in graduated cylinders, and periphyton aerial
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14 194 cover (%) was measured as the estimated percentage of the surface area enclosed by the
15
16 195 throw trap that was covered by periphyton. Separate periphyton samples (3 samples per
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18 196 site, corresponding to locations of throw-trap samples) were obtained to determine total
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20 197 phosphorus content (TP) ($\mu\text{g}\cdot\text{g dry}^{-1}$), ash-free dry mass (AFDM) ($\text{g}\cdot\text{m}^{-2}$) as an estimate
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22 198 of biomass, percent nitrogen and organic content, chlorophyll *a* concentration ($\mu\text{g}\cdot\text{g dry}^{-1}$)
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24 199 and density ($\mu\text{g}\cdot\text{m}^{-2}$) and algal species composition as described by Gaiser *et al.* (2006;
25
26 200 see also Stevenson *et al.* 2002). Total phosphorus from periphyton is a valuable indicator
27
28 201 of nutrient enrichment because phosphorus is quickly absorbed by biota and does not
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30 202 remain in the water column (Gaiser *et al.*, 2006). Algal species were categorized as green
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32 203 algae, diatoms, non-filamentous bluegreen algae (cyanobacteria), filamentous bluegreen
33
34 204 algae, and the combined relative abundance of diatoms and green algae was used in
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36 205 analyses because those species are thought to be more palatable to consumers (Geddes &
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38 206 Trexler, 2003). Using the Everglades Depth Estimation Network (EDEN) hydrological
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40 207 estimation tool (<http://sofia.usgs.gov/eden/stationlist.php>), we calculated time since
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42 208 flooding as the number of days since flooding after the most recent drying event (water
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44 209 levels <5 cm). Using this as a measure of time to recover following a drought,
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46 210 hydrological disturbance is inversely related to time since flooding. Sampling occurred
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3 211 in the late wet season when marshes were near peak water depths following summer
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5 212 rains.
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10 214 *Data Analysis*
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13 215 To examine complex interactions between these variables in a food-web context,
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15 216 we used structural equation modeling to identify relationships between TP levels, time
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17 217 since flooding, periphyton AFDM, the relative abundance of green algae and diatoms, the
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19 218 density of periphyton macroinvertebrate infauna and the densities of small consumers
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21 219 (fish and large invertebrates from throw-trap samples). Structural equation modeling
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23 220 enables analysis of systems involving multiple simultaneous cause-effect relationships, in
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25 221 contrast to reductionist approaches that examine these relationships singly, with the
26
27 222 potential to improve understanding of interaction networks typical of ecological
28
29 223 communities (Grace, 2006). For example, it can be used to identify species interactions
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31 224 and their direct, indirect and total effects (Johnson, Huggins, & DeNoyelles, 1991;
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33 225 Wootton, 1994a,b). This method can be applied to experiments (e.g., Johnson *et al.*,
34
35 226 1991; Wootton, 1994a,b) or observational data recorded along gradients of natural
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37 227 variability (e.g., Elmhagen & Rushton, 2007; Riginos & Grace, 2008).
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43 228 We developed seven *a priori* models describing hypothesized causal mechanisms
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45 229 for how disturbance, productivity and trophic interactions may determine the densities of
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47 230 small consumers via direct and indirect pathways, based on results of previous studies
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49 231 and theoretical expectations (see Supporting Information Appendix S2 for detailed
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51 232 descriptions of each model and rationale). Models were based on bottom-up control only
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53 233 or reciprocal relationships (both bottom-up and top-down controls) between consumers
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3 234 and prey. Specifically, top-down control was proposed between 1) omnivores and
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5 235 infauna, 2) infauna and periphyton biomass, 3) herbivores and periphyton biomass, and
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8 236 4) omnivores and periphyton biomass. The relationship between herbivores and
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10 237 omnivores was evaluated by comparing models that contained a causal path from
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12 238 herbivores to omnivores to models that assumed no causal link between them. We were
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14
15 239 unable to include a possible top-down relationship between omnivore density and
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17 240 herbivore density due to empirical underidentification. A model is considered identified
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19 241 if unique estimates can be determined for all of its parameters, which requires a sufficient
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21 242 number of observed variables given the number of parameters to solve (Grace, 2006). In
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23 243 some cases, a model can be theoretically identified but empirically underidentified
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25 244 because of correlations inherent in the data that effectively reduce the number of
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27 245 observations (Kline, 2005; Grace, 2006). However, the small omnivores in question may
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29 246 be unlikely to limit herbivores of similar size.
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34 247 Structural equation modeling (path analysis) was conducted using AMOS 7.0
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36 248 (Amos Development Corporation, Spring House, PA, USA). The site was considered the
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38 249 unit of observation ($n=28$), with the periphyton, hydrological and consumer variables
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40 250 calculated for each site. All variables were $\log_{10}(y + 1)$ transformed to improve
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42 251 univariate normality and reduce nonlinearities in relationships. Despite transformations,
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44 252 the data continued to show signs of deviation from normality (as indicated by univariate
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46 253 analyses, Mardia's coefficient for multivariate kurtosis, and Mahalanobis d), so we used
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48 254 bootstrapping (based on 2000 bootstrap samples) to test absolute model fit using the
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50 255 Bollen-Stine chi-square test. When data are highly non-normal, traditional chi-square
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52 256 tests of model fit can be overly conservative and the Bollen-Stine chi-square test, which
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3 257 uses bootstrapping to determine the probability of model fit, is recommended as an
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5 258 alternative (Byrne, 2000; Grace, 2006). Models were compared using the Bayesian
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8 259 Information Criterion (BIC) (lower BIC values indicate better fit), which weighs
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10 260 improvement in model fit against model complexity (Claeskens & Hjort, 2008). We
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12 261 report BIC instead of the more common Akaike's Information Criterion (AIC) because
13
14 262 BIC provides more consistent model selection as model complexity increases; BIC
15
16 263 applies a higher penalty than AIC for adding parameters (Claeskens & Hjort, 2008:
17
18 264 Chapter 4) and is more conservative than AIC in the presence of model uncertainty
19
20 265 (Burnham and Anderson 2010: pp 271-273). Because we used a model-comparison
21
22 266 approach, path coefficients are presented, but were not tested for statistical significance
23
24 267 (e.g., Gotelli & Ellison, 2006). We present the unstandardized and standardized path
25
26 268 coefficients fitted by maximum likelihood for each direct causal path in the final models.
27
28 269 Path coefficients in the model represent partial regression coefficients. Reported total
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30 270 effects of environmental gradients are the sum of direct and indirect causal paths. Our
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32 271 approach should be viewed as exploratory and hypothesis-generating rather than
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34 272 confirmatory given our limited trophic specification made necessary by high sample-size
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36 273 requirements of our model fitting and comparison approach.
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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

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3 280 sites of the omnivorous species and was present in more than 70% of the sites. Least
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5 281 killifish (*Heterandria formosa*, Girard), mosquitofish (*Gambusia holbrooki*, Girard) and
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8 282 bluefin killifish (*Lucania goodei*, Jordan) were also very common and thus typically
9
10 283 contributed notably to omnivore density. Herbivorous fish and large invertebrates were
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12 284 lower in density, dominated by planorbid snails (*Planorbella* spp.) with the highest mean
13
14 285 density, and flagfish (*Jordanella floridae*, Goode and Bean) at the largest number of sites.
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17 286 Cladocerans, nematodes, copepods, water mites, ostracods, amphipods and dipteran
18
19 287 larvae comprised the largest numbers of infaunal macroinvertebrates inhabiting
20
21 288 periphyton. Larger beetles, dragonfly larvae and snails were less numerous in periphyton
22
23 289 and found at fewer sites.
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26

27 290 Sites spanned a wide range of hydrological and nutrient levels (Table 1), and time
28
29 291 since flooding was positively correlated with periphyton TP (Spearman correlation: $r_s =$
30
31 292 0.68). Consistent with several other studies in the Everglades, many attributes of
32
33 293 periphyton were associated with time since flooding and/or periphyton TP (Table 2).
34
35 294 Increases in nutrient levels and time since flooding were correlated with decreases in
36
37 295 periphyton biomass, periphyton volume and the relative abundances of bluegreen and
38
39 296 filamentous bluegreen algae, but also with increases in organic content, chlorophyll *a*
40
41 297 concentration, and the relative abundances of green algae and diatoms. The density of
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43 298 omnivores increased coincident with nutrient levels and (to a lesser extent) recovery time
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45 299 following drought, while infaunal and herbivore densities did not exhibit strong
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47 300 correlations with either variable (Table 2; Figs. 2 and 3).
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53 301 A comparison of model BIC values indicated that one model (Model 6 in
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55 302 Supporting Information Appendix S2) was preferred to the others (the difference between
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3 303 the BIC of this model and the next best model was >2) (Table 3). Two other models
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5 304 (Model 1 and Model 7 in Supporting Information Appendix S2) had slightly higher BIC
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8 305 values, but only Model 6 and Model 1 showed adequate absolute fit to the data (Bollen-
9
10 306 Stine chi-square tests were not statistically significant at the 0.05 level; Table 3).

11
12 307 In Model 6 (Fig. 4), changes in periphyton biomass and community structure,
13
14 308 driven by increasing phosphorus, are transmitted to omnivores indirectly. Increases in
15
16 309 the relative abundance of diatoms and green algae, and increases in periphyton biomass,
17
18 310 increased infauna density, which in turn had a positive effect on omnivore density.
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20 311 Omnivores had a negative top-down effect on infauna, and infauna had a small but
21
22 312 negative effect on periphyton biomass. Both periphyton biomass and the relative
23
24 313 abundance of diatoms and green algae were negatively related to herbivore density, while
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26 314 increasing herbivores increased omnivore density with no reciprocal top-down effect.

27
28 315 Model 1 (Fig. 5) included only bottom-up effects and incorporated direct effects
29
30 316 of periphyton biomass and relative abundance of diatoms and green algae on omnivore
31
32 317 density. Direct effects of time since flooding and periphyton TP were generally similar
33
34 318 to those in Model 6. Relationships between trophic groups were bottom-up and mostly
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36 319 positive (increases in prey resulted in increases in consumers) or weak, with the
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38 320 exception of herbivores.

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40 321 Some patterns were shared by Model 6 and Model 1. Herbivore density was
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42 322 negatively related to periphyton biomass and the relative abundance of diatoms and green
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44 323 algae in both models. The total effect of periphyton TP was positive for omnivores and
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46 324 herbivores, but was nearly zero for infauna (Table 4). In Model 1 this resulted only from
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48 325 phosphorus's effect on periphyton community structure and biomass, but in Model 6 the
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3 326 negligible total effect of phosphorus was largely driven by top-down effects. Time since
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5 327 flooding increased infauna density and omnivore density directly, but decreased
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8 328 herbivore density directly in both models. However, time since flooding increased
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10 329 periphyton biomass and decreased the relative abundance of diatoms and green algae,
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12 330 making the total effect of hydrological disturbance negative for infauna and omnivores
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14
15 331 (Table 4). The effect of time since flooding was more complex for herbivores. In Model
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17 332 6, the negative effect was caused by a strong direct path and multiple indirect effects. In
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19 333 Model 1, the total effect was weaker, and the negative direct effect was moderated by
20
21 334 positive indirect effects through periphyton. The total effects of periphyton TP on
22
23 335 periphyton and consumers were larger than those of time since flooding in both models
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25 336 (Table 4), with the exception of infauna density.
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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,

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3 349 our findings emphasize a greater role of nutrient gradients in contributing to consumer
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5 350 densities across large spatial scales in the late wet season, when direct effects of previous
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8 351 drying were relatively weak. Further, the structural equation models identified the effects
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10 352 of food quality (indicated by algal community structure) and food or habitat quantity
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12 353 (indicated by periphyton biomass), allowed effects of nutrient enrichment and hydrology
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15 354 to be disentangled, and provided insight into direct versus indirect effects in this system.
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17 355 Both models incorporated bottom-up effects initiated by increases in nutrients
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19 356 (measured by total phosphorus levels in periphyton). Increasing phosphorus appeared to
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22 357 drive compositional changes in periphyton, including shifts in the dominant algal species,
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24 358 the proportion of organic content and the overall biomass and volume of periphyton.
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27 359 These findings mirror those of several other studies correlating phosphorus addition with
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29 360 increases in the relative abundance of diatoms and green algae and organic content, but
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31 361 decreases in the relative abundance of filamentous bluegreen algae and biomass of
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33 362 bluegreen algae and periphyton (McCormick *et al.*, 1996; Gaiser *et al.*, 2005, 2006). The
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35 363 proportion of periphyton comprised of organic material, diatoms and green algae may
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37 364 reflect food quality since these components are probably more palatable than inorganic
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39 365 components, bluegreen algae or filamentous bluegreen algae (Geddes & Trexler, 2003).
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41 366 Phosphorus addition increases these palatable elements, but decreases the total organic
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43 367 biomass of periphyton (e.g., food quantity and habitat for infauna).
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47 368 These changes in periphyton quality and quantity appear to be the indirect link
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49 369 between phosphorus enrichment and consumer densities. In both models, infaunal
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51 370 density directly increased with periphyton biomass and the proportion of green algae and
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53 371 diatoms. In Model 1, where primary production was directly linked to omnivore density,
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3 372 omnivores responded positively to the relative abundance of diatoms and green algae,
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5 373 and negatively to periphyton biomass (although this latter relationship was quite weak in
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8 374 magnitude). This is in contrast to Model 6, in which changes in food are transmitted to
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10 375 omnivores indirectly through infauna and herbivores. Interestingly, periphyton biomass
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12 376 and the relative abundance of diatoms and green algae had strong negative direct effects
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14 377 on herbivore density in both models, generally contrasting with their effects on infauna
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16 378 and omnivores. A possible explanation may be found in the composition of the herbivore
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18 379 community; flagfish comprised a significant portion of the herbivores in our samples and
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20 380 they may be poor competitors (Trexler *et al.*, 2005). Nonetheless, herbivore density
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22 381 actually increased with nutrient enrichment (i.e., the total effect of periphyton TP) due to
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24 382 the indirect pathways via periphyton biomass. Both models indicate that the quality of
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26 383 periphyton is as important as total food biomass, consistent with previous work
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28 384 demonstrating an increased ability of some consumers to feed on palatable elements
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30 385 following a physical break-up in the periphyton mat (Geddes & Trexler, 2003).

36 386 In the Everglades, the maintenance of large expanses of periphyton mats and
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38 387 apparent limits on infaunal density even in the face of nutrient enrichment may be
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40 388 evidence for a trophic cascade (Turner *et al.*, 1999; Liston, 2006). Trophic cascades are
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42 389 widespread in aquatic systems (Shurin *et al.*, 2002), often driven by predation of
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44 390 macroinvertebrates by fish (e.g., Wootton & Power, 1993). Few studies of top-down
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46 391 effects have been conducted in wetlands, but some show that small fish and insect
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48 392 predators can reduce invertebrate numbers (Batzer, 1998; Peck & Walton, 2008), while
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50 393 others have not found effects of small predators (Corti *et al.*, 1997). Empirical support
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52 394 for trophic cascades in the Everglades has been lacking (Dorn, Trexler, & Gaiser, 2006;
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3 395 Chick, Geddes, & Trexler, 2008). In the current study, small fish and invertebrates, but
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6 396 not infauna, increased with nutrients, a pattern potentially consistent with a trophic
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8 397 cascade based on predictions from food web theory (Power, 1992). The relative strength
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10 398 of Model 6 suggests that both bottom-up and top-down forces are important in shaping
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12 399 the densities of basal consumers in the Everglades. Like all the models considered,
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14 400 Model 6 includes bottom-up relationships between primary production (periphyton) and
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16 401 higher trophic levels. Increases in phosphorus levels drive changes in periphyton
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18 402 community structure, increasing the proportion of highly palatable algal species while
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20 403 simultaneously reducing the total organic biomass of periphyton. Model 6 assumes that
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22 404 these changes in primary production are transmitted indirectly, through primary
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24 405 consumers (infaunal macroinvertebrates and herbivorous fish, invertebrates, and
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26 406 tadpoles), to omnivorous fish and invertebrates. Omnivores, in turn, limit infauna
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28 407 density, and infauna density has a negative effect on periphyton biomass. These
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30 408 relationships are likely to underpin the pattern of increasing omnivore density, but not
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32 409 infauna density, with nutrient enrichment (e.g., Fig. 3). The positive effect of omnivores
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34 410 (through macroinvertebrate infauna) on periphyton biomass implies that a trophic cascade
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36 411 helps maintain periphyton mats, but herbivores may simultaneously act to stimulate
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38 412 periphyton growth (see below), indicating that multiple factors are important in
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40 413 controlling periphyton biomass.

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48 414 This contrasts with the exclusively bottom-up structure of Model 1. The fact that
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50 415 two very different models had similar support may be explained by the role of omnivory.
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52 416 Model 1 allows for omnivores to feed directly on periphyton, and this may result in
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54 417 similar net effects of periphyton TP as are found in Model 6 in which omnivory is
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3 418 removed. Trophic cascades are generally thought to be limited by omnivory (Polis &
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5 419 Strong, 1996), and could also be restricted in the Everglades by the associative resistance
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7 420 afforded palatable algae by the physical or algal composition of periphyton mats (Geddes
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9 421 & Trexler, 2003; Chick *et al.*, 2008). However, past studies have not found support that
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11 422 omnivorous fishes and invertebrates assimilate more periphyton as nutrients increase
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13 423 (Williams & Trexler, 2006).

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17 424 Herbivorous small fish and invertebrates played a different role than other
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19 425 consumer groups in both models. Herbivore density had a positive effect on omnivore
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21 426 density, presumably via predation where predators were unable to limit prey numbers.
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23 427 The similar size of individuals in the omnivore and herbivore groups may have prevented
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25 428 top-down control; some of the herbivores may have been too large or well-defended for
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27 429 the small omnivores to consume them. In Model 6, herbivores had a positive top-down
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29 430 effect on periphyton biomass, seemingly inconsistent with an expected predator-prey
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31 431 relationship. While a negative effect of predation may be more expected, positive effects
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33 432 could occur through nutrient regeneration (Geddes & Trexler, 2003).

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37 433 Previous studies of Everglades fauna have frequently found negative correlations
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39 434 between small fish and/or macroinvertebrate densities and measures of disturbance
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41 435 (Trexler *et al.*, 2002, 2005; Liston, 2006). The direct effect of time since flooding was
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43 436 positive for infauna and omnivore density in both models, suggesting their numbers
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45 437 increased with recovery time following droughts. However, the opposite pattern was
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47 438 found for herbivores, probably stemming from dominance of flagfish, which tend to
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49 439 decrease with time following droughts (Trexler *et al.*, 2005). Time since flooding was
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51 440 important in contributing to algal community structure, reducing the proportion of
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3 441 diatoms and green algae. Our results are potentially inconsistent with a previous study
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5 442 (Gottlieb *et al.*, 2006) reporting higher relative abundance of diatoms in long-hydroperiod
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7 443 sites, but that study did not separate effects of phosphorus from those of hydrology,
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9 444 which tend to be correlated. Despite a negative direct effect, the overall correlation
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11 445 between time since flooding and the relative abundance of green algae and diatoms was
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13 446 positive, possibly explaining the differences in results between studies. Effects of
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15 447 hydrological disturbance were somewhat weaker than the effects of nutrient enrichment,
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17 448 and the total effect of time since flooding was negative for all three consumer groups as a
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19 449 result of numerous indirect effects. Reduced effects of hydrology relative to nutrients in
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21 450 this study may have resulted from focusing on spatial, rather than temporal, variability
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23 451 and by sampling at the end of the wet season when few sites had been recently dry. This
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25 452 study also used partial regression coefficients to estimate effects of hydrology and
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27 453 nutrients, possibly resulting in different findings than studies relying on correlation alone.
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34 454 Structural equation models can provide important advances in understanding
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36 455 Everglades food webs. However, there are some shortcomings of our study. As is the
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38 456 case for all studies examining open, natural food webs, a limitation of our analysis is that
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40 457 models were necessary simplifications of the true food web. We were unable to include
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42 458 the effects of larger predators, which may have exerted further top-down control on
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44 459 consumers, and detritus-based components of the food web. Effects of predatory fish,
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46 460 such as gar, may actually be included in direct effects of time since flooding, since they
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48 461 are limited to deeper refugia when water levels are low (Chick, Ruetz, & Trexler, 2004).
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50 462 In addition, although we gained some resolution by categorizing consumers into three
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52 463 groups based on size and diet, individual species may exhibit unique and contrasting
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3 464 patterns not fully described by this analysis. For example, Liston (2006) identified
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5 465 effects of hydrology and/or nutrient levels on certain infaunal groups that were
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8 466 sometimes at odds with patterns observed for infauna as a whole. Finally, our study did
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10 467 not incorporate sites with phosphorus levels greater than $760 \mu\text{g g}^{-1}$ dry periphyton
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12 468 tissue; at higher levels periphyton mats can completely disappear and densities of fish
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15 469 and macroinvertebrates can be reduced (King & Richardson, 2007; Liston *et al.*, 2008;
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17 470 Rejmánková, Macek, & Epps, 2008). Future research should address food-web structure
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19 471 at artificially high nutrient levels, and ideally incorporate larger predatory fishes and
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21 472 wading birds as a fourth trophic level.
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24 473 By using a multi-model, structural equation modeling approach (Grace, 2006),
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26 474 this study provides insight into direct and indirect effects and the apparently limited role
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28 475 of top-down control in shaping consumer densities. To our knowledge, this is the first
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30 476 such analysis of a natural wetlands food web incorporating multiple trophic levels. Our
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32 477 results should guide future research to on the mechanisms underlying our proposed causal
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34 478 pathways.
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Table 1 Descriptive statistics for environmental gradients and consumer densities ($n = 28$)

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

Table 2 Spearman correlations between major environmental gradients (time since flooding and periphyton total phosphorus [TP]) and periphyton characteristics and consumer densities ($n = 28$)

	Time since flooding, r_s	Periphyton TP, r_s
Total periphyton volume (ml)	-0.59	-0.88
Total periphyton aerial cover (%)	-0.67	-0.87
Periphyton biomass (AFDM) ($\text{g}\cdot\text{m}^{-2}$)	-0.68	-0.92
Percent organic content (%)	+0.64	+0.82
Percent carbon (%)	+0.66	+0.84
Percent nitrogen (%)	+0.64	+0.86
Chlorophyll <i>a</i> concentration ($\mu\text{g}\cdot\text{g dry}^{-1}$)	+0.57	+0.78
Chlorophyll <i>a</i> density ($\mu\text{g}\cdot\text{m}^{-2}$)	-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 ($\text{number}\cdot\text{m}^{-2}$)	+0.31	+0.65
Small herbivore density ($\text{number}\cdot\text{m}^{-2}$)	+0.20	+0.29
Periphyton infauna density ($\text{number}\cdot\text{m}^{-2}$)	-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

¹number 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.

Figure Legends

Fig. 1 Map of the study area with the location of sampling sites in the Florida Everglades

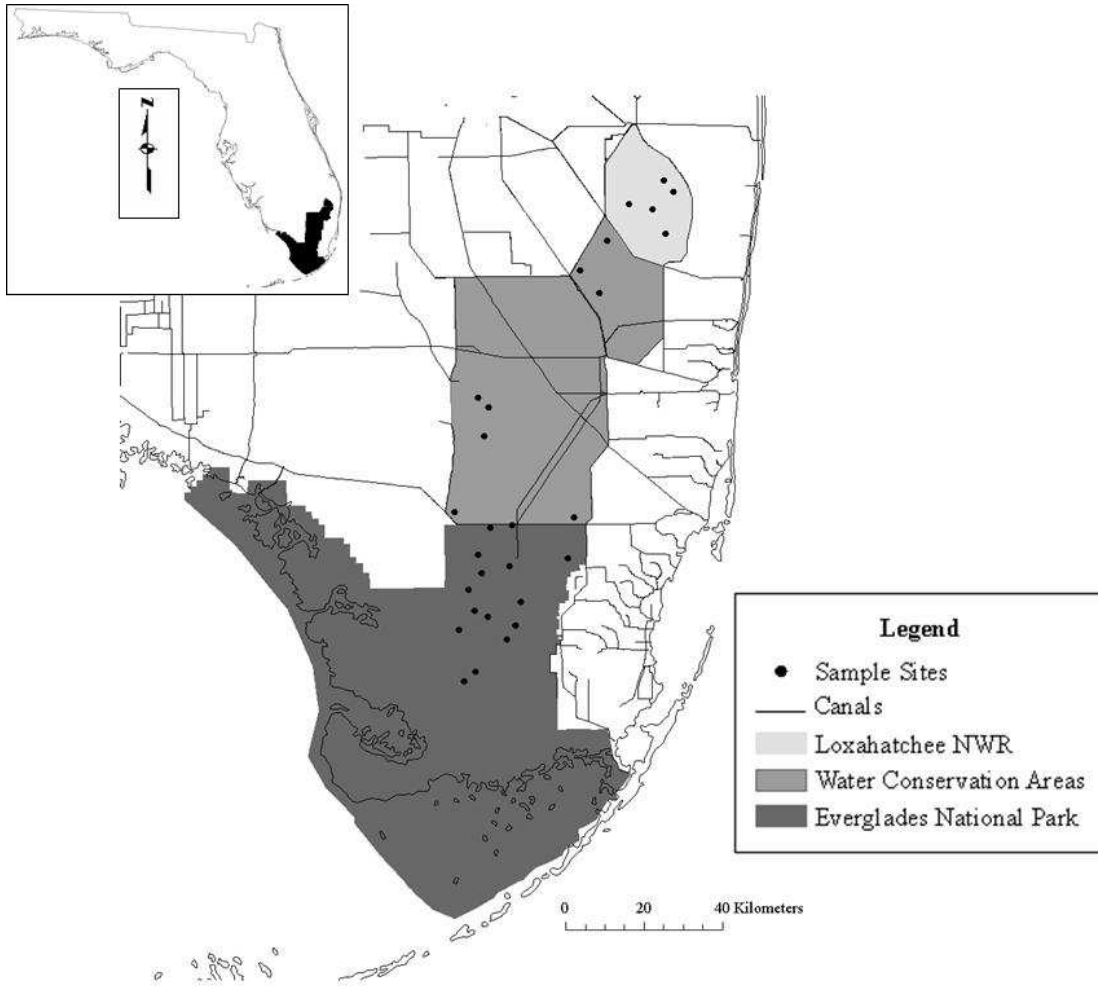
Fig. 2 Relationships between consumer densities and time since flooding

Fig. 3 Relationships between consumer densities and periphyton total phosphorus (TP) levels

Fig. 4 Model with the lowest BIC value (Model 6), incorporating bottom-up and top-down effects and no omnivory. All variables were log-transformed. Unstandardized and standardized (in parentheses) path coefficients are shown, along with squared multiple correlation coefficients (R^2) at the upper right corner of each endogenous variable. The bidirectional arrow between periphyton total phosphorus and time since flooding represents their non-causal bivariate covariance (correlation if standardized)

Fig. 5 Model with the second lowest BIC value (Model 1), incorporating bottom-up effects only and omnivory. All variables were log-transformed. Unstandardized and standardized (in parentheses) path coefficients are shown, along with squared multiple correlation coefficients (R^2) at the upper right corner of each endogenous variable. The bidirectional arrow between periphyton total phosphorus and time since flooding represents their non-causal bivariate covariance (correlation if standardized)

Fig. 1



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Fig. 2

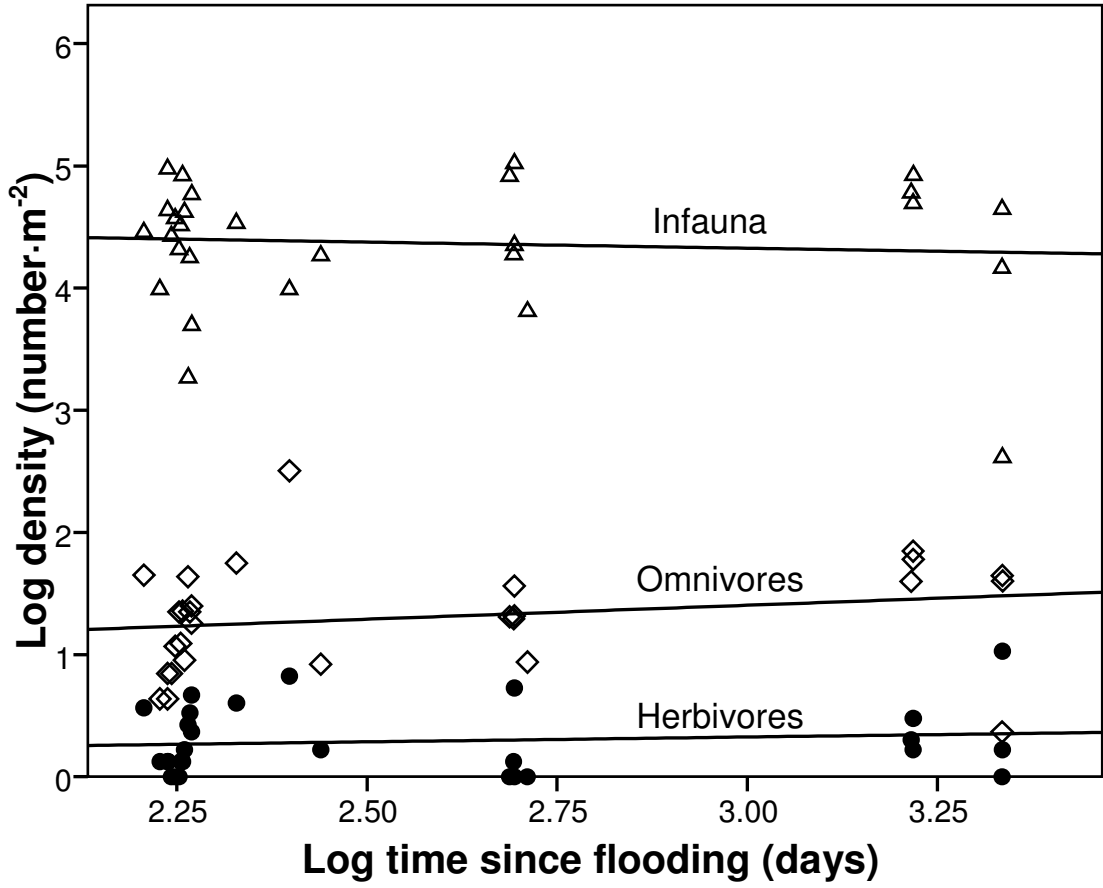
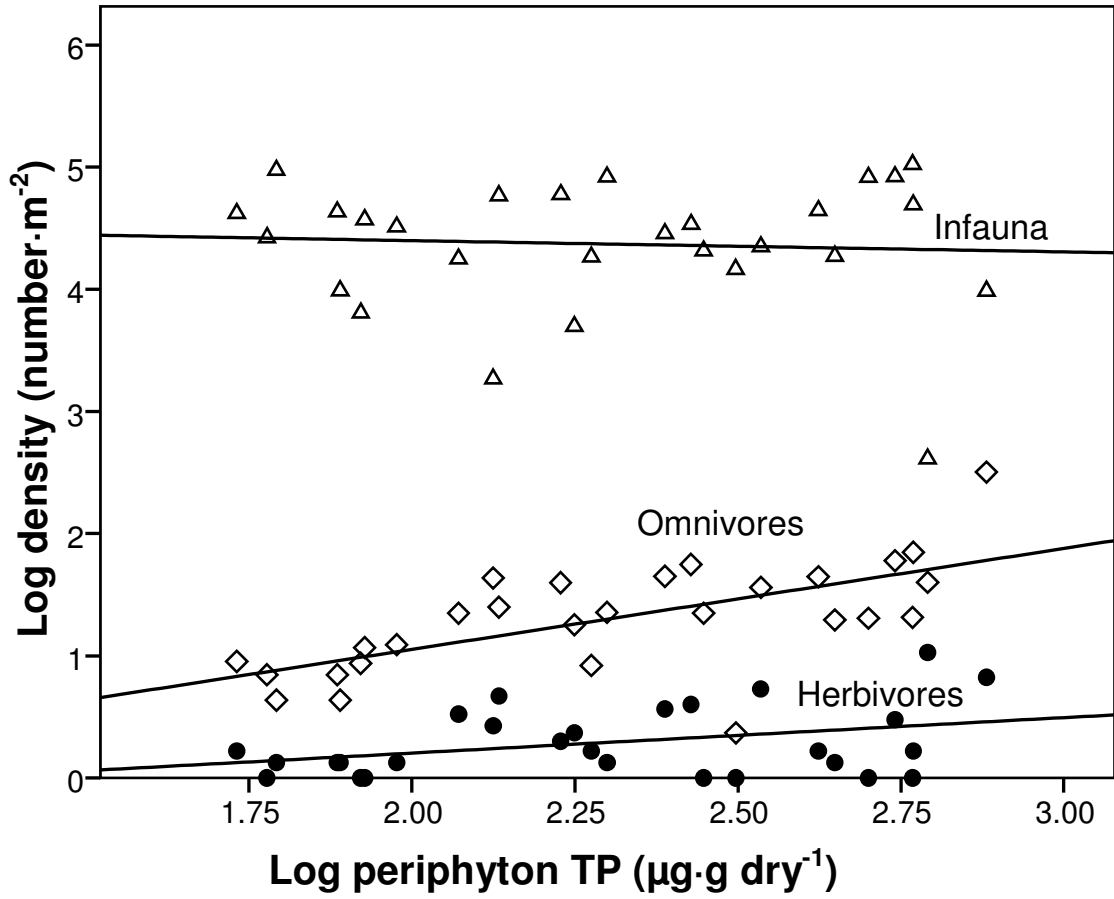


Fig. 3



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Fig. 4

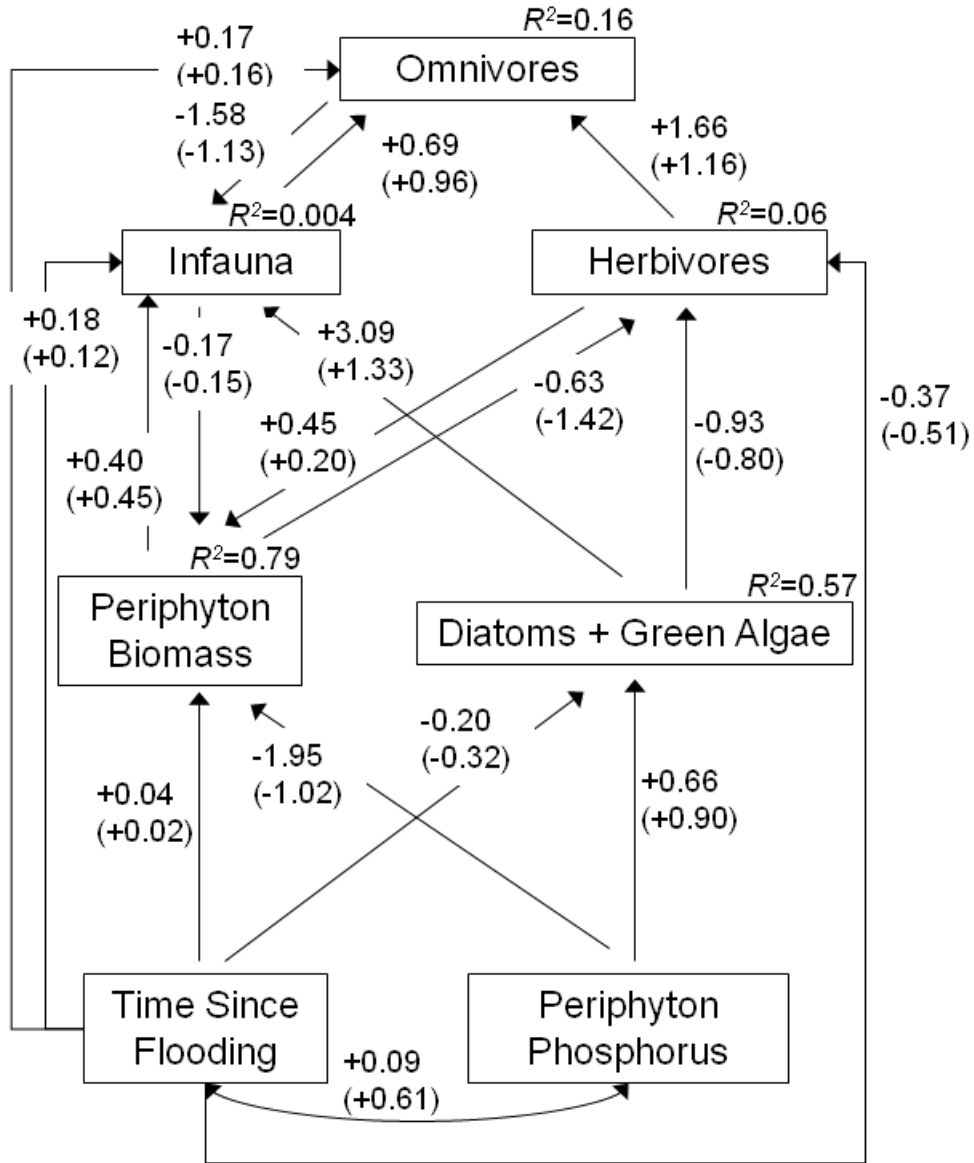
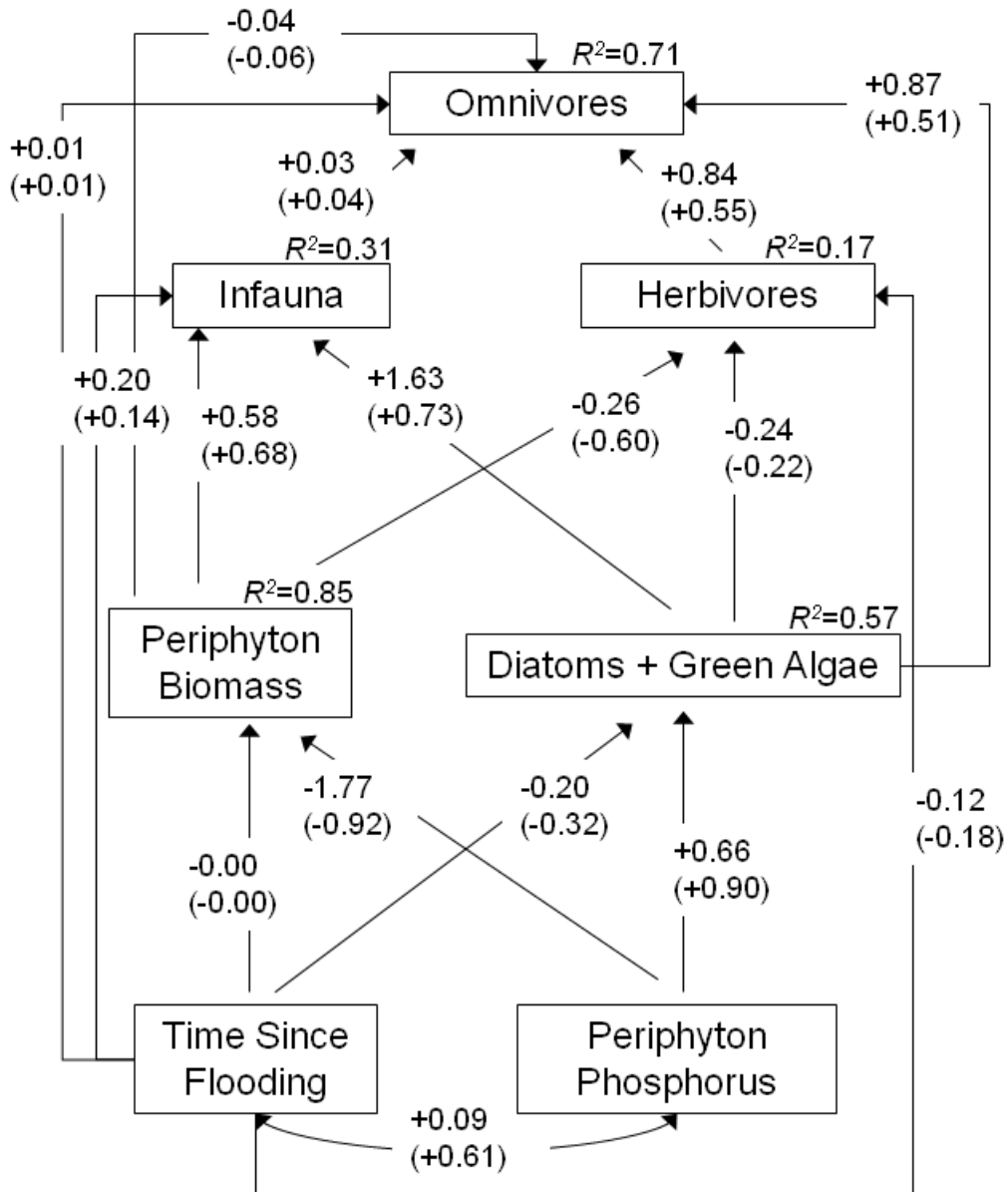


Fig. 5



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

Taxonomic group	Common name	Mean density (# m ⁻²) (SE)	Number of sites
<i>Noturus gyrinus</i>	Tadpole madtom	0.01 (0.012)	1
<i>Cybister</i> spp. (larva)	Water beetle	0.01 (0.012)	1
<i>Pseudobranchius axanthus</i>	Dwarf siren	0.01 (0.012)	1
Throw-trap herbivores			
<i>Planorbella</i> spp.	Planorbid snail	0.6 (0.36)	7
<i>Jordanella floridae</i>	Flagfish	0.4 (0.12)	17
<i>Poecilia latipinna</i>	Sailfin molly	0.18 (0.079)	5
<i>Rana</i> 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
<i>Haitia</i> spp.	Unidentified physid snail	0.06 (0.049)	2
<i>Pomacea paludosa</i>	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 Tanytopodinae)	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
Tanytopodinae (larva)	Chironomid; non- biting midge	800 (150)	27
<i>Dasyhelea</i> spp. (larva)	Biting midge	600 (140)	27
<i>Bezzia</i> spp. (larva)	Biting midge	500 (140)	20
Cyclopoida	Cyclopoid copepod	220 (62)	23
<i>Haitia</i> 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

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

1 Supporting Information, Appendix S2

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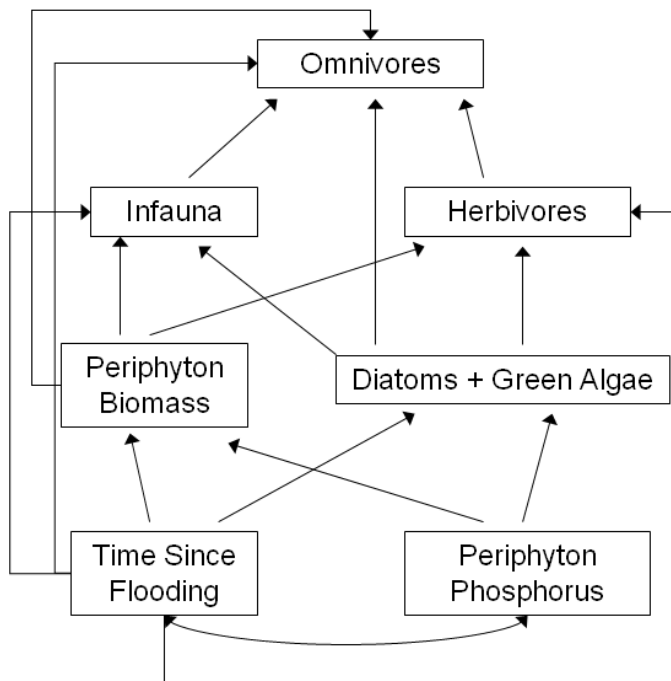
3 Candidate Models

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

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3 24 herbivores on omnivores. Models 5-7 included both bottom up effects and reciprocal
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5 25 top-down effects (e.g., effect of omnivore density on infauna density), and also differed
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8 26 in their inclusion of omnivory and relationships between herbivores and omnivores. We
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10 27 were unable to test models containing reciprocal relationships between omnivore density
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18 *Model 1: Bottom-up control, omnivory present*



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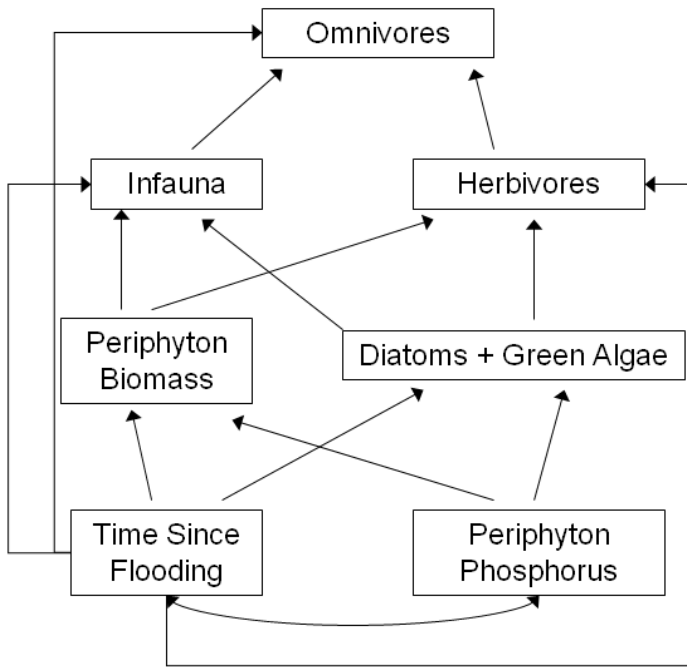
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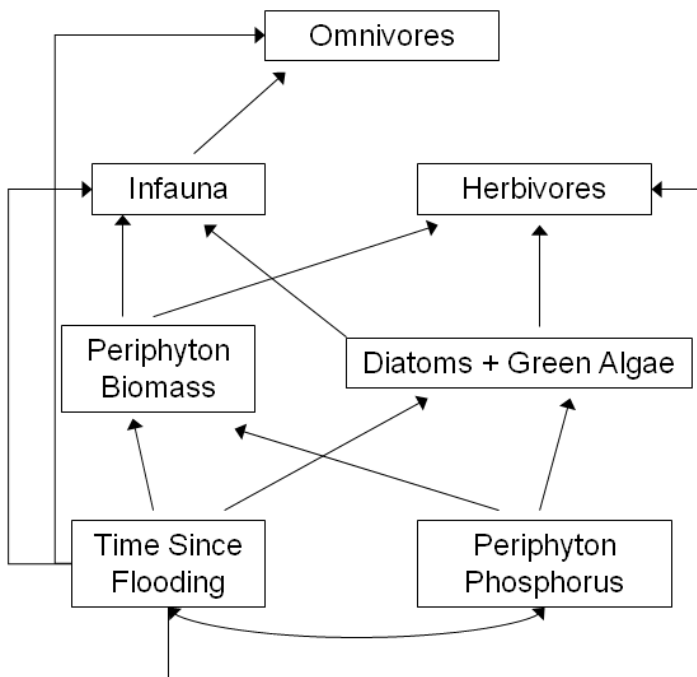
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38 *Model 2: Bottom-up control, omnivory absent*



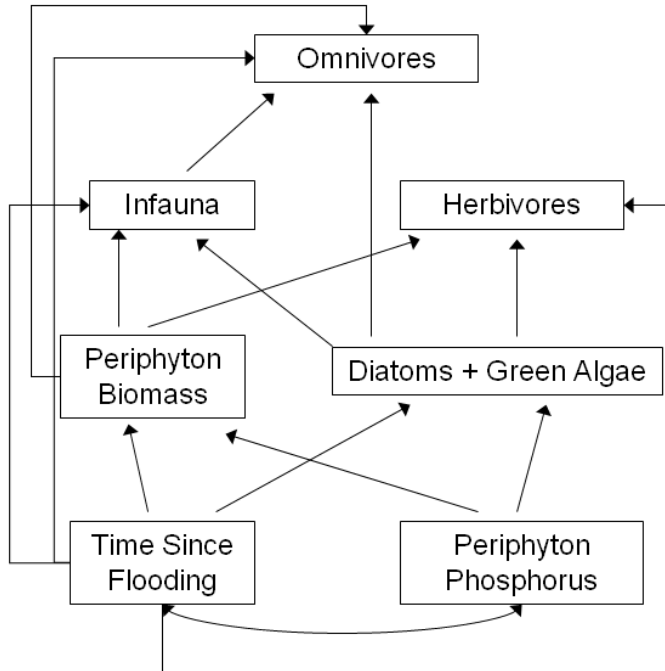
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40 *Model 3: Bottom-up control, omnivory absent, no path between herbivores and*
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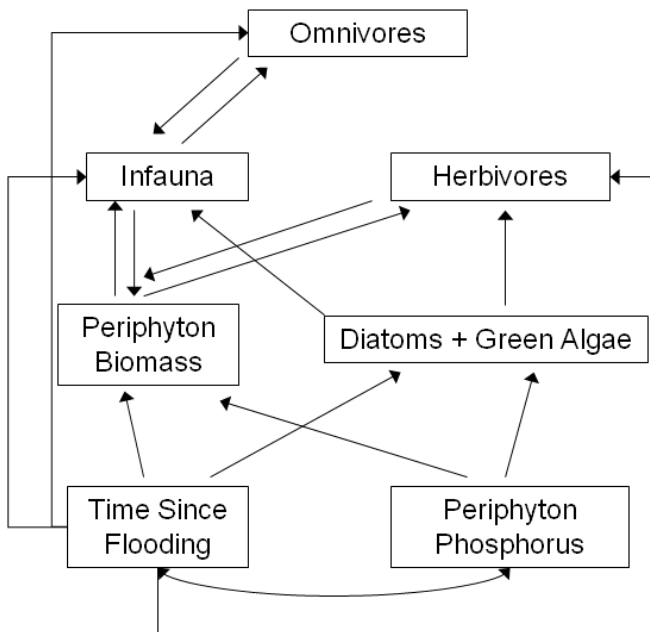


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43 *Model 4: Bottom-up control, omnivory present, no path between herbivores and*
 44 *omnivores*

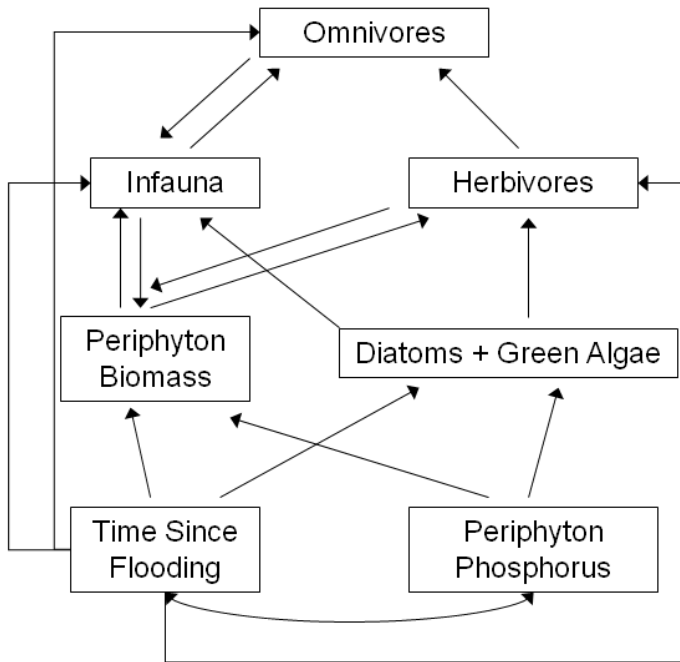


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 46 *Model 5: Bottom-up and top-down control, omnivory absent, no path between herbivores*
 47 *and omnivores*

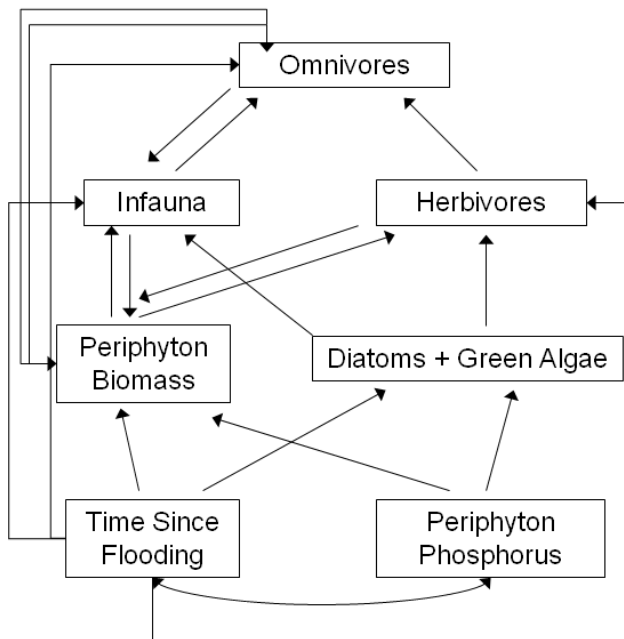


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32 52 *Model 7: Bottom-up and top-down control, omnivory present, only bottom-up control*
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34 53 *between herbivores and omnivores*
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