

1 **On the Dynamic Nature of Omnivory in a Changing World**

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9 **Abstract**

10 Nature's variability plays a major role in maintenance of biodiversity. As global change is
11 altering variability, understanding how key food web structures maintain stability in the face of
12 variation becomes critical. Surprisingly, little research has sought to mechanistically understand
13 how key food web structures are expected to operate in a noisy world, and what this means for
14 stability. Omnivory, for example, has been historically well studied but largely from a static
15 perspective. Recent empirical evidence suggests the strength of omnivory varies in response to
16 changing conditions in ways that may be fundamental to stability. Here, we extend existing
17 omnivory theory to i) predict how omnivory responds to variation, and; ii) show that dynamic
18 omnivory responses are indeed a potent stabilizing structure in the face of variation. We end by
19 synthesizing empirical examples within this framework, demonstrating the ubiquity of the
20 theoretical mechanisms proposed across ecosystem types, spatial scales and taxa.

21

22 **Key Words:** Dynamic omnivory, food web structure, global change, stability

23 **Introduction**

24 Ecosystems are notably variable and subject to regular polyrhythmic swings in abiotic
25 conditions that drive bottom-up shifts in resource density (e.g., diurnal, seasonal, decadal
26 changes in temperature, precipitation etc.) and create patterned mosaics of spatial heterogeneity
27 (Mougi 2020). The intensity of resource consumption by predators can also change through time
28 and space, leading to top-down shifts in resource density (Sommer et al. 1986). The ubiquity of
29 these varying (non-equilibrium) conditions, predictable to some extent, mean that organisms
30 within ecosystems have likely adapted in numerous ways to respond to changing conditions
31 (Levin 1998).

32 Despite the well-known fact that ecosystems are subject to such non-equilibrium conditions,
33 ecological theory and empiricism have tended to focus on understanding stability and function
34 from a static equilibrium perspective until relatively recently (Ushio et al. 2018). The
35 equilibrium simplification is understandable as it allows elegant analysis for high diversity
36 systems (May 1972, Allesina and Tang 2012, Gellner and McCann 2012) but potentially misses
37 out on dynamic responses of species that play fundamental roles in maintaining their persistence
38 in a noisy world (Neubert and Caswell 1997, Hastings 2004, Hastings et al. 2018).
39 Understanding the multidimensional nature of ecological stability requires examining dynamic
40 responses from multiple perspectives (e.g., equilibrium and non-equilibrium; (Ives and Carpenter
41 2007, Donohue et al. 2016). Importantly, these dynamic responses are measurable in empirical
42 systems, promising the ability to develop a dynamic theory that can be linked to empirical
43 research. Given that climate change is altering these underlying abiotic polyrhythms (Myneni et
44 al. 1997, Cai et al. 2018) and homogenizing spatial heterogeneity (Olden et al. 2006), it is

45 essential that theory and empiricism understand the role of responsive food web structure in
46 mediating ecosystem stability and function.

47 Recent research has argued that the generalist module (defined as the coupling of micro or
48 macrohabitats in space by a mobile, generalist consumer; figure 1a) is a clear example of a food
49 web architecture that can be a potent stabilizing force in a variable world (McCann and Rooney
50 2009, McMeans et al. 2015, 2016). Here, at any given time, a generalist consumer tends to move
51 in space towards the most profitable habitat (Pyke et al. 1977). Given that different habitats tend
52 to have resource dynamics that are asynchronised, then this simple adaptive behavioural
53 response by the consumer allows it to consume the resource in the highly productive habitat
54 while releasing the resource from consumption in the less productive habitat (figure 1a). This
55 asynchronous flux in predation pressure is known to enhance persistence of all species in the
56 generalist module and contribute to the adaptive capacity (ability of systems to alter structure in
57 response to external variation) of whole food webs (McCann and Rooney 2009, McMeans et al.
58 2016).

59 Akin to the portfolio effect in primary producers (Tilman 1999), generalist predators employ
60 a consumptive portfolio effect (see table 1 for definition) by altering their foraging behaviour
61 across multiple prey sources in a manner that ensures they get a relatively steady resource
62 supply. This stabilization is due to a mixture of bottom-up processes (e.g., differences in habitat
63 conditions that yield non-synchronous resource dynamics; figure 1a) and the top-down rapid
64 behaviour of the predator capable of generating resource asynchrony and integrating over their
65 resources in space (figure 1a). While the generalist module shows how a mobile consumer in
66 space may play a role in mediating variation, omnivory has qualitatively similar underlying
67 conditions in that it is also a module comprised of a generalist predator capable of foraging on

68 alternative resources that can vary asynchronously (figure 1b). Notably, while the generalist
69 predator can be envisioned as a spatial generalist, omnivores can be envisioned as trophic
70 generalists that may also be capable of reducing variation (figure 1).

71 Over the last two decades, ecologists have increasingly recognized the importance of
72 omnivorous interactions (see table 1 for definition of omnivory). Early theoretical arguments that
73 found omnivory was destabilizing (Pimm and Lawton 1978) have been replaced by the nuanced
74 understanding that while moderate to strong interactions are indeed destabilizing, weak
75 interactions can be powerfully stabilizing (Neutel et al. 2002, Emmerson and Yearsley 2004,
76 Gellner and McCann 2016). Over the same period, empirical work has shifted from suggesting
77 omnivory is rare (e.g., Pimm and Lawton 1978, but note that weak omnivorous interactions were
78 ignored in their methodology), to showing that omnivory is rampant throughout food webs and
79 increases in frequency with trophic level (Thompson et al. 2007). Nonetheless, empirical
80 investigations have largely considered omnivory as a static trait within these systems (Kratina et
81 al. 2012) while theory has also largely focused on the equilibrium stability implications of
82 omnivory (Pimm and Lawton 1978). However, it is increasingly recognized that changing
83 conditions can influence omnivorous interactions in space and time (Kratina et al. 2012, Tunney
84 et al. 2012).

85 Here, we expand on this idea that omnivory ought to change in response to environmental
86 variation (figure 1b). In what follows, we employ two general types of behavioural responses to
87 changing conditions (passive and active omnivores sensu Kalinkat et al. 2011) to bracket a large
88 range in foraging possibilities and ask if dynamic omnivory is robustly stabilizing under these
89 two differing foraging responses. Further, following existing omnivory theory (Tunney et al.
90 2012, Ward and McCann 2017), we define two general categories of mechanisms that produce

91 omnivorous responses (bottom-heavy and top-heavy omnivory). We review and synthesize
92 theory within this novel dynamic context (e.g., responses to perturbations) to show how different
93 conditions drive bottom-heavy and top-heavy driven changes in omnivory and that this dynamic
94 omnivory may be an under-studied stabilizing mechanism in the face of variation. We then
95 empirically demonstrate that both passive and active omnivores, and bottom-heavy and top-
96 heavy mechanisms, manifest themselves in the real world by re-examining well-studied food
97 webs within our dynamic omnivory framework. Furthermore, we demonstrate the ubiquity of
98 dynamic omnivory by providing an extensive empirical catalogue of examples that extends
99 across ecosystem types, trophic levels, and spatial/temporal scales. We end by arguing that, like
100 the generalist module, this dynamic understanding of omnivory allows us to consider how
101 omnivory contributes to the adaptive capacity of food webs and how global change will impact
102 omnivorous interactions, potentially altering carbon transfer, stability and production in whole
103 food webs.

104

105 **Theory: A Dynamic Omnivory Framework**

106 **i. A Base Framework for Dynamic Omnivory Responses: Definitions**

107 Here, we draw from longstanding foraging ecology that has been embedded in consumer-
108 resource and food web models through functional and numerical responses (Abrams 1982,
109 Chesson 1983). Consistent with much behavioral ecology literature that has found that
110 experimental data is consistent with optimal foraging theory (Pyke et al. 1977), consumer-
111 resource and food web theory have motivated models that maximize energy intake either
112 formulated explicitly as an optimal foraging model (Abrams 1982, Kondoh 2003, Abrams and

113 Matsuda 2004, Beckerman et al. 2006, 2010) or as a “rule of thumb” preference model that
114 approximates energy maximization in the functional and numerical response (Chesson 1983,
115 McCann et al. 2005, Kalinkat et al. 2011). For simplicity, we employ an omnivory model that
116 uses the preference function of Chesson (1983) adopted in many food web papers (Post et al.
117 2000, Faria and Costa 2010). We point out that both optimal foraging models (Krivan 2000, van
118 Baalen et al. 2001, Kondoh 2003) and the preference models (McCann and Hastings 1997,
119 McCann et al. 2005) used here have tended to consistently find that energy maximization
120 foraging is often stabilizing.

121 Omnivory, the feeding on more than one trophic level (Pimm and Lawton 1978), is
122 perhaps easiest envisioned in a simple food chain (figure 2a; see table 1 for all important
123 dynamic omnivory definitions discussed in this section). Here, towards a simple dynamic
124 framework of dynamic omnivory, we employ a tri-trophic level perspective, and we use
125 extensions of the Rosenzweig-MacArthur food chain model (see supplemental material S1 for
126 equations) to outline some of the key aspects of omnivory that mediate its dynamic response in
127 nature to changing conditions. Following empirical patterns that show that omnivory tends to
128 increase as we go up the food web (Thompson et al. 2007, Zheng et al. 2021), we focus on an
129 omnivory module that assumes omnivory occurs through the top predator. The omnivory model
130 and assumptions therein are based on McCann & Hastings (1997). Consistent with empirical
131 work, we do all dynamic theory with weak to intermediate average omnivorous interaction
132 strengths (Thompson et al. 2009).

133 In our dynamic framework, degree of omnivory is a measure of the contribution of R to
134 P’s diet (table 1; see S1 for equation). We note that this simple metric equates with commonly
135 employed empirical estimates of omnivory (e.g., stable isotopes) that also estimate the

136 percentage of carbon that comes from different trophic levels (Cabana and Rasmussen 1996).
137 Here, as discussed above, we assume foraging preference and therefore the degree of omnivory
138 is driven by the relative densities of potential prey items for an omnivorous predator (i.e.,
139 omnivory increases as R/C increases; figure 2c). In our example, we show how densities change
140 as the level of top-down control varies, as we move from a bottom-heavy Eltonian biomass
141 pyramid (left of figure 2a) to a top-heavy wasp-waisted biomass pyramid that emerges out of
142 strong top-down control (right of figure 2a). Across such a gradient in top-heaviness– that arises
143 from increasing resource productivity (K), predator attack rate (a), predator biomass conversion
144 rate (e) or reducing predator mortality (m) – densities of Resource (R) and Consumer (C) in
145 Predator (P) diet change in predictable ways as shown in figure 2b (McCauley et al. 2018).
146 Notably, the pyramid gets more top-heavy with a significant change in the relative prey densities
147 for the omnivorous top predator (i.e., lots of R relative to C, see figure 2a). Here, the top-down
148 pressure has indirectly driven an increase in the degree of omnivory (right figure 2c). Further, as
149 the resource densities increase relative to C densities and the degree of omnivory increases, the
150 food chain length decreases (left to right in figure 2a). Alternatively, if the ratio of R to C
151 (hereafter R:C) decreases, omnivory decreases and the food chain length increases (right to left
152 in figure 2a) – the food chain dynamically expands and contracts with changes in R:C.

153 Within this framework, we argue there are two simple, but qualitatively distinct, behavioural
154 responses of the potential omnivore to changing prey densities which ought to alter the effect of
155 changing densities on the degree of omnivory. Importantly, these two behavioural responses
156 bracket a continuum of possible functional responses under changing prey densities and have
157 been used experimentally by Kalinkat et al. (2011). First, an omnivore may be a **passive**
158 **omnivore** in that it never changes its preference for C or R but consumes more or less of them

159 depending on their relative densities (i.e., proportionally; see table 1 for definition and
160 supplemental material S1 for details). In other words, a passive omnivore exhibits a density-
161 independent preference. We note that even a passive feeding organism like a filter feeder may
162 still have preference (e.g., gill sizes select for certain size prey over others; Rouillon and Navarro
163 2003). Alternatively, the omnivore can modify its preference continuously such that the
164 preference increases when R:C increases. This altered preference makes the omnivore an **active**
165 **omnivore** (see table 1 for definition and supplemental material S1 for equation) in that it adjusts
166 its preference in line with the most abundant resource, generating a non-linear preference in the
167 functional and numerical responses (Chesson 1983, Kalinkat et al. 2011). As an example, if there
168 is a pulse in R then the top predator may increase its foraging on R briefly to tap into this
169 resource increase and do so in manner that reduces its consumption on C even more than the
170 proportional change in R:C densities. As a result, an active omnivore can have a much larger
171 change in the degree of omnivory compared to a passive omnivore with changing prey densities
172 (figure 2c).

173 Finally, and discussed further in the next section, we define two qualitatively distinct
174 mechanisms driving dynamic omnivory. The first occurs when the ratio of consumer and
175 resource densities change solely due to bottom-up abiotic influences that drive bottom-heavy
176 biomass distribution. As an example, a pulse of nutrients may immediately fuel resource growth
177 with other trophic levels lagging behind in response (compare increased omnivory between
178 region 1 and region 2; figure 3a-c); thus, during the early transient period after a pulse in
179 nutrients (region 2 in figure 3a-c) the increased R:C is arguably purely bottom-up driven and
180 such a shift in R:C promotes an omnivorous response whether passive or active ($om_B > om_{Eq}$;
181 figure 3b,c). We will refer to this as **bottom-heavy omnivory** (table 1). After this early transient

182 period, the densities of C and R eventually dynamically respond to the nutrient pulse (figure 3a-
183 c; region 3). In the example here, where the transmission of energy up the food chain is driven by
184 relatively strong interactions (i.e., a strongly top-down system; relatively high K_{ae}/m (Rip and
185 Mccann 2011, Gilbert et al. 2014), theory suggests this delayed transient response would yield a
186 strong top-down cascade with a top-heavy biomass pyramid and a high R:C (figure 3b,c; region
187 3). During this transient top-heavy phase, we would therefore expect what we will refer to as an
188 increase in **top-heavy omnivory**, since the degree of omnivory would increase due to the
189 cascading influence of a now inflated top predator (i.e., $om_T > om_{Eq}$; table 1). Here, we have
190 imagined a changing pulse in resources as one may expect due to seasonality, but we can also
191 apply our rationale to a press perturbation (defined table 1; figure 3d-f) that increases K
192 indefinitely. For example, press perturbations could also be conceptualized as spatial variation
193 where some systems are permanently more productive than others. With these definitions, we are
194 ready to consider the implications of dynamic omnivory on the response of food chain densities,
195 the degree of omnivory and the local and non-local stability properties of the food web.

196

197 **ii. Implications: Omnivory and Stability under Changing Conditions**

198 We now consider the omnivory response of the predator, P, under a pulse perturbation of
199 resource productivity, K (figure 3a-c) and press perturbations in K (mimicking permanently
200 altered conditions in space or time; figure 3d-f; see supplemental material S1 for analysis
201 details). While we look at local equilibrium stability (local return time, based on max
202 eigenvalues), for all cases we are also interested in non-equilibrium dynamics, so we restrict our
203 analysis to dynamics that show overshoot (i.e, equilibrium has complex eigenvalues) that readily
204 produce quasi-cycles from perturbations. Here, we see both the press and pulse perturbations as

205 directly related to common empirical measurements in the same ecosystem over time (e.g., a
206 seasonal pulse in K), or a given ecosystem type over space (e.g., one habitat has higher
207 production permanently as in a press). We will use these theoretical results to begin to synthesize
208 empirical dynamic omnivory results with the goal of motivating future work on dynamic food
209 web structure in general.

210 Figure 3a-c depicts the time series of the omnivory model over four time periods: prior to
211 a pulse addition of K (region 1), during its early transient bottom-heavy response (region 2),
212 during its later transient response after higher trophic level densities respond (region 3), and after
213 its return to equilibrium (i.e., back to region 1 type dynamics). In each case (i.e., food chain,
214 passive and active omnivore (figure 3a-c, respectively), the time series show the predator
215 (green), consumer (orange) and resource (blue) dynamics. As discussed above, we point out that
216 even in this simple pulse perturbation case there is a clear temporal bottom-heavy driven increase
217 in maximum degree of omnivory (passive omnivore: $om_B = 0.166$, active omnivore: $om_B =$
218 0.216 ; region 2 in figure 3b,c respectively) followed by a change in maximum omnivory that
219 occurs when the top predator has driven a subsequent cascading transient response that releases
220 the resource while suppressing the consumer (passive omnivore: $om_T = 0.233$; active omnivore:
221 $om_T = 0.326$; region 3 in figure 3b,c respectively). Thus, we see both a short-term bottom-heavy
222 omnivory response, and longer-term top-heavy response driven by the cascading impacts of the
223 pulse perturbation.

224 To understand how dynamic omnivory impacts stability, we look at both local metrics
225 (i.e., return time) and non-local metrics (i.e., degree of overshoot, max-min; Neubert & Caswell,
226 1997) of variation after a perturbation of K (see table 1 for all definitions and supplemental
227 material S1 for more details on these metrics). Recognize that in both cases of passive and active

228 omnivory, all metrics of local and non-local stability tend to show stabilizing responses (i.e.,
229 faster return time, lower degree of overshoot and smaller max-min) to the pulse perturbation
230 relative to the food chain, and the active omnivore demonstrates a stronger stabilizing response
231 relative to the passive omnivore (figure 4a-c). We would argue that this stabilization is much
232 akin to the generalist predator discussed above, whereby the generalist predator and omnivorous
233 predator are both harnessing the asynchronous response of C and R that is naturally occurring in
234 the food chain (i.e., when C is held in check R increases and vice versa). Note, that this dynamic
235 stabilizing response is amplified with stronger top-down pressure in that stronger top-down
236 pressure generates more asynchronous C and R dynamics. This top-down driven asynchrony sets
237 up conditions for the top predator to surf the different trophic levels in a manner that is
238 stabilizing. In a sense, this effect is another manifestation of asynchrony generation driven by
239 generalist predators in a noisy world, previously discussed for the diamond module (i.e., a
240 generalist module with strong and weak pathways where the predator inherently drives
241 asynchrony under stochastic or deterministic conditions; McCann and Rooney 2009). We note
242 that theory has consistently found that the active switching tends to be more stabilizing (McCann
243 et al. 2005), and indeed we see that active omnivory is even more stabilizing than passive as the
244 active predator is able to respond quickly and strongly to changing densities in C and R and
245 reduce the overshoot (figure 4a-c).

246 Similarly, Figure 3d-f depicts the time series of the omnivory model over four time
247 periods: prior to a press addition of K (region 1), during its early transient bottom-heavy
248 response (region 2), during its later transient response after higher trophic level densities respond
249 (region 3), and the return to a now new equilibrium (i.e., region 4 type dynamics of elevated K).
250 Here, for empirical reasons discussed below, we draw our attention to the final new equilibrium

251 state (region 4 in figure 3d-f) and ignore the transient response as it is consistent with figure 3a-c.
252 This new equilibrium state following a press is akin to comparing two separate lakes with
253 different abiotic conditions (e.g., total nutrient availability). We note that this final equilibrium
254 state occurs after all the transient dynamics are complete and so therefore shows the full
255 cascading implications of density from omnivory after the press perturbation of a sustained
256 increase in K . The press perturbation has effectively increased the top-down predation driving an
257 overall increase in R relative to C for both the passive and active top-heavy omnivory. Again,
258 and importantly, local and non-local stability tends to be enhanced by omnivory whether passive
259 or active (figure 4d-f). Note that the stabilizing response of the active omnivorous predator has
260 appeared to completely eliminate the oscillatory decay and returns extremely rapidly relative to
261 the food chain or passive omnivore case (figure 3d-f). This is an example of stronger interactions
262 driving asynchronous R and C dynamics that are harnessed by the omnivorous predator
263 employing a consumptive portfolio effect.

264 Finally, to understand the stability implications of dynamic omnivory more generally and
265 determine the robustness of these patterns, we investigated local and non-local stability metrics
266 (Neubert and Caswell 1997) across a wide parameter space for both pulse and press scenarios
267 (see supplemental material S1 for details on stability analysis). We individually altered all
268 parameters that increase top-down pressure of the predator (i.e., increasing the ratio Kae/m) on
269 its prey while keeping track of the local and non-local stability after a pulse perturbation (figure
270 S2) and a press perturbation (figure S3) of resource productivity, K . As expected from existing
271 omnivory theory (McCann and Hastings 1997, Gellner and McCann 2012) we find that our
272 results (figure 4) are robust under wide parameter spaces and the stabilizing potential (i.e., faster
273 return time, lower degree of overshoot and smaller max-min) of adaptive omnivory is greatest as

274 the system gets more top heavy (i.e., increasing K , a or e , or decreasing m ; figure S2, S3). We
275 point out that the above results rely on the underlying assumption that we employ weak to
276 moderate average omnivory strengths, which tend to occur in nature and are known to be
277 stabilizing (McCann and Hastings 1997, Emmerson and Yearsley 2004, Gellner and McCann
278 2012). Choosing strong ones means omnivory strengths remain destabilizing even within this
279 dynamic framework. As an example, a pulse in K that drives strong bottom-up responses in R
280 can exaggerate increases in top predator densities when omnivorous interaction strengths are too
281 strong allowing for the suppression of C to local extinction. Similarly, press perturbation
282 increases in K can make the strong P-R interaction oscillatory and less stable.

283 In summary, we have shown that omnivory increases through two qualitatively distinct
284 mechanisms (bottom-heavy and top-heavy changes in density), and differential behavioural
285 responses of the predator (passive and active). Omnivory within this dynamic context tends to
286 play a significant stabilizing role in the face of environmental noise, making it another potential
287 adaptive food web structure like the generalist module. A key mechanism is the asynchronous
288 responses of C and R (i.e., a portfolio effect) as P changes in density and averages energy uptake
289 over these waves. We now turn to empirical work to discuss this dynamic omnivory framework,
290 a framework that is intentionally used to intersect with emerging empirical omnivory results.

291

292 **Emerging Empirical Examples of Dynamic Omnivory**

293 Since evidence of widespread omnivorous interactions became apparent, omnivory has
294 been reasonably well studied in empirical food webs (Thompson et al. 2007). Recently, emphasis
295 on changing conditions has increasingly documented varying levels of omnivory across space

296 and time (Kratina et al. 2012). However, dynamic omnivory remains underappreciated in
297 empirical food webs due to the historical difficulty in quantifying omnivorous interactions and
298 the lack of a guiding theoretical framework. Detecting dynamic omnivory in real food webs
299 requires measurement of an omnivores diet in response to changes in relative densities of
300 trophically distinct prey under varying environmental conditions through space and/or time.
301 While this requires large amounts of data, advancements in empirical techniques, such as stable
302 isotope analysis and telemetry, combined with more historical approaches like stomach content
303 analysis, have enhanced ecologist's ability to measure such responses in omnivorous behaviour
304 under changing conditions (see table 2 for examples). Here, guided by our dynamic omnivory
305 framework, we draw on existing data to propose examples of dynamic omnivory in empirical
306 webs and demonstrate the apparent ubiquity of dynamic omnivory across ecosystem types,
307 trophic levels, and spatial/temporal scales (table 2). By outlining our framework in empirical
308 food webs, we hope to motivate future research to undertake the non-trivial task of collecting
309 such high-resolution data necessary to quantify dynamic omnivory in real systems.

310 **i. Passive & Active Omnivores in Empirical Webs**

311 As outlined in the theoretical framework, passive and active omnivores bracket a
312 continuum of possible functional responses to changing prey densities. In nature, determining the
313 endpoints of the gradient in passive and active omnivores is difficult as it requires rigorous data
314 on resource densities and the response of consumer preference to changing resource densities
315 which tend to be rare in empirical food web data (but see Kalinkat et al. 2011). Recall from the
316 above theoretical results, both passive and active omnivores exhibit stabilizing responses under
317 changing conditions.

318 Passive omnivores are characterized by a density-independent preference that passively
319 forage on their trophically distinct prey sources. Filter feeders are known to exhibit linear
320 functional responses driven by fixed preference (Jeschke et al. 2004), and so omnivorous filter
321 feeders may be perfect examples of passive omnivores. For example, Bighead carp
322 (*Hypophthalmichthys nobilis*) are mobile, filter-feeding fish whose diet and trophic position
323 varies seasonally in response to changing relative densities of zooplankton and phytoplankton
324 (e.g., higher trophic position under high zooplankton densities in spring and autumn, figure 5a;
325 Yu et al. 2019). This seasonal shift that follows relative densities patterns with a fixed preference
326 would classify these big-head carp as passive omnivores. However, their potential ability to
327 spatially track high abundances of their preferred prey indicates they may exhibit some active
328 behaviours (Yu et al. 2019).

329 Active omnivores on the other hand, can readily shift their density-dependent preference
330 across their trophically distinct prey sources to maximize energy intake. For example, American
331 black bears were shown to actively alter their foraging behaviour and move across the landscape
332 to target caribou calving grounds at certain periods of the year, despite other food sources still
333 being readily available (Rayl et al. 2018). At other times of the year, when caribou calves are not
334 as available, the bears appear to feed more passively on plants and ants in relation to their density
335 (Rayl et al. 2018). Within our dynamic omnivory framework, we would consider, these
336 American black bears primarily active omnivores, while exhibiting some passive behaviours. We
337 can characterize organisms by the dominant omnivorous behaviour by empirically examining
338 how omnivores respond to varying prey densities across space and time (i.e., how omnivore diets
339 and behaviours change across spatial and temporal variation in resource densities; table 2).
340 However, it is important to remember that these behaviours exist along a continuum and many

341 organisms will fall somewhere in between and can exhibit both active and passive behaviours
342 (Kalinkat et al. 2011).

343 **ii. Bottom-Heavy & Top-Heavy Omnivory in Empirical Webs**

344 As discussed above, any mechanism that inflates R relative to C densities should elicit
345 omnivory. In our dynamic omnivory framework, such inflated R:C can arise by two qualitatively
346 distinct mechanisms, bottom-heavy and top-heavy omnivory. Both types of mechanisms appear
347 to operate in empirical food webs based on evidence from existing literature (table 2). For
348 example, seasonal changes that produce pulses of nutrients can increase R densities and alter R:C
349 and drive changes in the predators' degree of omnivory. As shown in the theoretical framework
350 this change in R:C and subsequent change in omnivory is driven by bottom-heavy biomass
351 distribution. We see evidence of this bottom-heavy driven omnivory in Arctic marine food webs
352 where dramatic increases in light in open-water months lead to pulses in productivity that drive
353 higher availability of lower trophic level resources (i.e., phytoplankton). In response, omnivorous
354 amphipod species can switch from consuming higher trophic level zooplankton under winter ice
355 cover towards consumption of lower trophic level phytoplankton during the open water season
356 (Werner and Auel 2005, McMeans et al. 2015; figure 5c). In this example, a purely bottom-
357 heavy mechanism, akin to a pulse perturbation in our theoretical system (figure 3a-c), appears to
358 be driving the dynamic omnivory response to seasonal changes in resource density.

359 Alternatively, other conditions can increase the top-heaviness of food webs through time
360 or space and drive top-heavy dynamic omnivory as our theory suggests. For example, lake trout
361 are an omnivorous top predator that feed on both fish and invertebrates in nearshore and offshore
362 zones of a lake (vander Zanden et al. 1999). In lakes where access to highly productive nearshore
363 prey is high (e.g., small lakes), energy flow to lake trout increases, increasing the top-heaviness

364 of the food web (high nearshore access = high top-heaviness) (vander Zanden et al. 1999). High
365 densities of lake trout are likely to suppress their fish prey, making omnivorous foraging on
366 lower trophic level zooplankton beneficial (Tunney et al. 2012). Under these conditions, top-
367 heavy omnivory is therefore expected to dominate (figure 5e). Higher lake trout density and
368 increased omnivory in lakes with permanently higher nearshore access is consistent with
369 predictions from our theory that press perturbations can lead to top-heavy food webs that then
370 fuel omnivorous responses (figure 3d-f).

371 So far, we have considered empirical examples of bottom-heavy and top-heavy omnivory
372 in isolation. Our theory shows, however, bottom-heavy and top-heavy omnivory can also be tied
373 together (a bottom-up pulse leads first to bottom-heavy and then to top-heavy omnivory; figure
374 3) We can see this manifest in the real world, as real systems also undergo changes in top-down
375 and bottom-up dominated periods of omnivory. For example, in temperate agricultural stream
376 systems there are strong seasonal changes in resource densities driving bottom-heavy omnivory
377 (Hellmann et al. 2013), as well as strong changes in top-heaviness of webs through space (driven
378 by varying nutrient level inputs) that exhibit top-heavy mechanisms of omnivory (Champagne et
379 al. [in revision], van der Lee et al. 2021) (figure 5d). While we have outlined only a few specific
380 examples here, table 2 presents a catalogue of empirical examples across ecosystem types,
381 trophic levels, and spatial/temporal scale, to demonstrate the ubiquity of dynamic omnivory in
382 empirical food webs. We note that existing empirical examples of dynamic omnivory seem to
383 dominate in aquatic ecosystems, however as there is widespread evidence of omnivory in
384 terrestrial ecosystems (Thompson et al. 2007) the lack of examples in terrestrial systems may be
385 a factor of less work focused on examining terrestrial omnivore responses to changing
386 conditions.

387 **Discussion**

388 Here, we have examined the role of omnivory from a dynamic perspective. By assuming
389 two plausible behavioural omnivory responses (i.e., passive and active), we use theory to predict
390 temporal changes in the degree of omnivory after a perturbation, and the local/non-local stability
391 implications of these changes. We find that dynamic omnivory responses, whether passive or
392 active, often act as a potent stabilizer in complex ecosystems in the face of environmental
393 variation. Importantly, active omnivores have a stronger stabilizing potential relative to passive
394 omnivores as their density-dependent preference allows for rapid prey-switching, which is
395 known to drive stabilizing sigmoidal functional responses akin to Type III (McCann 2000, Post
396 et al. 2000). Further, similar to arguments that generalist couplers can stabilize lower trophic
397 level variation by integrating over two asynchronous habitat pathways (McCann and Rooney
398 2009), we show that omnivory responses to perturbations can naturally generate asynchronous
399 consumer and resource dynamics that the omnivore can integrate over (in a simplified sense the
400 omnivore harnesses a consumptive portfolio effect). Consistent with classic understanding of
401 trophic dynamics across gradients in productivity (Oksanen et al. 1981), our results argue that
402 changes in the degree of omnivory, and thus the stabilizing responses, are likely driven by a
403 combination of bottom-up and top-down cascading changes in resource and consumer densities,
404 both of which predictably alter the ratio of resources and consumers.

405 While we employed a single chain tri-trophic model, our results are consistent with
406 mechanisms proposed in other omnivory models (McLeod and Leroux 2021). Specifically,
407 multi-chain omnivory theory has found that top-heavy omnivory can increase across a gradient
408 in productivity (K) or changes in accessibility in attack rate (a) both which were argued to

409 increase the R/C ratio and thus omnivory (Tunney et al. 2012, Ward and McCann 2017).

410 Importantly, this multi-chain omnivory appears to play a role in building up biomass in the top
411 predator in empirical studies (e.g., lake trout; Tunney et al. 2012) leading to reductions in their
412 preferred prey (cisco) that drives increased omnivory.

413 Most traditional empirical omnivory approaches have been static and focused on
414 comparing the average strength of omnivory across species and ecosystems (Kratina et al. 2012),
415 resulting in theoretical and empirical arguments that omnivory is now believed to be widespread
416 (Thompson et al. 2007) but often weak (Emmerson and Yearsley 2004, Gellner and McCann
417 2016). Nonetheless, our empirical understanding of how the strength of omnivory responds to
418 changing conditions is only beginning to emerge. Here, our theoretical dynamic omnivory
419 framework provides us with a novel tool to empirically investigate omnivory responses of real
420 food webs (table 2). Specifically, we show that temporal shifts in resources across seasons have
421 predictable implications for changes in omnivory that match theory – strong bottom-up shifts in
422 production alter the degree of omnivory seasonally, for example. Further, since our theory
423 highlights short-term responses (that are often bottom-up driven) and long-term responses (that
424 occur after top-down responses have equilibrated), we are able to determine spatial variation in
425 omnivory of a species across a gradient in changing conditions (e.g., ecosystem size) that reflect
426 the “equilibrated” omnivory responses of the same species. These empirical results again
427 resonate with theory showing, for example, that in small strongly interacting ecosystems, top-
428 heavy omnivory can generate significantly increased omnivory responses relative to larger
429 systems assumed to have weaker interactions (Emmerson and Yearsley 2004, Gellner and
430 McCann 2016).

431 The theoretical framework we have outlined is a starting point to understand empirical
432 responses of organisms and food webs to changing conditions. Given that we are in a world
433 replete with global change driving novel temporal and spatial perturbations, theoretical
434 development of dynamic responses in key food web modules promises to allow us to further
435 understand the resilience implications of changing environmental conditions (Neubert and
436 Caswell 1997, Hastings 2004, Hastings et al. 2018). Our work adds the omnivory module to the
437 generalist module as another fundamental food web structure that can mute variation in space
438 and time. In a sense, the behavioural responses of predation in both cases act as adaptive capacity
439 capable of giving resilience to diverse webs in a noisy world (McMeans et al. 2016). Further
440 work identifying other food web structures (both low and high diversity structures) can add to
441 this critical developing framework for adaptive food webs. Our work shows the importance of
442 harnessing the variability of ecosystems by understanding how fundamental food web structures
443 change in space and time to variation.

444 Further, we point out that “dynamic responses” are empirically measurable and so
445 importantly facilitate the interaction of theory and empirical research – an area that has hindered
446 the rapid development of food web research (Kratina et al. 2012). By outlining the framework
447 and stability implications of dynamic omnivory, we hope to motivate future research to consider
448 food web structure and behaviour through this dynamic lens and expand data collection to
449 robustly examine these mechanisms in empirical food webs. As food webs are rewiring under
450 global change (Bartley et al. 2019), our framework is a significant step towards a better
451 understanding of the future stability of tomorrow’s ecosystems.

452

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453 **Code availability:** The code to reproduce this study is available as an archived compen-
454 dium (<https://doi.org/10.5281/zenodo.5776233>) and the corresponding development reposi-
455 tory is available at the following URL <https://github.com/McCannLab/Labmnivory>.

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634
635 **Acknowledgments**

636 This project was funded by the University of Guelph’s Canada First Research Excellence Fund
637 project “Food from Thought”, awarded to K.S.M. and a Discovery Grant from the National
638 Science and Engineering Research Council of Canada awarded to K.S.M. Thank you to Caden
639 McCann for all animal artwork used in figures.

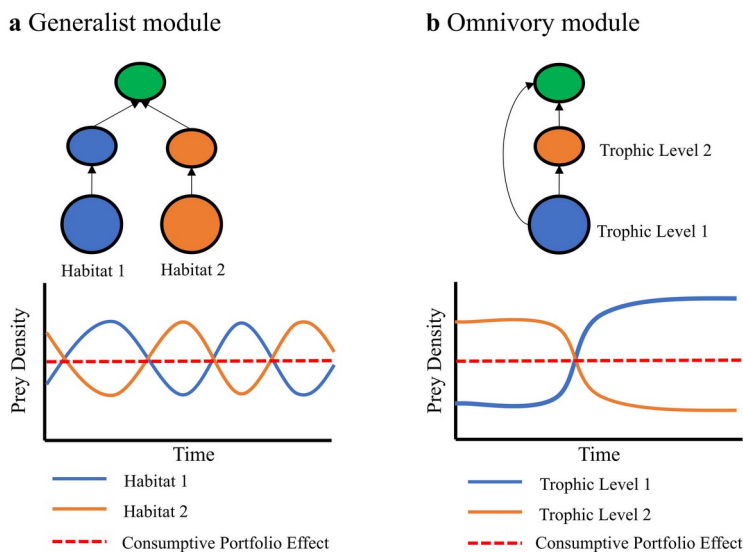
640 **Biographical Narrative**

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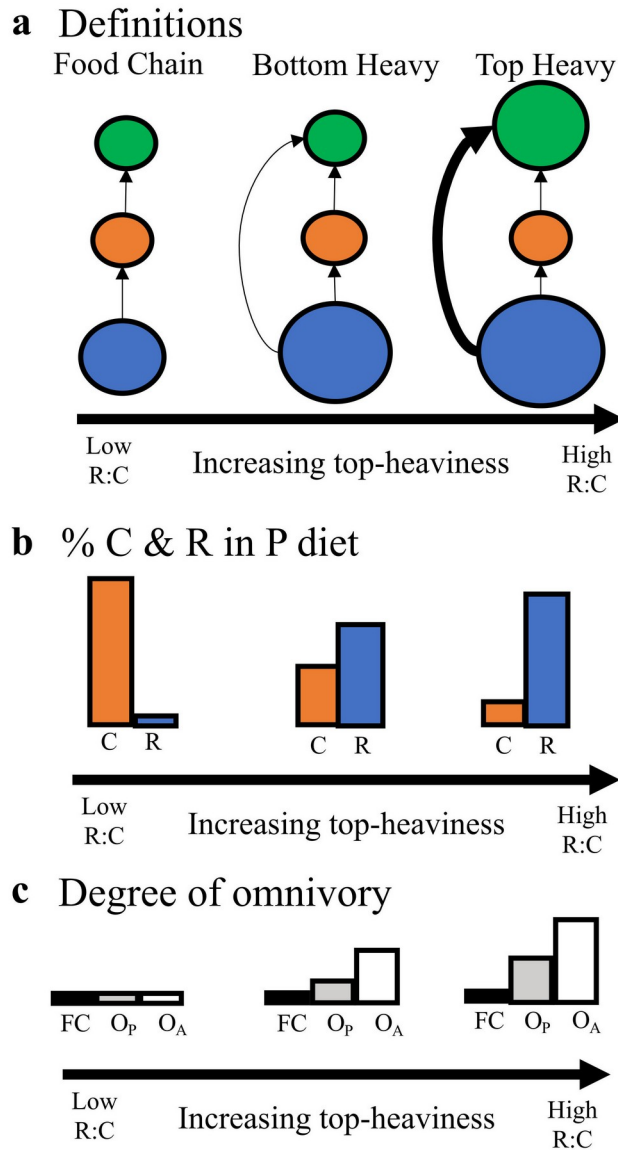
646 **Competing Interests**

647 In relation to the work here, the authors acknowledge no competing interests.

648 **Figures**
649

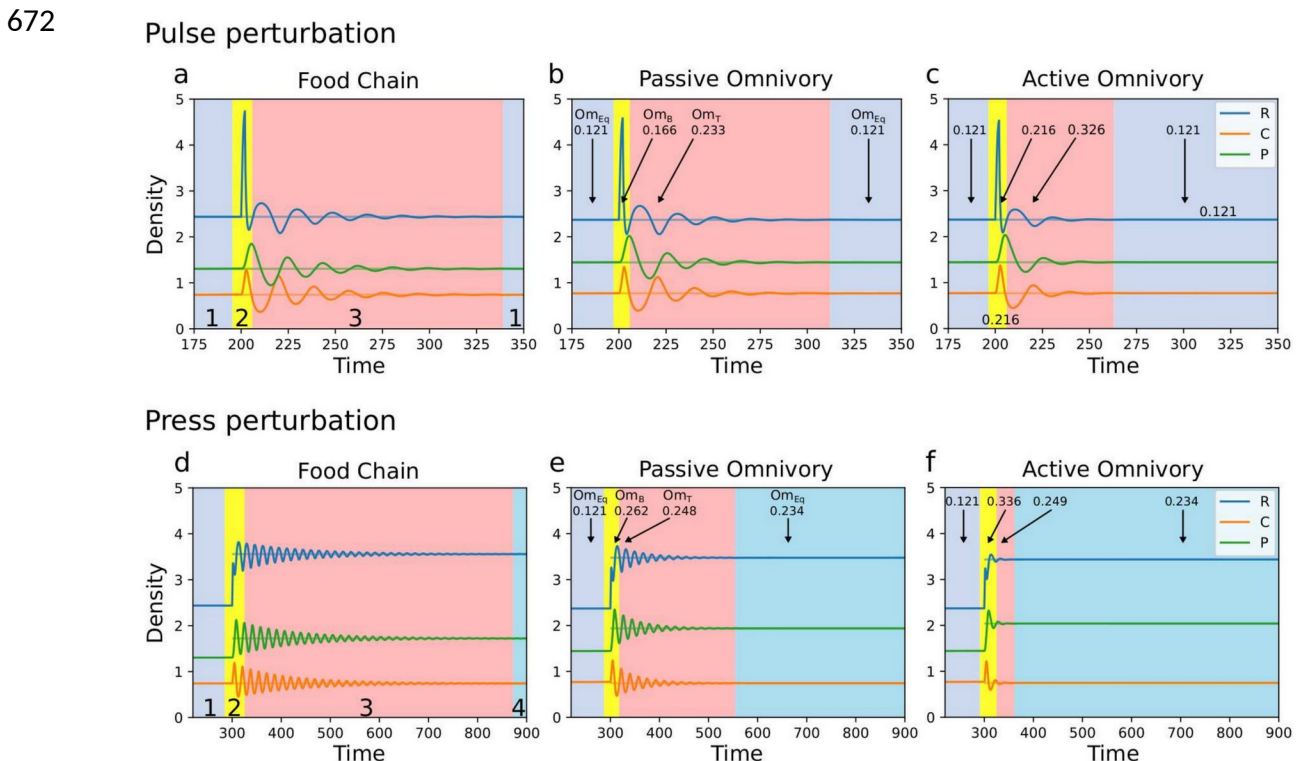


651 **Figure 1.** Similarities in the generalist and omnivory module, where **(a)** the generalist (green)
652 consumes prey (blue and orange) across multiple habitat compartments and employ a
653 consumptive portfolio effect harnessing the asynchronous flux of prey biomass across two
654 habitats through time. **(b)** The omnivore (green) consumes prey (blue and orange) across
655 multiple trophic levels and employ a consumptive portfolio effect harnessing the asynchronous
656 flux of prey biomass across two trophic levels through time.



657 **Figure 2.** The dynamic omnivory framework. **(a)** Change in tri-trophic food web module under
 658 increasing R:C conditions (i.e., increasing productivity/top-heaviness). Low R:C biomass ratios
 659 are characterized by a linear food chain with an Eltonian biomass pyramid distribution (left), as
 660 the R:C ratio increases, bottom-up changes in R density increase bottom-heavy omnivory
 661 (middle), and at high R:C ratio omnivores exhibit strong top-down pressure that drive cascades
 662 that increase top-heavy omnivory (right). **(b)** Change in % of C and R in the diet of omnivore

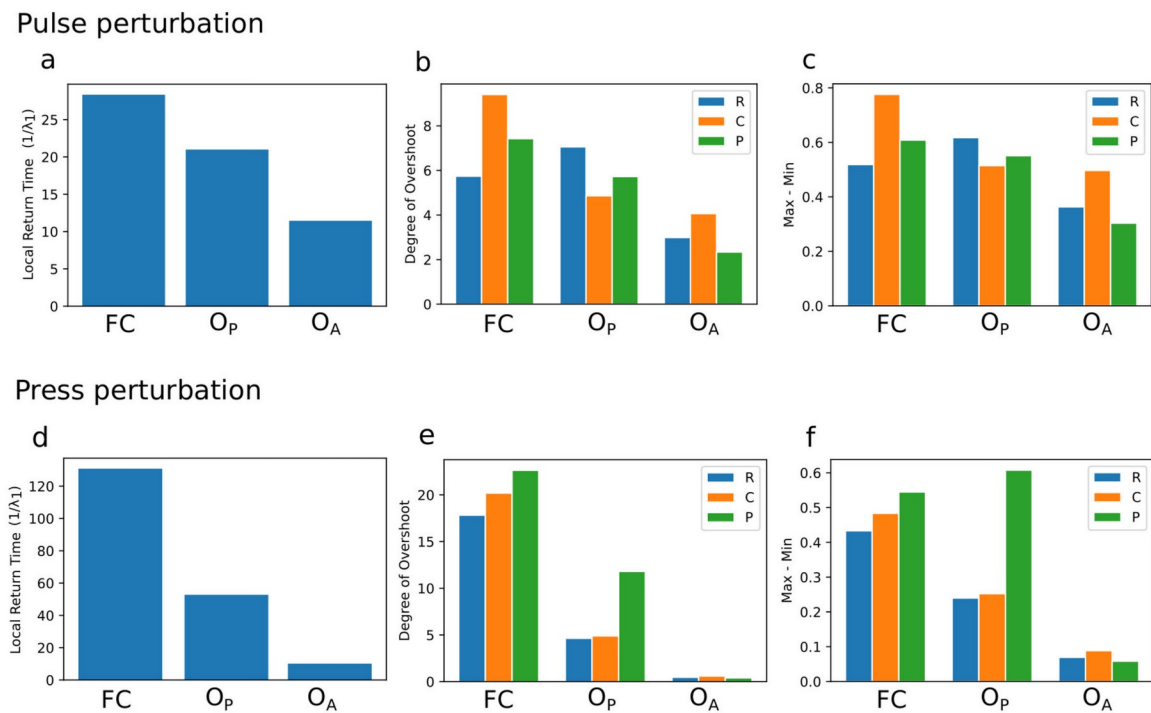
663 (P) under increasing R:C conditions (i.e., increasing productivity/top-heaviness). As the R:C
 664 ratio increases, the omnivores diet changes from being dominated by C (linear food chain) to
 665 being dominated by R (top-heavy omnivory). (c) Change in the degree of omnivory under
 666 increasing R:C conditions (i.e., increasing productivity/top-heaviness). As R:C increases and tri-
 667 trophic modules transition from a linear food chain to a top-heavy omnivory module the degree
 668 of omnivory increases. In a linear food chain (left), all omnivores (FC = food chain omnivore
 669 (black), O_P = passive omnivore (grey), O_A = active omnivore (white)) exhibit no degree of
 670 omnivory. As R:C increases both O_P and O_A increase their degree of omnivory, with O_A being
 671 higher due to ability to rapidly respond to changing prey densities.



673 **Figure 3.** Temporal dynamics of P, C, and R densities following a pulse perturbation in K
 674 (perturbation at t = 200) (a-c) and a press perturbation in K (perturbation at t = 300) (d-f). Each
 675 time series depicts initial equilibrium starting conditions before perturbation in K (region 1 in

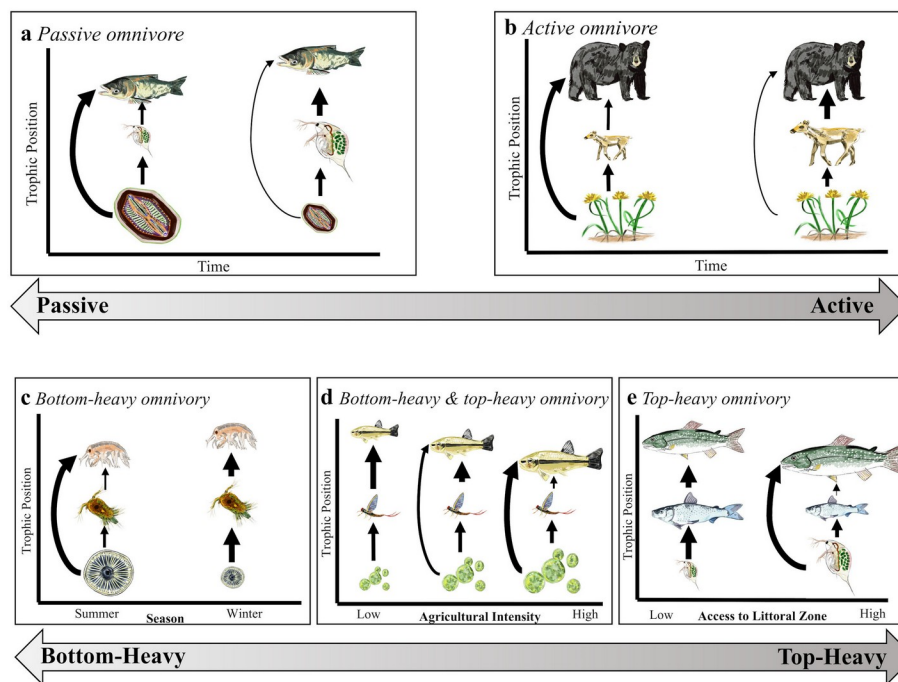
676 light blue), transient bottom-heavy response to perturbation (region 2 in yellow; note this region
 677 has been overemphasized to make visualization easier), transient phase where system oscillates
 678 between top-heavy and bottom-heavy (region 3 in pink) and after equilibrated (region 4 in blue
 679 shading on right) for (a) and (d) a food chain, (b) and (e) a passive omnivore, and (c) and (f) an
 680 active omnivore. Example degrees of omnivory in each region for the passive and active
 681 omnivore is given by om_{Eq} = degree of omnivory at equilibrium, om_B = degree of omnivory at
 682 low R:C (bottom-heavy omnivory), and om_T = degree of omnivory at max R:C (top heavy
 683 omnivory). Note under the pulse perturbation dynamics return to original equilibrium conditions
 684 and under the press perturbation a new equilibrium is reached.

685



686 **Figure 4.** Local and non-local stability metrics of food chain (FC), passive omnivory (O_P) and
 687 active omnivory (O_A) modules following a pulse perturbation (a-c) and press perturbation (d-f).
 688 (a) and (d) show local return time after pulse perturbation, measured as $1/\max(\text{Re}|\lambda_1|)$. (b) and (e)

689 show the degree of overshoot of the resource (R), consumer (C), and omnivore (P) following the
690 perturbation and (c) and (f) show the difference in maximum and minimum density of resource
691 (R), consumer (C), and omnivore (P).



692 **Figure 5.** Empirical examples of dynamic omnivory along passive-active (a,b) and bottom-
693 heavy-top-heavy continuums (c-e). (a) Bighead carp demonstrate passive omnivory as they
694 consume trophically distinct prey sources relative to their density through time with a fixed
695 preference. (b) American black bears demonstrate active omnivory as they shift preference and
696 actively forage on caribou calves during caribou calving season. (c) Seasonal changes in relative
697 zooplankton and phytoplankton availability drive bottom-heavy shifts in degree of omnivory as
698 amphipods. (d) Agricultural land-use change increases nutrient loading in streams and drives
699 bottom-heavy increases in degree of omnivory in creek chub, increasing their biomass and
700 driving top-heavy omnivory. (e) Increasing access to littoral zone (productivity gradient)
701 increases biomass of lake trout and drives top-heavy increases in their degree of omnivory.

702 **Table 1. Definitions of Key Terms Related to Dynamic Omnivory**

Key Term	Definition
Omnivory	Feeding at more than one trophic level by generalist predator (P).
Consumptive Portfolio effect	Statistical averaging of community biomass, where the sum of several random and independently varying population biomass' is less variable than an average population's biomass. Adapted from a long-standing economic principle that more diversified portfolios are less volatile.(Doak et al. 1998, Tilman 1999) Here, the consumptive portfolio effect is the average prey density available to omnivores harnessing asynchronous fluxes in consumer (C) and resource (R) biomass.
Degree of omnivory	A measure of the contribution of R to P's diet, measured as the ratio of R/(R+C) consumed by P. Equation: $\text{Deg}_{\text{om}} = \Omega a_{\text{RP}} R / (\Omega a_{\text{RP}} R + (1 - \Omega) a_{\text{CP}} C)$; see supplemental material S1 for parameter definitions.
Passive omnivore	The omnivore has a fixed preference (Ω) (scaling of its attack rate) on R relative to C. The degree of omnivory passively tracks changes in R and C densities. Equation: $\text{Deg}_{\text{om}} = \Omega a_{\text{RP}} R / (\Omega a_{\text{RP}} R + (1 - \Omega) a_{\text{CP}} C)$, where Ω is constant; see supplemental material S1 for parameter definitions.
Active omnivore	The omnivore modifies preference (scaling of attack rates on R and C respectively), depending on the ratio of $\omega R / (\omega R + (1 - \omega) C)$, where ω measures the speed with which the omnivore's attack rates on R and C respond to changes in their availability. Equation: $\text{Deg}_{\text{om}} = \Omega a_{\text{RP}} R / (\Omega a_{\text{RP}} R + (1 - \Omega) a_{\text{CP}} C)$, where $\Omega = \omega R / (\omega R + (1 - \omega) C)$; see supplemental material S1 for parameter definitions.
Bottom-heavy omnivory	Changes in degree of omnivory are driven purely by bottom-up abiotic influences (e.g., seasonal changes in productivity) that alter densities of R and C.
Top-heavy omnivory	Changes in the degree of omnivory are driven by cascading impacts of increasing top-heaviness after a change in resource availability.

703

704

705 **Table 2. Empirical Examples of Dynamic Omnivory.**

Ecosystem	Omnivory Mechanism	Type of Omnivore	Changing Condition	Taxa	Metric of Changing Omnivory	Reference
Freshwater						
Lake	Bottom-Heavy	Passive	Temporal: temporal changes in fish trophic position and diet composition in response to seasonal changes in resource availability	Silver Carp (<i>Hypophthalmichthys molitrix</i>) & Bighead Carp (<i>Hypophthalmichthys nobilis</i>); Zooplankton; Phytoplankton	Stable Isotope & Stomach Content Analysis	(Yu et al. 2019)
Stream	Bottom-Heavy	Passive & Active	Temporal: temporal changes in amphipod and caddisfly trophic position in response to seasonal changes in aquatic & terrestrial resource availability	Amphipod (<i>Gammarus pulex</i>) & Caddisfly larvae (<i>Hydropsyche spp.</i>); Benthic macroinvertebrates; Algae/Detritus	Stable Isotope Analysis	(Hellmann et al. 2013)
Lake	Bottom-Heavy	Active	Temporal: temporal changes in Dolly Varden diet composition in response to seasonal pulse in salmon eggs during salmon spawning migration	Dolly Varden (<i>Salvelinus malma</i>); Sockeye salmon eggs (<i>Oncorhynchus nerka</i>); Macroinvertebrates	Stomach Content Analysis & Physiological changes in gut size	(Armstrong and Bond 2013)
River	Bottom-Heavy	Active	Temporal: temporal changes in Rudd trophic position in response to seasonal changes in resource availability driven by temperature	Rudd (<i>Scardinius erythrophthalmus</i>); Emerald Shiner (<i>Notropis atherinoides</i>); Macrophyte (<i>Stuckenia pectinata</i>)	Stable Isotope Analysis	(Guinan et al. 2015)
Lake	Bottom-Heavy	Active	Spatial & Temporal: spatial and temporal changes in cisco diet composition in response to seasonal & spatial changes in resource availability	Cisco (<i>Coregonus artedii</i>); Round Goby (<i>Neogobius melanostomus</i>) & Alewife (<i>Alosa pseudoharengus</i>); <i>Bythotrephes longimanus</i>	Stomach Content Analysis	(Breaker et al. 2020)
Lake	Bottom-Heavy	Undetermined	Temporal: temporal changes in fish diet composition in	Roach (<i>Rutilus rutilus</i>); Macroinvertebrates;	Stomach Content	(Persson 1983)

			response to seasonal changes in resource availability	Algae/Detritus	Analysis	
Floodplain	Bottom-Heavy	Undetermined	Temporal: temporal changes in omnivorous fish diet & trophic position in response to seasonal changes in resource availability driven by seasonal flood pulse	Omnivorous fish species (e.g., <i>Channa</i> spp.); Prey fish; Invertebrates; Plant material	Stomach Content & Stable Isotope Analysis (Field Collection & Literature Synthesis)	(McMeans et al. 2019)
Stream	Bottom-Heavy	Undetermined	Spatial: spatial change in macroinvertebrate omnivores trophic position driven by gradient in agricultural eutrophication along stream	Stream secondary consumers; stream primary consumers; stream primary producers	Stable Isotope Analysis	(van der Lee et al. 2021)
Stream	Bottom-Heavy	Undetermined	Temporal: temporal changes in fish diet composition in response to seasonal changes in resource availability and temperature	Omnivorous Fish Species (<i>Bryconamericus iheringii</i>); Fish/Aquatic & Terrestrial Invertebrates; Algae/Plants/Detritus	Stomach Content Analysis	(González-Bergonzoni et al. 2016)
Stream	Bottom-Heavy & Top-Heavy	Undetermined	Spatial: spatial heterogeneity in trophic position of creek chub in response to changing resource availability along an agricultural land-use gradient	Creek chub (<i>Semotilus atromaculatus</i>); Benthic Invertebrates (e.g., <i>Ephemeroptera</i> spp.); Algae	Stable Isotope Analysis	(Champagne et al.)
Lake	Top-Heavy	Active	Spatial: spatial change in lake trout trophic position in response to changing prey availability driven by increasing lake size	Lake trout (<i>Salvelinus namaycush</i>); Cisco (<i>Coregonus artedii</i>); Zooplankton	Stable Isotope & Biomass Analysis	(Tunney et al. 2012)
Mesocosm Experiment	Top-Heavy	Undetermined	Spatial & Temporal: spatial and temporal heterogeneity in prey biomass density patterns in response to differential omnivorous fish densities	Bighead Carp (<i>Aristichthys nobilis</i>); Invertebrates (<i>Leptodora richardi</i>); Zooplankton (e.g., <i>Daphnia</i>); Phytoplankton	Biomass Density Analysis (Mesocosm Experiment)	(Zhao et al. 2016)
Marine						

Strait	Bottom-Heavy	Passive	Temporal: temporal changes in diet, stable isotope and fatty acid composition of jellyfish in response to seasonal changes in resource availability	Scyphozoan Jellyfish (<i>Pelagia noctilica</i>); Fish Larvae/Fish eggs; Zooplankton; Phytoplankton	Stomach Content, Stable Isotope, & Fatty Acid Analysis	(Milisenda et al. 2018)
Arctic	Bottom-Heavy	Undetermined	Temporal: temporal change in benthic omnivore diet in response to seasonal changes in resource availability	Amphipod <i>spp.</i> ; Zooplankton; Phytoplankton/Algae	Fatty Acid Analysis	(Werner and Auel 2005)
Fjord	Bottom-Heavy & Top-Heavy	Passive & Active	Spatial: spatial heterogeneity in lobster trophic position along resource productivity & availability gradient driven by kelp bed habitat density	Red Rock Lobster (<i>Jasus edwardsii</i>); Mussels (e.g., <i>Mytilus edulis galloprovincialis</i>); Kelp (<i>Ecklonia radiata</i>)	Field Density Surveys/Stable Isotope Analysis	(Jack and Wing 2011)
Mesocosm Experiment	Top-Heavy	Undetermined	Spatial: heterogeneity in shrimp diet & biomass dynamics of algae & amphipod in response to a shrimp presence/absence & resource availability gradient mesocosm experiment	Shrimp (<i>Palaemon elegans</i>); Amphipod (<i>Gammarus spp.</i>); Ephemeral Macroalgae	Biomass Density Analysis (Mesocosm Experiment)	(Eriksson et al. 2011)
Inter-tidal Zone	Bottom-Heavy	Active	Spatial: spatial changes in crab diet composition & trophic position in response to spatial heterogeneity in resource availability along beach width gradient	Ghost Crabs (<i>Ocypode quadrata</i>); Mole crabs (<i>Emerita talpoida</i>) & Coquina clams (<i>Donax variabilis</i>) & Amphipods (<i>Talorchestia sp.</i>); Macrophyte wrack	Stable Isotope Analysis	(Tewfik et al. 2016)
Estuary	Bottom-Heavy	Passive	Temporal: temporal changes in copepod diet composition in response to seasonal changes in resource biomass distributions	Copepod (<i>Centropages hamatus</i> & <i>Labidocera aestiva</i>); Nauplii (<i>Acartia tonsa</i> & <i>A. hudsonica</i>); Phytoplankton	Grazing Rate & Stable Isotope Analysis	(Conley and Turner 1985)
Terrestrial						
Coastal River Watershed	Bottom-Heavy	Active	Temporal: temporal changes in brown bear diet composition and habitat use in response to	Kodiak Brown Bears (<i>Ursus arctos middendorffi</i>); Sockeye	Habitat Use (aerial surveys, telemetry,	(Deacy et al. 2017)

Mix of bogs, heaths, barrens, & coniferous and mixed forest	Bottom-Heavy	Active	seasonal changes in resource availability driven by resource phenology patterns Spatial & Temporal: temporal changes in black bear diet composition & habitat use in response to spatial heterogeneity & seasonal changes in resource availability driven by calving season	Salmon (<i>Oncorhynchus nerka</i>); Red Elderberry (<i>Sambucus racemosa</i>) American Black Bear (<i>Ursus americanus</i>); Caribou Calves (<i>Rangifer tarandus</i>); Ants (family <i>Formicidae</i>); Vegetation	cameras) & Scat Analyses Habitat Use (telemetry) & Scat Analyses	(Rayl et al. 2018)
Arctic	Bottom-Heavy	Undetermined	Spatial & Temporal: spatial & temporal (seasonal) changes in polar bear diet composition in response to seasonal changes in resource availability driven by ice-on/ice-off	Polar Bear (<i>Ursus maritimus</i>); Animals (e.g., seals, seabirds, rodents); Vegetation/Algae	Scat Analysis	(Gormezano and Rockwell 2013)
Boreal Forest	Top-Heavy	Passive	Spatial: spatial heterogeneity in diet composition & habitat use in response to spatial heterogeneity in resource distribution during calving season	American Black Bear (<i>Ursus americanus</i>); Caribou fawns (<i>Rangifer tarandus caribou</i>) & Moose calves (<i>Alces alces</i>); Vegetation	Movement and habitat selection analyses (telemetry)	(Bastille-Rousseau et al. 2011)