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1 QUANTIFYING ECOLOGICAL AND SOCIAL DRIVERS OF ECOLOGICAL SURPRISE

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19 Key-words: fishery collapse, eutrophication, mountain pine beetle, natural resource management,  
20 social-ecological system, spatial temporal mismatch, structural equation model

21 **Abstract**

- 22 1. A key challenge facing ecologists and ecosystem managers is understanding what drives  
23 unexpected shifts in ecosystems and limits the effectiveness of human interventions  
24 during these events. Research that integrates and analyzes data from natural and social  
25 systems can provide important insight for unraveling the complexity of these dynamics,  
26 and is a critical step towards development of evidence-based, whole systems management  
27 approaches.
- 28 2. To examine our ability to influence ecosystems that are behaving in unexpected ways, we  
29 explore three prominent cases of ‘ecological surprise’. We capture the social-ecological  
30 systems using key variables and interactions from Ostrom’s social-ecological systems  
31 framework, which integrates broader ecosystem processes (e.g. climate, connectivity),  
32 management variables (e.g. quotas, restrictions, monitoring), resource use behaviours  
33 (e.g. harvesting), and the resource unit (e.g. trees, fish, clean water) being managed.
- 34 3. Structural equation modelling (SEM) revealed that management interventions often  
35 influenced resource use behaviours (e.g. rules and limits strongly affected harvest or  
36 pollution), but they did not have a significant effect on the abundance of the resource  
37 being managed. Instead, most resource variability was related to ecological processes and  
38 feedbacks operating at broader spatial or temporal scales than management interventions,  
39 which locked the resource system into the degraded state.

40 4. *Synthesis and applications.* Mismatch between the influence of management systems and  
41 ecosystem processes can limit the effectiveness of human interventions during periods of  
42 ecological surprise. Management strategies should shift from a conventional focus on  
43 removal or addition of a single resource towards solutions that influence the broader  
44 ecosystem. Operationalizing Ostrom's framework to quantitatively analyze social-  
45 ecological systems using SEMs shows promise for testing solutions to navigate these  
46 events.

47

## 48 INTRODUCTION

49 Resource and ecosystem managers continually make decisions with imperfect  
50 information regarding how ecosystems function, what drives observed ecological changes, and  
51 the degree to which their actions will produce the intended ecological results. The ability to  
52 predict ecological dynamics is arguably improving (Biggs, Carpenter & Brock 2009; Drake &  
53 Griffen 2010; Pace, Carpenter & Cole 2015). However, managers are frequently trying to effect  
54 change in an ecosystem (1) on short time scales (Cumming, Cumming & Redman 2006;  
55 Contamin & Ellison 2009), (2) at spatial scales smaller than the ecosystem itself (Cumming,  
56 Cumming & Redman 2006), or are (3) attempting to revert ecosystems back to their original  
57 state after unexpected change has occurred (Folke et al. 2004). These management targets are  
58 difficult to achieve because natural systems that are coupled with human systems are inherently  
59 complex, often fraught with uncertainty and difficult to predict (Underdal 2010; Fulton et al.

60 2011). The challenge of understanding – let alone managing – the multiple components and  
61 processes underlying ecosystem behaviour is no small task (Peters 1991; Costanza 2000;  
62 Waltner-Toews et al. 2003), and requires a holistic understanding of the dynamics that drive  
63 change in both social and ecological systems.

64 Management of ecological systems is further complicated by the occurrence of  
65 ‘ecological surprises’, which are defined as situations where human expectations or predictions  
66 of ecosystem behaviour deviate from observed ecosystem behaviour (King 1995; Doak et al.  
67 2008; Lindenmayer et al. 2010). Examples of ecological surprise include unanticipated critical  
68 transitions in ecosystems and management interventions that fail to influence ecosystem as  
69 expected (Filbee-Dexter et al. 2017). The threat of ecological surprise is of particular concern  
70 given the increasing frequency and severity of environmental changes globally which can have  
71 unforeseen consequences on ecological systems locally (IPCC 2014, Österblom et al. 2017).  
72 Often during ecological surprise, new or altered ecosystem dynamics appear to limit the  
73 effectiveness of management rules and regulations from influencing the ecological system  
74 (Levin 1998; Folke 2006). Resource managers and scientists have increasingly recognized the  
75 need to consider a broader range of factors when attempting to understand or predict these  
76 unexpected changes. This has prompted calls for a more complete understanding of the  
77 interactions among social systems of management and ecological components and processes  
78 during unexpected ecological change.

79           It is common for management systems to be characterized by fragmented, multi-level  
80 governance structures with sector-specific decision-making processes (e.g. Crowder et al. 2006;  
81 Morrison 2017), while ecosystems are characterized by multiple known and unknown biotic and  
82 abiotic components with complex interactions that vary in time and space (Levin 1998;  
83 Cumming, Morrison & Hughes 2017). The differences in scale and structure between these  
84 social and ecological systems determine the set of possible interactions among different  
85 components (Brondizio, Ostrom & Young 2009; Schlüter et al. 2012), and mismatch between  
86 systems may limit our ability to influence ecosystems during periods of rapid change (Pittman et  
87 al. 2015; Epstein et al. 2015; Alexander et al. 2017). For example, the legacies of past  
88 management decisions or structures may contribute to contemporary ecological change and limit  
89 the effectiveness of recent management interventions (Jackson et al. 2001; Liu et al. 2007).  
90 Similarly, ecological changes or forces, operating at larger spatial scales than managers can  
91 influence, may limit effectiveness of localized management interventions (Cumming, Cumming  
92 & Redman 2006; Koch et al. 2009; Epstein et al. 2013).

93           The ability of humans to effectively respond and adapt to observed ecological change can  
94 be limited by numerous other social factors as well. For example, a lack of compliance with rules  
95 can result in continued removal of a resource (Leader-Williams & Albon 1988; Rowcliffe, de  
96 Merode & Cowlishaw 2004; Mukul, Rashid & Khan 2017) or degradation of an ecosystem  
97 (Hauck & Sweijd 1999; Kideghesho et al. 2013). Similarly, governance systems may have

98 limited options for action due to restrictive policies, economic constraints, lack of knowledge, or  
99 other considerations (Costanza 2000; Gadgil Madhav et al. 2003; Berkes & Turner 2006).

100         In order to understand drivers of change in managed ecosystems, there is growing  
101 awareness of the need to consider ecological, social, and social-ecological processes in an  
102 integrated fashion (Hughes et al. 2017). Research that integrates quantitative social and  
103 ecological data to test hypotheses on social-ecological systems (SES) is rare (Vogt et al. 2015;  
104 but see Leslie et al. 2015; Laborde et al. 2016; Ziegler et al. 2017). However, combining data  
105 from social systems and ecosystems can reveal further complexity and a broader range of  
106 dynamics than analyses that focus on just one of the two systems (Schlüter et al. 2012; Moore et  
107 al. 2014; Hicks et al. 2016). In this study, we apply two conceptual and methodological tools to  
108 quantitatively explore the relative role of human and ecological drivers of change on natural  
109 systems.

110         First, in order to classify and integrate social and ecological data we used a conceptual  
111 framework developed by Ostrom, which is widely used by social-ecological researchers (Ostrom  
112 2007, 2009; McGinnis & Ostrom 2014). At its most general, Ostrom's framework describes an  
113 SES as a governance system that interacts with a specific resource unit that exists within a  
114 broader resource system (i.e., ecosystem). The framework also categorizes components of SES  
115 into multiple possible variables used to describe the system (McGinnis & Ostrom 2014). The  
116 framework facilitates synthesis across different systems or case studies, which allows for

117 comparison of key relationships among common, standardized system components (McGinnis &  
118 Ostrom 2014).

119 We then use structural equation models (SEMs) to quantify the potential relationships  
120 between different social and ecological variables in an SES. SEM is an analytical tool that  
121 enables us to link empirical data (e.g. abundance, limits) and theoretical constructs (e.g.  
122 ownership or connectivity) of SESs using ecological theory and known attributes or dynamics of  
123 the system (Grace et al. 2010). In our application, SEMs quantify the relative importance  
124 (strength of relationships) of ecological and social variables in driving change in the resource of  
125 interest.

126 We apply these tools to prominent cases of ecological surprise to understand how  
127 multiple factors and processes influence ecosystem behavior during these events. We selected  
128 three well-studied cases of ecological surprise from different ecological contexts (marine,  
129 freshwater, terrestrial) that demonstrate the limits of management capacity to influence or  
130 mitigate ecological change and variability: (1) the mountain pine beetle infestation currently  
131 occurring in the Western Boreal Forest in interior British Columbia (BC); (2) the persistent  
132 eutrophication of Lake Champlain's Missisquoi Bay in the Northeastern United States and  
133 Quebec, Canada; and (3) the collapse of the cod fishery in Atlantic Canada's Bay of Fundy  
134 (Figure 1). In all the managed systems, the resource of interest is expected to be influenced by  
135 both the larger resource system and actions of management. We use SEM to explore the extent  
136 that unexpected ecological behavior in each of these cases is the result of social or ecological



137 dynamics. Social dynamics may include a lack of management interventions, limited user  
138 response to management interventions, or user responses that do not produce the desired  
139 outcomes on short time scales or at small spatial scales. Ecological dynamics may include legacy  
140 effects, hysteresis, climate-driven impacts, or ecosystem changes at broader spatial scales. By  
141 quantifying relationships using a common framework we are able to directly compare among  
142 cases to understand generalities in these SESs.

143

## 144 **MATERIALS AND METHODS**

145 This work is the result of a multi-year synthesis project undertaken by an  
146 interdisciplinary team of researchers. Our approach draws on different theory and perspectives  
147 from both natural and social sciences.

148

### 149 **SES framework**

150 We use Ostrom's (2007) SES framework as a starting point to select variables in our  
151 focal SES case studies. We selected variables that encapsulate key management and ecosystem  
152 components for our three SES, and verified their importance using published literature  
153 (Appendix S1, S2). The management component of the SES includes a resource unit, harvest,  
154 and/or quota, which correspond to Ostrom's variables 'RU5', 'I1' and 'GS6' (McGinnis &  
155 Ostrom 2014). The ecological component includes a resource system, resource unit, and climate  
156 conditions, which correspond to Ostrom's variables 'RS', 'RU5' and 'ECO1' (McGinnis &

157 Ostrom 2014). In the context of the SES, the resource unit is the linking component, as its  
158 characteristics or abundance are theorized to be influenced directly by both ecological and social  
159 system components. Because management procedures and ecological dynamics differed among  
160 case studies, we selected additional variables from Ostrom’s framework that were important for  
161 specific cases. These included a flow variable describing the influx of the resource unit for the  
162 Bay of Fundy and the Western Boreal Forest, a monitoring variable for Lake Champlain and Bay  
163 of Fundy, and an ownership variable for the Bay of Fundy (Ostrom: ‘ECO3’, ‘GS6’, and ‘GS7’)  
164 (Appendix S2). Inclusion of these additional variables did not impact the core components of our  
165 SES, but rather provided context and accounted for known sources of variability within the  
166 social system or ecosystem. Here there were clear benefits to using well-studied systems, as we  
167 were able to ensure that we could acquire adequate data and evidence of these relationships to  
168 build our models. Further, it also enabled us to explore or validate previous narratives and/or  
169 hypotheses regarding the relative strengths of social and ecological drivers in these cases. We  
170 choose to exclude “Actor” variables (McGinnis and Ostrom, 2014), which represent entities that  
171 are directly or indirectly interacting with the resource unit (e.g. harvesting or producing resource  
172 units), in our models because 1) their actions were largely represented by our other management  
173 variables and 2) our hypotheses were not focused on individual-level variables.

174

175 **Data selection**

176 To quantify the key social and ecological variables in each case study we obtained time-  
177 series data that best captured the variable over the period of ecological surprise (Table S1;  
178 Appendix S2).

179 For the Bay of Fundy, we characterized the resource unit by the average biomass of cod  
180 caught during random stratified trawl surveys, conducted annually by the Canadian Department  
181 of Fisheries and Oceans (DFO) each July from 1984–2014 within the 2 fishing zones of the Bay  
182 of Fundy (zones 4Xsr) (DFO 2017). For the ecosystem variables, we defined climate as the  
183 average water temperature measured at depth during these trawl surveys, flow as the number of  
184 one-year-old cod entering the fishery, and resource system as the average trophic level of the  
185 benthic food web in the larger Nova Scotia bioregion each year (Bundy, Fanning & Zwanenburg  
186 2005). We used trophic level to summarize trends occurring in the resource system during the  
187 period of interest, because this indicator captures large changes in the species composition of  
188 marine ecosystems (Shannon et al. 2014). For the management variables, we defined quota as the  
189 total allowable catch (TAC) set by the DFO, harvest as the total biomass of cod landed by Bay of  
190 Fundy fishers, ownership as the number of fishing licenses, and monitoring as the number of  
191 research trawls each year.

192 For Lake Champlain’s Missisquoi Bay, we characterized the resource unit by the summer  
193 abundance of algae (measured as the mean June-September concentration of Chl-*a*) from 1979–  
194 2015. We defined climate as the average June-September air temperature, and resource system as

195 the total phosphorus concentration in the water. For the management variables, we defined quota  
196 as the total maximum daily load (TMDL) for phosphorus set by the United States Environmental  
197 Protection Agency, and monitoring as the frequency of water quality measures.

198 For the Western Boreal forest, we characterized the resource unit by the total cumulative  
199 area of forest in the province of BC affected by the mountain pine beetle annually between  
200 1975–2009. We defined harvest as the annual volume of timber harvested and quota as the  
201 annual allowable cut set by the BC Ministry of Forests, Lands and Natural Resources, resource  
202 system as area of forest containing trees greater than 80-years-old, and flow as the annual net  
203 change in forest area (area of forest reforested minus the area of forest burned). Finally, we  
204 defined the climate variable using minimum temperature thresholds for mountain pine beetle  
205 mortality that are hypothesized to be a primary factor driving continued population outbreaks of  
206 beetles. To account for seasonal change in cold tolerance of beetle larvae we summed the  
207 number of days over three thresholds for 100 % mortality of mountain pine beetle larvae in  
208 lodgepole pine forests: 1)  $\leq -25^{\circ}\text{C}$  from April to June, 2)  $\leq -40^{\circ}\text{C}$  from December to March, and  
209 3)  $\leq -25^{\circ}\text{C}$  from September to November (Safranyik & Wilson 2006).

210 For our case studies, an increase in the quantity of the resource unit (i.e. outcome  
211 variable) is considered to be desirable in the case of cod biomass in the Bay of Fundy and  
212 undesirable in the case of area affected by Mountain Pine Beetle in Western Boreal forest and  
213 phytoplankton biomass in Lake Champlain.

## 214 **Analytical approach**

215           To identify thresholds or points of sudden non-linear change in ecological data we  
216 performed trend analyses on time-series data of the resource units for each case study. For each  
217 case we fitted a generalized additive model (GAM). GAMs are nonparametric extensions of  
218 generalized models that fit a smoothing term to the data using maximum likelihood. To reduce  
219 the possibility of over-fitting our model (in the case of linear change) we used a penalized thin  
220 plate regression spline that enables the smoothing term to be reduced to zero (Wood 2004). We  
221 examined the first and second derivatives of the GAM to identify trends of increasing or  
222 decreasing response over time for each case (periods when the first derivative is significantly  
223 different from 0) and tipping points/critical transitions (periods when the second derivative is  
224 significantly different from 0) (Toms and Lesperance 2003).

225           For each case study, we constructed SEMs that described and measured the strength of  
226 the relationships leading from components of the ecological and social systems to the resource  
227 unit of interest (cod biomass, algal biomass, area of beetle-infested trees). SEM is a multivariate  
228 statistical approach used in a wide variety of ecological and social applications to explore  
229 relationships between dependent and independent variables (e.g. Byrnes et al. 2011; Seidl,  
230 Schelhaas & Lexer 2011; Dainese et al. 2017). SEMs are similar to regression models (e.g.  $\{X_1,$   
231  $X_2\} \rightarrow Y$ ), but they are more flexible and can test ‘path models’ consisting of multiple variables  
232 linked using multiple direct and indirect paths (e.g.  $\{X_1, X_2\} \rightarrow M \rightarrow Y$ ) (Pugesek, Tomer & Eye  
233 2003; Grace et al. 2010; Shipley 2016). SEM estimates variance and covariance matrices to

234 characterize the structure of relationships among variables, which provides increased flexibility  
235 for incorporating diverse types of variables and estimation techniques that reflect underlying  
236 assumptions about variable distributions and the degree or shape of paths between variables  
237 (Kline 2011). In addition, because SEM takes a structural or multi-level approach to estimating  
238 relationships among variables, both single empirical measurements (‘indicators’) and constructs  
239 (‘latent factors’ that are estimated using a combination of multiple empirical measurements) can  
240 be included in analyses (Kline 2011; Shipley 2016).

241         The paths in our SEM are based on known empirical links within systems of management  
242 and ecosystems (e.g. total allowable catch → landed cod) and our understanding of these  
243 systems, as well as the links theorized by Ostrom’s SES framework (Appendix S1, S2). We used  
244 time-series data (Figure 2;  $n > 30$  years for each case) to estimate the direct and indirect effects  
245 of climate, resource system, external flows, quota, harvest, monitoring, and ownership on the  
246 abundance of the resource unit. To confirm that non-independence of our time-series  
247 observations would not impact model structure we tested for temporal autocorrelation in the  
248 resource unit in each case study. We found no significant temporal autocorrelation for the  
249 resource unit in Bay of Fundy and Lake Champlain (Figure S1). However, we did find  
250 significant temporal autocorrelation for the Western Boreal forest resource unit. To account for  
251 this we included a 1-year lagged resource unit variable that linked directly to the resource unit in  
252 this case study ( $RU_{t-1} \rightarrow RU$ ).

253 We fit the SEMs using the lavaan package in R (Rosseel 2012). We report standardized  
254 path coefficients to allow comparison of the relative importance of ecological and social  
255 variables contributing to variability in the resource unit. The SEM figures presented here use  
256 standard reporting practices, with latent factors depicted as ovals and empirical indicators as  
257 rectangles (McDonald & Ho 2002). For additional details on SEM analysis, data sources, and  
258 unstandardized path coefficients see Appendix S2.

259

## 260 **RESULTS**

261 Our time-series analysis results indicate that there were significant changes in the  
262 resource unit in the Bay of Fundy and Western Boreal Forest case studies, but not in the Lake  
263 Champlain case study (Table 1; Figure 1). In the Bay of Fundy, cod biomass declined  
264 significantly from 1990 on, with a critical transition between 1980 and 1982. In the Western  
265 Boreal Forest, the amount of pine impacted by the mountain pine beetle increased significantly  
266 between 2002 on, with a critical transition between 2000 and 2002 (Figure 1). In Lake  
267 Champlain, chlorophyll-*a* concentration did not change significantly over the period of interest,  
268 and no critical transition was detected. For this case study, the timing of ecological surprise was  
269 defined as the year that the TMDL management intervention was implemented, because there  
270 was an expectation that this action would decrease the frequency and severity of algal blooms  
271 (but no change was detected).

272 Our SEM results demonstrate that the relationships theorized in the SES framework  
273 explained a large amount of the variation in the resource unit (RU) ( $r^2=0.95$  for the Bay of  
274 Fundy,  $r^2=0.80$  for the Mountain Pine Beetle,  $r^2=0.57$  for Lake Champlain). For these three cases  
275 of ecological surprise, the management variables within the social system had significant effects  
276 on the behaviour and decisions of resource users, but these decisions had little direct effect on  
277 the resource unit itself (Quota/Harvest→RU; Figures 3-5, Table 2). For all SEMs, the paths  
278 describing the effects of management actions on the resource unit during the period of surprise  
279 were not significant (Table 2). Specifically, the amount of cod caught by fishers in a given year  
280 was not significantly related to the abundance of cod in the Bay of Fundy in that year, restricting  
281 P inputs into Lake Champlain in a given year did not affect the biomass of algae (chlorophyll-*a*  
282 concentration) in the lake that year, and the quantity of trees harvested by logging companies in a  
283 given year did not affect the area of Western Boreal forest affected by the mountain pine beetle  
284 in that year.

285 In all SEMs, the paths describing management actions (paths between monitoring and  
286 quota or harvest) during the period of unexpected ecological change were statistically significant.  
287 For the Bay of Fundy, the increasing number of surveys on declining cod stock had a negative  
288 effect on the total allowable catch set by managers. The quota, which was lowered over this  
289 period, had a significant positive effect on the biomass of cod harvested (Figure 3). For Lake  
290 Champlain, the frequency of monitoring also had a significant negative relationship with quota.  
291 In the Western Boreal forest, the quota varied significantly with harvest, but this relationship was



292 negative such that harvest was low when the quota was high (Figure 5), likely driven by the  
293 inability of loggers to meet high ‘salvage logging’ quotas (B.C. Ministry of Forests, Mines, and  
294 Lands, 2010).

295 Most variability in the resource unit was related to variability in ecosystem processes  
296 during the period of interest (Resource system or  $RU_{t-1} \rightarrow RU$ ). The paths describing the effects of  
297 the broader resource system on the resource unit were significant in 2 of the 3 models (partial  $r^2$   
298  $> 0.80$  for Bay of Fundy and Lake Champlain, Table 2). In other words, the average trophic level  
299 of the benthic food web in the Nova Scotian bioregion had a positive effect on the biomass of  
300 cod (Figure 3). Food webs with lower average trophic levels (dominated by smaller fish and  
301 invertebrates) in the larger coastal region were associated with fewer cod in the Bay of Fundy.  
302 Similarly, in Lake Champlain the total P in the water had the strongest influence on the amount  
303 of algae in the lake. In contrast, the amount of Western Boreal forest containing trees  $> 80$  years-  
304 old had no significant effect on the amount of forest impacted by mountain pine beetle (Figure  
305 5). Instead, the abundance of trees  $> 80$  years-old was strongly influenced by the area of forest  
306 reforested or burned each year. Most variability in the amount of forest impacted by mountain  
307 pine beetle was explained by the area impacted by disease the previous year, indicating that  
308 internal feedbacks on the resource unit were stronger than the effects of management  
309 interventions or changes in the larger resource system.

310 Paths between the climate variable and the resource unit were only significant for the Bay  
311 of Fundy (Table 2). In the Bay of Fundy, water temperature had a negative effect on the biomass

312 of cod, which is a cold-water species. In Lake Champlain, air temperature had no effect on the  
313 concentration of chlorophyll-*a* in the lake, but did significantly impact the total phosphorus in  
314 the lake (Figure 4). In the Western Boreal forest, temperature conditions associated with beetle  
315 mortality had no significant effect on the area of forest impacted by the mountain pine beetle  
316 (Figure 5).

317

## 318 **DISCUSSION**

319 By quantitatively operationalizing Ostrom's SES framework, our results show that in all  
320 three cases the managed resource (RU) responded to short-term ecological changes, not to short-  
321 term changes in human behavior (i.e., people responded to management interventions, but the  
322 ecosystem did not). In particular, the strong link between the ecosystem (resource system) and  
323 the resource unit in the Bay of Fundy and Lake Champlain case studies suggests that, at the  
324 scales we examined, short-term changes in ecological dynamics had a stronger influence  
325 compared to localized management interventions (Figures 3, 5, Table 2). This is consistent with  
326 ecological feedbacks driving ecosystem structure, and these results coupled with past studies,  
327 suggest that broader spatial and temporal dynamics may limit the ability of management  
328 interventions to influence ecological surprise.

329 Although there was not a significant relationship between the social systems of  
330 management and the resource unit, we found that the governance variables capturing rules of use  
331 in Bay of Fundy and Western Boreal Forest, co-varied significantly with user behaviour (i.e.,

332 harvest affected by ownership and quota) (Table 2). This result suggests that the users being  
333 monitored by the managers adhered to the strong management interventions for these systems  
334 (e.g. cod quota was dramatically reduced to 6% of initial harvesting levels). It also indicates that  
335 failure of the management systems to produce the intended effect on the resource unit was not  
336 because users did not comply with rules or policies (or at least the users that were tracked).  
337 However, it is worth noting that illegal fishing and illegal cutting are not included in the harvest  
338 variable, so this relationship does not capture all user behaviour.

339

#### 340 **Ecological dynamics, reinforcing feedbacks and hysteresis**

341 The strong link between the ecological variables and RU in all case studies is consistent  
342 with an ecological surprise whereby the ecosystem undergoes an abrupt shift and/or is stabilized  
343 by ecological dynamics that create hysteresis. Research on sudden changes in ecosystem  
344 structure indicates that when ecosystems are pushed beyond tipping points of stability, human-  
345 driven recovery can be difficult because reinforcing feedback mechanisms or altered ecological  
346 dynamics can lock the ecosystem into the new configuration (Scheffer et al. 2001; Folke et al.  
347 2004; Berkes, Colding & Folke 2008). This is termed hysteresis, and occurs when an alternate  
348 ecosystem state persists after the initial driver of ecosystem change has been relaxed because of  
349 new reinforcing mechanisms (Scheffer et al., 2001). Missisquoi Bay of Lake Champlain typifies  
350 a classic example of hysteresis, where shallow lakes transition between macrophyte dominance  
351 and clear conditions to phytoplankton dominance and turbid conditions at different threshold

352 levels of nutrients (Jeppesen et al., 1990; Scheffer et al., 1993). A number of mechanisms  
353 stabilize lake systems in turbid states (reviewed in Scheffer and van Nes, 2007). For example,  
354 nutrient loading can induce anoxia in lake sediments causing phosphorus to become more  
355 bioavailable, reinforcing the turbid state even once external nutrient loading is reduced. There is  
356 evidence that the collapsed cod population is also experiencing some level of hysteresis.  
357 Following the dramatic loss of cod, planktivorous forage fishes and invertebrates increased in  
358 abundance (Bundy et al. 2009). Through direct predation and competition for resources with cod,  
359 these groups likely delayed the recovery of cod stocks (Petrie et al. 2009). In both cases, our  
360 resource system variables are related to these stabilizing feedback mechanisms maintaining the  
361 new ecosystem states (e.g. water phosphorus concentrations, average trophic level of the benthic  
362 food web). This suggests that during tipping points, shifting the focus away from directly  
363 controlling the availability of the resource, to focusing on ways to influence the broader resource  
364 system may be enable managers to navigate these events more successfully (Biggs et al. 2012).

365         In the Western Boreal Forest, the resource unit was strongly influenced by the mountain  
366 pine beetle disease in the previous year. This represents another type of ecological tipping point,  
367 where the forest is pushed past a threshold for a disease outbreak that sets the ecosystem on a  
368 trajectory that is difficult to deviate from, regardless of changes in harvest, climate, or in the  
369 broader resource system. This is consistent with positive feedbacks that lead to non-linear  
370 population outbreaks of insects or rapid spread of invasive species (Washington-Allen and Salo  
371 2007, Gibbs and Grant 1987).

372

**373 Underlying social drivers of ecological dynamics**

374         Although SEM results show that proximate management decisions have been ineffective  
375 at preventing or responding to ecological surprise, previous work on these systems indicate that  
376 the drivers of surprise are linked to a combination of historic management decisions and external  
377 social and ecological changes. These drivers occur at larger spatial and temporal scales than the  
378 managed system, which may be hindering the effectiveness of management interventions. For  
379 example, in all cases, the resource system variables are related to past management decisions.  
380 Our models are not able to directly test the relationships between past management, external  
381 changes, and the resource system (see Appendix S2 on why our models do not explicitly account  
382 for lagged effects of management). However, they are supported by a considerable breadth of  
383 scholarship that has focused on each specific case, as well as on understanding general  
384 ecosystem processes affected by management decisions (Appendix S1). This highlights a  
385 potential pitfall of a traditional single resource unit or single location management approach,  
386 whereby decisions and assessments are made for single resource units and do not account for  
387 processes occurring at larger spatial scales or those affecting multiple components of the  
388 ecosystem. In cases such as ours, where the resource is strongly influenced by internal feedbacks  
389 or the broader resource system in which it is embedded, management interventions in relation to  
390 ecological surprise should occur earlier or be stronger, or management should develop new  
391 strategies that act on the ecosystem in a different way (i.e. focus on the whole ecosystem such as

392 protecting critical habitat or using multispecies maximum sustainable yield in fisheries, (e.g.  
393 Levin & Lubchenco 2008; Worm et al. 2009; Hughes et al. 2017)). For example, rules in the Bay  
394 of Fundy could have cut quotas when other stocks showed first indications of overexploitation,  
395 forestry managers in BC could have prioritized diverse planting strategies, and managers of Lake  
396 Champlain could have focused on removing phosphorus and imposed stricter limits in areas of  
397 the lake that were below the critical thresholds of P loading required to trigger algal blooms.

398         Quantifying the relative importance of different management and ecological variables can  
399 also provide valuable information to managers. If an ecological variable is having a strong effect  
400 on the resource unit then managers can refocus their efforts accordingly. Alternatively, if the  
401 important variables are larger in scale than those that are under control of the manager then this  
402 information can be used as quantitative evidence to argue for expanded reach, collaboration with  
403 other managing bodies, or adapting to the ‘new normal’. This also reinforces the importance of  
404 ongoing information sharing, data collection, and analysis in determining appropriate  
405 management responses to ecological surprise.

406

#### 407 **Quantitative applications of Ostrom’s framework: insights and challenges**

408         Despite its frequent application in SES research, few studies have quantitatively tested  
409 ecological hypotheses using Ostrom’s framework (McGinnis & Ostrom 2014; Hinkel, Bots &  
410 Schlüter 2014). Our study uses a novel approach that combines Ostrom’s conceptual framework  
411 and advanced statistical tools to integrate ecological and social data, which enables us to quantify

412 relative drivers of unexpected ecological behaviour. In this way, we provide a broader  
413 perspective from those provided by ecological or social science alone. Although there are widely  
414 accepted narratives of what drives resource unit dynamics in each of these cases, these narratives  
415 are often created in the absence of formal statistical tests or are based on a narrow set of data. For  
416 example, climate has been identified as a contributing factor of shifts in all three case studies  
417 (Appendix S2), but the relative importance of climate in influencing the resource unit in our  
418 models was small compared to other ecological processes, suggesting that a sole focus on  
419 climate as the explanation of these events is not a complete nor correct conclusion.

420         The technique of quantitatively operationalizing Ostrom's SES framework provides a  
421 useful 'self-check' for managers on their management capacity and a way to determine the  
422 relative importance of variables affecting the managed resource. SEM is an ideal analytical tool  
423 to pair with SES dynamics because it is a highly adaptable framework that can be used to explore  
424 many different hypotheses. We focused on direct effects of the resource unit, however, other  
425 types of relationships can be modelled using SEMs, such as lagged effects, indirect effects and  
426 feedbacks, any of which may be of interest to managers.

427         Conceptually, we found two clear drawbacks of Ostrom's framework. First, it does not  
428 easily capture ecosystem-based management because it is focused towards a single resource unit,  
429 and not to the resource system. As a result, this framework will reproduce the inherent biases in  
430 single resource management approaches. Second, the possible variables are weighted towards the  
431 social system, and the framework is missing important ecological components (e.g. abiotic

432 conditions, biological diversity, energy transfer) that should be included and directly linked to  
433 the RU if it is to properly capture the SES. For example, there were no internal flows on the  
434 resource system, so we used an external flow 'ECO3' variable to capture these dynamics. These  
435 findings are consistent with other suggestions to improve the ecological components of the  
436 framework (Epstein et al. 2013; Vogt et al. 2015). Developing a more robust and comprehensive  
437 framework will ensure that these tools can have better application in SES research and  
438 quantitative hypothesis testing.

439         There also are limitations to our analytical approach. To explore the SES in a quantitative  
440 manner we simplified both the social system managing the resource and the ecosystem  
441 containing the resource to its key components, which loses fine-scale dynamics. This in turn  
442 limits our conclusions to the relative impacts of both systems, and does not allow us to fully  
443 examine the drivers of these dynamics within either system (e.g. attributes of the systems of  
444 governance, specific actors, species interactions, environmental forcing, etc.). Additionally,  
445 despite the relatively long-term datasets available for all the variables of interest in our case  
446 studies, the number of data points still limited our analyses, which were therefore not able to  
447 fully capture important historic processes. This highlights the importance of maintaining and  
448 collecting long-term data sets to understand dynamics, which are operating on multi-decadal  
449 scales. Finally, selecting appropriate data for Ostrom's SES variables (which are the result of a  
450 whole suite of dynamics) can be challenging, and requires knowledge of the social and  
451 ecological system that may be based on ecological theory or contain assumptions. However,



452 considering the complexity of the SESs in our case studies, it is remarkable that our models  
453 explained such a large amount of the variation in our resource units. This approach shows  
454 promise, and could be used to explore similar hypotheses about what drives socio-ecological  
455 outcomes in other systems.

## 456 **Conclusions**

457         The integration of data from natural and social sciences is a critical step in the shift  
458 towards evidence-based, whole systems management approaches. Our results reveal clear  
459 limitations on management's capacity to avoid an impending ecosystem shift or navigate an  
460 ongoing surprise at the time scale and spatial scale of these management interventions. Although,  
461 the additional information gained through SES modelling may not provide a 'silver bullet' for  
462 many of our current sustainability challenges, we would reiterate Ostrom's (2007) argument that  
463 there are no panaceas, and that these dynamics will be dependent on the specifics of each system.  
464 However, understanding the impacts of management decisions on the entire ecological system  
465 and their potential to create legacy effects should continue to be an important part of ecosystem  
466 management. Further use of these analytical methods should provide a useful tool for managers,  
467 allowing for a 'self check' on their management capacity, informing the type and scale of  
468 solutions that may be most effective and responsive in the face of rapid environmental change  
469 and surprise.  
470

471 **Authors' contributions**

472 All authors conceived the ideas and designed methodology; SA, JP and MB obtained social data  
473 and KFD, CS, and HAH obtained ecological data for the case studies. KFD, CS, and KJ analyzed  
474 and interpreted the data; KFD, CS, KJ and HAH led the writing of the manuscript. All authors  
475 contributed critically to the drafts and gave final approval for publication.

476

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485

486 **Data accessibility**

487 Data will be made available from the Dryad Digital Repository

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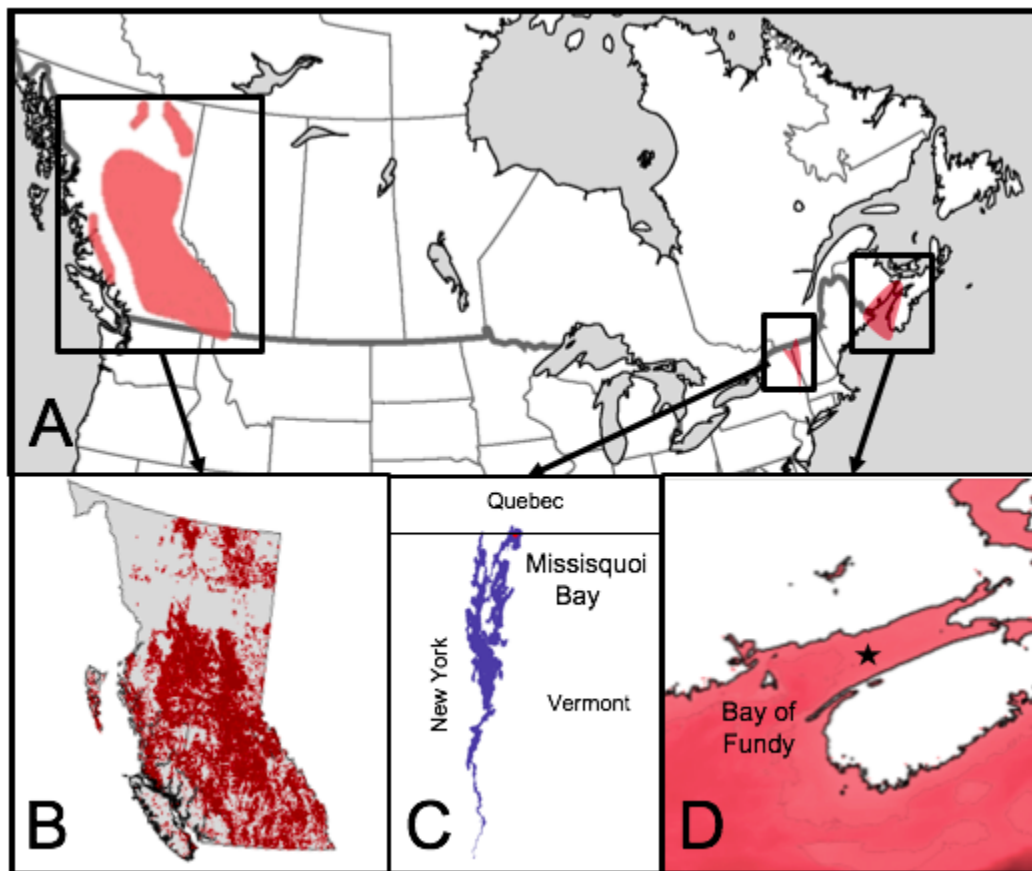
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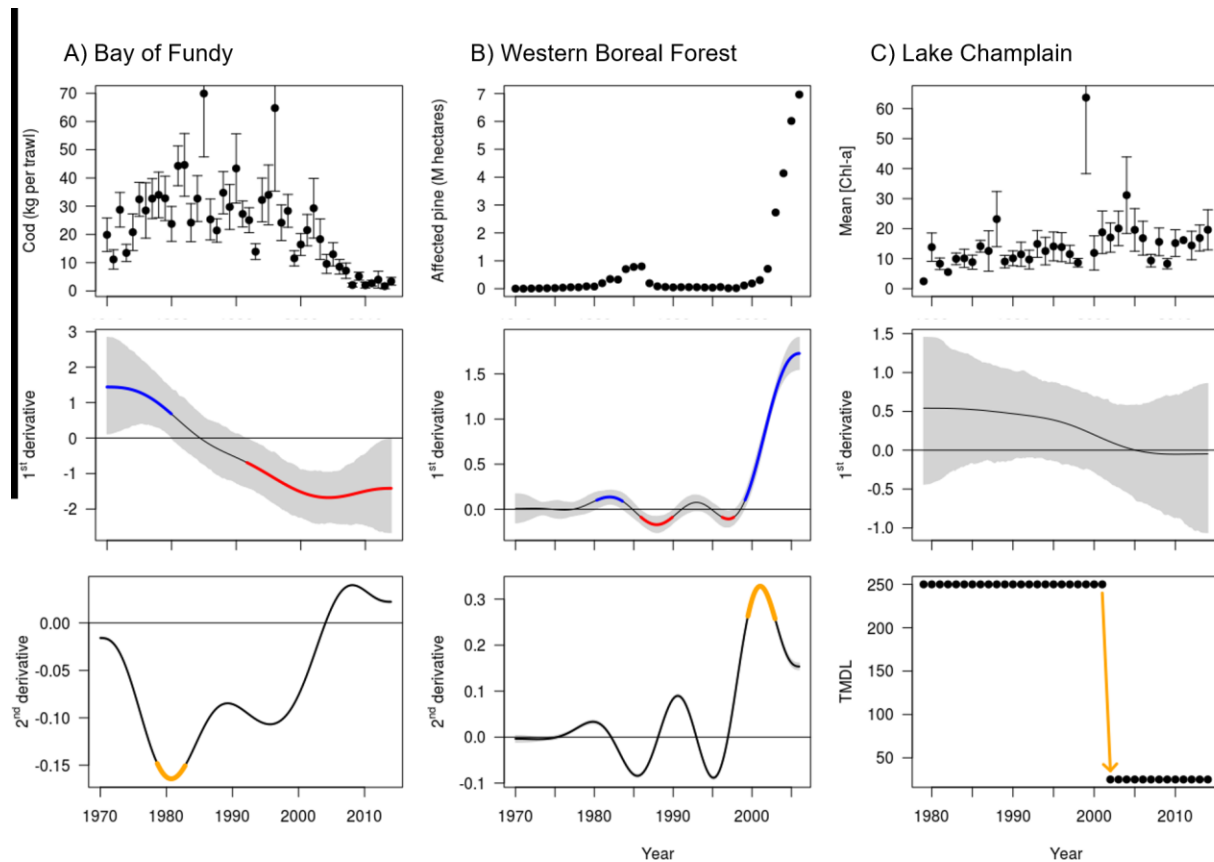
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- 695

696 **Figures and Tables**

697  
 698 **Figure 1.** (A) Map of case studies depicting the (B) area of forest impacted by mountain pine  
 699 beetle in 2016 in British Columbia, (C) Missisquoi Bay in Lake Champlain and (D) the Bay of  
 700 Fundy.

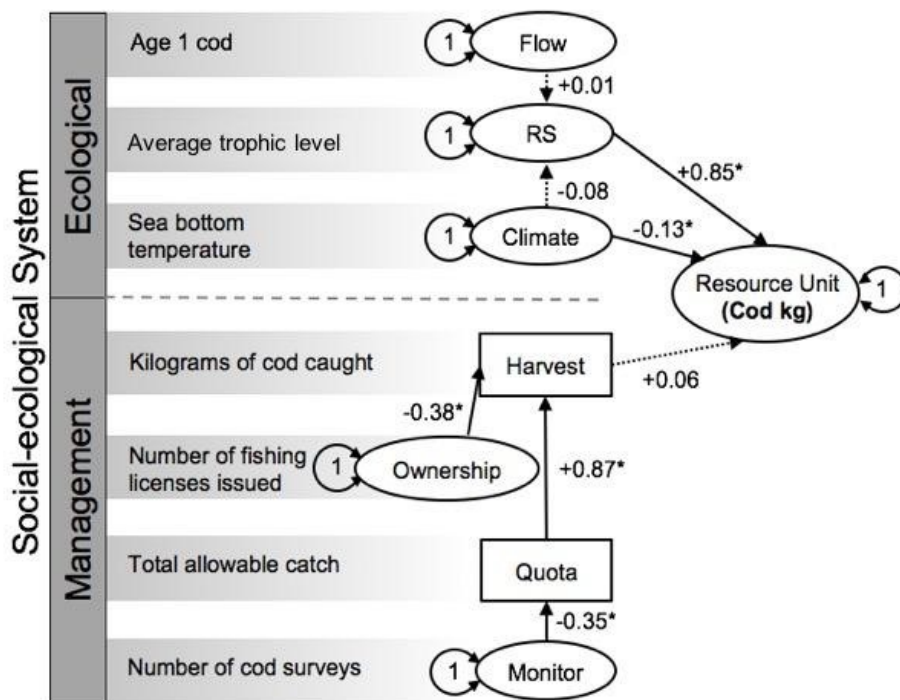
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703 **Figure 2.** Time-series of the resource units for each case study (top panel). (a) Cod biomass in  
 704 the Bay of Fundy, (b) the area of pine trees affected by mountain pine beetle in interior British  
 705 Columbia, and (c) mean summer chlorophyll-*a* in Missisquoi Bay of Lake Champlain.  $N = 31,$   
 706  $36, 37,$  respectively. Error bars in (a) and (c) represent standard errors and are cut off for 3  
 707 outlier data points. Middle panel shows 1st derivative of GAM model with 95% CI (gray). Blue  
 708 and red indicate the period over which the resource was significantly increasing and decreasing  
 709 (respectively). Bottom left and middle panels shows 2nd derivative of GAM which indicates  
 710 tipping points (orange) for cod abundance and area of diseased pine trees.

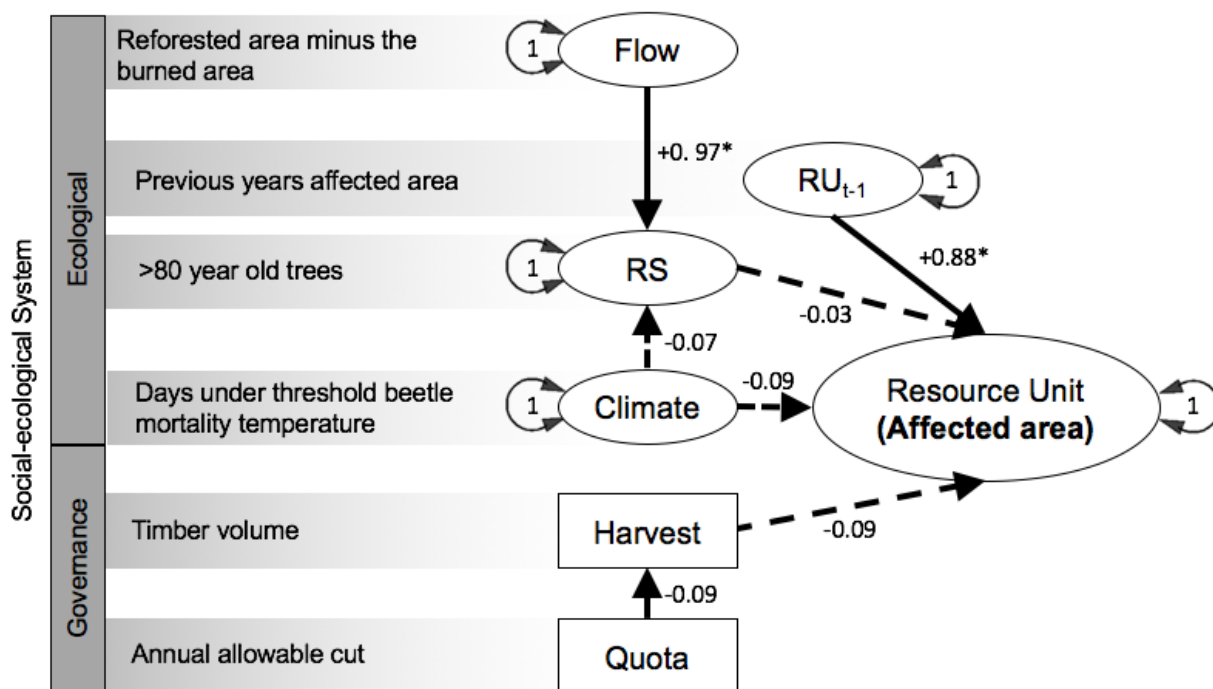
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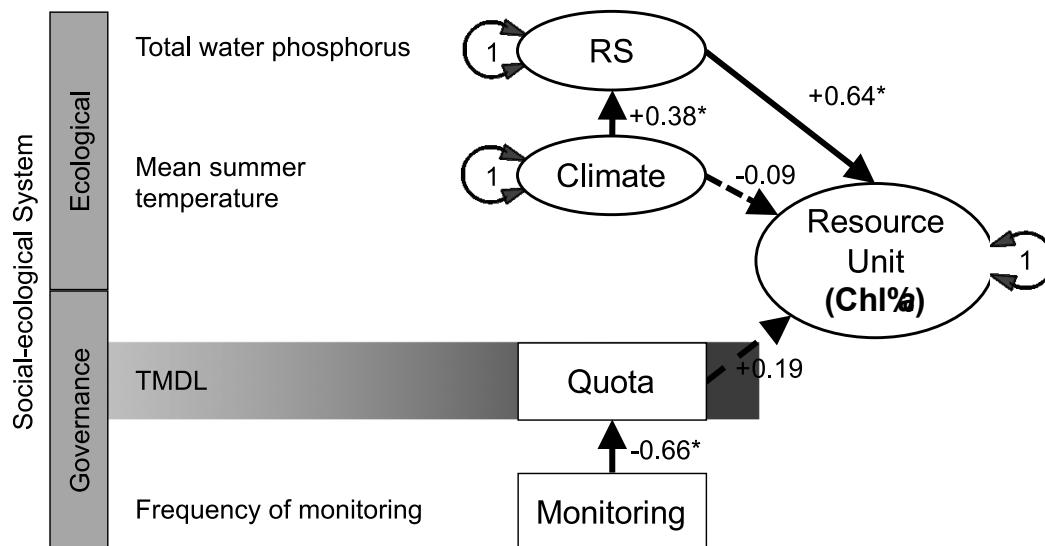
713 **Figure 3.** Structural equation model (SEM) of Bay of Fundy cod collapse showing how  
 714 variation in the resource unit (cod biomass) is associated with management and ecological  
 715 variables. Numbers next to arrows are standardized path coefficients. Solid arrows denote paths  
 716 that are significant ( $p > 0.05$ ). Latent factors with fixed variance are denoted by ovals, while  
 717 variables without fixed variance are denoted by rectangles. The data used for each variable is  
 718 shown in the grey boxes on the left.





719

720 **Figure 4.** Structural equation model (SEM) of interior British Columbia mountain pine beetle  
 721 infestation showing how variation in the resource unit (affected area of forest) is associated with  
 722 management and ecological variables. Numbers next to arrows are standardized path  
 723 coefficients. Solid arrows denote paths that are significant ( $p > 0.05$ ). Latent factors with fixed  
 724 variance are denoted by ovals, while variables without fixed variance are denoted by rectangles.  
 725 The data used for each variable is shown in the grey boxes on the left.



726

727 **Figure 5.** Structural equation model (SEM) of persistent eutrophication in Missisquoi Bay of  
 728 Lake Champlain showing how variation in the resource unit (mean summer Chl-*a* concentration)  
 729 is associated with management and ecological variables. Numbers next to arrows are  
 730 standardized path coefficients. Solid arrows denote paths that are significant ( $p > 0.05$ ). Latent  
 731 factors with fixed variance are denoted by ovals, while variables without fixed variance are  
 732 denoted by rectangles. The data used for each variable is shown in the grey boxes on the left.

733 **Table 1.** GAM results for each case. Models were in the form of  $RU \sim s(\text{Year})$  and were fit by  
 734 maximum likelihood using residual deviance. Significant  $p$ -values are in bold

Case	$r^2$		Est. $df$	F	$p$
Bay of Fundy	0.67	Intercept		t=20	<0.001
		Year	3.2	F=22.3	<0.001
Western Boreal Forest	0.99	Intercept		t=264	<0.001
		Year	8	F=3095	<0.001
Lake Champlain	0.10	Intercept		t=9.6	<0.001
		Year	1.7	F=2.2	0.122

735

736

737 **Table 2.** SEM standardized path coefficients for the three case studies: cod collapse in the Bay  
 738 of Fundy (BF), mountain pine beetle infestation in the Western Boreal Forest, interior British  
 739 Columbia (MPB) and the persistent eutrophication of Missisquoi Bay in Lake Champlain (LC).  
 740 Bolded standardized path coefficients are significant at  $p < 0.05$ . If a path was not present in the  
 741 SEM for a given case study the path is denoted NA.

	<b>Path</b>	<b>BF</b>	<b>MPB</b>	<b>LC</b>
Ecological	Flow → Resource System	0.01	<b>0.97</b>	NA
	Resource System → Resource Unit	<b>0.85</b>	-0.03	<b>0.64</b>
	Climate → Resource System	-0.08	-0.07	<b>0.38</b>
	Climate → Resource Unit	<b>-0.13</b>	-0.09	0.18
	Resource Unit (t-1) → Resource Unit	NA	<b>0.88</b>	NA
Management	Harvest → Resource Unit	0.06	-0.09	NA
	Ownership → Harvest	<b>-0.38</b>	NA	NA
	Quota → Harvest	<b>0.87</b>	-0.09	NA
	Quota → Resource Unit	NA	NA	0.19
	Monitoring → Quota	<b>-0.35</b>	NA	<b>-0.66</b>

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