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1   QUANTIFYING ECOLOGICAL AND SOCIAL DRIVERS OF ECOLOGICAL SURPRISE

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Abstract

1. A key challenge facing ecologists and ecosystem managers is understanding what drives unexpected shifts in ecosystems and limits the effectiveness of human interventions during these events. Research that integrates and analyzes data from natural and social systems can provide important insight for unraveling the complexity of these dynamics, and is a critical step towards development of evidence-based, whole systems management approaches.

2. To examine our ability to influence ecosystems that are behaving in unexpected ways, we explore three prominent cases of 'ecological surprise'. We capture the social-ecological systems using key variables and interactions from Ostrom's social-ecological systems framework, which integrates broader ecosystem processes (e.g. climate, connectivity), management variables (e.g. quotas, restrictions, monitoring), resource use behaviours (e.g. harvesting), and the resource unit (e.g. trees, fish, clean water) being managed.

3. Structural equation modelling (SEM) revealed that management interventions often influenced resource use behaviours (e.g. rules and limits strongly affected harvest or pollution), but they did not have a significant effect on the abundance of the resource being managed. Instead, most resource variability was related to ecological processes and feedbacks operating at broader spatial or temporal scales than management interventions, 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°C from April to June, 2) $\leq$ -40°C from December to March, and

209   3) $\leq$ -25°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

Underlying social drivers of ecological dynamics

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

Authors' contributions

All authors conceived the ideas and designed methodology; SA, JP and MB obtained social data

and KFD, CS, and HAH obtained ecological data for the case studies. KFD, CS, and KJ analyzed

and interpreted the data; KFD, CS, KJ and HAH led the writing of the manuscript. All authors

contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data will be made available from the Dryad Digital Repository

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696 **Figures and Tables**
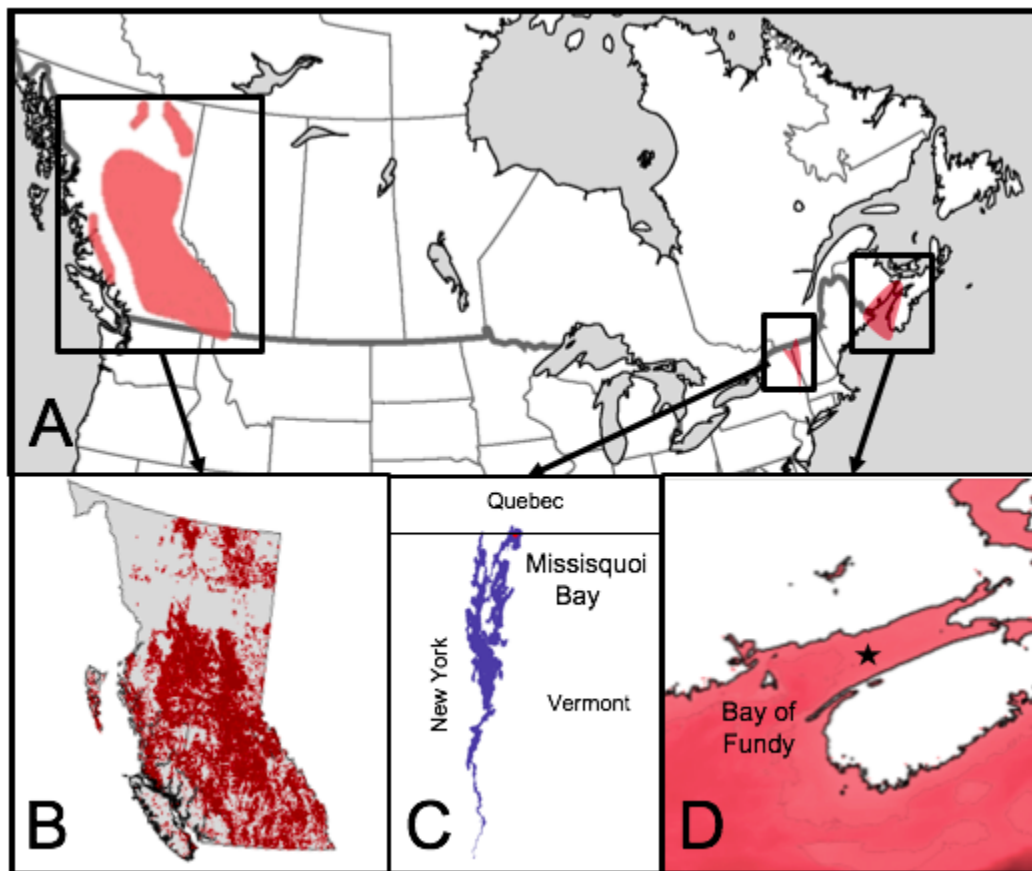
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698 **Figure 1**. (A) Map of case studies depicting the (B) area of forest impacted by mountain pine

699 beetle in 2016 in British Columbia, (C) Missisquoi Bay in Lake Champlain and (D) the Bay of

700 Fundy.

701
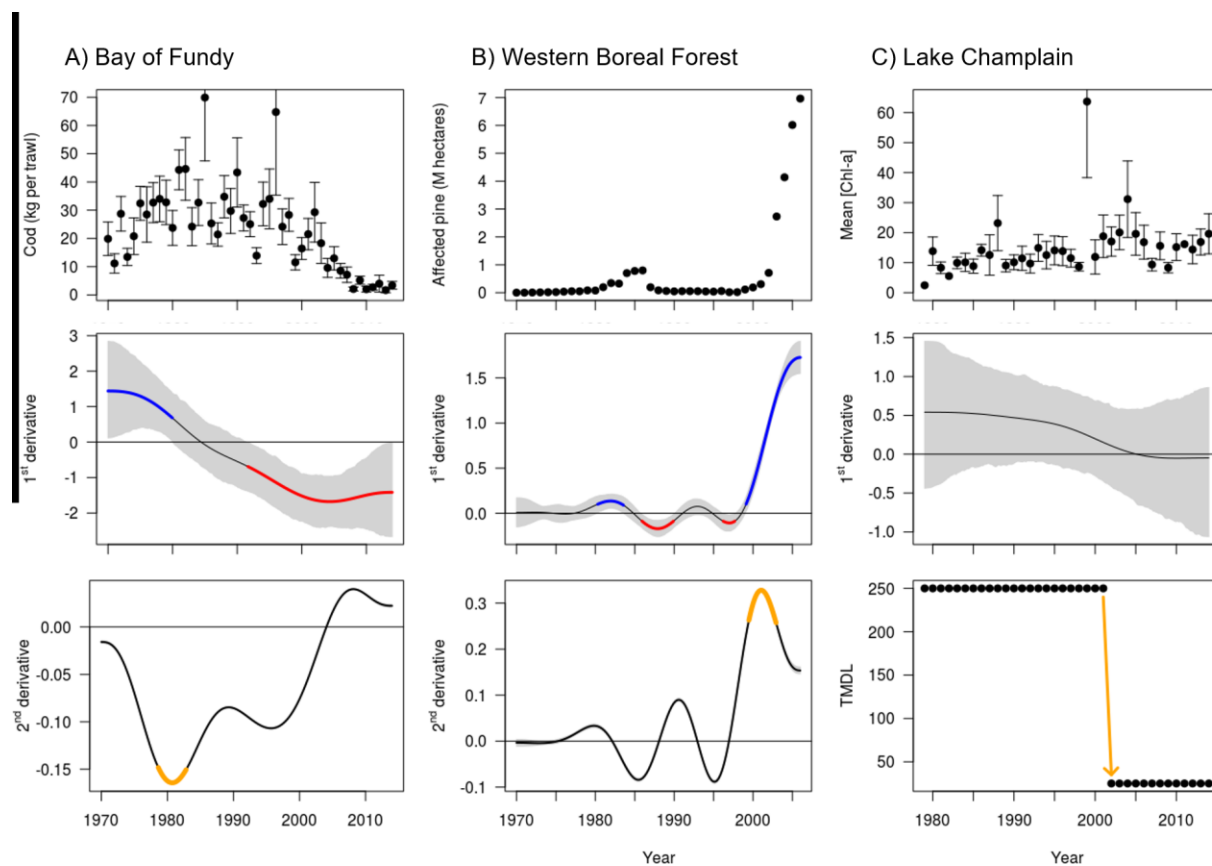
Figure 2. Time-series of the resource units for each case study (top panel). (a) Cod biomass in the Bay of Fundy, (b) the area of pine trees affected by mountain pine beetle in interior British Columbia, and (c) mean summer chlorophyll-*a* in Missisquoi Bay of Lake Champlain. N = 31, 36, 37, respectively. Error bars in (a) and (c) represent standard errors and are cut off for 3 outlier data points. Middle panel shows 1st derivative of GAM model with 95% CI (gray). Blue and red indicate the period over which the resource was significantly increasing and decreasing (respectively). Bottom left and middle panels shows 2nd derivative of GAM which indicates tipping points (orange) for cod abundance and area of diseased pine trees.
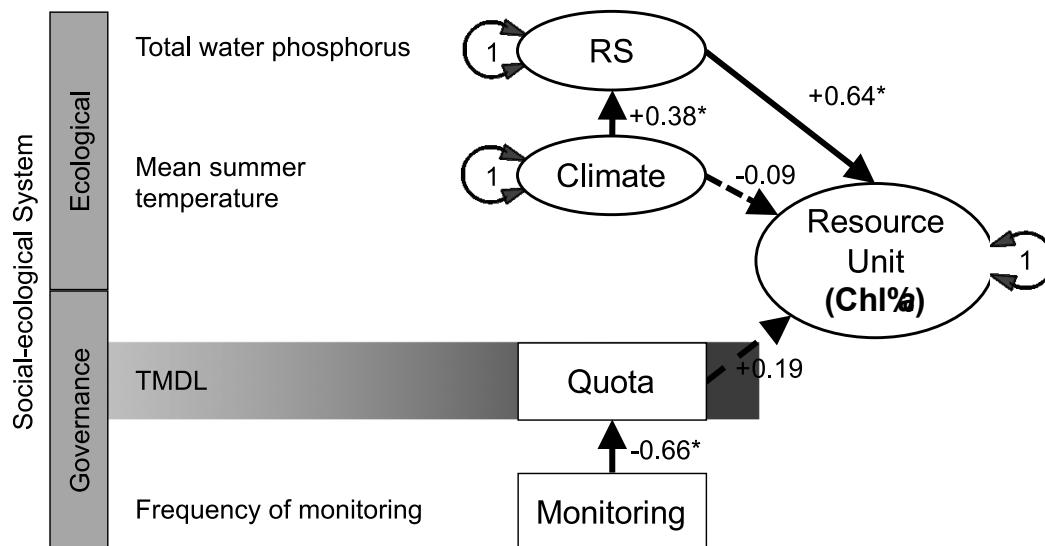
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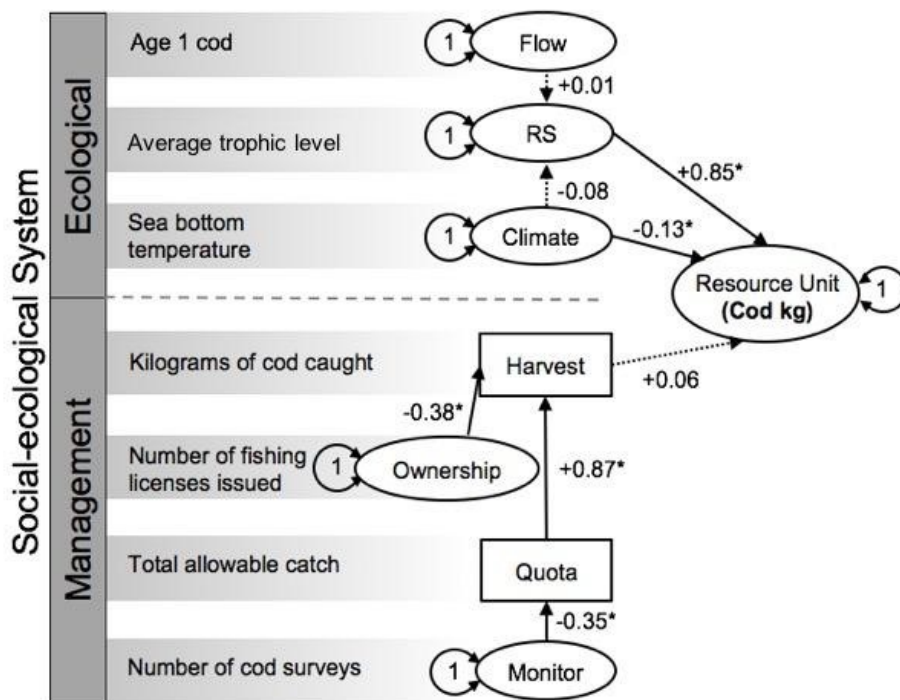
712

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.
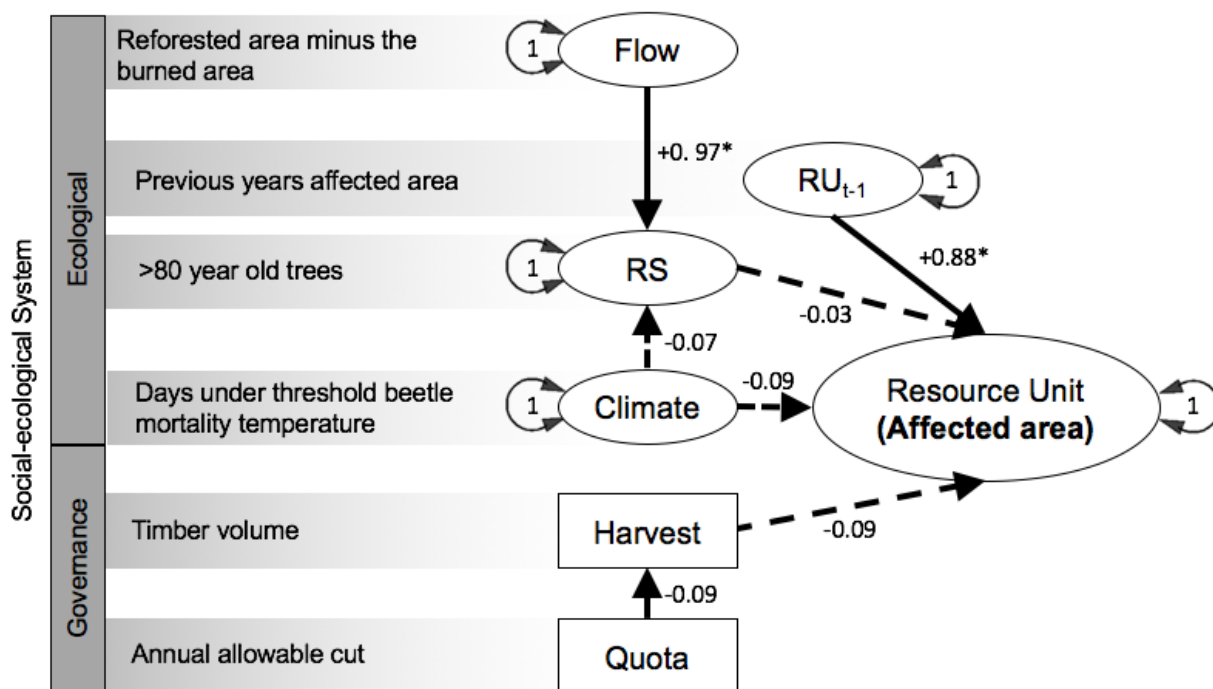
Figure 4. Structural equation model (SEM) of interior British Columbia mountain pine beetle infestation showing how variation in the resource unit (affected area of forest) is associated with management and ecological variables. Numbers next to arrows are standardized path coefficients. Solid arrows denote paths that are significant (p > 0.05). Latent factors with fixed variance are denoted by ovals, while variables without fixed variance are denoted by rectangles. 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~s(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.

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

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