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Ecological surprise: concept, synthesis, and social dimensions

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Authors
Filbee-Dexter, Karen
Pittman, Jeremy
Haig, Heather A
et al.

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Quantifying ecological and social drivers of ecological surprise

Karen Filbee-Dexter[1] (iD) | **Celia C. Symons**[2] (iD) | **Kristal Jones**[3] | **Heather A. Haig**[4] | **Jeremy Pittman**[5] | **Steven M. Alexander**[3,6] | **Matthew J. Burke**[7]

[1]Marine Section, Norwegian Institute of Water Research, Oslo, Norway; [2]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, California; [3]National Socio-Environmental Synthesis Center, University of Maryland, Annapolis, Maryland; [4]Limnology Laboratory, Department of Biology, University of Regina, Regina, SK, Canada; [5]School of Planning, Faculty of Environment, University of Waterloo, Waterloo, ON, Canada; [6]Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden and [7]Department of Natural Resource Sciences & McGill School of Environment, McGill University, Montreal, QC, Canada

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. Research that integrates and analyses data from natural and social systems can provide important insight for unravelling the complexity of these dynamics. It is, therefore, a critical step towards the development of evidence-based, whole-system 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 captured the social-ecological systems (SES) using key variables and interactions from Ostrom's SES 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 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 managed resource. 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.

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

KEYWORDS
ecological surprise, eutrophication, fishery collapse, mountain pine beetle, natural resource management, social–ecological system, spatial temporal mismatch, structural equation model

Karen Filbee-Dexter and Celia C. Symons contributed equally to this work.

1 | INTRODUCTION

Resource and ecosystem managers continually make decisions with imperfect information regarding how ecosystems function, what drives observed ecological changes and the degree to which their actions will produce the intended ecological results. The ability to predict ecological dynamics is arguably improving (Biggs, Carpenter, & Brock, 2009; Drake & Griffen, 2010; Pace, Carpenter, & Cole, 2015). However, managers are frequently trying to effect change in an ecosystem (a) on short time-scales (Contamin & Ellison, 2009; Cumming, Cumming, & Redman, 2006), (b) at spatial scales smaller than the ecosystem itself (Cumming et al., 2006), or are (c) attempting to revert ecosystems back to their original state after unexpected change has occurred (Folke et al., 2004). These management targets are difficult to achieve because natural systems that are coupled with human systems are inherently complex, often fraught with uncertainty and difficult to predict (Fulton, Smith, Smith, & van Putten, 2011; Underdal, 2010). The challenge of understanding—let alone managing—the multiple components and processes underlying ecosystem behaviour is no small task (Costanza, 2000; Peters, 1991; Waltner-Toews, Kay, Neudoerffer, & Gitau, 2003) and requires a holistic understanding of the dynamics that drive change in both social and ecological systems.

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

It is common for management systems to be characterized by fragmented, multilevel governance structures with sector-specific decision-making processes (e.g. Crowder et al., 2006; Morrison, 2017), while ecosystems are characterized by multiple known and unknown biotic and abiotic components with complex interactions that vary in time and space (Cumming, Morrison, & Hughes, 2017; Levin, 1998). The differences in scale and structure between these social and ecological systems determine the set of possible interactions among different components (Brondizio, Ostrom, & Young,

2009; Schlüter et al., 2012), and mismatch between systems may limit our ability to influence ecosystems during periods of rapid change (Alexander, Armitage, Carrington, & Bodin, 2017; Epstein et al., 2015; Pittman, Armitage, Alexander, Campbell, & Alleyne, 2015). For example, the legacies of past management decisions or structures may contribute to contemporary ecological change and limit the effectiveness of recent management interventions (Jackson et al., 2001; Liu et al., 2007). Similarly, ecological changes or forces, operating at larger spatial scales than managers can influence, may limit effectiveness of localized management interventions (Cumming et al., 2006; Epstein, Vogt, Mincey, Cox, & Fischer, 2013; Koch et al., 2009).

The ability of humans to effectively respond and adapt to observed ecological change can be limited by numerous other social factors as well. For example, a lack of compliance with rules can result in continued removal of a resource (Leader-Williams & Albon, 1988; Mukul, Rashid, & Khan, 2017; Rowcliffe, Merode, & Cowlishaw, 2004) or degradation of an ecosystem (Hauck & Sweijd, 1999; Kideghesho, Rija, Mwamende, & Selemani, 2013). Similarly, governance systems may have limited options for action due to restrictive policies, economic constraints, lack of knowledge or other considerations (Berkes & Turner, 2006; Costanza, 2000; Gadgil, Olsson, Berkes, & Folke, 2003).

In order to understand drivers of change in managed ecosystems, there is growing awareness of the need to consider ecological, social and social-ecological processes in an integrated fashion (Hughes et al., 2017). Research that integrates quantitative social and ecological data to test hypotheses on social-ecological systems (SESs) is rare (Vogt, Epstein, Mincey, Fischer, & McCord, 2015; but see Laborde et al., 2016; Leslie et al., 2015; Ziegler, Golebie, Jones, Weidel, & Solomon, 2017). However, combining data from social systems and ecosystems can reveal further complexity and a broader range of dynamics than analyses that focus on just one of the two systems (Hicks, Crowder, Graham, Kittinger, & Le Cornu, 2016; Moore et al., 2014; Schlüter et al., 2012). In this study, we apply two conceptual and methodological tools to quantitatively explore the relative role of human and ecological drivers of change on natural systems.

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

We, then, use structural equation models (SEMs) to quantify the potential relationships between different social and ecological variables in an SES. SEM is an analytical tool that enables us to link
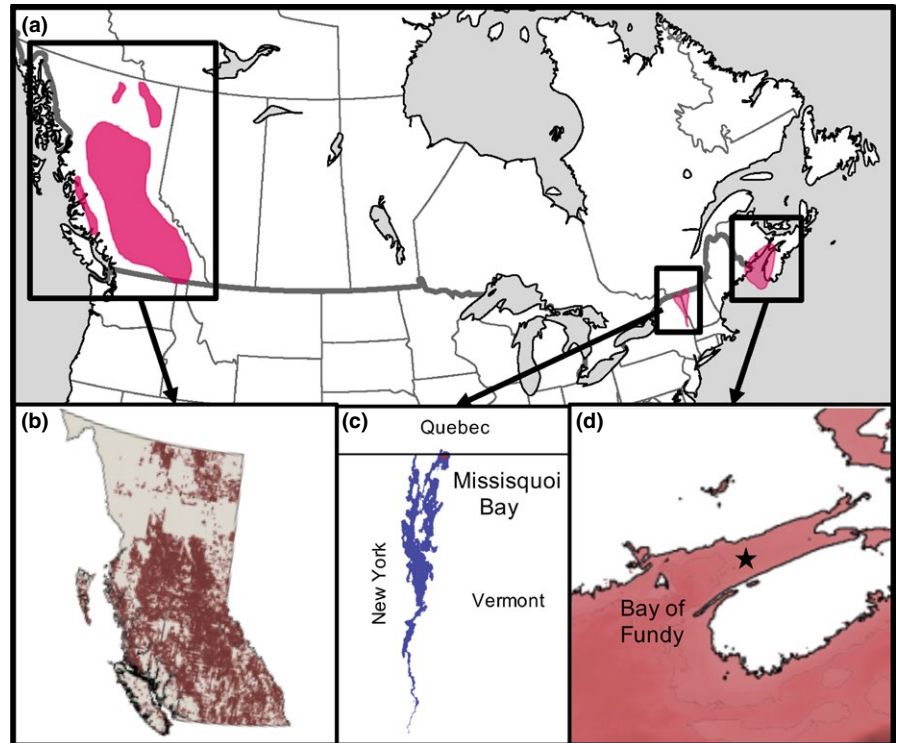
FIGURE 1 (a) Map of case studies depicting the (b) area of forest impacted by mountain pine beetle in 2016 in British Columbia, (c) Missisquoi Bay in Lake Champlain and (d) the Bay of Fundy [Colour figure can be viewed at wileyonlinelibrary.com]

empirical data (e.g. abundance, limits) and theoretical constructs (e.g. ownership or connectivity) of SESs using ecological theory and known attributes or dynamics of the system (Grace, Anderson, Olff, & Scheiner, 2010). In our application, SEMs quantify the relative importance (strength of relationships) of ecological and social variables in driving change in the resource of interest.

We apply these tools to prominent cases of ecological surprise to understand how multiple factors and processes influence ecosystem behaviour during these events. We selected three well-studied cases of ecological surprise from different ecological contexts (marine, freshwater, terrestrial) that demonstrate the limits of management capacity to influence or mitigate ecological change and variability: (a) the mountain pine beetle infestation currently occurring in the Western Boreal Forest in interior British Columbia (BC); (b) the persistent eutrophication of Lake Champlain's Missisquoi Bay in the Northeastern United States and Quebec, Canada; and (c) the collapse of the cod fishery in Atlantic Canada's Bay of Fundy (Figure 1). In all the managed systems, the resource of interest is expected to be influenced by both the larger resource system and actions of management. We use SEM to explore the extent that unexpected ecological behaviour in each of these cases is the result of social or ecological dynamics. Social dynamics may include a lack of management interventions, limited user response to management interventions, or user responses that do not produce the desired outcomes on short time-scales or at small spatial scales. Ecological dynamics may include legacy effects, hysteresis, climate-driven impacts or ecosystem changes at broader spatial scales. By quantifying relationships using a common framework, we are able to directly compare among cases to understand generalities in these SESs.

2 | MATERIALS AND METHODS

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

2.1 | SES framework

We use Ostrom's (2007) SES framework as a starting point to select variables in our focal SES case studies. We selected variables that encapsulate key management and ecosystem components for our three SESs and verified their importance using published literature (Appendices S1 and S2). The management component of the SES includes a resource unit, harvest and/or quota, which correspond to Ostrom's variables "RU5," "I1" and "GS6" (McGinnis & Ostrom, 2014). The ecological component includes a resource system, resource unit and climate conditions, which correspond to Ostrom's variables "RS," "RU5" and "ECO1" (McGinnis & Ostrom, 2014). In the context of the SES, the resource unit is the linking component, as its characteristics or abundance are theorized to be influenced directly by both ecological and social system components. Because management procedures and ecological dynamics differed among case studies, we selected additional variables from Ostrom's framework that were important for specific cases. These included a flow variable describing the influx of the resource unit for the Bay of Fundy and the Western Boreal Forest, a monitoring variable for Lake Champlain and Bay of Fundy, and an ownership variable for the Bay of Fundy (Ostrom: "ECO3," "GS6" and "GS7"; Appendix S2). Inclusion of these additional variables did

not impact the core components of our SESM, but rather provided context and accounted for known sources of variability within the social system or ecosystem. Here, there were clear benefits to using well-studied systems, as we were able to ensure that we could acquire adequate data and evidence of these relationships to build our models. Further, it also enabled us to explore or validate previous narratives and/or hypotheses regarding the relative strengths of social and ecological drivers in these cases. We choose to exclude "Actor" variables (McGinnis & Ostrom, 2014) in our models, which represent entities that are directly or indirectly interacting with the resource unit (e.g. harvesting or producing resource units), because (a) their actions were largely represented by our other management variables and (b) our hypotheses were not focused on individual-level variables.

2.2 | Data selection

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

For the Bay of Fundy, we characterized the resource unit by the average biomass of cod caught during random stratified trawl surveys, conducted annually by the Canadian Department of Fisheries and Oceans (DFO) each July from 1984 to 2014 within the two fishing zones of the Bay of Fundy (zones 4Xsr; DFO, 2017). For the ecosystem variables, we defined climate as the average water temperature measured at depth during these trawl surveys, flow as the number of 1-year-old cod entering the fishery, and resource system as the average trophic level of the benthic food web in the larger Nova Scotia bioregion each year (Bundy, Fanning, & Zwanenburg, 2005). We used trophic level to summarize trends occurring in the resource system during the period of interest, because this indicator captures large changes in the species composition of marine ecosystems (Shannon et al., 2014). For the management variables, we defined quota as the total allowable catch (TAC) set by the DFO, harvest as the total biomass of cod landed by Bay of Fundy fishers, ownership as the number of fishing licenses, and monitoring as the number of research trawls each year.

For Lake Champlain's Missisquoi Bay, we characterized the resource unit by the summer abundance of algae (measured as the mean June–September concentration of chlorophyll *a*) from 1979 to 2015. We defined climate as the average June–September air temperature and resource system as the total phosphorus concentration in the water. For the management variables, we defined quota as the total maximum daily load (TMDL) for phosphorus set by the United States Environmental Protection Agency, and monitoring as the frequency of water quality measures.

For the Western Boreal forest, we characterized the resource unit by the total cumulative area of forest in the province of BC affected by the mountain pine beetle annually between 1975 and 2009. We defined harvest as the annual volume of timber harvested and quota as the annual allowable cut set by the BC Ministry of Forests, Lands and Natural Resources, resource system as area of

forest containing trees greater than 80-years-old, and flow as the annual net change in forest area (area of forest reforested minus the area of forest burned). Finally, we defined the climate variable using minimum temperature thresholds for mountain pine beetle mortality that are hypothesized to be a primary factor driving continued population outbreaks of beetles. To account for seasonal change in cold tolerance of beetle larvae, we summed the number of days over three thresholds for 100% mortality of mountain pine beetle larvae in lodgepole pine forests: (a) ≤−25°C from April to June, (b) ≤−40°C from December–March, and (c) ≤−25°C from September to November (Safranyik & Wilson, 2006).

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

2.3 | Analytical approach

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

For each case study, we constructed SEMs that described and measured the strength of the relationships leading from components of the ecological and social systems to the resource unit of interest (cod biomass, algal biomass, area of beetle-infested trees). SEM is a multivariate statistical approach used in a wide variety of ecological and social applications to explore relationships between dependent and independent variables (e.g. Byrnes et al., 2011; Dainese et al., 2017; Seidl, Schelhaas, & Lexer, 2011). SEMs are similar to regression models (e.g. $\{X_1, X_2\} \rightarrow Y$), but they are more flexible and can test "path models" consisting of multiple variables linked using multiple direct and indirect paths (e.g. $\{X_1, X_2\} \rightarrow M \rightarrow Y$) (Grace et al., 2010; Pugesek, Tomer, & von Eye, 2003; Shipley, 2016). SEM estimates variance and covariance matrices to characterize the structure of relationships among variables, which provides increased flexibility for incorporating diverse types of variables and estimation techniques that reflect underlying assumptions about variable distributions and the degree or shape of paths between variables (Kline, 2011). In addition, because SEM takes a structural or multilevel approach to estimating relationships among variables, both single empirical measurements ("indicators") and constructs ("latent factors" that are
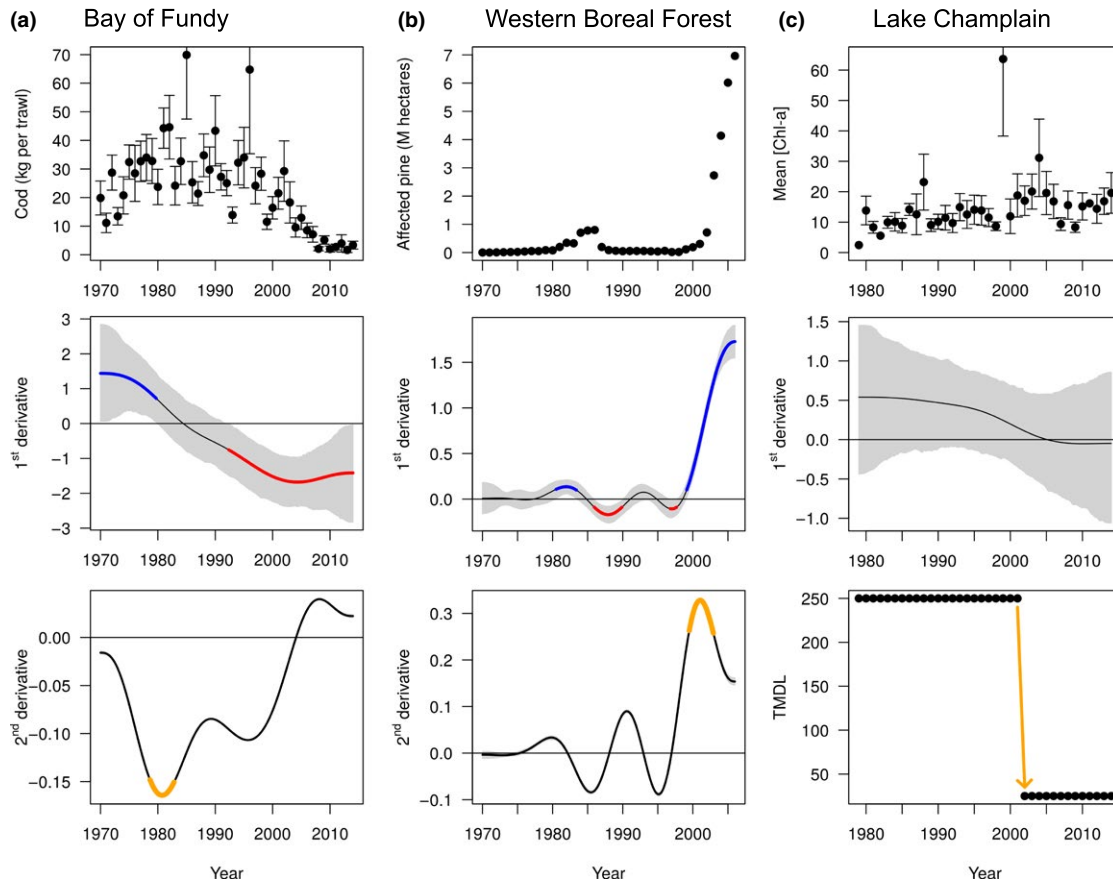
FIGURE 2 Time series of the resource units for each case study (top panel). (a) Cod biomass in the Bay of Fundy, (b) the area of pine trees affected by mountain pine beetle in interior British Columbia and (c) mean summer chlorophyll-*a* in Missisquoi Bay of Lake Champlain. *N* = 31, 36, 37, respectively. Error bars in (a) and (c) represent standard errors and are cut off for three outlier data points. Middle panel shows first derivative of GAM model with 95% CI (grey). Blue and red indicate the period over which the resource was significantly increasing and decreasing (respectively). Bottom left and middle panels show second derivative of GAM which indicates tipping points (orange) for cod abundance and area of diseased pine trees [Colour figure can be viewed at wileyonlinelibrary.com]

estimated using a combination of multiple empirical measurements) can be included in analyses (Kline, 2011; Shipley, 2016).

The paths in our SEMs are based on known empirical links within systems of management and ecosystems (e.g. total allowable catch → landed cod) and our understanding of these systems, as well as the links theorized by Ostrom's SES framework (Appendices S1 and S2). We used time-series data (Figure 2; *n* > 30 years for each case) to estimate the direct and indirect effects of climate, resource system, external flows, quota, harvest, monitoring and ownership on the abundance of the resource unit. To confirm that noninde-pendence of our time-series observations would not impact model structure, we tested for temporal autocorrelation in the resource unit in each case study. We found no significant temporal autocor-relation for the resource unit in Bay of Fundy and Lake Champlain (Figure S1). However, we did find significant temporal autocorrela-tion for the Western Boreal forest resource unit. To account for this, we included a 1-year lagged resource unit variable that linked di-rectly to the resource unit in this case study ($RU_{t-1} \rightarrow RU$).

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

3 | RESULTS

Our time-series analysis results indicate that there were signifi-cant changes in the resource unit in the Bay of Fundy and Western Boreal Forest case studies, but not in the Lake Champlain case study (Table 1; Figure 2). In the Bay of Fundy, cod biomass declined sig-nificantly from 1990 on, with a critical transition between 1980 and 1982. In the Western Boreal Forest, the amount of pine impacted by the mountain pine beetle increased significantly from 2002 on, with a critical transition between 2000 and 2002 (Figure 2). In Lake Champlain, chlorophyll-*a* concentration did not change significantly over the period of interest, and no critical transition was detected.

Case	r^2			Est. *df*	F	*p*
Bay of fundy	0.67	Intercept			t = 20.0	**<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

TABLE 1 GAM results for each case. Models were in the form of RU~s(Year) and were fit by maximum likelihood using residual deviance. Significant *p*-values are in bold
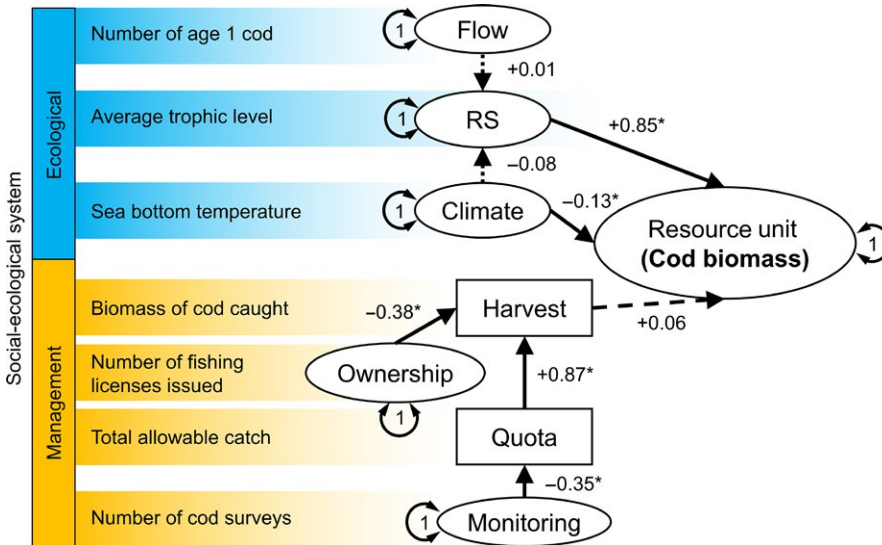
FIGURE 3 Structural equation model (SEM) of Bay of Fundy cod collapse showing how variation in the resource unit (cod biomass) is associated with management and ecological variables. Numbers next to arrows are standardized path coefficients. Solid arrows denote paths that are significant (*p* > 0.05). Latent factors with fixed variance are denoted by ovals, while variables without fixed variance are denoted by rectangles. The data used for each variable are shown in the shaded boxes on the left [Colour figure can be viewed at wileyonlinelibrary.com]

For this case study, the timing of ecological surprise was defined as the year that the TMDL management intervention was implemented, because there was an expectation that this action would decrease the frequency and severity of algal blooms (but no change was detected).

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

In all SEMs, the paths describing management actions (paths between monitoring and quota or harvest) during the period of unexpected ecological change were statistically significant. For the Bay of Fundy, the increasing number of surveys on declining cod stock had a negative effect on the TAC set by managers. The quota, which was lowered over this period, had a significant positive effect on the biomass of cod harvested (Figure 3). For Lake Champlain, the frequency of monitoring also had a significant negative relationship with quota. In the Western Boreal forest, the quota varied significantly with harvest, but this relationship was negative such that harvest was low when the quota was high (Figure 5), likely driven by the inability of loggers to meet high "salvage logging" quotas (B.C. Ministry of Forests, Mines, and Lands, 2010).

Most variability in the resource unit was related to variability in ecosystem processes during the period of interest (Resource system or RU_{t-1} → RU). The paths describing the effects of the broader resource system on the resource unit were significant in two of the three models (partial r^2 > 0.80 for Bay of Fundy and Lake Champlain, Table 2). In other words, the average trophic level of the benthic food web in the Nova Scotian bioregion had a positive effect on the biomass of cod (Figure 3). Food webs with lower average trophic levels (dominated by smaller fish and invertebrates) in the larger coastal region were associated with fewer cod in the Bay of Fundy. Similarly, in Lake Champlain, the total P in the water had the strongest influence on the amount of algae in the lake. In contrast, the amount of Western Boreal forest containing trees >80-year-old had no significant effect on the amount of forest impacted by mountain pine beetle (Figure 5). Instead, the abundance of trees >80-year-old was
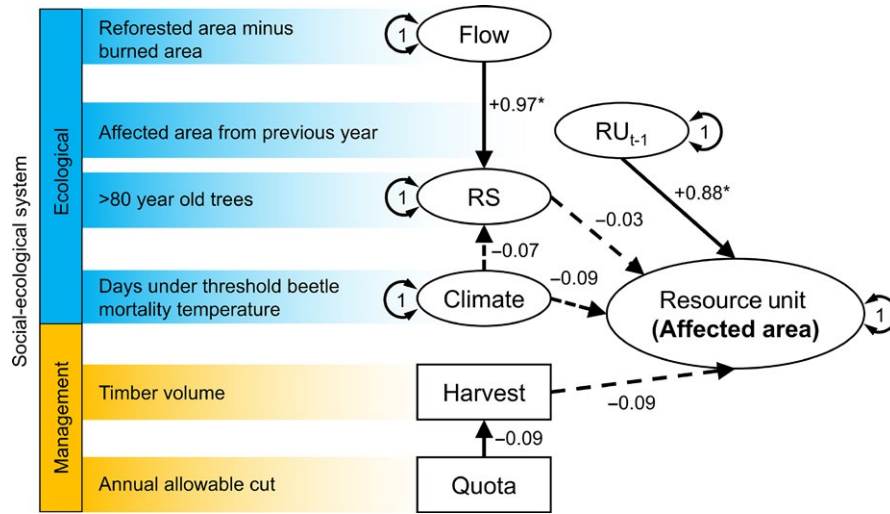
FIGURE 4 Structural equation model (SEM) of interior British Columbia mountain pine beetle infestation showing how variation in the resource unit (affected area of forest) is associated with management and ecological variables. Numbers next to arrows are standardized path coefficients. Solid arrows denote 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 are shown in the shaded boxes on the left [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 Structural equation model (SEM) of persistent eutrophication in Missisquoi Bay of Lake Champlain showing how variation in the resource unit (mean summer Chl-*a* concentration) 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 are shown in the shaded boxes on the left [Colour figure can be viewed at wileyonlinelibrary.com]
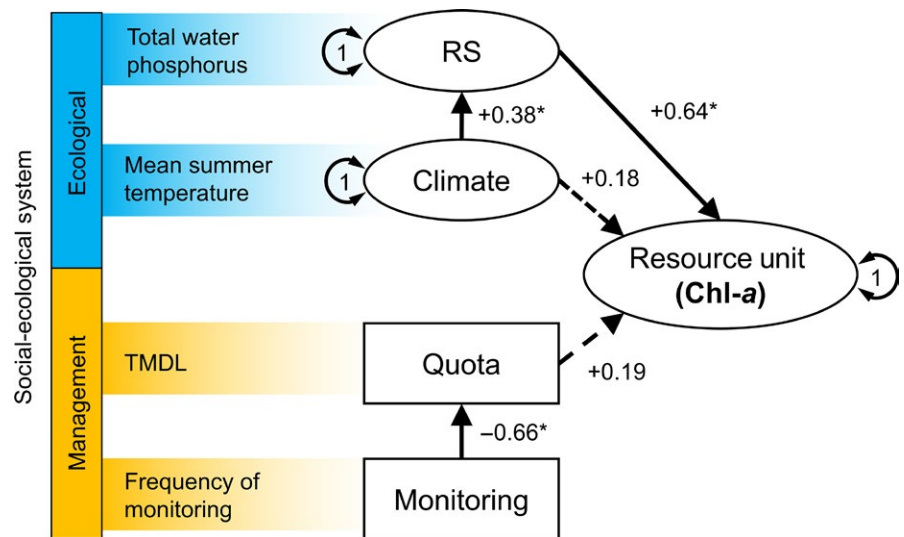
strongly influenced by the area of forest reforested or burned each year. Most variability in the amount of forest impacted by mountain pine beetle was explained by the area impacted by disease the previous year, indicating that internal feedbacks on the resource unit were stronger than the effects of management interventions or changes in the larger resource system.

Paths between the climate variables and the resource units were only significant for the Bay of Fundy (Table 2). In the Bay of Fundy, water temperature had a negative effect on the biomass of cod, which is a cold-water species. In Lake Champlain, air temperature had no effect on the concentration of chlorophyll-*a* in the lake, but did significantly impact the total phosphorus in the lake (Figure 5). In the Western Boreal forest, temperature conditions associated with beetle mortality had no significant effect on the area of forest impacted by the mountain pine beetle (Figure 4).

4 | DISCUSSION

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

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

Although there was not a significant relationship between the social systems of management and the resource unit, we found that the governance variables capturing rules of use in Bay of Fundy and Western Boreal Forest co-varied significantly with user behaviour (i.e. harvest affected by ownership and quota; Table 2). This result suggests that the users being monitored by the managers adhered to the strong management interventions for these systems (e.g. cod quota was dramatically reduced to 6% of initial harvesting levels). It also indicates that failure of the management systems to produce the intended effect on the resource unit was not because users did not comply with rules or policies (or at least the users that were tracked). However, it is worth noting that illegal fishing and illegal cutting are not included in the harvest variable, so this relationship does not capture all user behaviour.

4.1 | Ecological dynamics, reinforcing feedbacks, and hysteresis

The strong link between the ecological variables and RU in all case studies is consistent with an ecological surprise, whereby the ecosystem undergoes an abrupt shift and/or is stabilized by ecological dynamics. Research on sudden changes in ecosystem structure indicates that when ecosystems are pushed beyond tipping points of stability, human-driven recovery can be difficult because reinforcing feedback mechanisms or altered ecological dynamics can lock the ecosystem into the new configuration (Berkes, Colding, & Folke, 2008; Folke et al., 2004; Scheffer, Carpenter, Foley, Folke, & Walkerk, 2001). This is termed hysteresis and occurs when an alternate ecosystem state persists, even after the initial driver of ecosystem change has been relaxed, because of new reinforcing mechanisms (Scheffer et al., 2001). Missisquoi Bay of Lake

Champlain typifies a classic example of hysteresis, where shallow lakes transition between macrophyte dominance and clear conditions to phytoplankton dominance and turbid conditions at different threshold levels of nutrients (Jeppesen, Søndergaard, Sortkjær, Mortensen, & Kristensen, 1990; Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993). A number of mechanisms stabilize lake systems in turbid states (reviewed in Scheffer & van Nes, 2007). For example, nutrient loading can induce anoxia in lake sediments causing phosphorus to become more bioavailable, reinforcing the turbid state even once external nutrient loading is reduced. There is evidence that the collapsed cod population is also experiencing some level of hysteresis. Following the dramatic loss of cod, planktivorous forage fishes and invertebrates increased in abundance (Bundy, Heymans, Morissette, & Savenkoff, 2009). Through direct predation and competition for resources with cod, these groups likely delayed the recovery of cod stocks (Petrie, Frankt, Shackell, & Leggett, 2009). In both cases, our resource system variables are related to these stabilizing feedback mechanisms maintaining the new ecosystem states (e.g. water phosphorus concentrations, average trophic level of the benthic food web). This suggests that during tipping points, shifting the focus away from directly controlling the availability of the resource to focusing on ways to influence the broader resource system may enable managers to navigate these events more successfully (Biggs et al., 2012).

In the Western Boreal Forest, the resource unit was strongly influenced by the mountain pine beetle outbreak strength in the previous year. This represents another type of ecological tipping point, where the forest is pushed past a threshold for a disease outbreak that sets the ecosystem on a trajectory that is difficult to deviate from, regardless of changes in harvest, climate, or in the broader resource system. Although it is surprising that environmental conditions were not significant in this model, it is likely that temperature was critical in driving the initial outbreak of mountain pine beetle populations. However, once the system was pushed past this point, variation in annual temperature thresholds for mortality was a less important driver of the amount of affected forest. This is consistent with other positive feedbacks that lead to nonlinear population outbreaks of insects or rapid spread of invasive species (Gibbs & Grant, 1987; Washington-Allen & Salo, 2007).

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

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

4.3 | Quantitative applications of Ostrom's framework: Insights and challenges

Despite its frequent application in SES research, few studies have quantitatively tested ecological hypotheses using Ostrom's framework (Hinkel, Bots, & Schlüter, 2014; McGinnis & Ostrom, 2014). Our study uses a novel approach that combines Ostrom's conceptual framework and advanced statistical tools to integrate ecological and social data, which enables us to quantify relative drivers of unexpected ecological behaviour. In this way, we provide a broader perspective from those provided by ecological or social science alone. Although there are widely accepted narratives of what drives resource unit dynamics in each of these cases, these narratives are often created in the absence of formal statistical tests or are based on a narrow set of data. For example, climate has been identified as a contributing factor of shifts in all three case studies (Appendix S2), but the relative importance of climate in influencing the resource

unit in our models was small compared with other ecological processes, suggesting that a sole focus on climate as the explanation of these events is not a complete nor correct conclusion.

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

Conceptually, we found two clear drawbacks of Ostrom's framework. First, it does not easily capture ecosystem-based management because it is focused towards a single resource unit and not to the resource system. As a result, this framework will reproduce the inherent biases in single resource management approaches. Second, the possible variables are weighted towards the social system, and the framework is missing important ecological components (e.g. abiotic conditions, biological diversity, and energy transfer) that should be included and directly linked to the RU if it is to properly capture the SES. For example, there were no internal flows on the resource system, so we used an external flow "ECO3" variable to capture these dynamics. These findings are consistent with other suggestions to improve the ecological components of the framework (Epstein et al., 2013; Vogt et al., 2015). Developing a more robust and comprehensive framework will ensure that these tools can have better application in SES research and quantitative hypothesis testing.

There also are limitations to our analytical approach. To explore the SES in a quantitative manner, we simplified both the social system managing the resource and the ecosystem containing the resource to its key components, which loses fine-scale dynamics. This, in turn, limits our conclusions to the relative impacts of both systems and does not allow us to fully examine the drivers of these dynamics within either system (e.g. attributes of the systems of governance, specific actors, species interactions, environmental forcing). In addition, despite the relatively long-term datasets available for all the variables of interest in our case studies, the number of data points still limited our analyses, which were, therefore, not able to fully capture important historic processes. This highlights the importance of maintaining and collecting long-term datasets to understand these dynamics, which are operating on multidecadal scales. Finally, selecting appropriate data for Ostrom's SES variables (which are the result of a whole suite of dynamics) can be challenging and requires knowledge of the social and ecological system that may be based on ecological theory or contain assumptions. However, considering the complexity of the SESs in our case studies, it is remarkable that our models explained such a large amount of the variation in our resource units. This approach shows promise and could be used to explore similar hypotheses about what drives socioecological outcomes in other systems. For example, SES research using quantitative datasets should be highly useful for validating existing narratives

on which social or ecological interactions are most important a changing system, and determining whether local management strategies are effective in influencing systems facing both local and global stressors.

5 | CONCLUSIONS

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

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; S.M.A., J.P. and M.B. obtained social data and K.F.-D., C.C.S. and H.H. obtained ecological data for the case studies. K.F.-D., C.C.S. and K.J. analysed and interpreted the data; K.F.-D., C.C.S., K.J. and H.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.2c8f32s (Filbee-Dexter et al., 2018).

ORCID

Karen Filbee-Dexter http://orcid.org/0000-0001-8413-6797

Celia C. Symons http://orcid.org/0000-0003-4120-0327

REFERENCES

Alexander, S. M., Armitage, D., Carrington, P. J., & Bodin, Ö. (2017). Examining horizontal and vertical social ties to achieve social-ecological fit in an emerging marine reserve network. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27, 1209–1223. https://doi.org/10.1002/aqc.2775

B.C. Ministry of Forests, Mines and Lands. (2010). The state of British Columbia's forests. Victoria, Canada.

Berkes, F., Colding, J., & Folke, C. (2008) *Navigating social-ecological systems: Building resilience for complexity and change*. Cambridge, UK: Cambridge University Press.

Berkes, F., & Turner, N. J. (2006). Knowledge, learning and the evolution of conservation practice for social-ecological system resilience. *Human Ecology*, 34, 479–494. https://doi.org/10.1007/s10745-006-9008-2

Biggs, R., Carpenter, S. R., & Brock, W. A. (2009). Turning back from the brink: Detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 826–831. https://doi.org/10.1073/pnas.0811729106

Biggs, R., Schlüter, M., Biggs, D., Bohensky, E. L., BurnSilver, S., Cundill, G., … West, P. C. (2012). Toward principles for enhancing the resilience of ecosystem services. *Annual Review of Environment and Resources*, 37, 421–448. https://doi.org/10.1146/annurev-environ-051211-123836

Brondizio, E. S., Ostrom, E., & Young, O. R. (2009). Connectivity and the governance of multilevel social-ecological systems: The role of social capital. *Annual Review of Environment and Resources*, 34, 253–278. https://doi.org/10.1146/annurev.environ.020708.100707

Bundy, A., Fanning, P., & Zwanenburg, K. (2005). Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: Application of a 4D ecosystem exploitation index. *ICES Journal of Marine Science*, 62, 503–510. https://doi.org/10.1016/j.icesjms.2004.12.008

Bundy, A., Heymans, J. J., Morissette, L., & Savenkoff, C. (2009). Seals, cod and forage fish: A comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems. *Progress in Oceanography*, 81, 188–206. https://doi.org/10.1016/j.pocean.2009.04.010

Byrnes, J. E., Reed, D. C., Cardinale, B. J., Cavanaugh, K. C., Holbrook, S. J., & Schmitt, R. J. (2011). Climate-driven increases in storm frequency simplify kelp forest food webs. *Global Change Biology*, 17, 2513–2524. https://doi.org/10.1111/j.1365-2486.2011.02409.x

Contamin, R., & Ellison, A. M. (2009). Indicators of regime shifts in ecological systems: What do we need to know and when do we need to know it. *Ecological Applications*, 19, 799–816. https://doi.org/10.1890/08-0109.1

Costanza, R. (2000). Social goals and the valuation of ecosystem services. *Ecosystems*, 3, 4–10. https://doi.org/10.1007/s100210000002

Crowder, L. B., Osherenko, G., Young, O. R., Airamé, S., Norse, E. A., Baron, N., … Ogden, J. C. (2006) Resolving mismatches in U.S. governance. *Science*, 313, 617–618. https://doi.org/10.1126/science.1129706

Cumming, G. S., Cumming, D. H. M., & Redman, C. L. (2006). Scale mismatches in social-ecological systems: Causes, consequences, and solutions. *Ecology and Society*, 11(1), 14. https://doi.org/10.5751/ES-01569-110114

Cumming, G. S., Morrison, T. H., & Hughes, T. P. (2017). New directions for understanding the spatial resilience of social–ecological systems. *Ecosystems*, 20, 649–664. https://doi.org/10.1007/s10021-016-0089-5

Dainese, M., Riedinger, V., Holzschuh, A., Kleijn, D., Scheper, J., & Steffan-Dewenter, I. (2017). Managing trap-nesting bees as crop pollinators: Spatiotemporal effects of floral resources and antagonists. *Journal of Applied Ecology*, *55*, 195–204.

DFO. (2017). 2016 4X5Yb Atlantic Cod (Gadus morhua) Stock status update. *DFO Canadian Science Advisory Secretariat Science Response*, *24*, 2.

Doak, D. F., Estes, J. A., Halpern, B. S., Jacob, U., Lindberg, D. R., Lovvorn, J., … Novak, M. (2008). Understanding and predicting ecological dynamics: Are major surprises inevitable. *Ecology*, *89*, 952–961. https://doi.org/10.1890/07-0965.1

Drake, J. M., & Griffen, B. D. (2010). Early warning signals of extinction in deteriorating environments. *Nature*, *467*, 456–459. https://doi.org/10.1038/nature09389

Epstein, G., Pittman, J., Alexander, S. M., Berdej, S., Dyck, T., Kreitmair, U., … Armitage, D. (2015). Institutional fit and the sustainability of social–ecological systems. *Current Opinion in Environmental Sustainability*, *14*, 34–40. https://doi.org/10.1016/j.cosust.2015.03.005

Epstein, G., Vogt, J. M., Mincey, S. K., Cox, M., & Fischer, B. (2013). Missing ecology: Integrating ecological perspectives with the social-ecological system framework. *International Journal of the Commons*, *7*, 432. https://doi.org/10.18352/ijc.371

Filbee-Dexter, K., Pittman, J., Haig, H. A., Alexander, S. M., Symons, C. C., & Burke, M. J. (2017). Ecological surprise: Concept, synthesis, and social dimensions. *Ecosphere*, *8*(12), e02005. https://doi.org/10.1002/ecs2.2005

Filbee-Dexter, K., Symons, C. C., Jones, K., Haig, H. A., Pittman, J., Alexander, S. M., & Burke, M. J. (2018). Data from: Quantifying ecological and social drivers of ecological surprise. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.2c8f32s

Folke, C. (2006). Resilience: The emergence of a perspective for social–ecological systems analyses. *Global Environmental Change*, *16*, 253–267. https://doi.org/10.1016/j.gloenvcha.2006.04.002

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., & Holling, C. S. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 557–581. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711

Fulton, E. A., Smith, A. D. M., Smith, D. C., & van Putten, I. E. (2011). Human behaviour: The key source of uncertainty in fisheries management. *Fish and Fisheries*, *12*, 2–17. https://doi.org/10.1111/j.1467-2979.2010.00371.x

Gadgil, M., Olsson, P., Berkes, F., & Folke, C. (2003). Exploring the role of local ecological knowledge in ecosystem management governance: Three case studies. In F. Berkes, J. Colding, & C. Folke (Eds.), *Navigating social-ecological system building resilience for complexity and change* (pp. 189–209). Cambridge, UK: Cambridge University Press.

Gibbs, L. H., & Grant, P. R. (1987). Oscillating selection on Darwin's finches. *Nature*, *327*, 511–513. https://doi.org/10.1038/327511a0

Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, *80*, 67–87. https://doi.org/10.1890/09-0464.1

Hauck, M., & Sweijd, N. A. (1999). A case study of abalone poaching in South Africa and its impact on fisheries management. *ICES Journal of Marine Science*, *56*, 1024–1032. https://doi.org/10.1006/jmsc.1999.0534

Hicks, C. C., Crowder, L. B., Graham, N. A. J., Kittinger, J. N., & Le Cornu, E. (2016). Social drivers forewarn of marine regime shifts. *Frontiers in Ecology and the Environment*, *14*, 252–260. https://doi.org/10.1002/fee.1284

Hinkel, J., Bots, P. W. G., & Schlüter, M. (2014). Enhancing the Ostrom social-ecological system framework through formalization. *Ecology and Society*, *19*, art51. https://doi.org/10.5751/ES-06475-190351

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., … Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, *546*, 82–90. https://doi.org/10.1038/nature22901

IPCC. (2014). Climate Change 2014: Synthesis Report. In Core Writing Team, R. K. Pachauri & L. A. Meyer (Eds.), *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., … Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, *293*, 629 https://doi.org/10.1126/science.1059199

Jeppesen, E., Søndergaard, M., Sortkjær, O., Mortensen, E., & Kristensen, P. (1990). Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: A study of phytoplankton collapses in Lake Søbygård, Denmark. *Hydrobiologia*, *191*, 149–164. https://doi.org/10.1007/BF00026049

Kideghesho, J. R., Rija, A. A., Mwamende, K. A., & Selemani, I. S. (2013). Emerging issues and challenges in conservation of biodiversity in the rangelands of Tanzania. *Nature Conservation*, *6*, 1–29.

King, A. (1995). Avoiding ecological surprise: Lessons from long-standing communities. *The Academy of Management Review*, *20*(4), 961–985.

Kline, R. B. (2011). *Principles and practice of structural equation modeling*. New York, NY: Guilford Press.

Koch, E. W., Barbier, E. B., Silliman, B. R., Reed, D. J., Perillo, G. M., Hacker, S. D., … Wolanski, E. (2009). Non-linearity in ecosystem services: Temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment*, *7*, 29–37. https://doi.org/10.1890/080126

Laborde, S., Fernandez, A., Phang, S. C., Hamilton, I. M., Henry, N., Jung, H. C., … Moritz, M. (2016). Social-ecological feedbacks lead to unsustainable lock-in in an inland fishery. *Global Environmental Change*, *41*, 13–25. https://doi.org/10.1016/j.gloenvcha.2016.08.004

Leader-Williams, N., & Albon, S. D. (1988). Allocation of resources for conservation. *Nature*, *336*, 533–535. https://doi.org/10.1038/336533a0

Leslie, H. M., Basurto, X., Nenadovic, M., Sievanen, L., Cavanaugh, K. C., Cota-Nieto, J. J., … Aburto-Oropeza, O. (2015). Operationalizing the social-ecological systems framework to assess sustainability. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 5979–5984. https://doi.org/10.1073/pnas.1414640112

Levin, S. A. (1998). Ecosystems and the biosphere as complex adaptive systems. *Ecosystems*, *1*, 431–436. https://doi.org/10.1007/s100219900037

Levin, S. A., & Lubchenco, J. (2008). Resilience, robustness, and marine ecosystem-based management. *BioScience*, *58*, 27. https://doi.org/10.1641/B580107

Lindenmayer, D. B., Likens, G. E., Krebs, C. J., & Hobbs, R. J. (2010). Improved probability of detection of ecological "surprises". *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 21957–21962. https://doi.org/10.1073/pnas.1015696107

Liu, J., Dietz, T., Carpenter, S. R., Alberti, M., Folke, C., Moran, E., … Taylor, W. W. (2007). Complexity of coupled human and natural systems. *Science*, *317*, 1513–1516

McDonald, R. P., & Ho, M.-H. R. (2002). Principles and practice in reporting structural equation analyses. *Psychological Methods*, *7*, 64–82. https://doi.org/10.1037/1082-989X.7.1.64

McGinnis, M. D., & Ostrom, E. (2014). Social-ecological system framework: Initial changes and continuing challenges. *Ecology and Society*, *19*, art30. https://doi.org/10.5751/ES-06387-190230

Moore, M.-L., Tjornbo, O., Enfors, E., Knapp, C., Hodbod, J., Baggio, J. A., … Biggs, D. (2014). Studying the complexity of change: Toward an analytical framework for understanding deliberate social-ecological

transformations. *Ecology and Society*, *19*, art54. https://doi.org/10.5751/ES-06966-190454

Morrison, T. H. (2017). Evolving polycentric governance of the Great Barrier Reef. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, E3013–E3021. https://doi.org/10.1073/pnas.1620830114

Mukul, S. A., Rashid, A. Z. M. M., & Khan, N. A. (2017). Forest protected area systems and biodiversity conservation in Bangladesh. In S. A. Mukul, & A. Z. M. M. Rashid (Eds.), *Protected areas: Policies, management and future directions* (pp. 157–177). New York, NY: Nova Science.

Österblom, H., Crona, B. I., Folke, C., Nyström, M., & Troell, M. (2017). Marine ecosystem science on an intertwined planet. *Ecosystems*, *20*, 54–61. https://doi.org/10.1007/s10021-016-9998-6

Ostrom, E. (2007). A diagnostic approach for going beyond panaceas. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 15181–15187. https://doi.org/10.1073/pnas.0702288104

Ostrom, E. (2009). A general framework for analyzing sustainability of social-ecological systems. *Science*, *325*, 419–422. https://doi.org/10.1126/science.1172133

Pace, M., Carpenter, S., & Cole, J. (2015). With and without warning: Managing ecosystems in a changing world. *Frontiers in Ecology and the Environment*, *13*, 460–467. https://doi.org/10.1890/150003

Peters, R. H. (1991). *A critique for ecology*. Cambridge, UK: Cambridge University Press.

Petrie, B., Frankt, K. T., Shackell, N. L., & Leggett, W. C. (2009). Structure and stability in exploited marine fish communities: Quantifying critical transitions. *Fisheries Oceanography*, *18*, 83–101. https://doi.org/10.1111/j.1365-2419.2009.00500.x

Pittman, J., Armitage, D., Alexander, S., Campbell, D., & Alleyne, M. (2015). Governance fit for climate change in a Caribbean coastal-marine context. *Marine Policy*, *51*, 486–498. https://doi.org/10.1016/j.marpol.2014.08.009

Pugesek, B. H., Tomer, A., & von Eye, A. (2003). *Structural equation modeling: Applications in ecological and evolutionary biology*. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511542138

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, *48*, 1–36.

Rowcliffe, J. M., deMerode, E., & Cowlishaw, G. (2004). Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. *Proceedings of the Royal Society of London B: Biological Sciences*, *271*, 2631–2636.

Safranyik, L., & Wilson, B. (Eds.) (2006). The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In L. Safranyik & B. Wilson, *The mountain pine beetle: A synthesis of biology, management, and impacts on Lodgepole Pine*. Victoria, Canada: Pacific Forestry Centre.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walkerk, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*(6856), 591–596. https://doi.org/10.1038/35098000

Scheffer, M., Hosper, S. H., Meijer, M.-L., Moss, B., & Jeppesen, E. (1993). Alternative equilibria in shallow lakes. *Trends in Ecology & Evolution*, *8*, 275–279. https://doi.org/10.1016/0169-5347(93)90254-M

Scheffer, M., & van Nes, E. H. (2007). Shallow lakes theory revisited: Various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia*, *584*, 455–466. https://doi.org/10.1007/s10750-007-0616-7

Schlüter, M., Mcallister, R. R. J., Arlinghaus, R., Bunnefeld, N., Eisenack, K., Hölker, F., … Stöven, M. (2012). New horizons for managing the environment: A review of coupled social-ecological systems modeling. *Natural Resource Modeling*, *25*, 219–272. https://doi.org/10.1111/j.1939-7445.2011.00108.x

Seidl, R., Schelhaas, M.-J., & Lexer, M. J. (2011). Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Global Change Biology*, *17*, 2842–2852. https://doi.org/10.1111/j.1365-2486.2011.02452.x

Shannon, L., Coll, M., Bundy, A., Gascuel, D., Heymans, J., Kleisner, K., … Shin, Y. (2014). Trophic level-based indicators to track fishing impacts across marine ecosystems. *Marine Ecology Progress Series*, *512*, 115–140. https://doi.org/10.3354/meps10821

Shipley, B. (2016). *Cause and correlation in biology : A user's guide to path analysis, structural equations, and causal inference with R* (2nd ed., pp. 100–199). Sherbrooke, Canada: Université de Sherbrooke. https://doi.org/10.1017/CBO9781139979573

Toms, J. D., & Lesperance, M. L. (2003). Piecewise regression: A tool for identifying ecological thresholds. *Ecology*, *84*, 2034–2041. https://doi.org/10.1890/02-0472

Underdal, A. (2010). Complexity and challenges of long-term environmental governance. *Global Environmental Change*, *20*, 386–393. https://doi.org/10.1016/j.gloenvcha.2010.02.005

Vogt, J. M., Epstein, G. B., Mincey, S. K., Fischer, B. C., & McCord, P. (2015). Putting the "E" in SES: Unpacking the ecology in the Ostrom social-ecological system framework. *Ecology and Society*, *20*, art55. https://doi.org/10.5751/ES-07239-200155

Waltner-Toews, D., Kay, J. J., Neudoerffer, C., & Gitau, T. (2003). Perspective changes everything: Managing ecosystems from the inside out. *Frontiers in Ecology and the Environment*, *1*, 23–30. https://doi.org/10.1890/1540-9295(2003)001[0023:PCEMEF]2.0.CO;2

Washington-Allen, R. A., & Salo, L. F. (2007). Catastrophic thresholds: Perspectives, definitions, and applications. *Bulletin of the Ecological Society of America*, *88*, 219–226. https://doi.org/10.1890/0012-9623(2007)88[219:CTPDAA]2.0.CO;2

Wood, S. N. (2004). Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association*, *99*, 673–689. https://doi.org/10.1198/016214504000000980

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., … Zeller, D. (2009). Rebuilding global fisheries. *Science*, *325*, 578–585. https://doi.org/10.1126/science.1173146

Ziegler, J. P., Golebie, E. J., Jones, S. E., Weidel, B. C., & Solomon, C. T. (2017). Social-ecological outcomes in recreational fisheries: The interaction of lakeshore development and stocking. *The Ecological Applications*, *27*, 56–65. https://doi.org/10.1002/eap.1433

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.