

1 Integrating Economic dynamics into Ecological Networks: The case of
2 fishery sustainability

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14 Short Title: Economic-Ecological Network Dynamics

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24 **Keywords:** network ecology, coupled natural-human systems, open access fishery, bio-energetic model,

25 allometric-trophic-network model, linear-price model

26 **Summary/Abstract**

27 Understanding and sustainably managing anthropogenic impact on ecosystems requires studying the
28 integrated economic -ecological dynamics driving coupled human-natural systems. Here, we expand
29 ecological network theory to study fishery sustainability by incorporating economic drivers into food-web
30 models to evaluate the dynamics of thousands of single-species fisheries across hundreds of generated
31 food-webs and two management strategies. Analysis reveals harvesting high population biomass species
32 can initially support fishery persistence, but threatens long term economic and ecological sustainability by
33 indirectly inducing extinction cascades in non-harvested species. This dynamic is exacerbated in open
34 access fisheries where profit driven growth in fishing effort increases perturbation strength. Results
35 demonstrate the unique insight into both ecological dynamics and sustainability garnered from
36 considering economically dynamic fishing effort in the network.

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40 One Sentence Summary: Integrating economic drivers into ecological networks reveal non-linear drivers
41 of sustainability in fisheries.

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43 **Main**

44 The advent of network theory in ecology and environmental studies has greatly advanced the
45 study of ecological dynamics and complexity (1, 2). These advances have also translated into a growing
46 knowledge of how human caused disturbances can create far-reaching ecological impacts through indirect
47 effects (3-6). Often, however, the disturbances in these network studies have been studied as a one-time
48 event or a constant external rate of change, separate from the dynamic elements of the network (3, 6, 7).
49 We argue that developing both sustainable management practices and a fuller understanding of
50 anthropocene ecological dynamics require recognition that much of the ecological impact of
51 anthropogenic activity is determined by an integrated feedback process between ecological dynamics and

52 socio-economic conditions as a coupled natural-human system (8, 9). In short, the scope of ecological
53 networks should contain humans as dynamic elements when necessary (10, 11). Here, we expand
54 ecological network theory by incorporating economic dynamics into food-web models to evaluate the
55 coupled natural-human dynamics affecting sustainability in the case of fisheries.

56 Fisheries are an important example of natural-human integrated network systems given their
57 critical role in the economic stability and food security of billions of people (12). Both the available yield
58 and mobilized fishing effort in any fishery are products of a complex set of interacting socio-economic
59 and ecological factors (13, 14). Understanding the dynamics and consequences of these interactions is
60 particularly pressing as current management strategies have produced an over-exploitation crisis in a
61 multitude of fisheries across the globe (15, 16), threatening both aquatic biodiversity (17) and the
62 aforementioned food security (12). Traditionally, fishery sustainability goals have been implemented into
63 policy on a single-fishery basis as a yield optimization process called maximum sustainable yield (MSY)
64 (12). However, MSY's conventional consideration of harvested species in isolation, instead of part of a
65 broader food-web (14, 18, 19), has limited its ability to address the indirect effects of harvesting seen in
66 more network based approaches. Specifically, the population variability induced directly through fishing
67 effort on harvested species (20) can transfer to non-harvested species through trophic interactions (5, 21).
68 This variability has been linked to perturbations causing reductions in aquatic biodiversity (22, 23) and
69 ecosystem function (24). These reductions cycle back to further affect harvested species (5, 25) and the
70 potential economic returns harvested species provide (15, 26). Any effect on economic returns can
71 impact future fishing effort and the corresponding effect on harvested ecosystems, creating a bio-
72 economic feedback loop. While this bio-economic loop is understood in concept, limited work exists on
73 its actual dynamics, especially in the context of broader ecological networks (27). We propose that
74 attempts to understand and manage fishery dynamics must consider economic factors in the network as
75 integrated ecological economic models (13). Otherwise, until more is known about the complex
76 interactions between ecological and economic factors driving fishing efforts, policy makers risk
77 attempting to optimize a process we poorly understand.

78 In accordance with such concerns, we applied network theory to incorporate the ecological
79 complexity of species trophic interactions into the model. This differs from past approaches using
80 Ecopath with Ecosim (28) which rely on extensive lists of system- and species-specific parameters to
81 create models to effectively manage specific systems. The network approach allows for the development
82 of more fundamental, widely-applicable theory because network models can be run across an array of
83 ecological configurations, both empirical (5) and realistically generated (29), by parameterizing
84 metabolism and species interactions through allometry (30). In this study we generated networks as food
85 webs using the Niche Model (31), each with an initial 30 interacting trophic species. Species available for
86 harvest are labeled “fish” for ease of description (Fig 1a). Ecological dynamics in each web were
87 governed by a series of ordinary differential equations and parameterized through allometrically scaled
88 rates (30) creating Allometric-Trophic Network (ATN) models (see Methods, 32). Finally, the network
89 approach also provides a flexible framework which facilitates the integration of economic dynamics.

90 We incorporated two economic models driving fishing effort into the ATN’s ecological network
91 structure with fisheries functioning as an additional node in the networks. After an initialization period of
92 4000 time steps, roughly 11 years in model time (see Methods; 32) (Fig 1b), each “conserved” food-web
93 (see Methods; 32) is subjected to two fishery treatments (Fig 1c): (1) Fixed Effort and (2) Open Access.
94 The Fixed Effort treatment uses fixed levels of fishing effort starting immediately after the initialization
95 period and do not change within simulations (Fig 1d). In the Open Access treatment, on the other hand,
96 fishing Effort is unregulated (33). Instead, Effort adjusts in response to fishing profits, with Effort growth
97 and decline occurring in response to positive and negative net profits respectively (Fig 1e). Profits are
98 influenced by yield and market price. Market price is related to yield through a dynamic linear pricing
99 model (see Methods; 32) (Fig S1). The Fixed Effort treatment serves as a control to the dynamics of
100 Open Access fisheries, but it also has real world representations in strictly permitted fisheries used for
101 subsistence fishing (34). The Open Access treatments simulate fisheries from their initialization at $t=4000$
102 and therefore start from a low initial Effort of 1. Effects of different economic conditions are studied by
103 parameter sweeps across levels of price sensitivity to yield (b), Effort’s sensitivity to changes in profit (μ),

104 and maximum price (a) paid for the harvested species. See Methods section for more (32). Fisheries are
105 single-species, with the harvested fish per simulation labeled, H .

106 We use our dynamic model to evaluate the economic and ecological factors which determine: (1)
107 the impact of fishing on harvested and non-harvested species (ecological impacts), (2) the conditions for
108 fishery “success” (i.e., a sustained non-0 fishing effort), and (3) the different ecological impacts of
109 fisheries within Fixed and Open Access regimes.

110 When we implement fishing through the Fixed Effort treatment, higher Effort levels increase H
111 mortality, intuitively causing more biomass depletion (Fig S2), more extinctions (Fig S3), and quicker
112 times to extinction (Fig 2a) for the harvested species, H . Among the hundreds of ecological factors
113 analyzed (see Methods), we found those H extinctions to be more prevalent at higher trophic levels (Fig
114 S4; Fig 2b), reflecting numerous empirical examples (35-37). Interestingly though, the best ecological
115 predictor of H -extinctions, the population biomass of H at the start of fishing (B_{H0} ; Table S1), has a non-
116 linear effect (Fig 2b; Fig S5a). Compared to the lowest B_{H0} , moderate increases in starting population
117 biomass decreased H extinction prevalence, as more abundant harvested populations are resistant to the
118 extraction induced mortality. However, for all but the highest trophic levels, we saw that further increases
119 in B_{H0} escalate extinction risk of H .

120 This non-linearity occurs because fishing higher B_{H0} generally induces greater levels of
121 variability in the rest of the community’s populations (Fig S6; see Methods), mirroring past work that
122 finds greater population variability when removing species with higher biomasses (29) (Table S2). Higher
123 levels of variability generate extinction cascades of non-harvested species (N - H extinctions; Fig S7)
124 which threaten H through its prey items. The association of B_{H0} , population variability, and N - H
125 extinctions functions as the mechanism behind B_{H0} causing higher levels of N - H extinctions (Fig 2c; Fig
126 S5b; Fig S8). In fact, B_{H0} is also the best single pre-fishing predictor of N - H extinctions (Table S3) and
127 its effects are exacerbated when higher Effort levels induce stronger perturbations in the community (Fig
128 2c; Fig S6; Table S3). The majority of these N - H extinctions occur downstream from H (Fig S9a), and are

129 trophically close to H (Fig S9b) with the average distance becoming closer with a higher number of
130 trophic links to H (Fig S10). As such, we clearly see that the degree of losses in H 's prey options
131 increases proportionally with general N - H extinctions ($\beta = 1.5$, $p < .0001$, $R^2 = 0.75$; Fig 2d). The
132 relatively high level of downstream extinctions relative to upstream extinctions is at least partially due to
133 the size constraints on the food-webs and the fish trophic levels studied here, but these results do indicate
134 that perturbations due to fishing can cycle through the food web and threaten even highly abundant
135 harvested species through their prey items.

136 In the Open Access treatment, B_{H0} also played a critical role in fishery sustainability as it was a
137 principal driver of market dynamics. Open Access Effort is dynamic, capable of both declines and growth
138 (Fig 3a). Growth in Open Access Effort is a function of B_{H0} and the maximum price of H , the parameter
139 a . Higher max price reflects higher base demand for H and higher B_{H0} provides potential yield to meet
140 demand, thereby driving greater profits and Effort (Fig S11a). Dependent upon demand and yield, Effort
141 levels can range from low to high values. However, with sufficiently low demand or yield, net profit is
142 consistently negative, Effort declines to 0, meaning the fishery fails to sustain itself (Fig S12).
143 Consequently, harvesting the most abundant fish per web sustained more fisheries (78% of simulations)
144 than fishing randomly chosen fish populations (26% of simulations). Though, higher prices/demand can
145 sustain Effort on low abundance species by supporting higher profits on lower yield (Fig S13). This
146 growth potential in the combination of max price (a) and harvestable biomass (B_{H0}) strongly predicts the
147 peaks in Effort early in Open Access fisheries' time series (Fig 3a&3b; Table S4; Table S5).

148 However, growth itself, if unchecked, can also lead to Effort declines during the "cycle of
149 adjustment (38)," an empirically detected bio-economic process (39). That is, we see Effort reductions
150 (Fig 3a) when past fishing effort has either over-supplied and caused market-saturation (reductions
151 through price sensitivity to yield, b) or over-fished H (reductions through a lack of biomass from which to
152 profit). These mechanisms of reactionary Effort reduction can function as "self-corrections" that
153 potentially protect against excessive fishing Effort, allowing for regrowth in the harvested populations.

154 These self-corrections, coupled with the potential for Open Access fisheries to fail to sustain Effort at low
155 B_{H0} , explain the relative lack of H extinctions in the Open Access tests (Fig S11b). However, especially
156 in fisheries with high growth potential (high prices and B_{H0}) where Effort is highly sensitive to profit
157 (high μ), the combination of sufficiently high price (a) and high B_{H0} elevates Effort to levels (Fig 3b)
158 inducing H extinctions before self-correction occurs (Fig 3c). Analyzing Open Access fishery outcomes
159 reveals three general economic categories: (1) failed fisheries due to low B_{H0} and price (a) failing to
160 maintain or grow Effort, (2) failed fisheries due to high B_{H0} and price driving H extinctions through
161 excessive Effort, and (3) sustained fisheries existing in a middle ground between the two (Fig 3d).

162 These three general economic outcomes underpin much of the relationship between the harvested
163 species and fishing Effort in Open Access fisheries. In particular, these results indicate that H extinctions
164 were actually most common when harvesting highly abundant H (species with high B_{H0}) as unregulated
165 growth in Effort depleted fish reserves (Fig S14). This also formed the basis of the non-linear effect B_{H0}
166 had on Open Access fishery persistence (Fig 4a) and the level of Effort sustained by the end of the
167 simulation (Fig 4b). Additionally, while H extinctions were relatively less common, the link between
168 harvestable biomass and Effort growth reversed the relationship between B_{H0} and time to H extinction
169 seen in Fixed Effort fisheries (compare Fig 2a to Fig 4c). Finally, the dynamics of Effort in response to
170 yield also drive the different effects of fishing on the rest of the community between Open Access and
171 Fixed Effort fisheries.

172 The profit-driven growth in Effort caused by high B_{H0} means that (given sufficient demand)
173 economic factors incentivize subjecting food-webs to high levels of harvesting pressure on their more
174 abundant species. This induces more variability in the biomass of the rest of the community than Fixed
175 Effort fisheries (Fig S15). Expectedly (Fig S7), market generated variability induced more non-harvested
176 ($N-H$) extinctions than Fixed Effort simulations. This was the case whether comparisons between Fixed
177 Effort and Open Access results were made with attainable Efforts levels across all webs (Fig 4d; Fig S16;

178 Fig S17) or strictly within each web at the most comparable Effort levels between fishery treatments (Fig
179 4e).

180 While our model framework has not yet been applied to multi-species fisheries or to realistically
181 regulated fisheries, it can qualitatively reproduce past theoretical results (29) (Table S2), well-
182 documented empirical patterns (Fig S4), and output from models specifically trained on empirical data
183 (23) (Fig S18). This gives us confidence in vetting our results and further applying this framework
184 towards the study of operational ecosystem based fisheries management (EBFM) strategies (27). Model
185 output demonstrates the striking nonlinear effects of the population biomass of harvested species (B_{H0}) on
186 both the ecological and economic sustainability of fishing. It also reveals the role of B_{H0} in driving
187 variations in Effort and exacerbating the ecological costs of harvesting in Open Access fisheries.
188 Temporary fluctuations in Effort above sustainable levels are a known process in the cycles of adjustment
189 seen in Open Access fisheries (33), but we show here that the indirect effects of those fluctuations can
190 drastically change food-web structure. Overall, our results indicate that considering the sustainability of
191 even one aspect of an ecosystem service likely requires a holistic accounting of both the ecology that
192 provides the service and the economy that the service provides.

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Supplementary Material:

Materials and Methods
Figures S1 – S18
Tables S1 – S6
References (40 – 53)

Figures

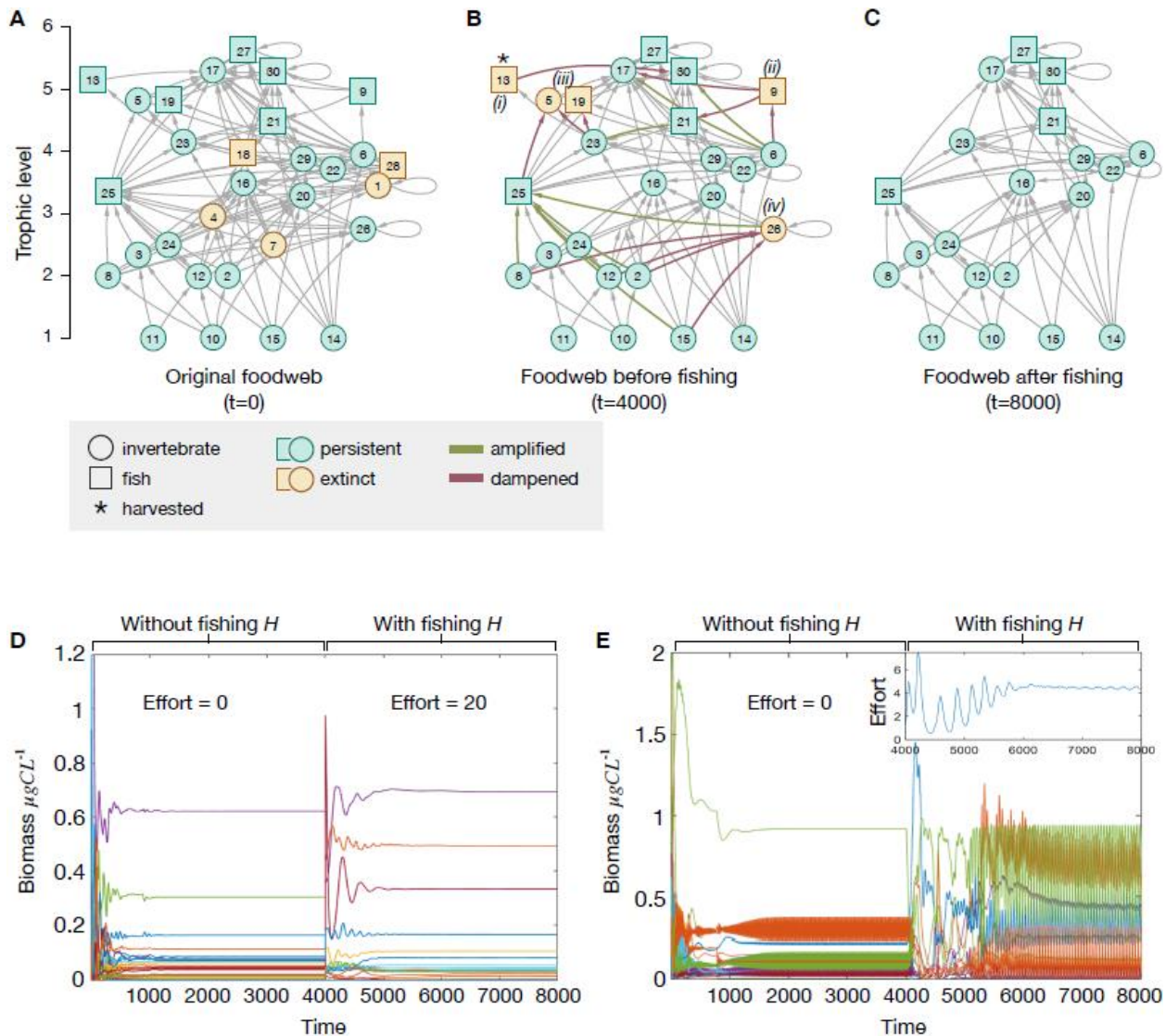
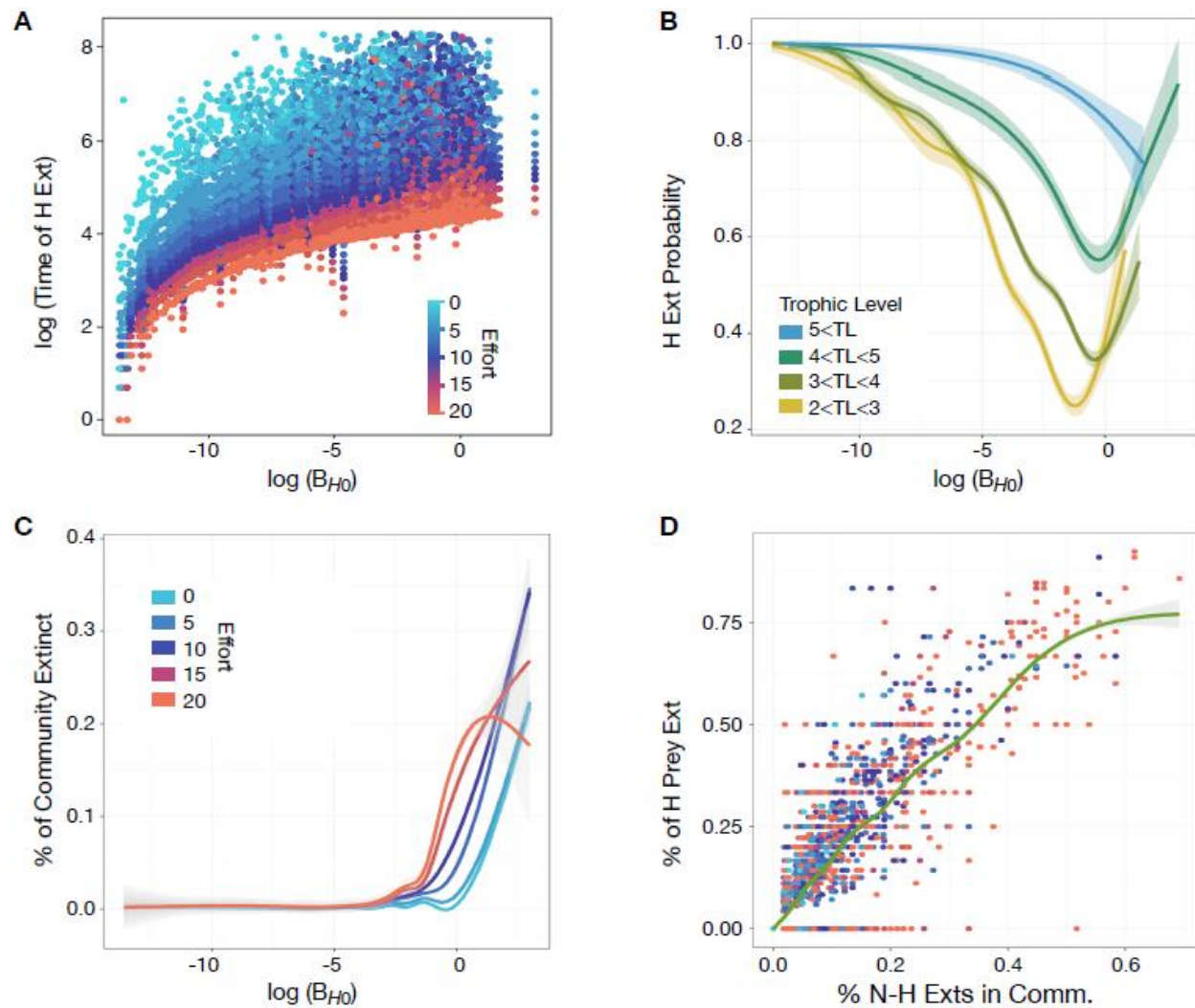
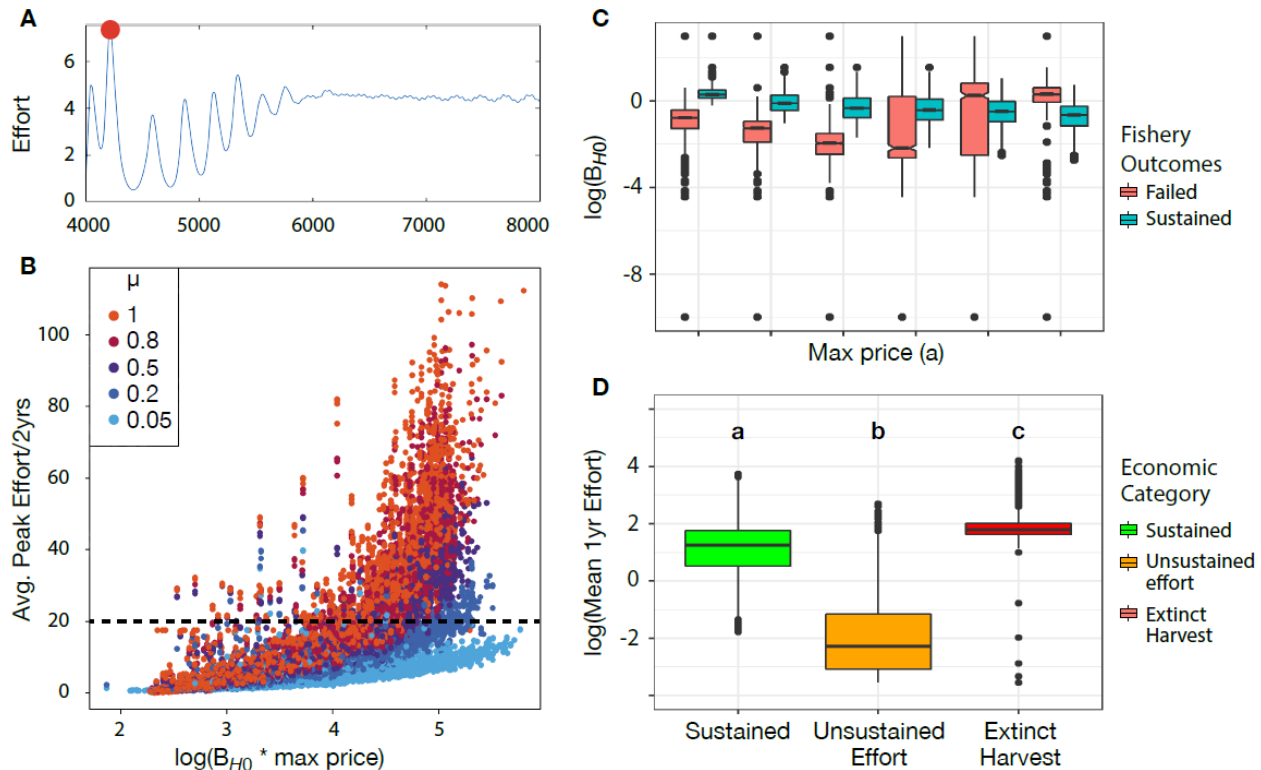


Figure 1: Diagrams of the experimental design. a-c) Example evolution of a food web structure across complete simulation process with a Fixed Effort of 5. Node sizes are logarithmically scaled to the biomass at each point in time of the simulation. Edges between nodes represent trophic interactions with arrows indicating the consumer. The vertical axis indicates the trophic level of trophic species. a) The example food web at initialization (t=0). Colors of nodes indicate species that will survive or go extinct after initialization. b) The example food web after initialization and before fishing effort (t=4000). Colors of nodes indicate species that will survive or go extinct after fishing. Indices (i) – (iv) indicate the order of extinctions during simulation. c) The final structure of the food web after the fixed harvesting effort (t=8000). d) Example simulation of a FE treatment simulation with effort set at 20. e) Example simulation of an Open Access treatment simulation.

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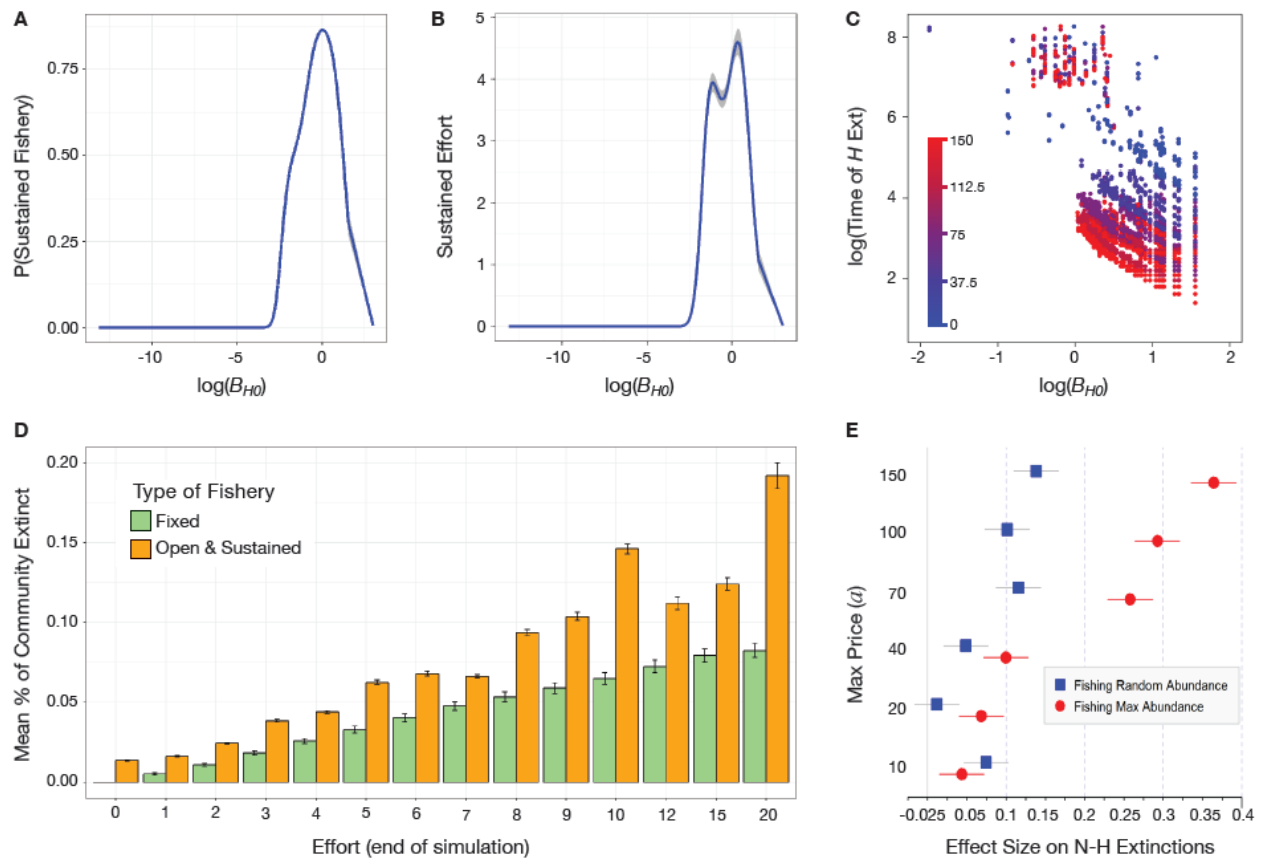
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 407 **Figure 2: Fixed Effort results.** a) Scatterplot showing the effect of $\log(B_{H0})$ on time to H extinction. b)
 408 Generalized additive model (GAM) binomial regression of the effects of $\log(B_{H0})$ on the probability of
 409 fishing resulting in H extinction across four trophic level groupings of H . Lines represent fit and shaded
 410 regions show 95% confidence interval. Including $\log(B_{H0})$, trophic level of H , and Fixed Effort level
 411 gives the binomial GAM results: 51.1% of variance explained at $R^2=0.57$, UBRE=-0.32. c) GAM
 412 regressions showing the percent of the community lost based on $\log(B_{H0})$. Lines represent fit and shaded
 413 regions show 95% confidence interval. Higher Effort levels (e.g. E=15, 20) do present a non-linear trend
 414 at high B_{H0} . This is due to the expedited H extinctions at high Effort levels ending the active fishing
 415 disturbance on the rest of the community quicker than lower Effort levels. See Fig S6 for more. d) Scatter
 416 plot showing positive relative relationship between the percent of community lost to $N-H$ extinctions
 417 and the percent of H 's prey items lost. Colors represent Fixed Effort values similar to Fig 2a and the
 418 green line represents GAM regression fit with 95% confidence interval.
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Figure 3: Open Access results. a) Example of effort dynamics where red dot represents a local peak effort. b) Peak efforts averaged across two years per the product of starting biomasses of harvested species (B_{H0}) and max price (a). Colors indicate the value of μ , economic sensitivity/reactivity of the Effort per simulation. c) Box-plot showing B_{H0} of failed and sustained fisheries across different Max Price (a) when fishing the max B_{H0} fish population per food-web. Increasing a supports sustained fishing effort in less abundant fisheries until spiking effort peaks produced by higher profits when fishing abundant species cause the H -extinctions and fishery failure. d) Three economic outcomes characterized by efforts averaged across the first fishing year. Sustained (green) fisheries exhibit intermediate efforts producing enough profit without collapsing the resource. Unsustained (orange) fisheries failed before causing species extinctions because their profits were lower than harvesting costs. Extinct (red) fisheries failed because high profits produce high effort peaks causing the harvested-species extinction. Significant differences indicated by different letters (Tukey HSD, $p < 2e^{-16}$). In boxplots of Fig 3c and 3d, boxes represent the interquartile range with the horizontal line showing the median, the lower box representing the 25 percentile, and the upper box showing the 75 percentile. Upper and lower lines extending from the boxes show the most extreme values within 1.5 times the 75th and 25th percentile respectively. Outliers are shown as single dots.

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Figure 4: Open Access fishery's economic and ecological sustainability results. a) Probability of producing a sustainable Open Access fishery across the B_{H0} of H . Graph depicts the non-linear output of a binomial GAM regression with 95% confidence interval ($R^2 = 0.47^{***}$, UBRE=-0.20). b) Sustained Open Access effort measured as average of final 400 time steps approaching $t=8000$. Graph depicts non-linear output of a gaussian GAM regression with 95% confidence interval ($R^2 = 0.37$, GCV=9.60). c) Scatterplot showing the effect of $\log(B_H)$ on time to H extinction in Open Access simulations. Note the qualitatively reversed relationship from Fixed Effort fisheries. Color gradient represents the max price effort (a)* the market reactivity (μ). d) Bar graph with standard error comparing the percent of the community lost through $N-H$ extinctions in Fixed Effort fisheries to Open Access fisheries with comparable effort levels at $t=8000$. E) Hedge's G effect size comparison of the two fishery treatments (Fixed and Open Access) on $N-H$ extinctions across different max prices (a). Dots represent effect size and lines show 95% confidence intervals. Comparisons are made within webs at comparable effort levels (see Methods; 32).