

Sustaining Economic Exploitation of Complex Ecosystems in Computational Models of Coupled Human-Natural Networks

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Abstract

Understanding ecological complexity has stymied scientists for decades. Recent elucidation of the famously coined "devious strategies for stability in enduring natural systems" has opened up a new field of computational analyses of complex ecological networks where the nonlinear dynamics of many interacting species can be more realistically modeled and understood. Here, we describe the first extension of this field to include coupled human-natural systems. This extension elucidates new strategies for sustaining extraction of biomass (e.g., fish, forests, fiber) from ecosystems that account for ecological complexity and can pursue multiple goals such as maximizing economic profit, employment and carbon sequestration by ecosystems. Our more realistic modeling of ecosystems helps explain why simpler "maximum sustainable yield" bioeconomic models underpinning much natural resource extraction policy leads to less profit, biomass, and biodiversity than predicted by those simple models. Current research directions of this integrated natural and social science include applying artificial intelligence, cloud computing, and multiplayer online games.

Introduction

The reduction of biodiversity and ecological productivity continues to degrade ecosystems' abilities to sustain human and non-human life (Millennium Ecosystem Assessment 2005). Ecosystems that provide such sustenance are complex systems comprised by networks of diverse interdependent and interacting species (Pascual and Dunne 2006). These networks include food webs that depict interconnected food chains within habitats such as lakes or forests (McCann 2012). Better understanding of ecosystems is required to help manage them. Only recently has this understanding enabled realistically complex ecosystems to be computationally modeled. This advance emerged from computational studies of ecosystems that uncovered how

such nonlinear high dimensional systems may dynamically persist despite their mathematical improbability recognized four decades ago. This improbability directly contradicted a dominant "diversity begets stability" paradigm at the time that held that diversity and complexity stabilize ecosystems (May 2006). The instability was based on some of the earliest computational studies that found that large random networks of higher complexity in terms of more nodes and links failed to persist (Gardner and Ashby 1970) due to increased probability of positive feedback loops associated with increased interactions (May 1973). This led to a famous challenge for diversity-begets-stability proponents to "elucidate the devious strategies that make for stability in enduring natural systems" (May 1973).

Over thirty years later, computational research addressing this challenge found that regularities in food web structure (Martinez, Williams and Dunne 2006), predator-prey body-size ratios (Brose, Williams and Martinez 2006, Otto, Ball and Brose 2007), and feeding behavior (Williams and Martinez 2004) put ecosystems in a highly non random parameter space where diversity begets stability (Brose, Williams and Martinez 2006). Whereas before, realistically complex models failed to persist, the new insights enabled such systems modeled as nonlinear, high dimensional, coupled ordinary differential equations to characterize the bioenergetic feeding and biomass dynamics of complex networks of persistently interacting species (Berlow et al. 2009, Gross et al. 2009). Such advances helped rejuvenate basic research on ecological stability and initiated new and highly active computational research focused on the ecological effects of species loss and pollution (Brose, Berlow and Martinez 2005, Berlow et al. 2009, Sahastrabudhe and Motter 2011).

Here, we push this research forward to analyze the sustainability of coupled human-natural systems comprised by humans that exploit ecosystems by extracting biomass such as fish, forests, and fiber for food and financial gain. Further advances in computational sustainability will help

conduct and analyze large numbers of models that generate huge amounts of data which describe coupled human-natural networks including ecosystems and help uncover more sustainable management strategies.

Background

The seriousness of the many stressors on ecosystems, which provide services critical for human life on Earth, is recognized by an increasingly large number of people across the world (Barnosky et al. 2012). Climate change and habitat degradation due to human activity are chief among these challenges (Millennium Ecosystem Assessment 2005). Some immediate and dramatic results of such perturbations are the loss of species native to ecosystems (Hughes, Daily and Ehrlich 1997), the invasion of ecosystems by species alien to them (Williamson 1996) and degradation of ocean productivity due to overfishing (Worm et al. 2009). Interacting species within ecosystems including humans form highly complex, non-linear, dynamically coupled systems, but scientists are only beginning to understand how this interdependence impacts the fundamental structure, dynamics, function, and stability of complex ecological systems (Carpenter et al. 2009).

Computational analyses of ecological systems that ignore humans have illuminated powerful structural regularities in the consumer-resource networks that comprise food webs (Dunne 2006, Williams and Martinez 2008, Dunne et al. 2008). Knowledge of this structure helped illuminate network dynamics that describe how species' abundances and feeding rates vary over time and the dynamic consequences of species loss, invasion, and environmental change for ecosystems. For example, computational studies of species loss can now quantitatively predict the effects on the abundance of other species in field experiments (Berlow et al. 2009) and suggest which additional species to eliminate in order to prevent extinction cascades resulting from the initial loss (Sahastrabudhe and Motter 2011). The theoretical and mathematical framework for these studies has been successfully extended to seasonal dynamics of 20 groups of species within a large natural ecosystem (Boit et al. 2012). These promising results suggest that computational models of specific habitats (e.g., coral reefs, lakes, forests, etc.) form a firm foundation for integrating human exploitation of these habitats. Here, we describe such advances focused on economic and subsistence exploitation of ecosystems that improve the power and usability of network modeling, data management, and visualization.

The urgency of environmental problems and complexity involved in solving them require new advances to computational approaches to these problems. More usable approaches are needed to enable ecologists and other non-computational experts to conduct computational research.

More powerful approaches are needed to explore more and larger networks of increased complexity that reflect more of the variability, interactions, and environmental problems found in nature. We address these goals by developing user friendly web-based approaches with client-based analyses including visualization that harness cloud computing for powerful and flexible computation. Client-based approaches provide rich functionality and fast response times. The inherently parallel nature of simulating many ecological networks and the vast data produced by these simulations combined with low economic cost make cloud-based approaches potentially ideal research solutions, especially when combined with platform independent browser-based access. However, while cloud computing has found widespread application in business environments, it has yet to demonstrate many scientific accomplishments (Fox 2011). This makes the harnessing of cloud-based approaches to scientific problems a novel computer science challenge deserving of innovative research efforts.

While both commercial and scientific computation typically requires users to buy and maintain computers appropriate to their computational needs, the establishment of server farms along with software platforms such as Microsoft's Azure can free researchers from the need to rewrite software as well as buy and maintain hardware and software. In its place, cloud computing promises relatively easy and cost-effective access to much greater and more quickly scalable computing power than users could otherwise afford, manage, or maintain. The activities described here incorporate cloud computing into ongoing computation which enhances the ability of domain specialists to simulate, analyze, and ultimately understand and predict the structure and function of complex ecological systems.

Non-cloud frameworks for simulation of complex ecological network dynamics are very time and personnel intensive. For example, simulations of 50-species networks require discussions with a model-coding expert, coding by that expert to set up the simulations, and about a week of computation time on 25 PCs in a cluster to achieve a reasonable amount of replication. Due to memory limitations, only a limited amount of the results can be saved and accessed in the future. Experience has shown that it is hard to know ahead of time which subsets of simulation data will be important for analyzing and interpreting simulation output. This can result in costly repetition of the coding and simulation cycle. The major benefits of running such simulations on a cloud-computing platform include the reduction of simulation time for complex network dynamics to a few hours, and the ability to save all results including the full simulation time series, which reduces the need to rerun simulations. Thus, cloud-based computing offers the opportunity for much greater efficiency in the workflow, reducing the demand on code-savvy group members and reducing barriers to research by domain scientists.

Methods

Allometric trophic network (ATN) modeling (Brose, Berlow and Martinez 2005, Brose, Williams and Martinez 2006, Berlow et al. 2009, Sahastrabudhe and Motter 2011) proceeds by first creating a food web of a certain size and complexity using a structural network models that determine who eats whom within the network. The structure formed by that food web is then used to assign body sizes to species within the food web based on empirically derived and highly variable consumer-resource body size ratios where predators are typically, but not always, larger than their prey. Allometric relationships between species' metabolic rates and body sizes are then used to parameterize ODEs that determine the temporal dynamics of species populations including extirpation where populations drop below an extinction threshold. Here, we apply this framework to a realistic case of fishing in a large lake by adopting several parameters derived from applying the ATN framework to the well-studied European Lake Constance (Boit et al. 2012). The parameters result in an excellent fit to the seasonal dynamics observed in the lake which supports the realism of our computational explorations.

The Niche Model (William and Martinez 2000, 2008) generates the initial realistic structure of the food webs and has two inputs: the number of species S and connectance C (Martinez 1992) where $C = L/S^2$ and L is the number of trophic links. The model assigns a uniformly random "niche value" ($0 \leq n_i \leq 1$) to each of S species. Consumer i eats only species whose niche values are contained within a range r_i with a center of $c_i < n_i$. c_i is randomly chosen from a uniform distribution between $r_i/2$ and $\min(n_i, 1 - r_i/2)$. $r_i = xn_i$, where x is a random variable defined on $[0,1]$ with a beta-distributed probability of $p(x) = \beta(1-x)^{\beta-1}$ with $\beta = 1/(2C) - 1$.

We use 17 network properties to describe food-web structure (William and Martinez 2000, 2008, Dunne et al. 2008): *Top*, *Int*, *Bas* are the proportions of species that are respectively without predators (top), with both predators and preys (intermediate), and without preys (basal); *Can*, *Herb*, *Omn* and *Loop* are the fractions of species that are cannibals, herbivore (only basal preys), omnivores (i.e. feeding on multiple trophic levels) and involved in loops (apart from cannibalism); *ChLen*, *ChSD* and *ChNum*, the mean length, standard deviation of length and log number of the food chains; *TL*, the mean short-weighted trophic level of species (Williams and Martinez 2004); *MaxSim*, the mean of the maximum trophic similarity of each species; *VulSD*, *GenSD* and *LinkSD* are the normalized standard deviations of vulnerability (number of predators), generality (number of preys) and total links; *Path* is the mean shortest food-chain length between two species and *Clust* is the clustering coefficient (Watts and Strogatz 1998).

The population dynamics within the food webs were simulated using (Berlow et al. 2009):

$$\dot{B}_i = r_i \left(1 - \sum_{j \in \text{autotrophs}} \frac{B_j}{K}\right) B_i - \sum_{j \in \text{consumers}} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}} \quad (1)$$

$$\begin{aligned} \dot{B}_i = & -x_i B_i + \sum_{j \in \text{resources}} x_i y_{ij} B_j F_{ij} - \sum_{j \in \text{consumers}} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}} \\ & - \sum_{k \in \text{firms}} q_k E_{ki} B_i \end{aligned} \quad (2)$$

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_0^h + c B_i B_0^h + \sum_{k \in \text{resources}} \omega_{ik} B_k^h} \quad (3)$$

Eq. (1) and (2) describe the changes in the biomass densities of, respectively, an autotroph and an heterotroph species. In these equations, r_i is intrinsic growth-rate of basal species i , K is the carrying capacity shared by all the basal species, x_i is i 's metabolic rate ($x_{\text{basal}} = 0$, Brose et al. 2006), y_{ij} is the maximum consumption rate of i eating j , e_{ij} is i 's assimilation efficiency when consuming j . We used a weak Holling-type III functional response (eq. 3) with B_0 as the half-saturation density, h is the Hill exponent set to 1.2, c is the predator interference and ω_{ij} is i 's relative inverse attack rate (i.e. i 's preference towards j).

Parameter values follow Berlow et al. (2009) and Boit et al. (2012): $S = 30$, $C = 0.15$. r_i is normally distributed with a mean of $0.6/d$ and an SD of 0.2. $K = 540 \mu\text{gC}/L$. $y_{ij} = 10/d$. $e_{ij} = 0.85$ for carnivores and 0.66 for herbivores. $B_0 = 80 \mu\text{gC}/L$. $\omega_{ij} = 1/\sum i$'s resources. Metabolic rates of non-basal species were calculated using a surprisingly accurate "short-weighted" measure of trophic level (TL_i) based on binary food webs (Williams and Martinez 2004a). Basal species' reference body masses (M_i) = 1. Consumers' M_i were calculated using the average predator-prey body-mass ratios, $Z: M_i = Z_i^{TL_i-1}$. Z was sampled from a lognormal distribution with mean=100 (SD=50) for fishes and mean=10 (SD=100) for invertebrates (Brose, Williams and Martinez 2006). Species with $TL_i < 3$ are always invertebrates and species with $TL_i > 3$ were usually (P=0.6) a fish. Metabolic rates follow -0.25 power-law relationships. $x_i = 0.314 M_i - 0.24$ for invertebrates. $x_i = 0.88 M_i - 0.24$ for fish (Brose, Williams and Martinez 2006).

Initial biomass densities were uniformly distributed within 5-500 $\mu\text{gC}/L$. The systems were then simulated for 2000 time steps before allowing economic exploitation in better mimic the establishment of a new fishery within a stable ecosystem. Approximately 25% of the species go extinct during this first period (extinction threshold = $10^{-6} \mu\text{gC}/L$). Only networks that were still connected after 2000 time steps were considered further. As the effort was always fixed, we set the catchability to 1% so that effort equals the percentage of extracted biomass.

After 2000 time steps, 3 relatively large species at high trophic levels were chosen by selecting the 3 species with the highest TL_i/x_i for exploitation under four different scenarios. Three of the scenarios were simply exploiting only 1 of the 3 species which were compared with a single-species logistic-growth model parameterized to reflect the chosen species. Species carrying capacity (K) was set to its biomass without exploitation and its intrinsic growth rate calculated from the species metabolic rate ($r = x(y - 1)$). In the fourth scenario, all 3 species were harvested simultaneously at the same exploitation rate. We varied the amount of biomass extracted from 0% to 100%.

We analyzed 100 food webs with a mean number of species of 25.5 (SD=2.0) and a mean connectance of 15.8% (SD=1.2%). The 17 structural properties of each of the 100 webs were calculated as well as the metabolic rate and trophic level of the exploited species and whether it is a fish, invertebrate, top, intermediate, herbivore and/or a cannibalistic species. We also calculated properties of network structure local to the exploited species including vulnerability, generality and connectivity of the exploited species, its prey and its predators. We conducted 120,000 simulations comprised by 300 simulations of finely varying percentage from 0% to 100% of biomass extracted from each of the 100 food webs under the 4 exploitation scenarios. Simulation lasted 4000 time steps including 2000 pre- and post-exploitation. Biomass results are means during the last 400 time steps which avoided transitional dynamics because no large, slow oscillations emerged in our simulations, all of which were performed in Matlab version 6.5 and 7.10 using ode45 for ODEs with the default settings.

Results

Given the wide range of stochastic variability in food-web structure and subsequent ecological function and exploitation, simulations yielded a wide range of results. The most consistent result was that exploited species almost always went extinct at lower rates of extraction than the logistic model predicts. With few but interesting exceptions, the biomass also decreases more with increased extraction than predicted by the logistic model. Only one of the many structural network properties, the mean vulnerability of exploited species' prey, appears related to the magnitude of this decrease (Fig. 1). Exploitation of a species often results in increases in the exploited species' prey. This increase in food supply can increase the exploited species growth rate which often compensates for losses to extraction. However, this compensation is typically much less when the exploited species prey is consumed by many other species. Such consumption typically limits greatly any potential increase of prey density in response to extraction of only one of its several predators. We show this by plotting the mean vulnerability of exploited species' prey

against the percent of exploited species' biomass that needs to be extracted to reduce its biomass to half its unexploited density (Fig. 1). Many exploited species with mean prey vulnerability ≥ 6 species go extinct when $< 5\%$ of its biomass is extracted. In contrast, many exploited species with mean prey vulnerability < 6 can be sustained despite extracting $> 5\%$ and $> 10\%$ of its biomass. Another general result is that smaller bodied species with higher metabolic rates can sustain extraction of larger fractions of their populations without going extinct (results not shown). This is due to fact that exploited species with higher metabolic rates generally inflict higher grazing pressure on their resources. Thus, a higher exploitation rate is needed to counterbalance this high grazing pressure.

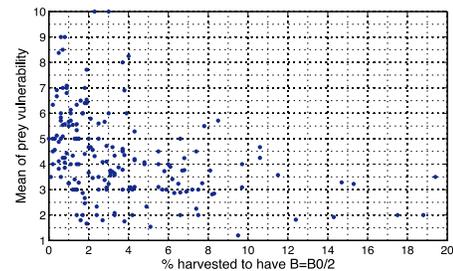


Figure 1: Influence of the vulnerability of exploited species' prey on the percent of the exploited species that can be extracted while sustaining half of its unexploited biomass density. Only results from exploiting only one species are presented.

Figure 2 illustrates two examples that depict many of our results including the consistent extirpation of exploited species at lower extraction rates than predicted by the logistic model. The vastly more frequent finding (Fig. 2a) is the surprising insensitivity to exploiting more than one species. The biomass of a species extracted under the single-species exploitation scenario is virtually identical to when two additional species are exploited at the same rate. This finding may be due to the use of an inappropriate benchmark. Each species is compared to its abundance in an unexploited food web. However, if one large bodied species at high trophic level is exploited, other similar species may compensate by increasing their abundance due to the reduced density of a similar presumably competing species. Our results are effectively blind to this type of interdependence. Additional simulations are needed to explore this possibility. Still, insensitivity observed suggests that economic benefits of exploiting multiple species within a network may be simply additive in comparison to an ecosystem free from exploitation.

The exception to these general results only incurred in one of the 100 food webs (Fig. 2b). Exploiting species in this web resulted in the very interesting "hydra effect" (Abrams 2009) where extraction of a species results in so much of an increase in its prey that the increased resource supply overcompensates for losses due to increased extraction. This results in increasing extraction counter intuitive-

ly increasing the exploited species' biomass. The magnitude of this overcompensation varies among species. In Fig. 2b, exploitation of just the red species results in a mild hydra effect presumably because the red species has no predators and only one (blue) prey. This allows it to exert very strong grazing pressure on its prey. Extracting the red species biomass probably enables the blue species to recover from very low abundance and thus allowing the red species growth to increase more than its biomass lost to extraction. This presumably allows the red species to increase with increasing extraction from ~2% to 7%. Exploiting only the blue species results in a hydra effect at a little over 10% extraction. Extracting the red and blue species alone results in higher biomasses than predicted by the logistic model over range of low extraction rates. In contrast, exploiting only the green species reduces its biomass well below that predicted by the logistic model.

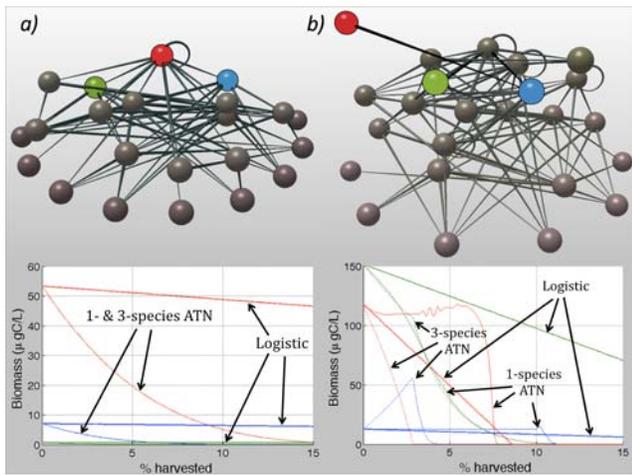


Figure 2: Two (a & b) examples of exploited food webs. Top: Food-web network (links are feeding relationships) with species (spheres) at higher trophic levels above basal species at the base. Results of exploiting the 3 colored species shown in same colors below. Bottom: Biomasses sustained in the web above as a function of exploitation rate when only 1 species at a time is fished, the 3 species are fished together, and each species is modeled as an isolated logistically growing species.

These results change dramatically when all 3 species are exploited. The red species is reduced well below that predicted by the logistic model because both it and its only prey, the blue species, is exploited. This may be expected when the red species mortality increases along with that of its only prey. However, the blue species increases to several times its unexploited density in this scenario when all 3 species are extracted at ~2-3% because its only predator is reduced and also, perhaps, due to other undetermined factors. The green species' biomass here is higher at ~3% extraction than when only the green species is exploited probably because it eats a cannibalistic species that eats the blue species. This may allow the green species to indirectly benefit from the large increase in the blue species.

Discussion

Extraction of biomass from realistically complex ecological systems can result in profoundly different effects that extraction from more simplistically modeled systems. Logistically growing species, usually one but sometimes several, provide much of the foundation for bioeconomic theory and modeling. Perhaps the most famous of these theories is that of "maximum sustainable yield" (MSY) that asserts maximum economic return is achieved when the exploited population is reduced to half of its carrying capacity (Larkin 1977). This almost always overestimates the sustainable exploitation rate of more realistically modeled species. In fact, most species would be driven entirely extinct at extraction rates recommended by MSY (Fig. 2). The one exception we found (red species Fig. 2b) appears unusual in that it is a large bodied specialist at a high trophic level. Still, more thorough analyses are needed to explore when similar but less dramatic results occur among networks occupying larger parameter spaces.

Perhaps a more surprising result is the lack of dependence among species in the same ecosystem on whether or not other species are also exploited. This too needs further exploration especially with analyses using benchmarks other than the completely unexploited state used here.

More generally, our results demonstrate the utility and necessity of computational analyses of human-natural networks. The wide range of variability in nature and the manner in which humans exploit nature mean that human-natural networks occupy huge parameter spaces for which computational analyses are particularly appropriate. The high dimensional, nonlinear, and nonrandom nature of these networks largely prohibit more analytical approaches from shedding much light on their behavior. Finally, the embarrassingly parallel structure of our analyses point towards the great potential of cloud computing approaches to human-natural networks. Not only can large parameter sweeps be conducted in short times using vast computational resources needing virtually no maintenance by the users or their institutions, but cloud computing can also store the times series from the simulations allowing analyses to focus on the data rather than rerunning simulations to output subsets of simulation data thought to be able to help answer research questions. If made generally accessible e.g., via browser-based queries of SQL Azure, such data-intensive ecological research (Michener and Jones 2012) would also open the research to non-computational experts such as statisticians, natural resource managers, and ecologists who could answer research questions not focused on or even imagined by the scientists conducting the simulations. Such inclusion of a wider range of researchers could greatly accelerate scientific progress on the critically important problems identified here as well as many other problems throughout science.

Future Directions

Results such as those presented here have helped motivate significant developments of cyberinfrastructure, including cloud computing infrastructure (Figure 3), to address complex ecological networks both with and without humans. Not only does it achieve many of the benefits suggested in the previous paragraph, it also provides a backend for multi-player online games to help explore and analyse complex ecological networks. We created such a game called World of Balance (WoB) based on managing the Serengeti ecosystems of Africa (de Visser, Freymann and Olf 2010) whose population dynamics are driven by Eq. (1) - Eq. (3). WoB is the first of a series of ecosystem management games that more realistically depict exploitation of forests, lakes, grasslands and oceans. Such games may contribute to ecology and conservation biology much of what Foldit has contributed to molecular biology. That is, the widespread inclusion of the complementary capabilities of players and computers in solving important research questions (Khatib et al. 2011).

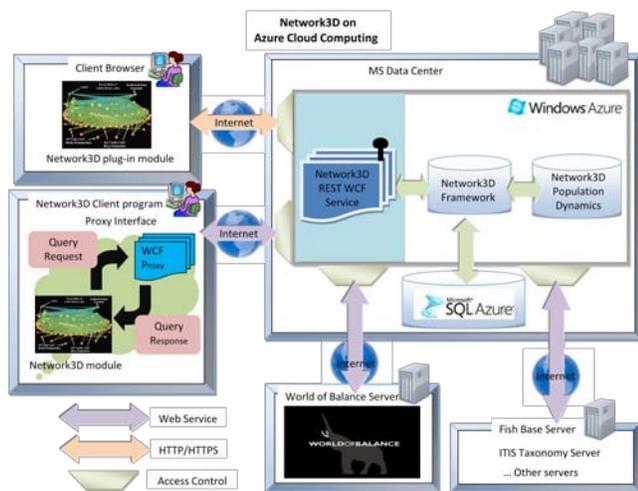


Figure 3. Cyberinfrastructure for ecological network analysis. The Microsoft Windows application "Network3D" now ported to Azure simulates and analyzes the structure and dynamics of ecological networks (Eq. 1-3). The Network3D engine uses Windows Workflow Foundation to implement long-running processes as workflows. Multiple manipulation requests cause each manipulation to be delivered to a worker instance to execute. Results of each manipulation is saved to SQL Azure. A web role provides the user with an interface where the user can initiate, monitor and manage their manipulations as well as web services for other sites and visualization clients. Once the request is submitted through the web role interface, the manipulation workflow starts the task and a manipulation is assigned to an available worker to process. The Network3D client communicates through web services and visualizes network structure and population dynamics.

A central goal of WoB is to maintain a higher environmental score. This is done by creating, growing and managing an ecosystem with many species and high bio-

mass. Such play also generates experience points and gold that further enables the player to more powerfully nurture and manage their ecosystem by e.g., buying individuals of different species and altering the weather. Network3D running in the Azure cloud simulates the population dynamics within the player's ecosystem and provides these dynamics to the WoB client for visualization. The client represents these dynamics by varying the number of individual plants and animals rendered in 3D within the user's zone. Individual plants' locations remain fixed while animals wander around the landscape. Players purchase individuals of species both existing and novel to their ecosystems. This mimics species migration and invasion. Players can also sell organisms within their zone to hunters, food, and firewood markets. Advanced players can use "superpowers" gained by playing to modify parameters such as carrying capacity, predation behavior, and prey resistance to consumption as well as growth and metabolic rates.

Due to the nature of population dynamics, players must pay careful attention to what's changing within their ecosystem and try to maintain it as best as possible to prevent it from collapsing due to the inherent dynamics of the systems. Players visually see the results of their activities throughout a given period. More broadly, WoB is about maintaining a healthy ecosystem and understanding ecological and economic interdependence. It is also about crowd sourcing the work of exploring parameter space by saving and analyzing easily accessible game results.



Figure 4. Screen shot of World of Balance game. Environment score (top right) increases with species diversity, biomass and trophic level in player's User Zone. This score increases the player's ability to purchase species from game shop (lower left) with Gold (top right), a form of in game currency. World and Team chat (lower right) enables player to communicate with different groups who cooperate or compete and can see each other's Zones. Game is in beta form while development and formal evaluation of design, usability and learning outcomes continue.

Play and research in this area continue to become more sophisticated. For example, instead of simply fixing

effort as described above, we have implemented more realistic models that make E a function of economic variables. This includes an important model of variable exploitation in an open access fishery (Conrad 2010): $\dot{E} = \mu (pqB_i - c_o) E$ where E is fishing effort for species i , p is the price per unit catch, q is the "catchability coefficient", B_i is the biomass density of exploited species i , c_o is the cost per unit effort, and μ is market openness which constrains how fast the effort changes based on profit or loss. As long as the fishery is at least partially open ($\mu > 0$), E increases at a rate determined by profit which is the difference between income ($pqB_i E$) and cost ($E c_o$). E decreases when this difference is negative indicating loss. Allowing E to vary would allow the fishery to seek a bioeconomic state where fishery income equals its costs. We also implemented three more realistic models of the influence of supply and demand on p by making p a linear [$p = a(1-bY)$], isoelastic [$p = aY^{-b}$], or non-linear and non-isoelastic [$p = a/(1+bY)$] function of catch ($Y = qE_i B_i$, Conrad 2010). Here, b quantifies the sensitivity of the price to the harvest. In the linear model, a is the maximum p which only reached when $Y = 0$ and p decreases as Y increases until $Y \geq 1/b$ when $p = 0$. With the isoelastic model, $p \rightarrow \infty$ when $Y \rightarrow 0$ and $p \rightarrow 0$ when $Y \rightarrow \infty$. The third model is non-linear as is the isoelastic model but prevents $p \rightarrow \infty$ and $p \rightarrow 0$.

A key concept in evaluating effects of economic exploitation of ecosystems is distinguishing such effects from effects of subsistence exploitation of ecosystems. Humans have sustainably exploited ecosystems free of formal economies for millennia (Maschner et al. 2009) and it is critical to understand these exploitation mechanisms in order to better manage the ecological sustainability of humans. Mechanisms of subsistence exploitation involve demographic rather than financial responses to ecosystem exploitation (Pulestron and Tuljapurkar 2008). These responses are largely determined by which species are exploited and ecological responses to the exploitation. The former has been well described for the Sanak Archipelago in Alaska (Maschner et al. 2009). Figure 5 shows subsistence exploitation of the intertidal food webs of the Archipelago. Such visualizations and related analyses demonstrate the unusual but not unprecedented role of humans in these food webs as extraordinary generalists highly connected to the ecological system. Future work should integrate the structural insights suggested by Fig. 5 with ecological and demographic mechanisms discussed above to better understand the dynamics of subsistence exploitation and distinguish them from those of economic exploitation.

Beyond increased sophistication of models and improved cyberinfrastructure for exploring them, computer science tools including constraint analysis and optimization could help greatly improve our understanding of these models (Gomes 2009). Such work could maximize multiple policy goals including employment in terms of extrac-

tion effort, carbon sequestration in terms of total ecosystem biomass and financial gain in terms of profit. The combination of increased computational power plus theoretical and analytical sophistication could contribute much to basic knowledge of integrated natural-social sciences and applied knowledge of coupled human-natural networks.

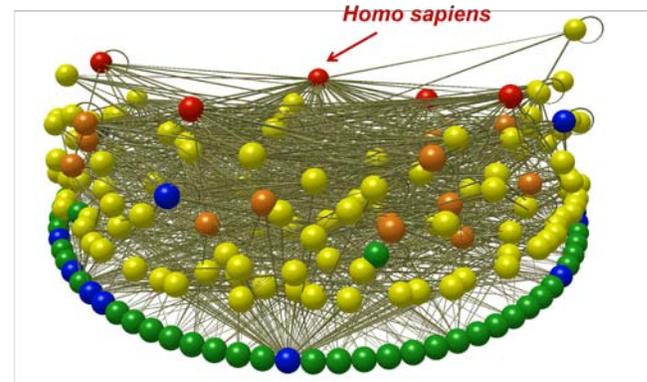


Figure 5. The intertidal food web of Sanak Island, Alaska. Spheres represent species or groups of species, and the links between them show feeding relationships. The colors of the spheres indicate types of taxa: green shows algae; blue shows seagrass, lichen, protozoa, bacteria, and detritus; yellow shows invertebrates such as snails, crabs, mussels, and octopus; orange shows fishes; and red shows mammals such as sea otters. The *Homo sapiens* node represents human hunter-gatherers (Aleut) who are among the most general consumers in the webs. Images produced using Network3D software (Yoon et al. 2004, Williams 2010).

An important application of such contributions concerns parameter estimation. While the results in this and a closely related paper (Boit et al. 2012) are based on the empirically specified parameters in Eq. (1) - (3), automatic determination of accurate parameter values is critical to the success of our simulations, especially for cases where optimal parameter values are difficult to be specified manually, are inaccurate or impossible to obtain from first principles and experiments, or are otherwise unavailable.

In general, parameter estimation can be an optimization problem where the optimal estimate minimizes the difference between the observed data and the model (Boit et al. 2012). Two formulations of the estimation problem are: *structure identification* and *parameter estimation*. The very structure of the model is unknown in the former while, in the latter, the functional form of the model is known and the challenge lies in obtaining the optimal values for the model parameter (e.g. Boit et al. 2012). Structure identification is seen as a highly complex problem. Solutions typically begin with canonical models which can provide local approximations. Examples include S-systems (Savageau 1969, 1969a), where the topology of the model and the magnitude of interactions are characterized by kinetic-order coefficients and Lotka-Volterra models (Lotka 1925). Unlike structure estimation, this paper focuses on

estimating parameters of models described by differential equations such as Eq. (1) – Eq. (3). Parameter estimation is also a crucial sub-problem in structure identification. The technical difficulty in parameter estimation for models such as those considered here emerge from three principal factors: the possible presence of a large number of parameters, noise in the data, and the need for numerical integration of the equations during iterative parameter update. The numerical integration can particularly and significantly impact the computational costs of the modeling process.

An effective approach for avoiding this numerical integration involves the use of slope substitution (Chou, Martens and Voit 2006, Vilela 2007). This approach recognizes that the derivatives on the left-hand side of Eq.(1) and Eq.(2) represent the respective slopes of the variable. If the slopes can be estimated, then the corresponding set of n coupled differential equations can be analyzed as a set of $n \times N$ uncoupled algebraic equations. Since real-world data contains noise which is amplified when computing slopes, techniques for data smoothing and robust slope estimation (Eilers 2003, Vilela 2007) improve the estimation process. Other numerical approaches to parameter estimation include the single shooting method (Saur 2006), the method of multiple shootings (Voss, Timmer, and Kurths 2006), and generalized smoothing (Ramsay et al. 2007).

In addition to numerical optimization-based methods, traditional AI methods such as expert systems, agent-based modeling, and concept-map modeling can also be utilized for structure identification and parameter estimation. Such methods can be especially powerful in encoding the intuitive and undocumented information and insights ecologists have about specific environments to obtain both the model structure and parameters. This advance could be effectively coupled to serious game playing (Khatib et al. 2011). Numerical-based optimization methods would do the heavy lifting of choosing the most likely parameter estimates while humans focus on model structure and behavioral choices involved in sustaining exploitation of ecological networks.

Conclusion

We have described a computational framework for analyzing the dynamics of complex human-natural networks where humans may extract biomass for economic gain. Initial analyses apply this framework to fisheries and suggest that application of the best known model of natural resource bioeconomics would lead to the destruction of the fishery which many fisheries have experienced (Worm et al. 2009). Our analyses also suggest a surprising amount of independence of the effects of exploiting one to three species within an ecosystem. However, much more sophisticated theory, computational capacity, and scientific

effort needs to determine the generality of these findings. Towards this and other ends, we describe advances in theory, cyberinfrastructure, and usability that are under development. These developments should lead to much broader scientific engagement with these critical problems and greater understanding and subsequence managing of the life support services provided by ecosystems.

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References

- Abrams, P.A. 2009. When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect. *Ecology Letters* 12: 462-474.
- Berlow, E.L., J.A. Dunne, R.J. Williams, N.D. Martinez, P. B. Stark, and U. Brose. 2009. Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences of the USA* 106: 187-191.
- Barnosky, A.D., J. Bascompte, E.L. Berlow, J.H. Brown, M. Fortelius, W.M. Getz, R. Gillespie, E. A. Hadly, J. Harte, A. Hastings, J. Kitzes, P.A. Marquet, C. Marshall, N.D. Martinez, N. Matzke, D. Mindell, A. Mooers, E. Revilla, P. Roopnarine, A.B. Smith, G. Vermeij, and J.W. Williams. 2012. A conceptual framework for forecasting biological impacts of global change. *Nature* Forthcoming.
- Boit, A., N.D. Martinez, R.J. Williams and U. Gaedke. 2012. Mechanistic theory and modeling of complex food-web dynamics in Lake Constance. *Ecology Letters* Forthcoming.
- Brose, U., E.L. Berlow, and N.D. Martinez. 2005. Scaling up keystone effects from simple modules to complex ecological networks. *Ecology Letters* 8: 1317-1325.
- Brose, U., R.J. Williams, and N.D. Martinez. 2006. Allometric scaling enhances stability in complex food webs. *Ecology Letters* 9: 1228-1236.
- Carpenter, S. R., Mooney, H. A., Agard, J., Capistrano, D., Defries, R. S., Díaz, S., Dietz, T., Duraiappah, A. K., Oteng-Yeboah, A., Pereira, H. M., Perrings, C., Reid, W. V., Sarukhan, J., Scholes, R. J., and Whyte, A. 2009. Science for managing ecosystem services: Beyond the millennium ecosystem assessment. *Proc. of the National Academy of Sciences* 106: 1305-1312.
- Chou, I.C., H. Martens, E.O. Voit. 2006. Parameter estimation in biochemical systems models with alternating regression. *Theoretical Biology and Medical Modelling* 3: 25
- Conrad, J.M. 2010. *Resource Economics*. Cambridge University.
- de Visser, S.N., B.P. Freymann, and H. Olf. 2010. The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *Journal of Animal Ecology* 80: 484-494.

- Dunne, J.A. 2006. The network structure of food webs. Pages 27-86 in Pascual and Dunne, eds. Oxford University.
- Dunne, J.A., R.J. Williams, N.D. Martinez, R. Wood, and D.E. Erwin. 2008. Compilation and network structure analyses of Cambrian food webs. *PLoS Biology* 6: 693-708.
- Eilers, P.H. 2003. A perfect smoother. *Anal. Chem.* 75:3631-36.
- Gomes, C. P., 2009. Computational Sustainability: Computational Methods for a Sustainable Environment, Economy, and Society. *The Bridge*, National Academy of Engineering, 39(4).
- Gross, T., L. Rudolf, S.A. Levin and U. Dieckmann. 2009. Generalized models reveal stabilizing factors in food webs. *Science* 325: 747-50.
- Fox, A. 2011. Computer science. Cloud computing--what's in it for me as a scientist? *Science* 331:406-7.
- Gardner, M.R. and W.R. Ashby. 1970. Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature* 228: 784.
- Hughes, J.B., G.D. Daily and P.R. Ehrlich. 1997. Population diversity: its extent and extinction. *Science* 278: 689-692.
- Khatib, F., et al. 2011. Crystal structure of a monomeric retroviral protease solved by protein folding game players. *Nature Structural and Molecular Biology* 18: 1175-1177.
- Larkin, P.A. 1977. An epitaph for the concept of maximum sustained yield. *Trans. of Amer. Fish. Soc.* 106: 1-11.
- Lee, C., and S. Tuljapurkar. 2008. Population and prehistory I: Food-dependent population growth in constant environments. *Theoretical Population Biology* 73: 473-482.
- Lotka, A.J. 1925. *Elements of Physical Biology*. Williams and Wilkins, Baltimore.
- Martinez, N.D. 1992. Constant connectance in community food webs. *The American Naturalist* 139: 1208-1218.
- Martinez, N.D., R.J. Williams, and J.A. Dunne. 2006. Diversity, complexity, and persistence in large model ecosystems. Pages 163-185 in Pascual and Dunne, eds. Oxford University Press.
- Maschner, H., M. Betts, J. Cornell and J. Dunne. (2009). An Introduction to the Biocomplexity of Sanak Island, Western Gulf of Alaska. *Pacific Science* 63: 673-709.
- McCann, K.S. 2012. *Food Webs*. Princeton U. Press, Princeton.
- May, R.M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.
- May, R.M. 2006. Network structure and the biology of populations. *Trends in Ecology and Evolution* 21: 394-399.
- Michener, W.K. & M.B. Jones. 2012. Ecoinformatics: supporting ecology as a data-intensive science. *Trends Ecol. & Evol.* 27:85-93
- Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-Being: Current State and Trends: Findings of the Condition and Trends Working Group*. Island Press.
- Otto, S., B. Rall and U. Brose. 2007. Allometric degree distributions facilitate food-web stability. *Nature* 450: 1226-1230.
- Pascual, M. and J.A. Dunne, eds. 2006. *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University.
- Puleston, C. and S. Tuljapurkar. 2008. Population and prehistory II: Food-dependent demography in variable environments. *Theoretical Population Biology* 74: 147-160
- Ramsay, J.O., G. Hooker, D. Campbell and J. Cao. 2007. Parameter estimation for differential equations: a generalized smoothing approach. *J. of Royal Statistical Society: Series B* 69: 741-796.
- Sahasrabudhe, S. and A.E. Motter. 2011. Rescuing ecosystems from extinction cascades through compensatory perturbations. *Nature Communications* 2: 170.
- Sauer, T. 2006. *Numerical Analysis*. Pearson Addison-Wesley
- Savageau, M.A. 1969. Biochemical systems analysis. I. Some mathematical properties of the rate law for the component enzymatic reactions. *Journal of Theoretical Biology* 25: 365-369.
- Savageau, M.A. 1969a Biochemical systems analysis. II. The steady-state solutions for an n-pool system using a power-law approximation. *Journal of Theoretical Biology* 25: 370-379.
- Vilela M, Borges CC, Vinga S, Vasconcelos AT, Santos H, Voit EO, Almeida JS, 2007 Automated smoother for the numerical decoupling of dynamics models. *BMC Bioinformatics*. 21(8): 305.
- Voss, H., J. Timmer, and J. Kurths. 2006. Nonlinear dynamical system identification from uncertain and indirect measurements. *International Journal of Bifurcation and Chaos* 14: 1905-1933.
- Watts, D. J., and S.H. Strogatz. (1998). Collective dynamics of "small-world" networks. *Nature* 393: 440-442.
- Williamson, M. 1996. *Biological Invasions*. Chapman and Hall.
- Williams, R. J. 2010. Network3D Software. Microsoft Research, Cambridge, UK.
- Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. *Nature*, 404: 180-183.
- Williams, R.J., and N.D. Martinez. 2004. Stabilization of chaotic and non-permanent food-web dynamics. *European Physical Journal, B* 38: 297-303.
- Williams, R.J., and N.D. Martinez. 2004a. Limits to trophic levels and omnivory in complex food webs: Theory and data. *The American Naturalist*, 16: 458-468.
- Williams, R.J., and N.D. Martinez. 2008. Success and its limits among structural models of complex food webs. *Journal of Animal Ecology*, 77: 512-519.
- Worm, B., R. Hilborn, J. K. Baum, T. A. Branch, J. S. Collie, C. Costello, M. J. Fogarty, E. A. Fulton, J. A. Hutchings, S. Jennings, O. P. Jensen, H. K. Lotze, P. M. Mace, T. R. McClanahan, C. Minto, S. R. Palumbi, A. M. Parma, D. Ricard, A. A. Rosenberg, R. Watson, and D. Zeller. 2009. Rebuilding Global Fisheries. *Science* 325: 578-585.
- Yoon, I., R.J. Williams, E. Levine, S. Yoon, J.A. Dunne, and N.D. Martinez. 2004. Webs on the Web (WoW): 3D visualization of ecological networks on the WWW for collaborative research and education. *Proc. of the IS&T/SPIE Symposium on Electronic Imaging, Visualization and Data Analysis* 5295: 124-132.