Selective enhancement of an exploited species undermines community stability

**Authors:** Akira Terui1,\*, Hirokazu Urabe2, Masayuki Senzaki3, Bungo Nishizawa4

\*Corresponding author: hanabi0111@gmail.com

**Affiliations:** 1 Department of Biology, University of North Carolina at Greensboro, Greensboro, NC 27412, USA 2 Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA 3 National Institute for Environmental Studies, Tsukuba, Ibaraki 305-8506, Japan 4 Shiraume Gakuen College, Kodaira, Tokyo 187-8570, Japan

## Maintext

Anthropogenic influences have caused global biodiversity crisis, such that human interventions are critical to sustainable management of natural resources. Captive breeding - DEFINE CAPTIVE BREEDING - is a common method to conserve or enhance wild populations of diverse plant and animal taxa. Although there is growing recognition that the selective enhancement with captive-bred organisms entails ecological risks (e.g., the accumulation of deleterious alleles), this method is still pervasive in conservation and fisheries. In fisheries for example, XXX have been spent annually to support hatchery programs globally. This is perhaps because of the “myth” that numerical benefits of released individuals may exceed the associated risks. The current debate, however, overlooks the fact that we have rarely assessed the community-wide impact of selective enhancement. Species are all embedded in the complex web of interacting organisms, and excessive release of particular species may have unforeseen consequences for ecological communities in the long term. Evidence for this hypothesis is lacking, however.

Here, we use a simple, general theory to show that the selective enhancement of a particular species undermines long-term community stability, which we define here as the relative size of fluctuations in total community density over time. The present study further demonstrates the relevance of this general theory to natural systems by illustrating its congruence with stream fish communities, in which an exploited species, masu salmon (*Oncorhynchus masou masou*), is supplemented by hatchery programs. Our findings paint a bleak picture for this form of ecosystem management, reinforcing the recurrent calls for alternative strategies.

We use a multispecies Ricker model to simulate community dynamics with selective enhancement of a constituent species. Specifically, population density of species at time , , is modeled as:

where is the intrinsic growth rate, the competition coefficient of species on species (intraspecific competition if ; ), the carrying capacity, the number of released individuals for the enhancement of species (species 1; set constant as for simplicity), and the species responses to stochastic environmental fluctuations. The parameter takes a value of one when (otherwise zero) to represent the reproductive contribution of released individuals to the next generation of the enhanced species. XX parameter combinations were used to represent ecological scenarios with different strength of competition and XX. Under each simulation scenario, we ran 1400 time steps of 1000 independent communities (i.e., simulation replicates) with varying , of which the last 1000 time steps were used to obtain the coefficient of variation, mean, and standard deviation of community density (). Temporal means and standard deviations were calculated for the enhanced species and the unenhanced species separately to infer mechanisms that underlie community-level responses.

Our model predicted a destabilizing effect of selective enhancement on ecological communities. With increasing released individuals , communities showed greater temporal fluctuations as illustrated by increased CV (Figure XX). Since CV is a ratio of SD to mean, the increase of CV can be driven by a decreased mean, an increased SD, or both. In our case, the group-level analysis depicted a major influence of the decreased means of enhanced and unenhanced species groups (Figure XX). For enhanced species, intraspecific competition is responsible for the decreased mean. That is, released individuals induce strong overcompensation, where the negative effect of reduced per-capita reproduction exceeds the numerical benefit of released individuals (increased reproducing individuals). Meanwhile, the decreased mean of unenhanced species is caused by interspecific competition between enhanced and unenhanced species. This negative effect of released individuals through competition was noticeable even with weak interspecific competition that would otherwise allow stable coexistence. Combined, the total community density decreased more sharply than individual species groups with increased numbers of released individuals (XX). The SDs showed a similar trend, but the relationship was flatter than the means. CONCLUDING SENTENCE

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EMPIRICAL ANALYSIS

### Methods

### Theory

We developed a multispecies Ricker model to simulate community dynamics with selective enhancement of a particular species. Population density of species at time , , is modeled as:

where is the intrinsic growth rate, the competition coefficient between species and (intraspecific competition if ; ), the carrying capacity, the number of released individuals for the enhancement of species 1, and the species responses to stochastic environmental fluctuations. The parameter takes a value of one when (otherwise zero) to represent the reproductive contribution of released individuals to the next generation of the enhanced species. The species-specific intrinsic growth rates and competition coefficients were drawn randomly from a uniform and exponential distribution, respectively, to allow for interspecific variation as and . The number of released individuals was assumed to be constant across time steps (). Environmental stochasticity was drawn from a normal distribution as

We varied values of four parameters: 10, 20; 1, 2; 0.1, 0.3, 0.5; 0.1, 0.5. For simplicity, we assumed identical carrying capacities among simulated species as 100. This setup resulted in 24 sets of parameter combinations that cover a range of ecological scenarios.

Under each parameter combination, we ran 1400 time steps of 1000 independent communities (i.e., simulation replicates) with the gradient of the number of released individuals (0 - 500). We initialized the community with populations of each species drawn from a poisson distribution with a mean of five. We repeated the seeding procedure every 10 time steps over the first 200 time steps to allow species to establish populations and reach an equilibrium without (initialization period). After the initialization period, we released individuals of the enhanced species every time step over the next 200 time steps to reach a new equilibrium with selective enhancement (burn-in period). We saved the last 1000 time steps to obtain the relative temporal fluctuations (i.e., the coefficient of variation) of the whole community (), the enhanced species (), and the unenhanced species (). We also calculated temporal means and standard deviations for each species group. Values of simulation parameters were summarized in XXX. We performed simulations using R version XXX.

### Empirical analysis

#### Data

**Time-series data.** We assembled time-series data of fish abundance across XX sites within XX protected watersheds of Hokkaido Island, Japan. In these watersheds, aquatic species are protected and no harvest is allowed. At these sites, the long-term monitoring program began in 1971 but effective sampling methods (a combination of electrofishing and cast net sampling) were implemented in 1999. Data were collected in summer to fall with irregular sampling intervals (0 to 3 year intervals for most cases). After careful data selection (Supporting Information), we used time-series data of fish abundance at XX sites during a period of 1999-2019. ADD SOME DETAILS

**Fish stocking.** At the protected watersheds, masu salmon were stocked to enhance the wild populations since XXX. A mixture of captive-bred and wild-born individuals were released in spring (fry [age 0+] and smolt [age 1+] stages) and fall (juvenile stage [age 0+]). We examined historical records of fish stocking and obtained annual stocking data (the number of individuals released) for a period of 1999-2019 at each watershed. We were unable to extract stocking data at the site level.

**Environmental data.** At each sampling site,we collected the following data as potential covariates: upstream watershed area (km2; a proxy for stream size), proportional land use in the upstream watershed (forest, agriculture, urban), local species richness, local climates (annual mean air temperature [unit] and cumulative precipitation [mm]), and ocean productivity (Chlorophyll a [unit]).

#### Statistical analysis

Our goal is to compare temporal dynamics of fish communities across sites. However, the data are not directly comparable because of artificial observation errors (e.g., different observers) and missing observations. To confront this challenge, we developed Bayesian state space models for three species groups separately: (1) whole community, summed abundance of all species, (2) enhanced species, abundance of masu salmon, (3) unenhanced species, summed abundance of all species except masu salmon. Bayesian state space models is best suited for our analysis because it can account for observation errors while imputing missing values given the long-term trend at the site. The model is composed of observation and state models as described below.

In the observation model, we model observation processes. Summed fish abundance of either whole community, enhanced species (masu salmon only), and unenhanced species at site in year , , was assumed to follow a Poisson distribution:

where is the expected fish density (individual m-2) and the sampling area (m2). Since fish sampling was conducted after the spring stocking of masu salmon, captured fish may include individuals released in the observation year. To avoid biases in estimating temporal community trends, we explicitly modeled this observation process:

is the “true” fish density excluding fish released in the spring, the number of salmon fry released in spring in watershed within which site is located, and the site-specific effect of released salmon fry on the observed fish density. The parameter is a random error variable drawn from a log-normal distribution as . The inclusion of this random variable allows us to account for site-specific and year-specific observation errors. The parameter equals one when we model the unenhanced species group (otherwise ). We included to exclude the term because the unenhanced species group does not include masu salmon.

In the state model, we model temporal dynamics of fish density as follows:

where is the average rate of change at site and is the process error that is assumed to follow a normal distribution as . The site-specific rate of change is random draws from a normal distribution as , assuming that community dynamics across Hokkaido have a shared temporal trend to some degree (the degree of shared trend is controlled by the standard deviation ). This hierarchical structure allows for improved estimates of by sharing information across sites. We used median estimates of fish density to calculate temporal CV, mean (), and SD ().

We developed the following linear regression models taking either log-transformed CV, mean, or SD as a response variable with a normal error distribution.

where is the watershed-specific intercept ( refers to site nested within watershed ) and is the regression coefficient of site-level predictor . The site-level predictors include upstream watershed area, air temperature, precipitation, forest land use, and local species richness (we excluded local species richness from the masu salmon model). The watershed-specific intercept was related to watershed-level predictors as:

The watershed-level predictors include the number of released masu salmon and ocean productivity (sea surface chlorophyll a).

We fitted the models to the data using JAGS version 4.1.0 through *runjags* package in R. Priors were summarized in XXX. Data manipulation and analysis were performed in R version 4.1.0.

## Data availability

## Acknowledgments

## References