

# Young Scientists Summer Program 2017

## Four Research Projects

**Evolution and Ecology Program  
International Institute for Applied Systems Analysis  
Laxenburg, Austria**



# Fisheries-induced life-history evolution in anadromous stocks

Perla Catalina Chaparro Pedraza

*Institute for Biodiversity and Ecosystem Dynamics,  
University of Amsterdam, The Netherlands*

## Goal

To understand how life-history traits of migratory species evolve under different mortality regimes, in particular to predict their fisheries-induced evolution.

## Background and motivation

Atlantic salmon and other salmonid species have a typical anadromous life cycle. Anadromous individuals are migratory, beginning their life cycle in freshwater (breeding habitat) and later moving to the ocean (non-breeding habitat), where they grow larger and eventually become mature. Mature individuals migrate back to the freshwater habitat in order to reproduce, before returning to the ocean.

Multiple anthropogenic disruptions – including overfishing, habitat degradation, and fragmentation, as well as global shifts in climate – affect the life cycle of anadromous species (Chapman *et al.*, 2011) and threaten their persistence. In particular, shifts in mortality regimes have likely impacted the evolution of the timing of the habitat switch between freshwater and the ocean and the timing of reproduction. After their transition to the ocean, salmonids experience increased food availability that elevates the energy they can allocate to energy reserves (Jonsson *et al.*, 1998). An early habitat switch thus enables high-energy reserves since early in life and consequently raises fecundity. However, small-sized salmon face elevated mortality from predation in the ocean (Friedland *et al.*, 2009). Conversely, a late habitat switch increases body size and consequently reduces predation risk after arrival in the ocean. Since both survival and fecundity are essential components of fitness, the timing of the habitat switch is subject to natural selection. Therefore, alterations in the fecundity-survival tradeoff may affect selection on this life-history trait and shift the evolutionary outcome.

Given the economic and cultural importance of salmonid species, policy measures have been taken to accomplish their conservation and sustainable exploitation. For instance, salmon fisheries at open sea were largely prohibited in the 1990s, with catches henceforth allowed only during the spawning migration near or in spawning rivers. Before the implementation of this policy, fishing was possible on both mature and immature individuals; conversely, after its implementation, only mature individuals returning to spawn are caught (Hard *et al.*, 2008). Therefore, it is of interest to understand the effects of different mortality regimes on the fecundity-survival tradeoff, and thereby, on fisheries-induced life-history evolution of the habitat switch and maturation.

Although several theoretical studies have addressed similar questions on the evolution of life-history traits related to migration, most of them have focused on birds (Chapman *et al.*, 2011). Fishes, in contrast to many wild birds, clearly exhibit food-dependent growth (Elliott and Hurley, 1997). Therefore, in the studies on birds the growth rate is not explicitly modeled as food-dependent, making most of the conclusions arising from this line of theory not applicable to fishes. The investigation of fisheries-induced life-history evolution requires a theoretical

framework in which the developmental rate is explicitly modeled as food-dependent and density dependence is accounted for as a consequence of the interaction of individuals with their environment.

I will use an adaptive dynamics approach in conjunction with physiologically structured population models to study the evolution of the timing of the habitat switch. By using adaptive dynamics theory, the evolutionary outcome will be a result of the underlying population dynamics, which arises from ecological factors such as mortality, cost of migration, and food availability, as well as from the interaction of individuals with their environment. In addition, by modeling the anadromous population as a physiologically structured population, the developmental rate can be explicitly modeled as food-dependent. I will compare the model predictions to data of Atlantic salmon populations that have undergone long-term monitoring of their life-history traits, especially those that include data before and after the prohibition of salmon fisheries at sea.

## Research questions

Using a physiologically structured population model in which the timing of the habitat switch and the timing of maturation can evolve, I will examine how these traits evolutionarily respond to fishing, addressing the following questions:

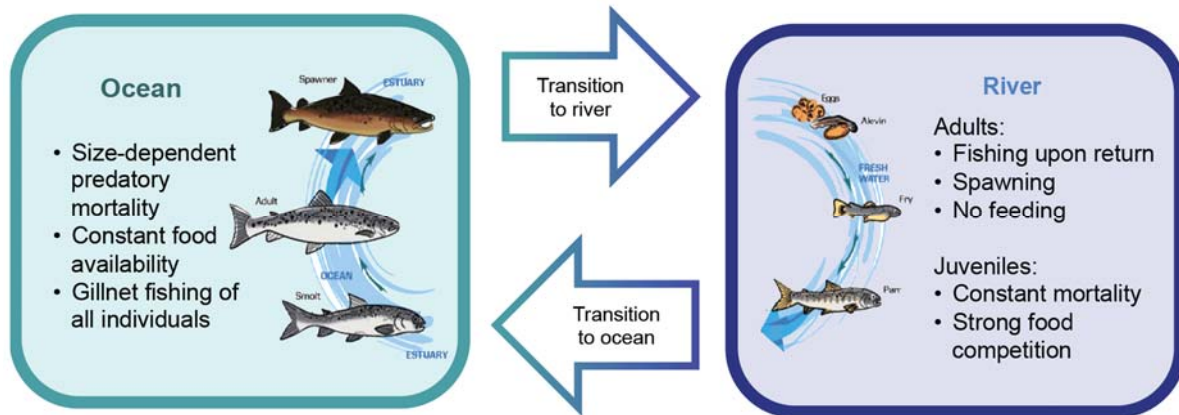
- What is the evolved timing of the habitat switch and of maturation for individuals facing different predation risks?
- How does fishing mortality shift the evolutionary outcome?
- How do changes in fishing policy shift the evolutionary outcome?
- How do predictions from the model compare to field data?

## Methods and work plan

### *Model overview*

I will devise a model of an anadromous population migrating between two habitats (breeding and non-breeding habitat). The food availability in the breeding habitat increases through growth and declines due to foraging by individuals, simulating the strong density dependence in this habitat (Jonsson *et al.*, 1998), while the food in the non-breeding habitat is constant, reflecting that density dependence is negligible (Jonsson *et al.*, 1998). The anadromous population is physiologically structured and follows a semi-discrete dynamics: continuous dynamics describe the resource consumption, somatic growth, stored energy reserves, and survival, and a discrete map describes the annually pulsed reproduction. We will use the bioenergetics approach described by Martin *et al.* (2017) to model individual consumption, somatic growth, stored energy reserves, and reproduction. Survival in the breeding habitat is constant, while in the non-breeding habitat it is assumed to be size-dependent (Pinder *et al.*, 1978), whereby large individuals experience low predation risk. In addition to predation mortality, individuals experience starvation, fishing, and background mortality. During the breeding season, individuals use their energy reserves to migrate upstream the river and spawn. All individuals that are born in the same breeding season are lumped into a single cohort and are assumed to grow at the same rate. After hatching, individuals stay in the breeding habitat until they reach a size threshold at which they switch to the non-breeding habitat (smolting). Similarly, maturation occurs at

a threshold size, when individuals start to accumulate energy that they will invest in reproduction in the next reproductive season. The two size thresholds for smolting and maturation are the evolving traits in the model.



Modified from: <http://salmonfactswork.weebly.com/salmon-life-cycle.html>

I will use adaptive dynamics theory (Geritz *et al.*, 1998) to study how the evolution of the thresholds for smolting and maturation are affected by predation risk, and how they will adapt under different fishing regimes.

Given that it is not possible to find analytic expressions for the equilibrium densities, I will numerically evaluate the model using Matlab and C-based programs.

### **Data**

To compare model predictions with empirical observations, I will use data collected on populations of Atlantic salmon of different fisheries in Scotland that include long-term information on the age and size at smolting and at first spawning, with the latter serving as a proxy of maturation.

### **Work plan**

There are four steps in this research project that will be carried out sequentially:

- Formulate and parameterize the model.
- Understand the effects of predation risk and different fishing regimes on the evolution of the timing of smolting and maturation.
- Compare model predictions with data on Atlantic salmon populations.
- Write the report and draft a corresponding publication.

### **Relevance and link to EEP's research plan**

The results of this project will contribute to improving our knowledge of the ecology and evolution of migratory fishes. Given mounting examples of population declines of anadromous salmonids (i.e., Atlantic salmon), this knowledge is key for their sustainable exploitation and conservation. Furthermore, because of the cultural and economic importance of these species, it is crucial to understand and predict the eco-evolutionary consequences of exploiting anadromous stocks. This project is in line with EEP's ongoing research on "Evolutionarily Sustainable Consumption".

## Expected output

The results of this work are intended for a coauthored publication in an international scientific journal and will also be a chapter of my PhD dissertation.

## References

- Chapman BB, Brönmark C, Nilsson JÅ & Hansson LA (2011). The ecology and evolution of partial migration. *Oikos* 120: 1764–1775.
- de Roos AM, Boukal DS & Persson L (2006). Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proceedings of the Royal Society B* 273: 1873–1880.
- Elliott JM & Hurley MA (1997). A functional model for maximum growth of Atlantic salmon parr (*Salmo salar*) from two populations in northwest England. *Functional Ecology* 11: 592–603.
- Friedland KD, MacLean JC, Hansen LP, Peyronnet AJ, Karlsson L, Reddin DG & McCarthy JL (2009). The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science* 66: 289–304.
- Geritz SAH, Kisdi E, Meszéna G, & Metz JAJ (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12: 35–57.
- Hard JJ, Gross MR, Heino M, Hilborn R, Kope RG, Law R & Reynolds JD (2008). Evolutionary consequences of fishing and their implications for salmon. *Evolutionary Applications* 1: 388–408.
- Jonsson N, Jonsson B, & Hansen LP (1998). The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon (*Salmo salar*). *Journal of Animal Ecology* 67: 751–762.
- Martin B, Heintz R, Danner E & Nisbet R (2017). Integrating lipid storage into general representations of fish energetics. *Journal of Animal Ecology* 86: 812–825.
- Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B & Dieckmann U (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428: 932–935.
- Pinder J, Wiener J & Smith M (1978). The Weibull distribution : a new method of summarizing survivorship. *Ecology* 59: 175–179.

# Emergence of efficient extraction in social-ecological models for fisheries

Daniel Cooney

*Program in Applied and Computational Mathematics,  
Princeton University, USA*

## Goal

To explore social-ecological models of fisheries as a case study for mitigating the “tragedy of the commons” in the management of common-pool resources, with the goal of understanding potential mechanisms for social institutions to facilitate the emergence of socially efficient resource use.

## Background and motivation

We are interested in studying the tragedy of the commons for common-pool resources, a social dilemma in which a group of rationally acting individuals overexploit a renewable resource and consequently are worse off than a group that extracts at a more sustainable level (Hardin, 1968; 2009). One prominent example of such a social dilemma is the case of fisheries, in which the motive of fishers to maximize catch profits can place a strain on the regeneration of fish stocks. The Food and Agriculture Department of the United Nations reported that in 2013, around 30 percent of the world’s fisheries were classified as overexploited or depleted, a dramatic increase from 1974 when less than 10 percent were (FAO 2016). With another 58 percent of fisheries considered fully exploited (FAO 2016), population growth and potential increases in demand could push a majority of global fisheries into an unsustainable exploitation regime.

Standard models for the dynamics of fisheries describe the natural growth of fish populations and the ecological feedback of extraction efforts on the regeneration of fish stocks (Gordon, 1954). A key feature of such models is the existence of an optimal level of fish extraction that maximizes the long-term availability of fish resources, whereas each fisher has an individual incentive to exceed this level of effort, resulting in unsustainable levels of fish extraction. Economists have studied this problem as a game-theoretic social dilemma, labeling the optimal level of extraction as “cooperation” and a higher level of extraction as “defection” (Sethi and Somanathan, 1996). Recent studies have derived conditions for when a social norm of cooperation can be sustained, given a large enough initial fraction of cooperators, by sanctioning defectors through costly punishment (Sethi and Somanathan, 1996) or by costless social ostracism (Tavoni *et al.*, 2012; Schlüter *et al.*, 2016). Furthermore, when social optimality cannot be sustained, there often exist second-best levels of extraction, which can be enforced as a norm via sanctioning of individuals with higher extraction levels (Tilman *et al.*, 2016).

Beyond studying the stability of efficient extraction, once established as a social norm, it is important to explore how efficiency can emerge from an inefficient state. While sanctioning has proven effective in the case of few defectors and many cooperators, a two-phase approach of initially rewarding cooperators and subsequently punishing defectors has been shown to outperform pure rewards or penalties for facilitating the establishment and resilience of cooperation in public-goods games (Chen *et al.*, 2014). Although much has been studied on the governance of common-pool resources by well-established social institutions (Ostrom, 2011), this strategy of “first carrot, then stick” has shown promise as a means for institutional emergence

by promoting cooperation and preventing second-order free-riding (Sasaki *et al.*, 2015; Cong *et al.*, 2016).

In particular, the creation of reward pools and pool punishment (Sasaki *et al.*, 2015) can be interpreted as the emergence of a centralized institution with multilateral incentive enforcement. Centralization of sanctioning authority has been shown experimentally in humans to promote cooperation and fairness (Baldassarri and Grossman, 2011), but has yet to receive the theoretical attention given to more traditional peer-to-peer sanctioning methods for overcoming social dilemmas (Sigmund, 2007), although the emergence of cooperative institutions has been studied in models of public-goods games (Hauert *et al.*, 2006; Sigmund *et al.*, 2010). A club structure has been proposed as a means for creating and enforcing climate-change agreements (Nordhaus, 2015), and it has been shown that collections of small clubs can confer enough social benefit to maintain enforcement of the agreements in the presence of first- and second-order free-riding (Hannam *et al.*, 2015).

In addition, the proper context for studying the emergence of efficient extraction should acknowledge that fish harvesting strategies are a continuous-valued behavioral trait. A key question is whether a population initially composed of inefficient extractors can evolve (or co-evolve with an emergent social institution) to yield a population consisting exclusively or primarily of efficient extractors. Analytical frameworks such as adaptive dynamics (Dieckmann and Law, 1996; Geritz *et al.*, 1997) or gradient dynamics (Friedman and Ostrov, 2013) can be used to study the evolution of extraction levels, and coevolution with a social norm requiring progressively more efficient extraction could be a mechanism for bootstrapping cooperation (Nakamaru and Dieckmann, 2009).

## Research questions

I aim to address the following research questions:

- Can the “first carrot, then stick” approach, combining rewarding early cooperators with punishing remaining defectors, be used to facilitate the emergence of efficient extraction in a fisheries model with two levels of extraction?
- Moreover, does such a policy increase the basin of attraction and decrease convergence times to or costs for reaching full or partial cooperation relative to policies that solely reward cooperators or punish defectors?
- What happens with such a policy when we allow for a continuum of extraction and sanctioning strategies? Can efficient extraction emerge from a previously overexploited state via bootstrapping and the evolution of social norms?
- Time permitting, I will also examine how we can best incorporate the possibilities of emergent social norms and social institutions into fisheries models, and how can we use available tools from dynamical systems and adaptive dynamics to study the tradeoffs between bilateral and multilateral mechanisms for rewards and sanctions?

## Methods and work plan

### *Resource model*

In our core model for the social-ecological dynamics of fisheries, we consider a population of  $N$  fishers that each invests the effort  $e_i$  into extracting fish. Following the Gordon-Schaefer model (Gordon, 1958; Tilman *et al.*, 2016), the size  $n$  of the fish population is governed by the

differential equation  $dn/dt = rn(1 - n/k) - qEn$ , where  $E = \sum_{i=1}^N e_i$  is the total effort exerted by the group,  $k$  is the carrying capacity of the fish population,  $r$  is the intrinsic growth rate of the fish population, and  $q$  measures the probability that a unit of fishing effort results in catching a fish.

### ***Fishery economics***

We model fisher payoff by assuming that fishers pay a cost  $w_i = w(e_i)$  per unit effort and receive a constant price  $p$  per caught fish, yielding the payoff function  $\pi_i = pqne_i - w_i e_i$  (Tilman et al. 2016). If fish dynamics are fast on the timescale of fisher decision-making, then effectively  $n = k(1 - qE/r)$ , and the fisher payoff  $\pi_i = pqk(1 - qE/r)e_i - w_i e_i$  is reminiscent of a static common-pool resource game.

### ***Institutional incentives***

Fisher utility  $U_i$  is then obtained by combining the fisher payoff with potential institutional incentives and costs of rewarding cooperation or punishing defection,  $U_i = \pi_i + I(e_i, e_{-i}, \pi_i, \pi_{-i}) - C(e_i, e_{-i}, \pi_i, \pi_{-i})$ , where  $I(\cdot)$  is the incentive meted out by the social institution,  $C(\cdot)$  is the cost associated with supporting the institution, and  $e_{-i}$  and  $\pi_{-i}$  denote, respectively, the effort levels and payoffs of all group members other than individual  $i$ .

### ***Two extraction levels***

When we consider only two possible extraction levels, we can label the more sustainable level “cooperation” (with fisher payoff  $\pi_C$  and utility  $U_C$ ) and the more exploitative level “defection” (with fisher payoff  $\pi_D$  and utility  $U_D$ ). Assuming that individuals update their strategies by imitating successful fishers, we can describe the changing fraction of cooperative fishers,  $x$ , using the replicator dynamics,  $dx/dt = x(1 - x)(U_C - U_D)$ , which, coupled with the dynamics for the fish population size  $n$  thus describes the evolution of this social-ecological system (Tavoni et al., 2012; Tilman et al., 2016). In this two-strategy context, with clearly defined cooperators and defectors, we can write the incentive function  $I(\cdot)$  in a more suggestive form as  $I_C(x) = \alpha(x)R(x)$  and  $I_D(x) = [1 - \alpha(x)]P(x)$ , where  $R(\cdot)$  and  $P(\cdot)$  are the institution’s rewards for cooperation and penalties for defection, and  $\alpha(x)$  is the proportion of institutional resources allocated to rewarding. One form of  $\alpha(x)$  of interest is the Heaviside function  $H(x^* - x)$ , corresponding to a “first carrot, then stick” policy exclusively rewarding cooperation if  $x < x^*$  and exclusively punishing defection for  $x > x^*$ . If the institution has a fixed budget  $B$  that it invests either into rewards with cost efficiency  $a$  or into penalties with cost efficiency  $b$ , this implies  $R(x) = B/(f + axN)$  and  $P(x) = B/[f + b(1 - x)N]$ , where  $f$  is the fixed cost of the social institution.

### ***Adaptive dynamics of continuous extraction levels***

We can extend this two-strategy model to describe the evolution of extraction levels amongst a set of continuous extraction strategies. First, we will study the evolution of extraction levels given fast fish dynamics and a fixed institutional incentive policy. In a resident population with  $N - 1$  fishers extracting at level  $e$ , a single fisher extracting at level  $e'$  receives the utility  $U(e', e) = \pi(e', e) + I(e', e) + C(e', e)$  with  $\pi(e', e) = \{kpq - w(e') - kpq^2r^{-1}[e' + (N - 1)e]\}e'$ . In the limit of rare strategy exploration, we can derive the canonical equation of adaptive dynamics for this model and study the resultant evolutionarily singular extraction levels to determine the impact of the social institution on the eventual level of fish extraction.



### ***Institutional incentives for continuous extraction levels***

To explore generalizations of the “first carrot, then stick” institutional incentive policy to continuous extraction levels, we plan to consider populations with a polymorphic distribution of extraction levels, and ask how a social planner can best utilize a fixed budget to promote efficient extraction through the mechanism of rewarding and punishing fishers based on their level of resource extraction. Specifically, we plan to examine an incentive policy with a switching threshold  $e^*$  such that the institution rewards the least-extracting fishers only when the population’s average extraction level  $\bar{e}$  exceeds the switching threshold  $e^*$  and punishes the most-extracting fishers only when  $\bar{e}$  is below  $e^*$ . Furthermore, we will assume that the fraction of rewarded individuals decreases with  $\bar{e}$ , while the fraction of punished individuals increases with  $\bar{e}$ . To start our explorations, we will choose the decrease and increase to be linear in  $\bar{e}$  and assume that the fraction of fishers rewarded when  $\bar{e}$  is just above  $e^*$  and the fraction of fishers punished when  $\bar{e}$  is just below  $e^*$  add up to 1. These specifications are meant to generalize key properties of the “first carrot, then stick” institutional incentive policy, which is based on recognizing that a social institution is best off allocating the bulk of its budget to rewarding when cooperation is rare and instead allocating it to punishing when defection is rare, so that individuals receiving institutional rewards or penalties are maximally affected by these incentives when cooperation needs to be started and defection needs to be ended, respectively. We plan to describe the dynamics of the polymorphic strategy distribution characterizing the fisher population under this incentive policy using the continuous-strategy extensions of the replicator dynamics (Bomze, 1990) or pairwise comparison dynamics (Cheung, 2014).

We also plan to explore more general continuous-strategy institutional incentive policies. Building on the fact that the “first carrot, then stick” incentive policy can be proved to be the optimal in the two-strategy case described above, we will strive to define a generalized sense of optimality for continuous-strategy incentive policies. On this basis, we will analyze the optimal control problem in the function space of all potential incentive policies sharing two general features: exclusivity, meaning that the institution uses either rewards or penalties, but no mixed incentives, and uniformity, meaning that the institution applies the same incentive levels uniformly across all rewarded or punished individuals. Before attempting to address this challenge in its full generality, we will explore variants of the aforementioned direct extension of the “first carrot, then stick” incentive policy, by considering linear functions that differ from those described above, by considering nonlinear functions for mapping the average extraction level to the fractions of rewarded and punished individuals, and by considering linear or nonlinear functionals of the strategy distribution for specifying those fractions. Using techniques such as optimal control for populations with heterogeneous agents (Nuno and Moll, 2017) or adaptive dynamics for function-valued traits (Parvinen *et al.*, 2006), we will thus seek to identify institutional incentive policies that are best suited for bringing about the emergence of efficient extraction in these social-ecological models of fisheries.

### **Work plan**

I plan to work on this project in the following steps:

- Analyze the two-strategy fisheries model under the “first carrot, then stick” incentive policy, by constructing bifurcation diagrams and comparing results to models with pure rewarding or punishing.

- Extend the two-strategy results to the adaptive dynamics of continuous extraction strategies.
- Develop institutional incentive policies for continuous strategies with rewards and penalties based on generalization of “first carrot, then stick”.
- Study the effectiveness of these institutional incentives in steering fisher populations towards efficient average levels of extraction.
- Time permitting, examine the evolution of institutional incentive policies in the context of optimal control theory or adaptive dynamics theory for function-valued traits.

## Relevance and link to EEP’s research plan

This proposed research is related to several of EEP’s core research themes, including the integrative understanding of the social-ecological dynamics of fisheries, the sustainable consumption of natural resources, and the management of public goods. In addition, the mathematical techniques from adaptive dynamics theory and evolutionary game theory are generally relevant and applicable for many of EEP’s research projects, and the methods and ideas used to study models of fisheries in this project can be further applied to many other societal problems involving common-pool resources, such as climate change or pollution of air or water, which are of general relevance to many of the major research goals addressed by EEP and by IIASA as a whole.

## Expected output and publications

The expected output from this project will be a manuscript that will be incorporated into my PhD thesis and submitted as a coauthored article for peer review to an international scientific journal.

## References

- Baldassarri D & Grossman G (2011). Centralized sanctioning and legitimate authority promote cooperation in humans. *Proceedings of the National Academy of Sciences of the USA* 108: 11023–11027.
- Bomze IM (1990). Dynamical aspects of evolutionary stability. *Monatshefte für Mathematik* 110: 189–206.
- Chen X, Sasaki T, Brännström Å & Dieckmann U (2015). First carrot, then stick: How the adaptive hybridization of incentives promotes cooperation. *Journal of the Royal Society Interface* 12: 20140935.
- Cheung MW (2014). Pairwise comparison dynamics for games with continuous strategy space. *Journal of Economic Theory* 153: 344–375.
- Cong R, Li K, Wang L & Zhao Q (2016). Cooperation induced by wise incentive allocation in spontaneous institution. *Europhysics Letters* 115: 38002.
- Dieckmann U & Law R (1996). The dynamical theory of coevolution: A derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34: 579–612.
- Food and Agriculture Organization of the United Nations (2016). *State of World Fisheries and Aquaculture (SOFIA) 2016*. FAO Fisheries Department.

- Friedman D & Ostrov DN (2013). Evolutionary dynamics over continuous action spaces for population games that arise from symmetric two-player games. *Journal of Economic Theory* 148: 743–777.
- Geritz SA, Kisdi E, Meszéna G & Metz JAJ (1997). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12: 35–57.
- Gordon HS (1954). The economic theory of a common-property resource: The fishery. *Journal of Political Economy* 62: 124–142.
- Hannam PM, Vasconcelos VV, Levin SA & Pacheco JM (2015). Incomplete cooperation and co-benefits: Deepening climate cooperation with a proliferation of small agreements. *Climatic Change*: 1–15.
- Hardin G (1968). The tragedy of the commons. *Science* 162 1243–1248.
- Hardin G (2009). The tragedy of the commons. *Journal of Natural Resources Policy Research* 1: 243–253.
- Hauert C, Traulsen A, Brandt H, Nowak MA & Sigmund K (2007). Via freedom to coercion: The emergence of costly punishment. *Science* 316: 1905–1907.
- Nakamaru M & Dieckmann U (2009). Runaway selection for cooperation and strict-and-severe punishment. *Journal of Theoretical Biology* 257: 1–8.
- Nordhaus W (2015). Climate clubs: Overcoming free-riding in international climate policy. *American Economic Review* 105: 1339–1370.
- Ostrom E (2011). *Governing the Commons: The Evolution of Institutions for Collective Action*. Cambridge University Press, USA.
- Sasaki T, Okada I, Uchida S & Chen X (2015). Commitment to cooperation and peer punishment: Its evolution. *Games* 6: 574–587.
- Schlüter M, Tavoni A & Levin S (2016). Robustness of norm-driven cooperation in the commons. *Proceedings of the Royal Society B* 283: 1–9.
- Sethi R & Somanathan E (1996). The evolution of social norms in common property resource use. *American Economic Review* 86: 766–788.
- Sigmund K (2007). Punish or perish: Retaliation and collaboration among humans. *Trends in Ecology and Evolution* 22: 593–600.
- Sigmund K, De Silva H, Traulsen A & Hauert C (2010). Social learning promotes institutions for governing the commons. *Nature* 466: 861–863.
- Tavoni A, Schlüter M & Levin S (2012). The survival of the conformist: Social pressure and renewable resource management. *Journal of Theoretical Biology* 299: 152–161.
- Tilman AR, Watson JR & Levin S (2017). Maintaining cooperation in social-ecological systems: Effective bottom-up management often requires sub-optimal resource use. *Theoretical Ecology* 10: 155–165.

# Cultural evolution of low fertility at high socio-economic status

Sara Li-Yen Loo

*School of Mathematics and Statistics,  
University of Sydney, Australia*

## Goal

To investigate the cultural evolution of low fertility at high socio-economic status, exploring the paradox of negative correlation of socio-economic status with fertility.

## Background and motivation

Cultural evolutionists have been fascinated by the global transition of fertility from high to low, as populations develop and move towards post-industrial societies. Improvements in socio-economic status are negatively correlated with fertility, measured in terms of surviving offspring. This paradox is counter-intuitive to assumptions embedded in life-history theory. Life-history theory expects individuals to invest in strategies that will maximize lifetime reproductive success, therefore implying that greater wealth would result in more surviving offspring. However, investigations of modern societies have demonstrated negative correlations (Livi-Bacci, 1986; Borgerhoff-Mulder, 1998; Bryant, 2007). In contemporary society, over half the global population live in countries with below-replacement fertility (Wilson, 2004).

Models of this shift from high to low fertility as countries develop has been investigated by evolutionary biologists, as well as cultural evolutionists. Demographic transition researchers argue that cultural, sociological, and economic factors are too intrinsically defined to be analyzed separately (review in Colleran, 2016; and references therein), and keenly dependent on different social interactions and networks. Models based in evolutionary anthropology have explored these different aspects of fertility decline (Barkow & Burley, 1980; Mace, 1996; Borgerhoff-Mulder, 1998; Kaplan, 1996). These studies have compared the effect of individual socioeconomic and sociocultural factors on fertility outcomes (Shenk, 2009; Shenk *et al.*, 2013; Alvergne *et al.*, 2011), and present models that are often based in economic optimization problems, resource-allocation strategies, and fitness optimization (Nettle, 2013; Brown, 2011). The underlying assumption with many of these models is that with less children, a parent can invest more time and effort into their survival. Individual fitness is increased by producing higher-quality offspring. There is a strong focus in the literature on the trade-off between quantity and quality of surviving offspring (Lack, 1968; Turke, 1989; Kaplan, 1996). This emphasizes the benefit of parental investment, and assumes that individuals with high relative fitness will produce offspring with a similarly high relative fitness. This does not follow the pattern displayed in modern societies.

Cultural evolutionists have pointed to the observed fertility decline as a key example of cultural transmission resulting in behaviors that do not maximize fitness (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985). Colleran (2016) highlights the following focuses of the study of demographic transition from a cultural evolution perspective: “(i) how individual learning biases that evolved to optimize social information transmission generate and maintain different frequencies of cultural traits in populations; (ii) how variation and interaction between groups at different cultural equilibria lead to between-group competition, selection and transmission; and (iii) how different channels (modes) of social transmission affect the dynamics of information flow in populations” (p. 4).

Investigations into the mechanisms underlying this cultural evolution need to consider not only trade-offs between the quantity and quality of offspring, but also the effects of status-seeking and social learning on the fertility decisions of parents. Separating transmission into genetic and cultural components can be difficult (Laland & Brown, 2002), but studies in the literature argue that cultural evolution can be explored by adjusting the theory of evolution by natural selection (e.g., Dawkins, 1976; Cavalli-Sforza & Feldman, 1981; Richerson & Boyd, 1984; Boyd & Richerson, 1985; Mesoudi *et al.*, 2004). These studies consider non-genetic Darwinian mechanisms of inheritance; traits of high-status individuals are selected for.

This inheritance of the traits of high-status individuals results in observed maladaptive effects of competition. This stems from the notion that strategies or traits that increase an individual's chance of outcompeting its competitors are selected for, despite the decrease in benefit to the overall population. In this case, the competition for higher socio-economic status brings about the decrease in fertility, as overcompensating one's wealth follows from the concept of the "arms race".

We adopt a dynamic model structured within a cultural evolution framework to explore these concepts of strategic selection, in order to establish how socio-economic status and cultural changes can coevolve.

Within this framework, an individual's target for how much wealth to endow or provide their children is a transmitted cultural trait. Thus, transmission is not restricted to the biological transfer of behavior through DNA. As culture is passed from one individual to another by nurture – through observation, imitation, teaching, etc. (Cavalli-Sforza & Feldman, 1981) – behaviors can be transmitted through any member of a population, including those other than one's genetic parents.

We examine these mechanisms using an integro-difference equation model, building on the work of a previous EEP YSSP project, where the fitness currency is in terms of wealth, rather than reproductive success. We seek to provide answers as to the mechanisms that drive the sacrifice of fertility for socio-economic status.

## Research questions

I will address the following questions:

- What are the conditions under which low fertility can evolve with high socio-economic status?
- How can we implement a continuous trait model to demonstrate the paradox observed in modern, post-transition societies?
- What happens when the total wealth available to a population increases with the total endowment to children?
- What traits are inherited?
- Is socio-economic assortment a key determinant of behavior? What happens if parents are allowed to choose role models preferentially from their own class?

## Methods and work plan

We aim to build on previous work in the EEP by refining and analyzing a cultural-evolution model for understanding conditions under which low fertility emerges at high socio-economic status. In particular, we will investigate three extensions through which (i) the disposable wealth

of parents depends on their own socio-economic status and on their parent generation's endowment to offspring, (ii) parents base their fertility decisions on decisions of other parents with similar socio-economic status, and (iii) role models for fertility decisions are chosen probabilistically across the whole range of socio-economic status with a gradual preference for imitating parents with high-socio economic status. We hope these extensions will provide a richer understanding of the mechanisms that drive the cultural evolution of low fertility at high socio-economic status.

### ***Model Overview***

We explore the evolution of two traits within a population: socio-economic status,  $s$ , and an endowment target,  $e$ . These are defined such that  $s \in [0,1]$  and  $e \in [e_{\min}, 1]$ . Socio-economic status describes the rank of an individual, reflecting their economic and social position in society relative to others in the population in that generation. This can be thought of in terms of income, education, and occupation, for example. Endowment target is a representation of the investment strategy to which a parent adopts, defining how much of their wealth to endow, or provide, to their children. This endowment can be thought of in terms of monetary or material inheritance, or of investment into the development of certain skills or values. Endowment here is an evolving trait, and the mechanisms by which either high or low endowment targets are selected for is dependent on the coevolution of and competition embedded within socio-economic status.

Between generations, the socio-economic ladder is determined as a relative metric between individuals in a given generation. Endowment target transmission can occur through learning from one's parent, or through an alternative role model via other mechanisms of social learning.

### ***Model Details***

The distribution of the population is defined as  $f(s, e)$ , a bivariate probability density. This population density is updated with the next generation of parents, and the evolution of the average endowment target investigated as it co-evolves with socio-economic status.

The number of children born to each individual in a population is given by

$$n(s_p, e_p) = \frac{W(s_p, \hat{e}_p)}{e_p}$$

where  $s_p$  is the socio-economic status of the parent,  $e_p$  is the endowment target of the parent, and  $W(s_p, e_p)$  is the total wealth belonging to a parent that can be endowed to their children, and is dependent on the parent's socio-economic status and the average endowment target of the population,  $\hat{e}_p$ . Wealth increases as the rank of socio-economic status increases, so  $\partial W / \partial s_p > 0$ . We define this wealth function as

$$W(s_p, \hat{e}_p) = [W_{\min, \min}(1 - R(\hat{e}_p)) + W_{\min, \max}R(\hat{e}_p)](1 - s_p) + [W_{\max, \min}(1 - R(\hat{e}_p)) + W_{\max, \max}R(\hat{e}_p)]s_p,$$

where

$$R(\hat{e}_p) = \frac{\hat{e}_p - e_{\min}}{1 - e_{\min}}$$

denotes the average endowment target of the population. This corresponds to the level of economic development or richness in a given population, defined on  $[0,1]$ . Other parameters within this function given by different indexes of  $W$  define the maximum or minimum wealth given

maximum or minimum endowment or socio-economic status. This function interpolates between the average endowment target of the population and socio-economic status, and is of a general form, such that special cases can be derived.

The overall transmission of socio-economic status is given by

$$S(s|s_p, e_p, f) = \frac{1}{Z_s(s_p, e_p, f)} N(s|r(e_p, f), D(s_p)),$$

where  $Z_s(s_p, e_p, f)$  normalizes socio-economic status such that  $\int_0^1 S(s|s_p, e_p, f) ds = 1$ , to maintain a stable population, and  $N(s|m, d)$  is the probability density of the normal distribution of socio-economic status,  $s$ , with mean  $m$  and standard deviation  $d$ , for the next generation. This normal distribution represents the moving average of inherited status,  $s$ , distributed about the rank  $r(e_p)$ , with standard deviation as a decreasing function of the parents' socio-economic status,  $D'(s_p) < 0$ .

Once the population is assigned specific ranks, and a degree of movement in the transmitted status allowed through this normal distribution, the overall transmission of status from one generation to the next is established.

The endowment rank above is defined as

$$r(e_p, f) = \frac{1}{Z_r(f)} \int_{e_{\min}}^{e_p} \int_0^1 n(s, e) f(s, e) ds de$$

where  $Z_r(f)$  normalizes the rank such that  $r(1, f) = 1$ , that is, the highest ranking individual holds the highest rank.

The endowment target inherited by the child can come from either the child's parent, or a role model in the population. The probability a child inherits its endowment target from a role model is given by an imitation kernel,  $K(s, s_M, f)$ . The subscript  $M$  corresponds to the role model, who therefore has socio-economic status  $s_M$ , and endowment target  $e_M$ . This is defined as the product of a normal distribution and a sigmoidal function. The endowment inherited from a role model is assortatively chosen from the parent generation, represented in the sigmoidal function. The softness of this curve can be interpreted as a form of perception or implementation error, where role models who are better than the individual are more likely to be chosen, with the steepness of the curve defined by the parameter,  $w \geq 0$ . The assortativeness of imitation with regards to status is modelled with  $a \geq 0$ . The imitation kernel is expressed

$$K(s, s_M, f) = \frac{1}{Z_i(s, f)} \frac{N(s_M|s, \frac{1}{a})}{1 + \exp(-w(s_M - s))},$$

where  $Z_i(s, f)$  normalizes the kernel so that

$$\int_0^1 \int_0^1 K(i, s_M, f) f(s_M, e_M) ds_M de_M = 1$$

We can obtain special cases of this imitation kernel by taking different values of  $a$  and  $w$ . For example, large values of  $a$  correspond to small variance in the normal distribution and therefore a non-assortative choice, and  $w \rightarrow \infty$  to a step function rather than the sigmoid Fermi function.

Overall endowment transmission is given by

$$E(e|s, e_p, s_M, e_M, f) = v \delta(e - e_p) + (1 - v)K(s, s_M, f)\delta(e - e_M),$$

where  $\delta$  is the Dirac delta function. This function describes the transmission of endowment target  $e$ , by expressing the probability density that a child adopts endowment target  $e$  when it has socio-economic status  $s$ , its parents have endowment target  $e_P$ , and it “learns” from a role model characterised by  $(s_M, e_M)$  in a population composed by  $f$ .

We combine these transmission functions to then assume the following intergenerational dynamics,

$$f_{t+1}(s, e) = \int_0^1 \int_0^1 S(s|s_P, e_P, f_t) f_t(s_P, e_P) \int_0^1 \int_0^1 E(e|s, e_P, s_M, e_M, f_t) f_t(s_M, e_M) ds_M de_M ds_P de_P,$$

where functions are described as above.

### **Work plan**

The envisaged work plan is as follows:

- Gain an understanding of model structure, coding and execution.
- Previous modelling produced oscillations in the average fertility of each generation. We will investigate how this oscillatory behaviour is obtained. Further simulations will be performed in order to understand the mechanisms behind this fluctuating behaviour.
- Implement novel wealth function, allowing the total population wealth to increase as the total endowment increases.
- Perform sensitivity analysis to determine the effect of model parameters.
- Include socio-economic assortment to allow parents to choose role models preferentially from their own class.
- Consider the effect of probability of choosing a role model as dependent on the socio-economic status of a parent.

### **Relevance and link to EEP’s research plan**

This project is related to EEP's interest in changes in living systems, particularly as is focused on evolutionary dynamics. Investigation into competitive interactions within communities is a major interest of the EEP program. Modelling of cultural evolution in this way is novel.

### **Expected output and publications**

The results obtained from this work will be published in a co-authored peer-reviewed international journal, and be included as a chapter in my doctoral thesis.

### **References**

- Alvergne A, Gurmu E, Gibson MA & Mace R (2011). Social transmission and the spread of modern contraception in rural Ethiopia. *PLoS ONE* 6: e22515.
- Barkow J & Burley N (1980). Human fertility, evolutionary biology, and the demographic transition. *Ethology and Sociobiology* 1: 163-180–183.
- Borgerhoff Mulder M (1998). The demographic transition: Are we any closer to an evolutionary explanation? *Trends in Ecology and Evolution* 13: 226–270.
- Boyd R & Richerson PJ (1985). *Culture and the evolutionary process*. University of Chicago Press, USA.



- Brown GR, Dickins TE, Sear R & Laland KN (2011). Evolutionary accounts of human behavioural diversity. *Philosophical Transactions of the Royal Society B* 366: 313–324.
- Bryant J (2007). Theories of fertility decline and the evidence from development indicators. *Population and Development Review* 33: 101–127.
- Cavalli-Sforza LL & Feldman MW (1981). *Cultural transmission and evolution: A quantitative approach*. Princeton University Press, USA.
- Colleran, H (2016). The cultural evolution of fertility decline. *Philosophical Transactions of the Royal Society B* 371: 20150152.
- Dawkins R (1976). *The Selfish Gene*. Oxford University Press, UK.
- Kaplan H (1996). A theory of fertility and parental investment in traditional and modern societies. *Yearbook of Physical Anthropology* 39: 91–135.
- Lack D (1968). *Ecological Adaptations for Breeding in Birds*. Methuen, London, UK.
- Laland N & Brown GR (2002). *Sense and nonsense: Evolutionary perspectives on human behaviour*. Oxford University Press, UK.
- Livi-Bacci M (1986). Social-group forerunners of fertility control in Europe. In AJ Coale and SC Watkins eds.: *The Decline of Fertility in Europe*. Princeton University Press, USA, pp. 182–200.
- Mace R (1996). Biased parental investment and reproductive success in Gabbra pastoralists. *Behavioural Ecology and Sociobiology* 38: 75–81.
- Mesoudi A, Whiten A & Laland K (2004). Is human cultural evolution Darwinian: Evidence reviewed from the perspective of the origin of species. *Evolution* 58: 1–11.
- Nettle D, Gibson MA, Lawson DW & Sear R (2013). Human behavioural ecology: Current research and future prospects. *Behavioural Ecology* 24: 1031–1040.
- Richerson PJ, Boyd R (1984). Natural selection and culture. *Bioscience* 34: 430–434.
- Shenk MK (2009). Testing three evolutionary models of the demographic transition: patterns of fertility and age at marriage in urban South India. *American Journal of Human Biology* 21: 501–511.
- Shenk MK, Towner MC, Kress HC & Alam N (2013). A model comparison approach shows stronger support for economic models of fertility decline. *Proceedings of the National Academic of Science of the USA* 110: 8045–8050.
- Turke P (1989). Evolution and the demand for children. *Population and Development Review* 15: 61–90.
- Wilson C (2004). Fertility below replacement level. *Science* 304: 207–209.
- Salvatella R, Irabedra P & Castellanos LG (2014). Interruption of vector transmission by native vectors and “the art of the possible”. *Memórias do Instituto Oswaldo Cruz* 109: 122–130.
- Sanchez-Martin MJ, Feliciangeli MD, Campbell-Lendrum D & Davies CR (2006). Could the Chagas disease elimination programme in Venezuela be compromised by reinvasion of houses by sylvatic *Rhodnius prolixus* bug populations? *Tropical Medicine and International Health* 11: 1585–1593.
- World Health Organization (2012). Accelerating work to overcome the global impact of neglected tropical diseases: A roadmap for implementation: Executive summary.

# Towards enhanced realism in models of biodiversity evolution

Takuji Oba

*Department of Advanced Mathematical Sciences,  
Graduate School of Informatics, Kyoto University, Japan*

## Goal

To investigate how biologically realistic functional responses affect the ecological and evolutionary dynamics in models of biodiversity.

## Background and motivation

Human societies depend on ecosystem services which are upheld by our planet's rich biodiversity (Naeem *et al.*, 1994; Loreau *et al.*, 2001; Kinzig *et al.*, 2001; Loreau *et al.*, 2002; Hooper *et al.*, 2005; Naeem *et al.*, 2009). However, species are currently becoming extinct at an unprecedented rate due to human activities and important ecosystem services may thus be at risk. In fact, the Millennium Ecosystem Assessment (MA), held in 2001 – 2005 aiming at assessing how changes in ecosystems and ecosystem services affect humans, has reported that, over the past few hundred years, humans have increased the species extinction rate by as much as 1,000 times over the background rate typical throughout our planet's history. Eco-evolutionary biodiversity models help address the challenge of rapid biodiversity loss and preserve ecosystem functions by allowing different conservation strategies to be tested and evaluated.

At the heart of eco-evolutionary biodiversity models is the representation of intra- and interspecific interactions in ecosystems. The networks describing trophic interactions, i.e., feeding relationships, among a community's species are called food webs. The biodiversity that is supported by a community may strongly depend on its food-web structure (May, 1972; Pimm and Lawton, 1977; Ives *et al.*, 2000; Jansen and Kokkoris, 2003; Kondoh, 2003; Worm and Duffy, 2003), which is determined by factors such as the level on which interactions occur (individuals, subpopulations of present species, present species, etc.), what kind of interactions take place (cooperative, competitive, trophic, etc.), and what phenotypic traits individuals express and how these traits influence the interactions. While food-web models have been studied for a long time (Cohen *et al.*, 1990; Williams and Martinez, 2000; Cattin *et al.*, 2004), evolutionary models, which capture the emergence of food-web structure through evolutionary processes, are increasingly drawing interest as they are able to link population dynamics to the structure of food webs (Caldarelli *et al.*, 1998; Drossel *et al.*, 2001; McKane, 2004; Tokita and Tasutomi, 2006; Loeuille and Loreau, 2005; Brännström *et al.*, 2013).

The effect of species abundances on the interactions among a community is known as density dependence, and the specific dependence of prey densities on the foraging rate of a predator is known as a functional response. Holling (1959a, 1959b) classified the functional response of a predator on a prey into three types I, II and III, where the first corresponds to linear dependence and the latter two to characteristic nonlinear dependencies. While type I functional responses can easily be extended to the case of many producer species, this is not the case for type II and III functional responses as straightforward generalizations often lack biological consistency in multispecies contexts (van Leeuwen *et al.*, 2007; van Leeuwen *et al.*, 2013).

The aim of this project is to investigate how biologically realistic functional responses affect the ecological and evolutionary dynamics in models of biodiversity. As described in more detail

below, I will determine consistency criteria that need to be fulfilled by multi-species functional responses, derive consistent nonlinear functional responses, and investigate numerically how the derived functional responses influence the ecological and evolutionary dynamics in one or more food-web models.

## Research questions

I will address the following questions.

- Which consistency criteria must biologically realistic multi-species functional responses satisfy?
- How can type II and type III functional responses be extended to multi-species contexts?
- How does biologically realistic functional responses affect the eco-evolutionary dynamics of food webs?

## Methods and work plan

My project will unfold in three interweaved layers. At first, I will determine consistency criteria that need to be fulfilled by multi-species functional responses. Next, I will derive consistent nonlinear functional responses. Finally, I will investigate numerically how the derived functional responses influence the ecological and evolutionary dynamics in food-web models.

### *Consistency of multi-species functional responses*

Functional responses are very common in the study of demographic dynamics, often in the setting of a single predator consuming a single prey. When the functional response describes consumption of two or more prey, biological consistency requires that arbitrary grouping of ecologically identical individuals into artificial species does not affect the consumption rate. Furthermore, the assumptions that are typically made in derivations of multi-species functional responses, such as the prey and predator abundance remaining approximately constant during the time-scale of searching and handling prey, do not always hold. As the first step of this project, I will investigate what consistency criteria multi-species functional responses and the derivation of these functional responses should fulfill.

### *Deriving biologically realistic multi-species functional responses.*

Holling (1959b) derived the standard Type II functional response by assuming that a predator is in either of two states, searching for prey or handling prey. As an important milestone in the development of biologically realistic multi-species functional responses, van Leeuwen *et al.* (2013) extended this classical derivation by assuming the predator is more likely to find prey it has previously consumed. Their derivation, however, makes the assumption that the prey and predator abundance remaining approximately constant during the time-scale of searching and handling prey, which may not hold in many real ecological systems. In this project, I will extend the derivation by van Leeuwen *et al.* (2013) to account for potentially changing densities of prey and predators also on shorter time scales. To address the issue that, the equations become too complicated to solve analytically, I will divide predator individuals into three stages: young individuals, which are too young to produce offspring, searching adult individuals, and handling adult individuals.

### ***Effects of biologically realistic functional responses on eco-evolutionary dynamics***

After deriving biologically realistic multi-species functional responses, I will investigate how the predicted eco-evolutionary dynamics change when they are used in the evolutionary food-web model of Brännström *et al.* (2011). After implementing the new functional responses, I will systematically explore the parameter space, in particular increasing the handling time to see how this affects the outcome. I will pay particular attention to how well-known consequences of non-linear functional responses in two-species predator-prey systems, such as the emergence of limit cycles, manifest themselves in a multispecies context and on evolutionary time scales.

### ***Work plan***

I will take the following three steps to reach my goals:

- Determine consistency criteria that need to be fulfilled by multi-species functional responses, derive consistent nonlinear functional responses.
- Derive consistent nonlinear functional responses extending van Leeuwen *et al.* (2013).
- Investigate how the derived functional responses influence the ecological and evolutionary dynamics in the eco-evolutionary food-web model of Brännström *et al.* (2011).
- If time allows, I will also consider one more food-web model and/or explore the consequences of using other functional responses. All numerical implementations will be done in Matlab.

### **Relevance and link to EEP's research plan**

This project is expected to contribute to Evolution and Ecology Program's (EEP) research project *Eco-evolutionary Dynamics of Living Systems* by developing key elements of biologically realistic biodiversity models and by clarifying their importance for model predictions.

### **Expected output and publications**

The results of this project will be a chapter of my PhD thesis and hopefully a co-authored article in a scientific international journal.

### **References**

- Brännström Å, Loeuille N, Loreau M & Dieckmann U (2011). Emergence and maintenance of biodiversity in an evolutionary food-web model. *Theoretical Ecology* 4: 467–478.
- Caldareli G, Higgs P & McKane A (1998). Modelling coevolution in multispecies communities. *Journal of Theoretical Biology* 193: 345 – 358.
- Cattin M, Bersier L, Banasek-Richter C, Baltensperger R & Gabriel J (2004). Phylogenetic constraints and adaptation explain food web structure. *Nature* 427: 835–839.
- Cohen J, Briand F & Newman C (1990). *Community food webs: Data and theory*. Springer Verlag, Berlin, Germany.
- Drossel B, Higgs P & McKane A (2001). The influence of predator-prey population dynamics on the long-term evolution of food web structure. *Journal of Theoretical Biology* 8: 293–320.
- Holling CS (1959a). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* 91: 293–320.

- Holling CS (1959b). Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91: 385–398.
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setl H, Symstad AJ, Vandermeer J & Wardle DA (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75: 3–35.
- Ives AR, Klug JL & Gross K (2000). Stability and species richness in complex communities. *Ecological Letters* 3: 399–411.
- Jansen VAA & Kokkoris GD (2003). Complexity and stability revisited. *Ecological Letters* 6: 498–502.
- Kinzig AP, Pacala SW & Tilman D (2001). *The functional consequences of biodiversity: empirical progress and theoretical extensions*. Princeton University Press, USA.
- Kondoh M (2003). Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299: 1388–1391.
- Loeuille N & Loreau (2005). Evolutionary emergence of size structured food webs. *Proceedings of the National Academy of Sciences of the United States of America* 102: 5761–5766.
- Loreau M, Naeem S & Inchausti P (2002). *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press, UK
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D & Wardle DA (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294: 804–808.
- May RM (1972). Will a large complex system be stable? *Nature* 238: 413–414.
- McKane AJ (2004). Evolving complex food webs. *The European Physical Journal B* 38: 287–295.
- Naeem S, Bunker DE, Hector A, Loreau M & Perrings C (2009). *Biodiversity, ecosystem functioning, and human well-being: An ecological and economic perspective*. Oxford University Press, UK.
- Naeem S, Thompson LJ, Lawler SP, Lawton JH & Woodfin RM (1994). Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734–737.
- Pimm SL & Lawton JH (1977). The number of trophic levels in ecological communities. *Nature* 268: 329–331.
- Tokita K & Yasutomi A (2006). Emergence of a complex and stable network in a model ecosystem with extinction and mutation. *Theoretical Population Biology* 63: 131–146.
- van Leeuwen E, Brännström A, Dieckmann U & Rossberg AG (2013). A generalized functional response for predators that switch between multiple prey species. *Journal of Theoretical Biology* 328: 89–98.
- van Leeuwen E, Jansen VA & Bright PW (2007). How population dynamics shape the functional response in a one-predator-two-prey system. *Ecology* 88: 1571–1581.
- Williams RJ & Martinez ND (2000). Simple rules yield complex food webs. *Nature* 404: 180–183.
- Worm B & Duffy JE (2003). Biodiversity, productivity and stability in real food webs. *Trends Ecology & Evolution* 18: 628–632.