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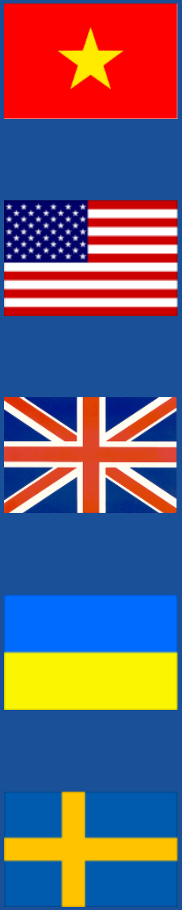

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Understanding Complex Adaptive Systems

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Complex Adaptive Systems

- Collections of individual agents
- Agents can be heterogeneous
- Agents interact locally and nonlinearly
- Agents adapt their features/strategies based on the outcomes of those interactions

Features of Complex Adaptive Systems

1. Rapid adaptation
2. Codependent agents
3. Emergent phenomena
4. Tipping points
5. Self-organized criticality
6. Social dilemmas
7. Stakeholder diversity

1

Rapid Adaptation

Two Types of Adaptation

- **Biological evolution**
  operates through genetic change (slower)
- **Cultural evolution**
  operates through social learning (faster)

Two Common Misperceptions

- Biological evolution is always slow

  On the contrary, rapid contemporary evolution is widespread, in particular in response to anthropogenic environmental change

- Biological evolution is always optimizing

  On the contrary, selection operates at the individual level, implying that population-level features will rarely get optimized by evolution

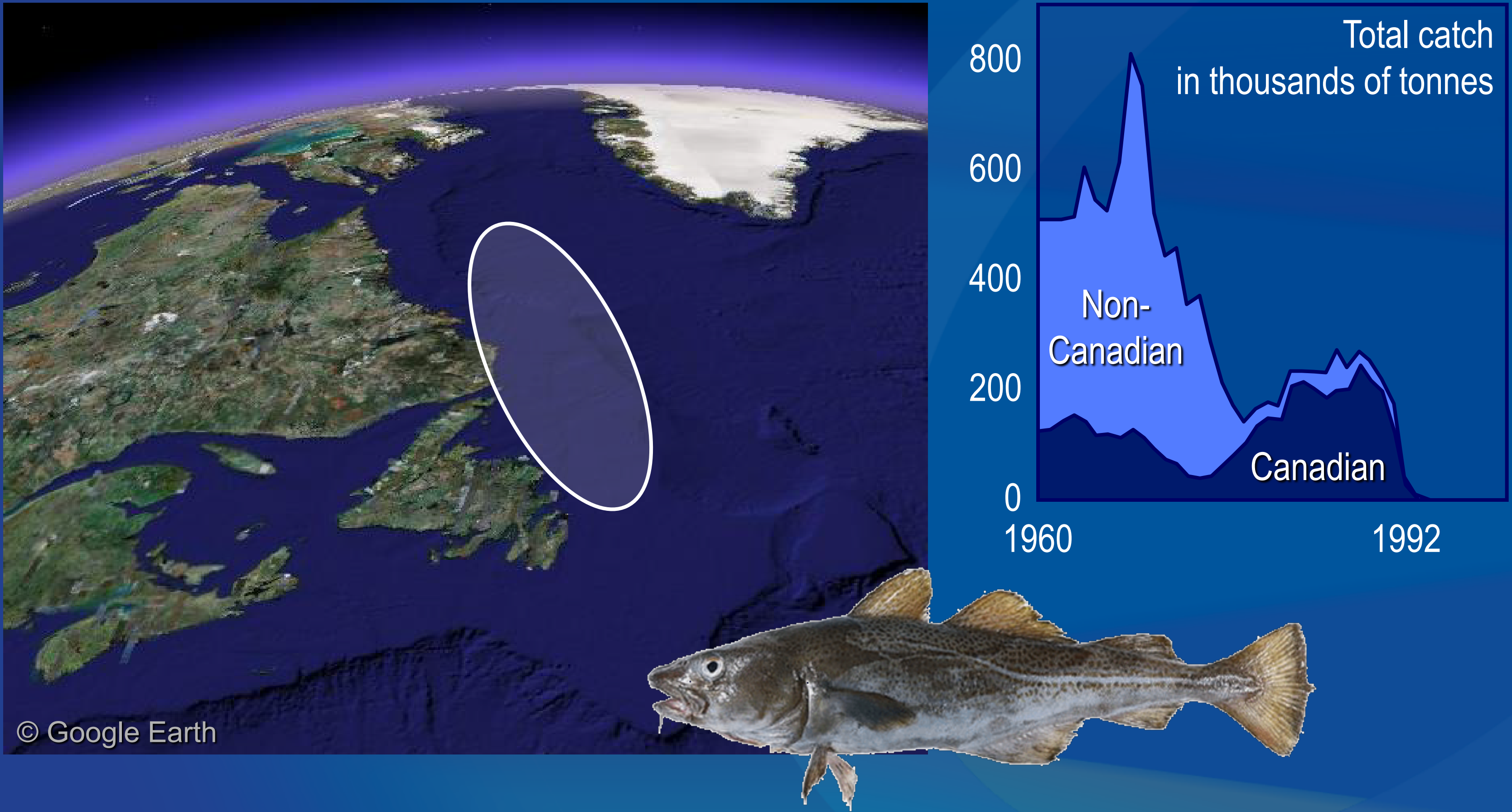
Example: Modern Fisheries

- Evolutionary responses of stocks to modern fishing pressures are inevitable
- Significant evolution can occur within just a few generations
- Evolutionary changes are not necessarily beneficial
- Evolutionary changes will often be difficult to reverse

Which Traits Are at Risk?

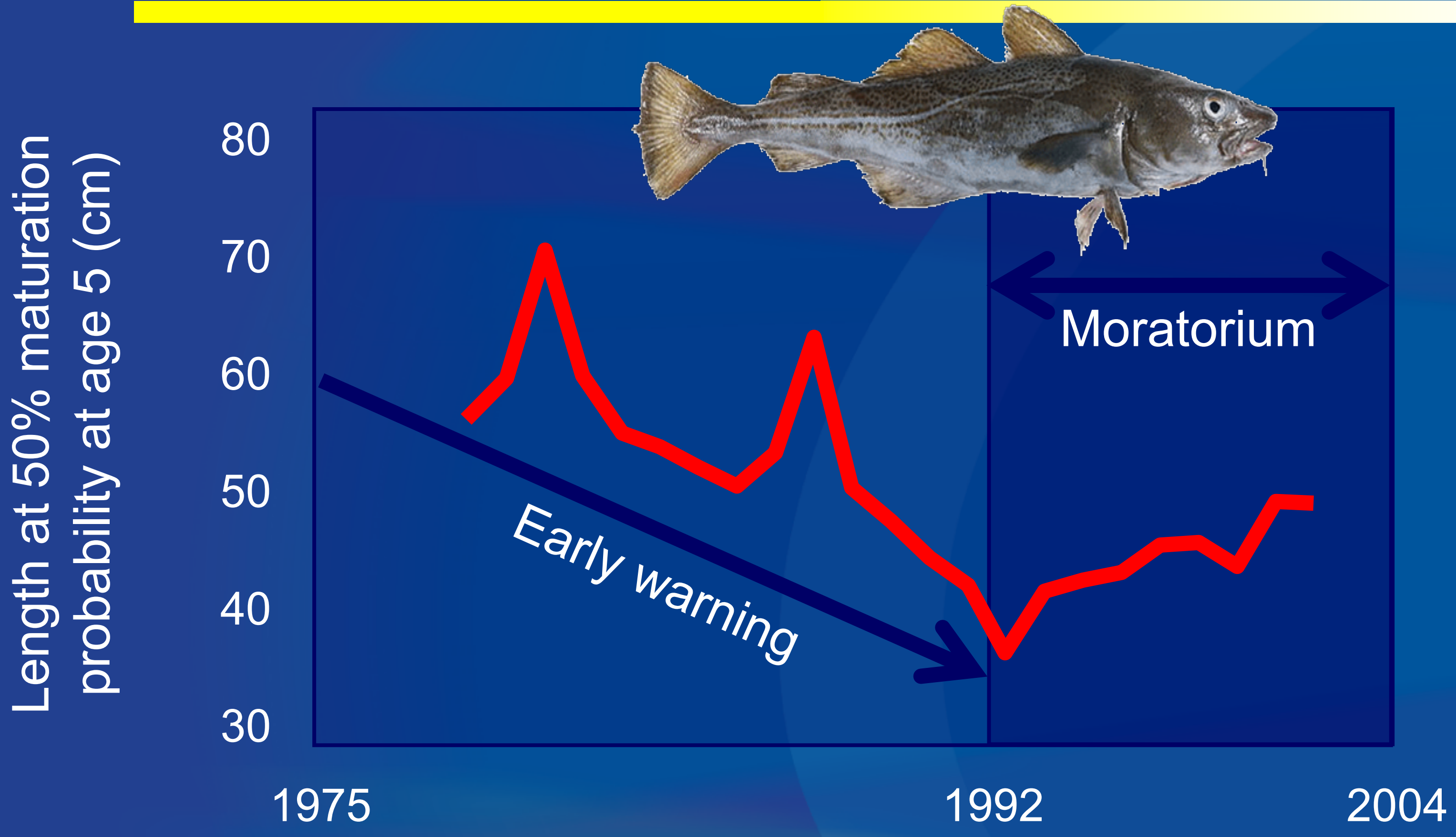
- Age and size at maturation
  - ⇨ Reproducing late is impossible
- Reproductive effort
  - ⇨ Saving for future seasons is futile
- Growth rate
  - ⇨ Staying below mesh size prolongs life
- Morphology and behavior
  - ⇨ Avoiding fishing gear is advantageous

Northern Cod: Fishing History



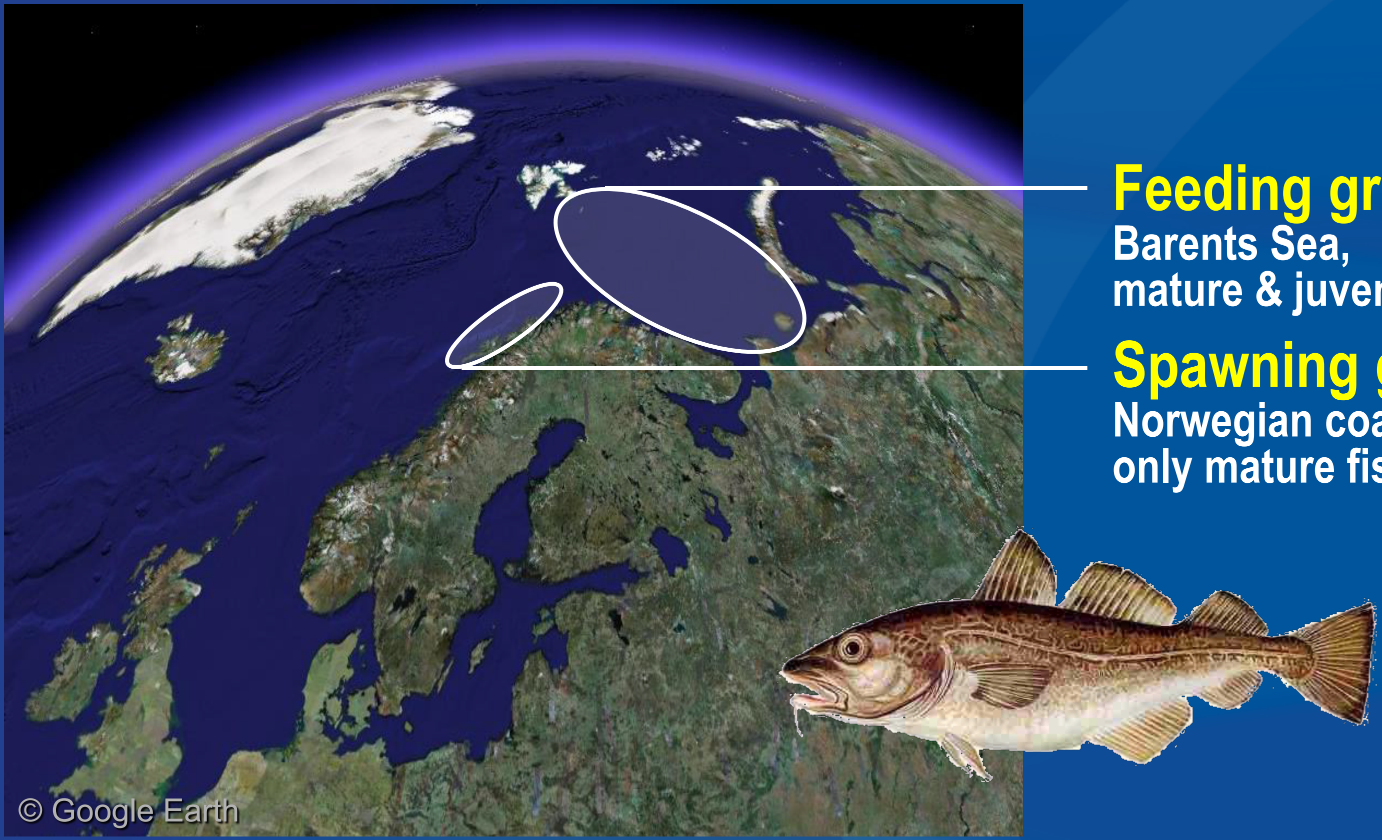
**The northern cod stock collapsed in 1992,
in one of the worst disasters of modern fishing**

Northern Cod: Evolutionary Change



A strong negative trend in maturation schedule, as predicted by theory

Northeast Arctic Cod: Stock Structure



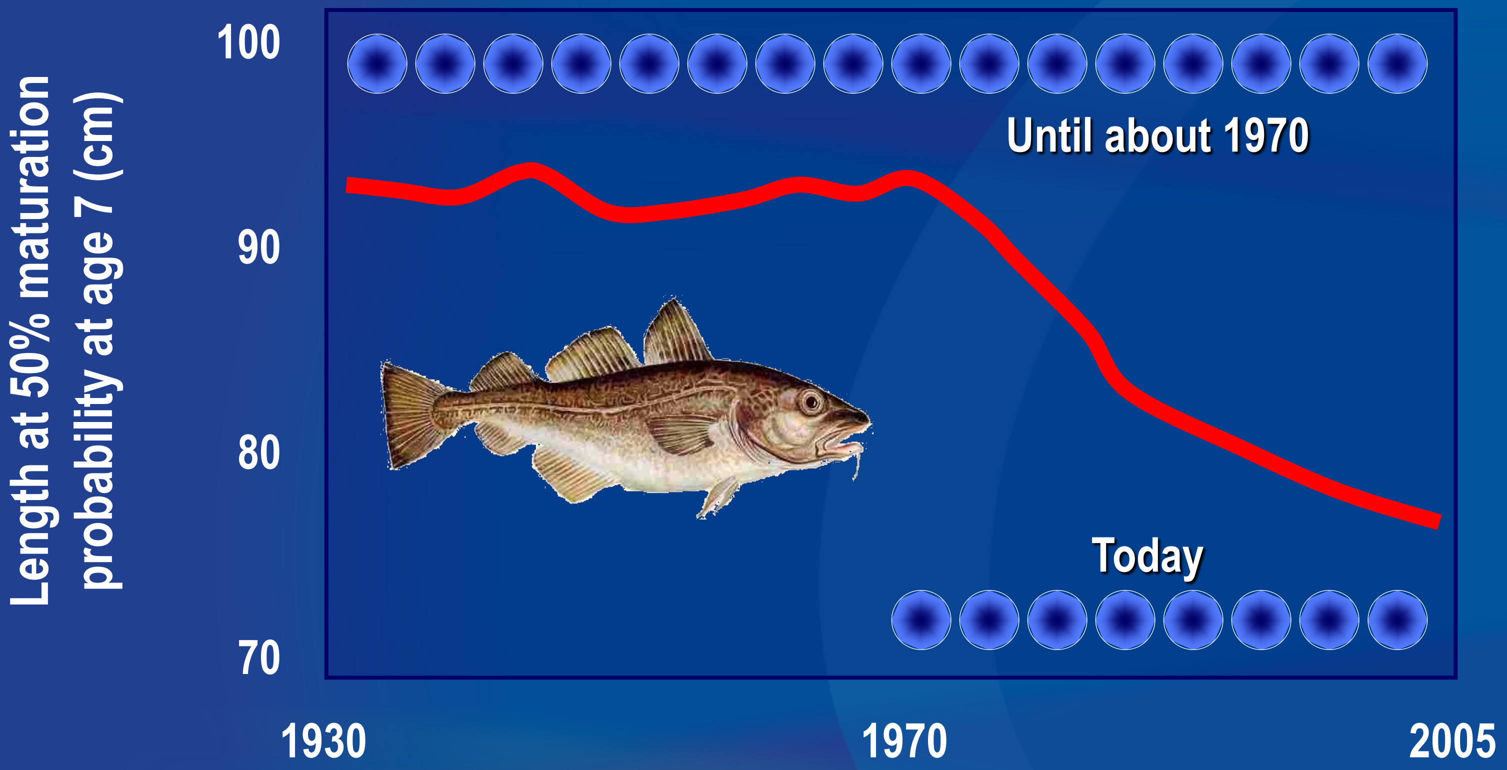
© Google Earth

Feeding grounds
Barents Sea,
mature & juvenile fish

Spawning grounds
Norwegian coast,
only mature fish

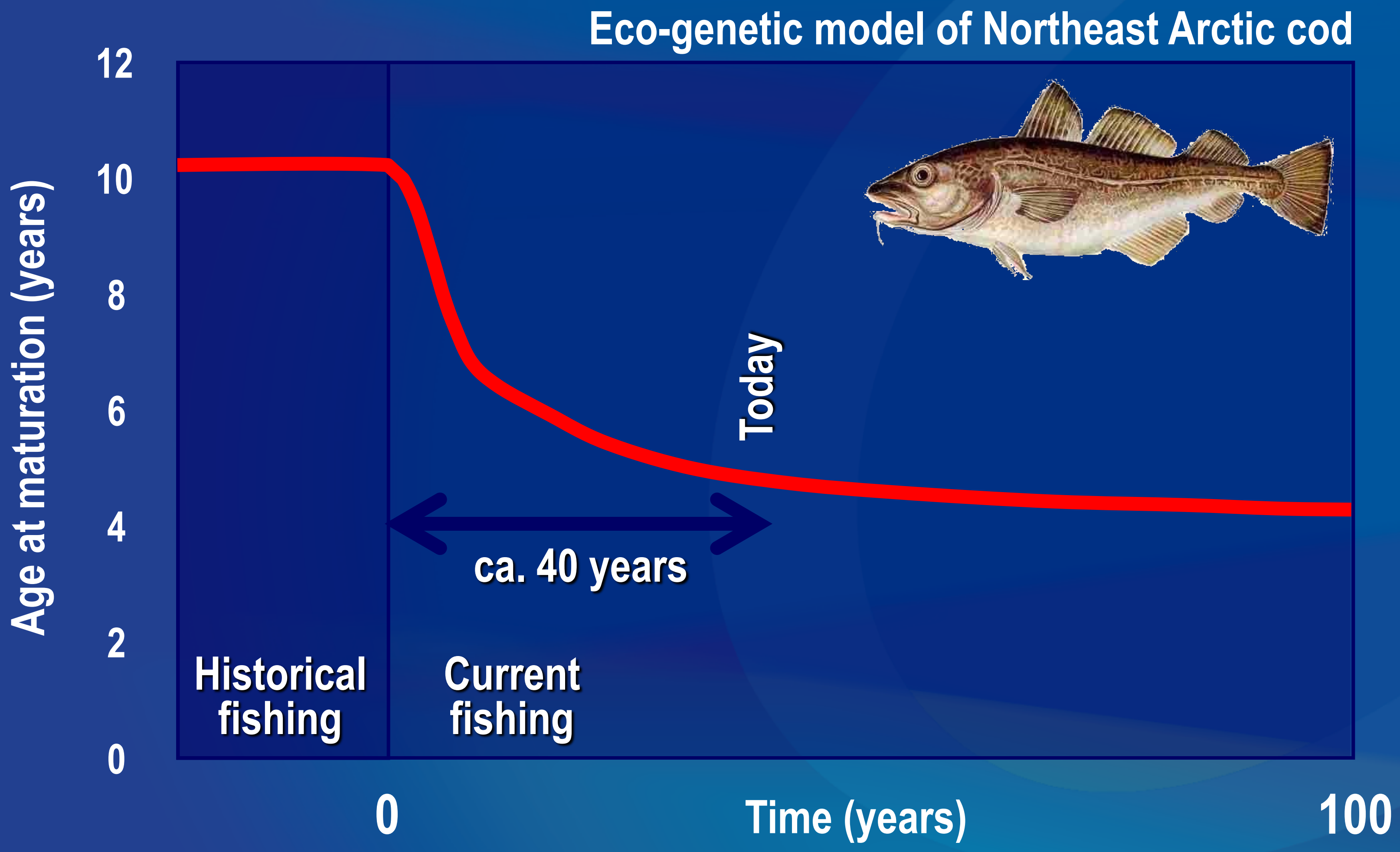
With a catch of 400,000 tonnes per year, Northeast Arctic cod is one of the most important European fish stocks

Northeast Arctic Cod: Evolutionary Change

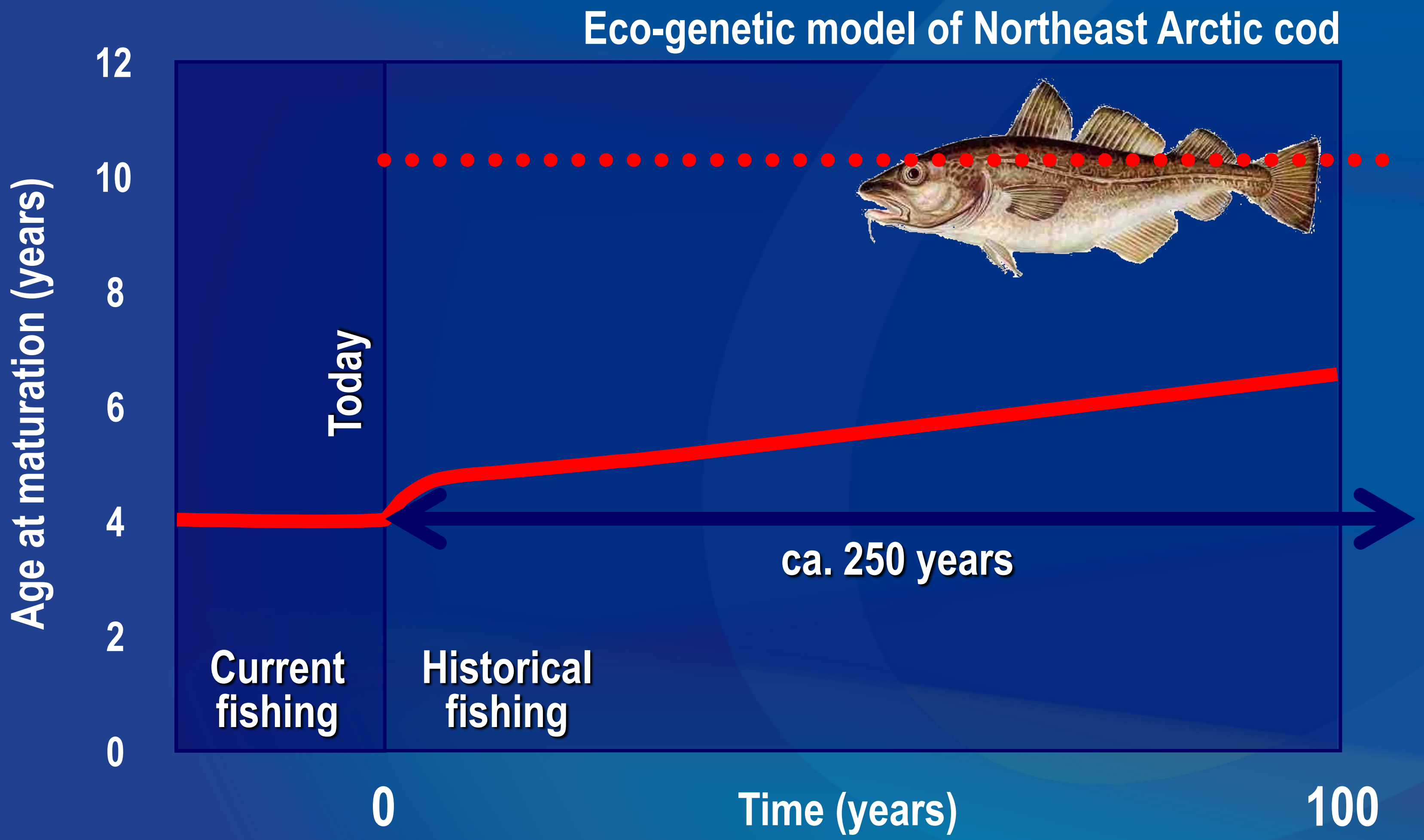


This shift in maturation schedule contributes to a drop in maturation age from 9-10 years to 6-7 years and reduces initial egg production by about 50%

Fast Pace of Evolutionary Decline



Slow Pace of Evolutionary Recovery



Evolution, 56(4), 2002, pp. 669–678

MEASURING PROBABILISTIC REACTION NORMS FOR AGE AND SIZE AT MATURATION

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Abstract.—We present a new probabilistic concept of reaction norms for age and size at maturation that is applicable when observations are carried out at discrete time intervals. This approach can also be used to estimate reaction norms for age and size at metamorphosis or at other ontogenetic transitions. Such estimations are critical for understanding phenotypic plasticity and life-history changes in variable environments, assessing genetic changes in the presence of phenotypic plasticity, and calibrating size- and age-structured population models. We show that previous approaches to this problem, based on regressing size against age at maturation, give results that are systematically biased when compared to the probabilistic reaction norms. The bias can be substantial and is likely to lead to qualitatively incorrect conclusions; it is caused by failing to account for the probabilistic nature of the maturation process. We explain why, instead, robust estimations of maturation reaction norms should be based on logistic regression or on other statistical models that treat the probability of maturing as a dependent variable. We demonstrate the utility of our approach with two examples. First, the analysis of data generated for a known reaction norm highlights some crucial limitations of previous approaches. Second, application to the northeast arctic cod (*Gadus morhua*) illustrates how our approach can be used to shed new light on existing real-world data.

Key words.—Body size, life history, logistic regression, maturation, metamorphosis, phenotypic plasticity, reaction norm.

nature
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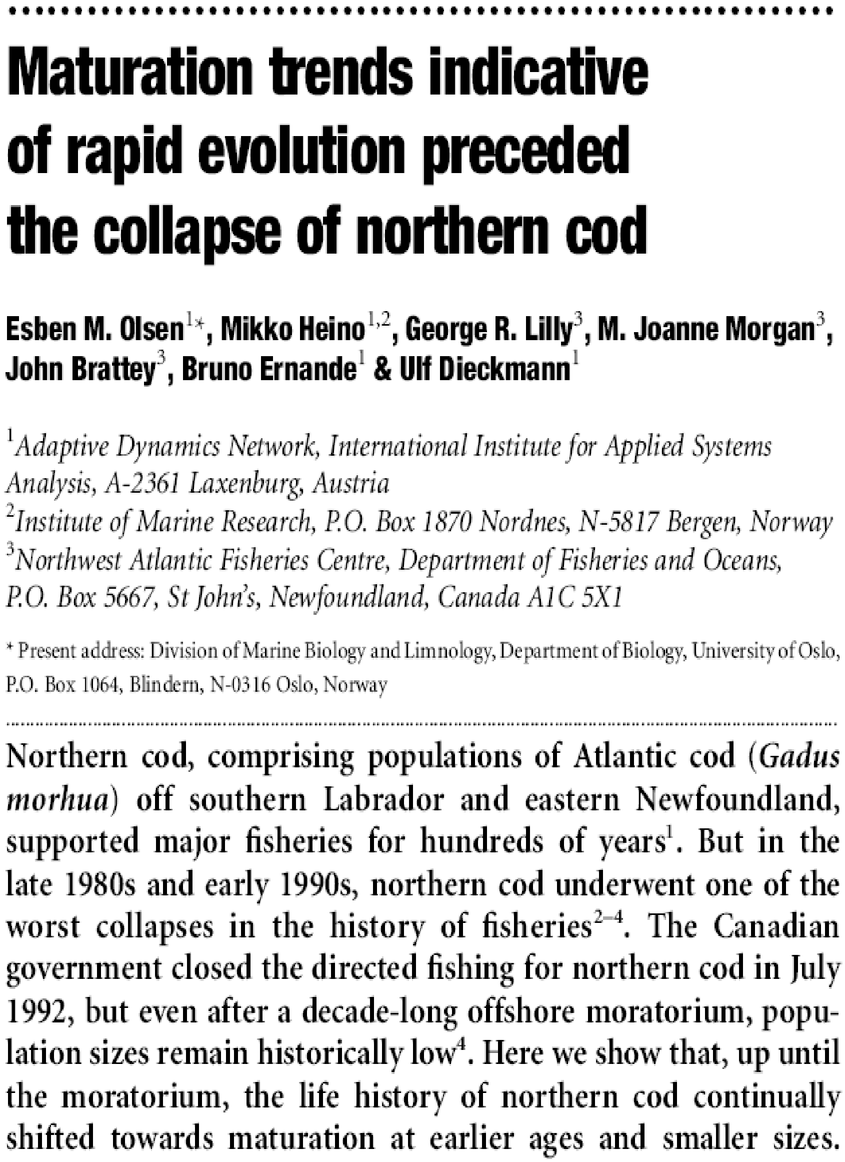

Maturation trends indicative of rapid evolution preceded the collapse of northern cod

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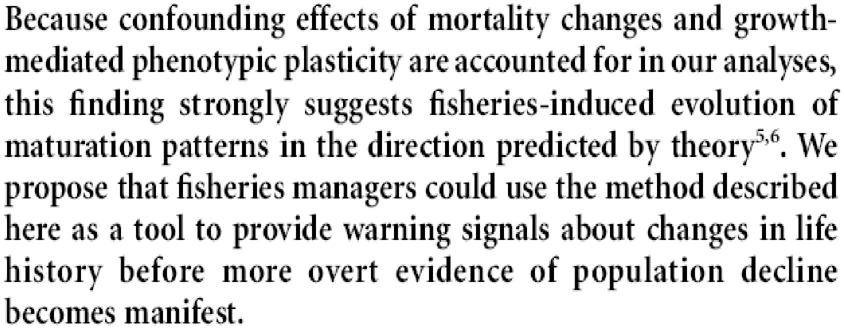
Northern cod, comprising populations of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, supported major fisheries for hundreds of years[1]. But in the late 1980s and early 1990s, northern cod underwent one of the worst collapses in the history of fisheries[2–4]. The Canadian government closed the directed fishing for northern cod in July 1992, but even after a decade-long offshore moratorium, population sizes remain historically low[4]. Here we show that, up until the moratorium, the life history of northern cod continually shifted towards maturation at earlier ages and smaller sizes.



Because confounding effects of mortality changes and growth-mediated phenotypic plasticity are accounted for in our analyses, this finding strongly suggests fisheries-induced evolution of maturation patterns in the direction predicted by theory[5,6]. We propose that fisheries managers could use the method described here as a tool to provide warning signals about changes in life history before more overt evidence of population decline becomes manifest.

Ecological Applications, 19(7), 2009, pp. 1815–1834

Eco-genetic modeling of contemporary life-history evolution

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Abstract. We present eco-genetic modeling as a flexible tool for exploring the course and rates of multi-trait life-history evolution in natural populations. We build on existing modeling approaches by combining features that facilitate studying the ecological and evolutionary dynamics of realistically structured populations. In particular, the joint consideration of age and size structure enables the analysis of phenotypically plastic populations with more than a single growth trajectory, and ecological feedback is readily included in the form of density dependence and frequency dependence. Stochasticity and life-history trade-offs can also be implemented. Critically, eco-genetic models permit the incorporation of salient genetic detail such as a population's genetic variances and covariances and the corresponding heritabilities, as well as the probabilistic inheritance and phenotypic expression of quantitative traits. These inclusions are crucial for predicting rates of evolutionary change on both contemporary and longer timescales. An eco-genetic model can be tightly coupled with empirical data and therefore may have considerable practical relevance, in terms of generating testable predictions and evaluating alternative management measures. To illustrate the utility of these models, we present as an example an eco-genetic model used to study harvest-induced evolution of multiple traits in Atlantic cod. The predictions of our model (most notably that harvesting induces a genetic reduction in age and size at maturation, an increase or decrease in growth capacity depending on the minimum-length limit, and an increase in reproductive investment) are corroborated by patterns observed in wild populations. The predicted genetic changes occur together with plastic changes that could phenotypically mask the former. Importantly, our analysis predicts that evolutionary changes show little signs of reversal following a harvest moratorium. This illustrates how predictions offered by eco-genetic models can enable and guide evolutionarily sustainable resource management.

Key words: Atlantic cod, Gadus morhua; *density-dependent growth; eco-evolutionary dynamics; evolution; fisheries-induced evolution; fishing-induced adaptive change; harvest; life-history theory; phenotypic plasticity; probabilistic maturation reaction norm; quantitative genetics; reproductive investment.*

POLICY FORUM

Science

ECOLOGY

Managing Evolving Fish Stocks

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David S. Boukal,[2,1] Keith Brander,[5] Bruno Ernande,[6,7] Anna Gårdmark,[8] Fiona Johnston,[7,3]
Shuichi Matsumura,[7,3] Heidi Pardoe,[9,10] Kristina Raab,[11,10] Alexandra Silva,[12]
Anssi Vainikka,[8] Ulf Dieckmann,[7] Mikko Heino,[2,1,7] Adriaan D. Rijnsdorp[13]

Evolutionary impact assessment is a framework for quantifying the effects of harvest-induced evolution on the utility generated by fish stocks.

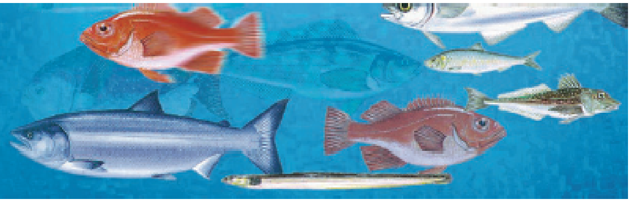
Darwinian evolution is the driving process of innovation and adaptation across the world's biota. Acting on top of natural selection, human-induced selection pressures can also cause rapid evolution. Sometimes such evolution has undesirable consequences, one example being the spreading resistance to antibiotics and pesticides, which causes suffering and billion-dollar losses annually (*1*). A comparable anthropogenic selection pressure originates from fishing, which has become the main source of mortality in many fish stocks, and may exceed natural mortality by more than 400% (*2*). This has, however, been largely ignored, even though studies based on fisheries data and controlled experiments have provided strong empirical evidence for fisheries-induced evolution over a range of species and regions (see table, page 1248). These evolutionary changes are unfolding on decadal time scales—much faster than previously thought.

Life-history theory predicts that increased mortality generally favors evolution toward earlier sexual maturation at smaller size and elevated reproductive effort. Fishing that is

question is not whether such evolution will occur, but how fast fishing practices bring about evolutionary changes and what the consequences will be.

Life-history traits are among the primary determinants of population dynamics, and their evolution has repercussions for stock biomass, demography, and economic yield (*5*, *6*). Fisheries-induced evolution may also be slow to reverse or even irreversible (*5*), with implications for recruitment and recovery (*7*). Consequently, predator-prey dynamics, competitive interactions, relative species

FISH and FISHERIES



Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management

Ane T Laugen[1,2], Georg H Engelhard[3], Rebecca Whitlock[4,5,6], Robert Arlinghaus[7,8], Dorothy J Dankel[9], Erin S Dunlop[9,10,11], Anne M Eikeset[12], Katja Enberg[9,10], Christian Jørgensen[10,13], Shuichi Matsumura[4,7,14], Sébastien Nusslé[15,16], Davnah Urbach[4,17], Loïc Baulier[9,10,18], David S Boukal[9,10,19], Bruno Ernande[4,20], Fiona D Johnston[4,7,8], Fabian Mollet[4,21], Heidi Pardoe[22], Nina O Therkildsen[23], Silva Uusi-Heikkilä[7,24], Anssi Vainikka[25,26], Mikko Heino[4,9,10], Adriaan D Rijnsdorp[21,27] & Ulf Dieckmann[4]

2

Codependent Agents

nature COMMUNICATIONS

ARTICLE

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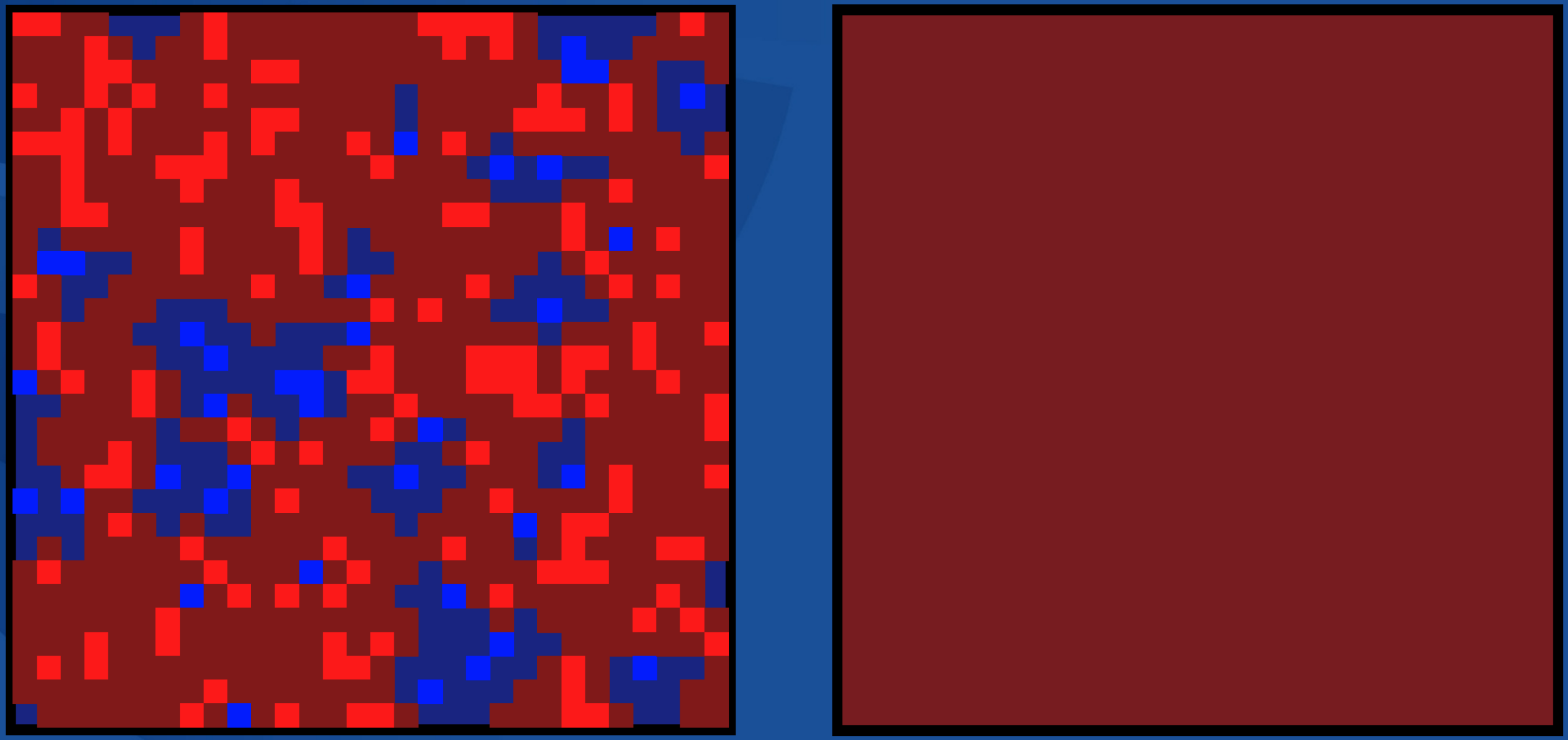
OPEN

Resource heterogeneity can facilitate cooperation

Ádám Kun[1,2,3,4] & Ulf Dieckmann[1]

Although social structure is known to promote cooperation, by locally exposing selfish agents to their own deeds, studies to date assumed that all agents have access to the same level of resources. This is clearly unrealistic. Here we find that cooperation can be maintained when some agents have access to more resources than others. Cooperation can then emerge even in populations in which the temptation to defect is so strong that players would act fully selfishly if their resources were distributed uniformly. Resource heterogeneity can thus be crucial for the emergence and maintenance of cooperation. We also show that resource heterogeneity can hinder cooperation once the temptation to defect is significantly lowered. In all cases, the level of cooperation can be maximized by managing resource heterogeneity.

A few rich cooperators suffice to enable cooperation under adverse conditions



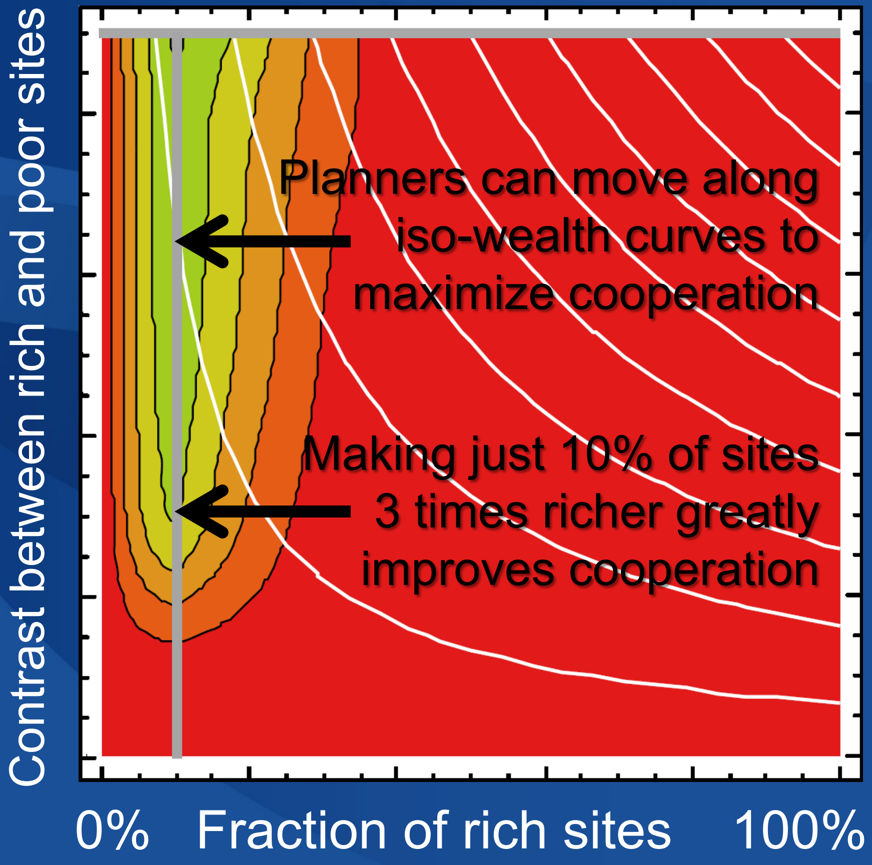
With wealth inequality

Without wealth inequality

Blue: cooperators, red: defectors, bright: rich sites, dark: poor sites

Social planners can maximize cooperation by managing wealth inequality

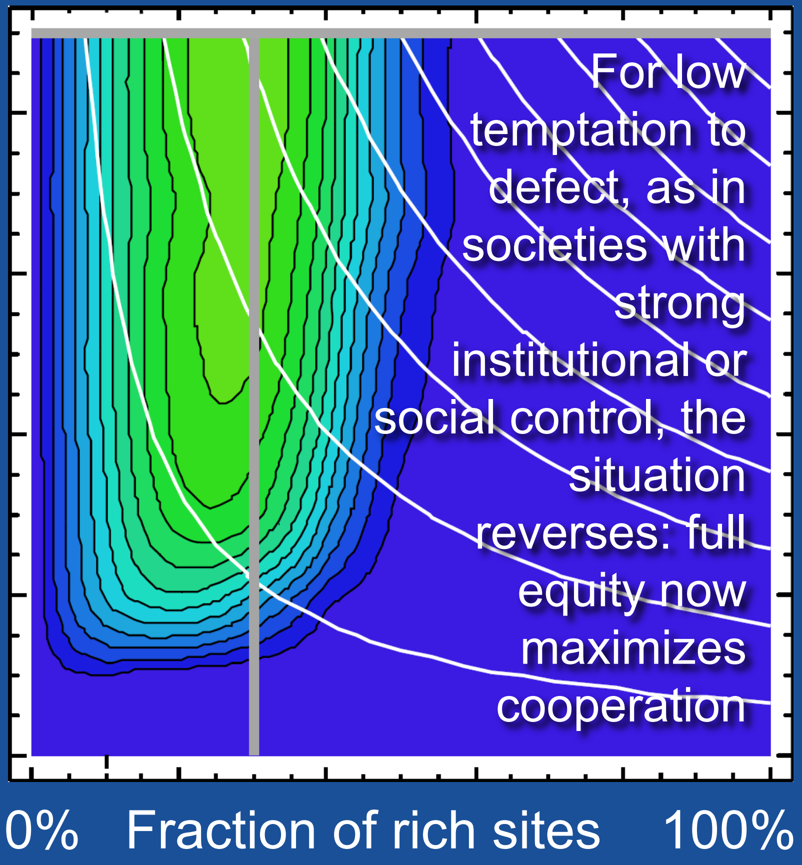
High temptation to defect



Planners can move along iso-wealth curves to maximize cooperation

Making just 10% of sites 3 times richer greatly improves cooperation

Low temptation to defect

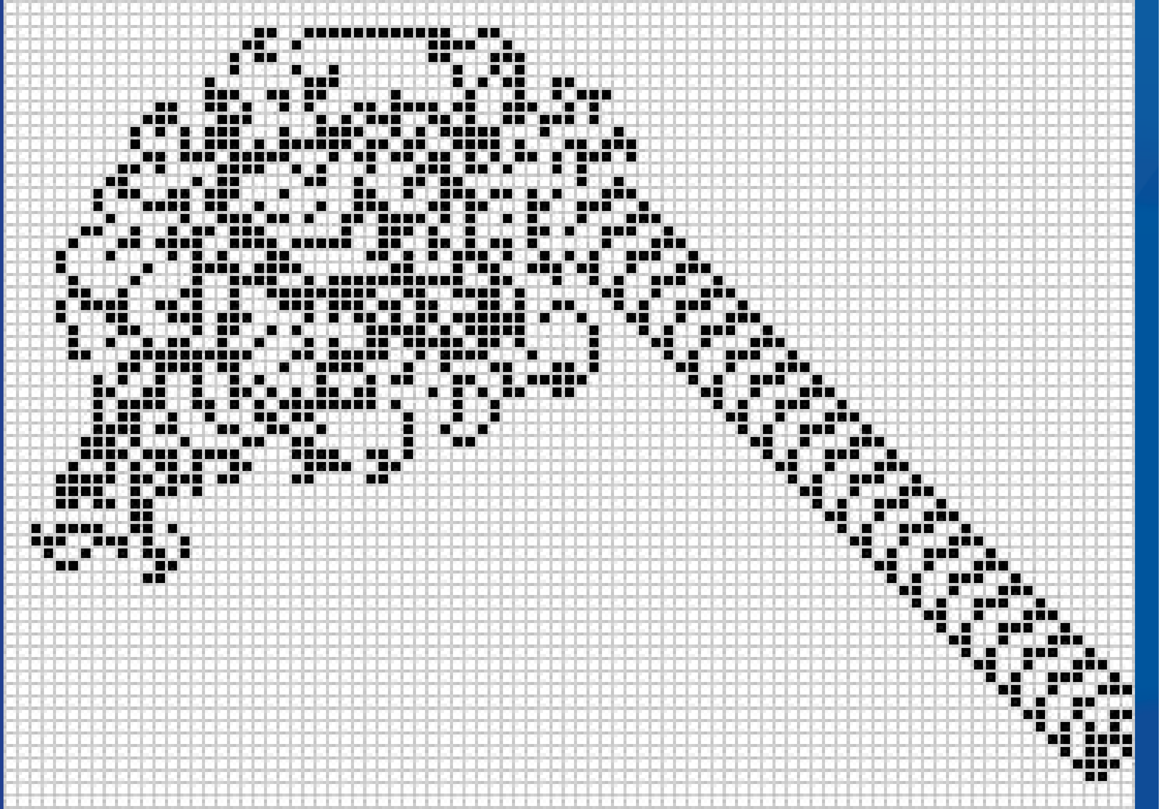


For low temptation to defect, as in societies with strong institutional or social control, the situation reverses: full equity now maximizes cooperation

3

Emergent Phenomena

Langton's Ant

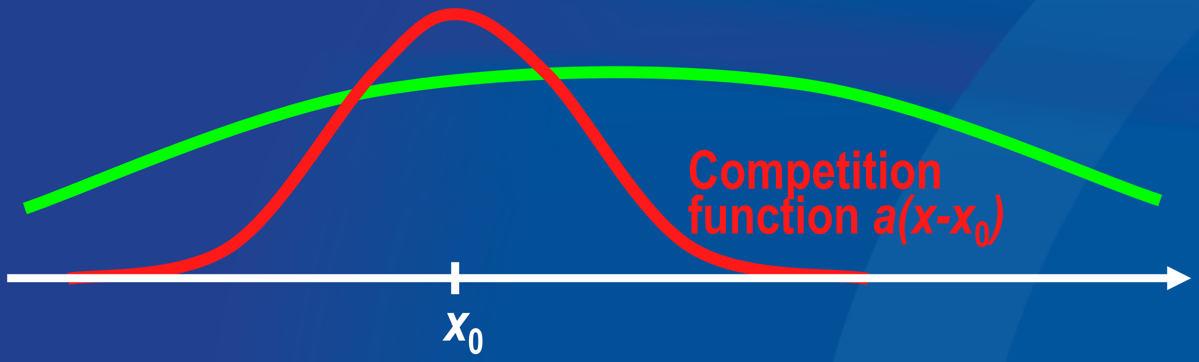


Ant moves:

(1) On a white square, turn 90° right, on a black square, turn 90° left

(2) Flip the color of the square and move forward one square

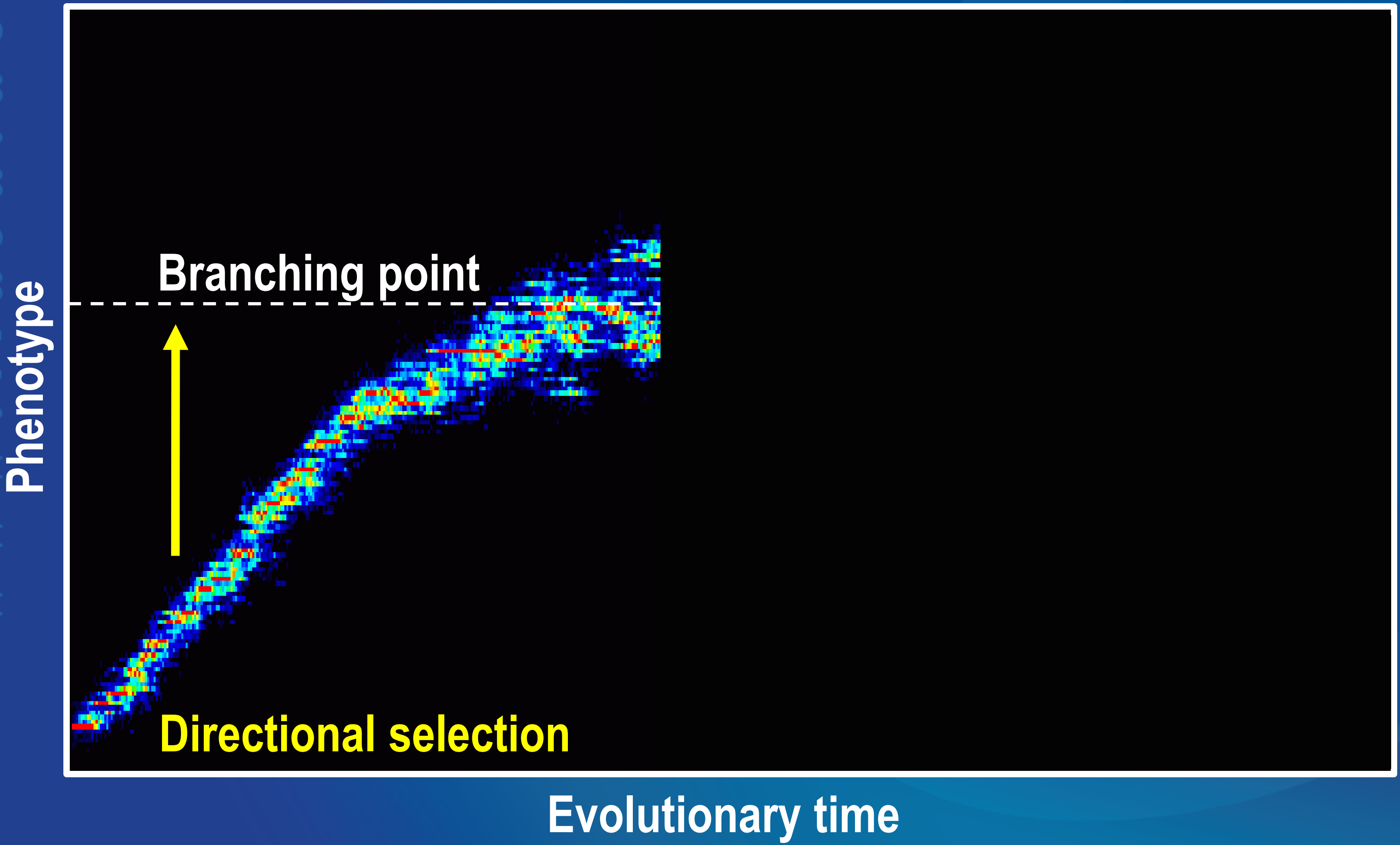
Evolution under Local Competition



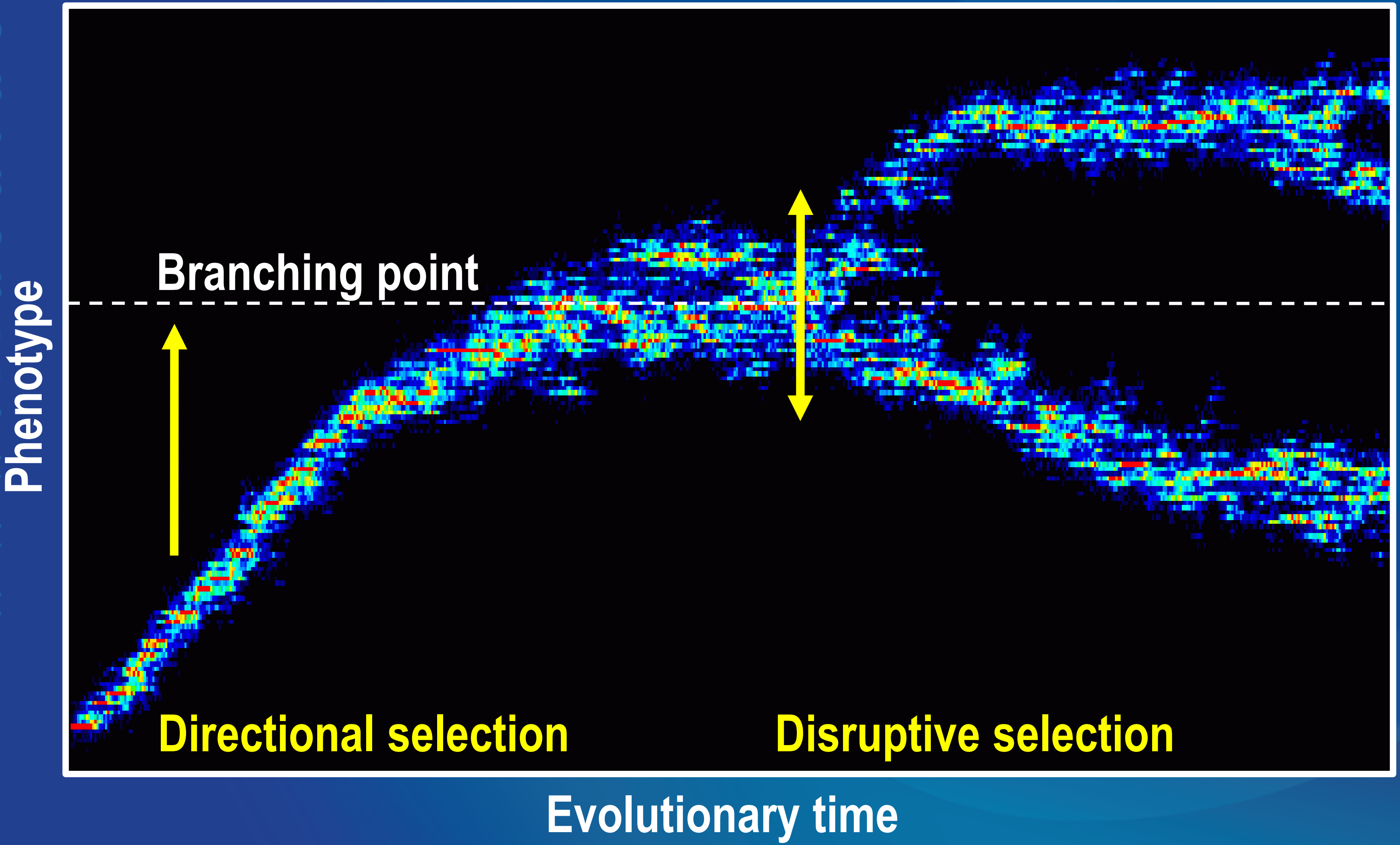
Dynamics of population sizes n_i of strategy x_i

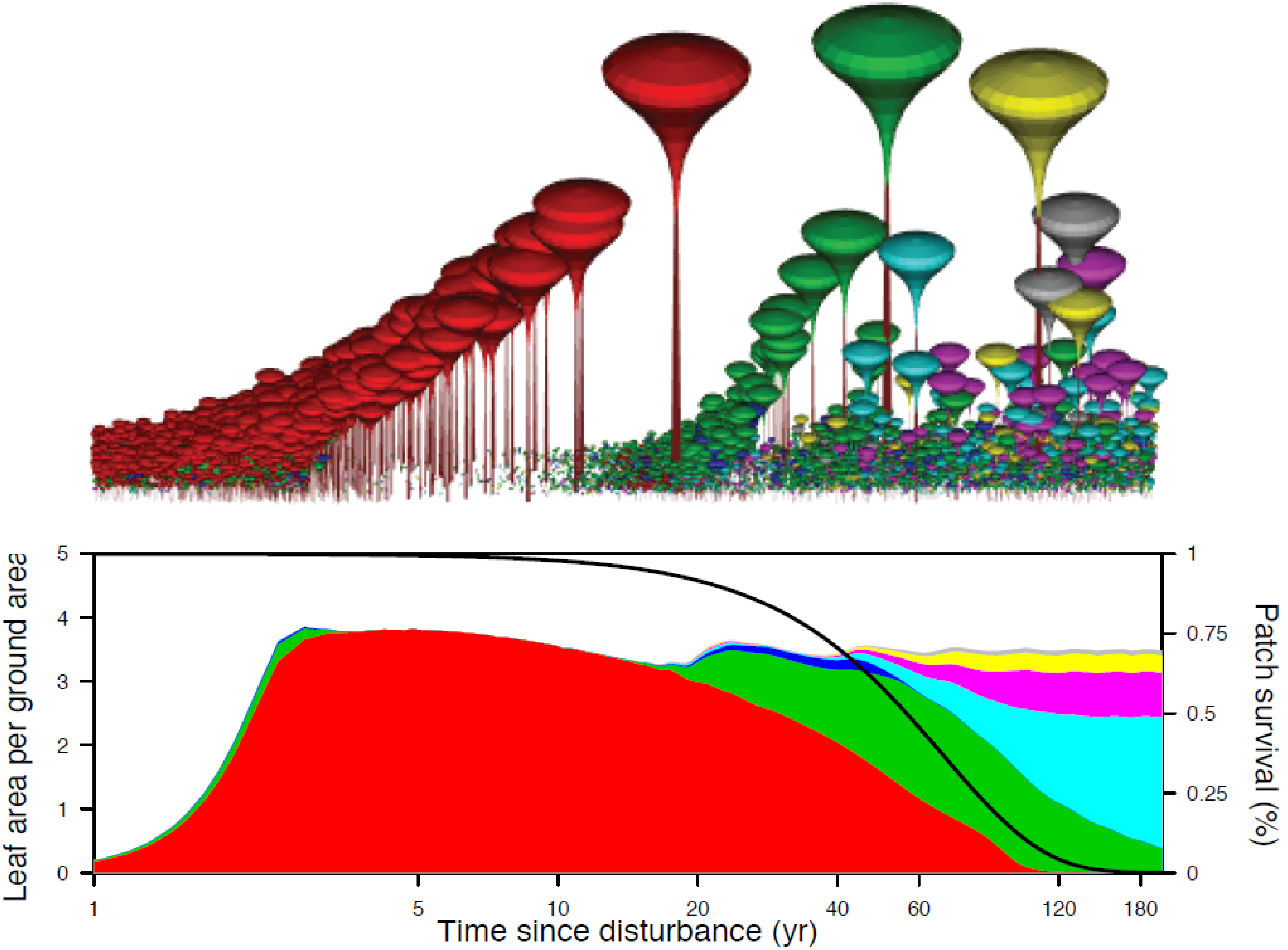
$$\frac{d}{dt}n_i = r\, n_i[1-\frac{1}{\underline{k(x_i)}}\sum_j \underline{a(x_i-x_j)}n_j]$$

Agent-based Evolution

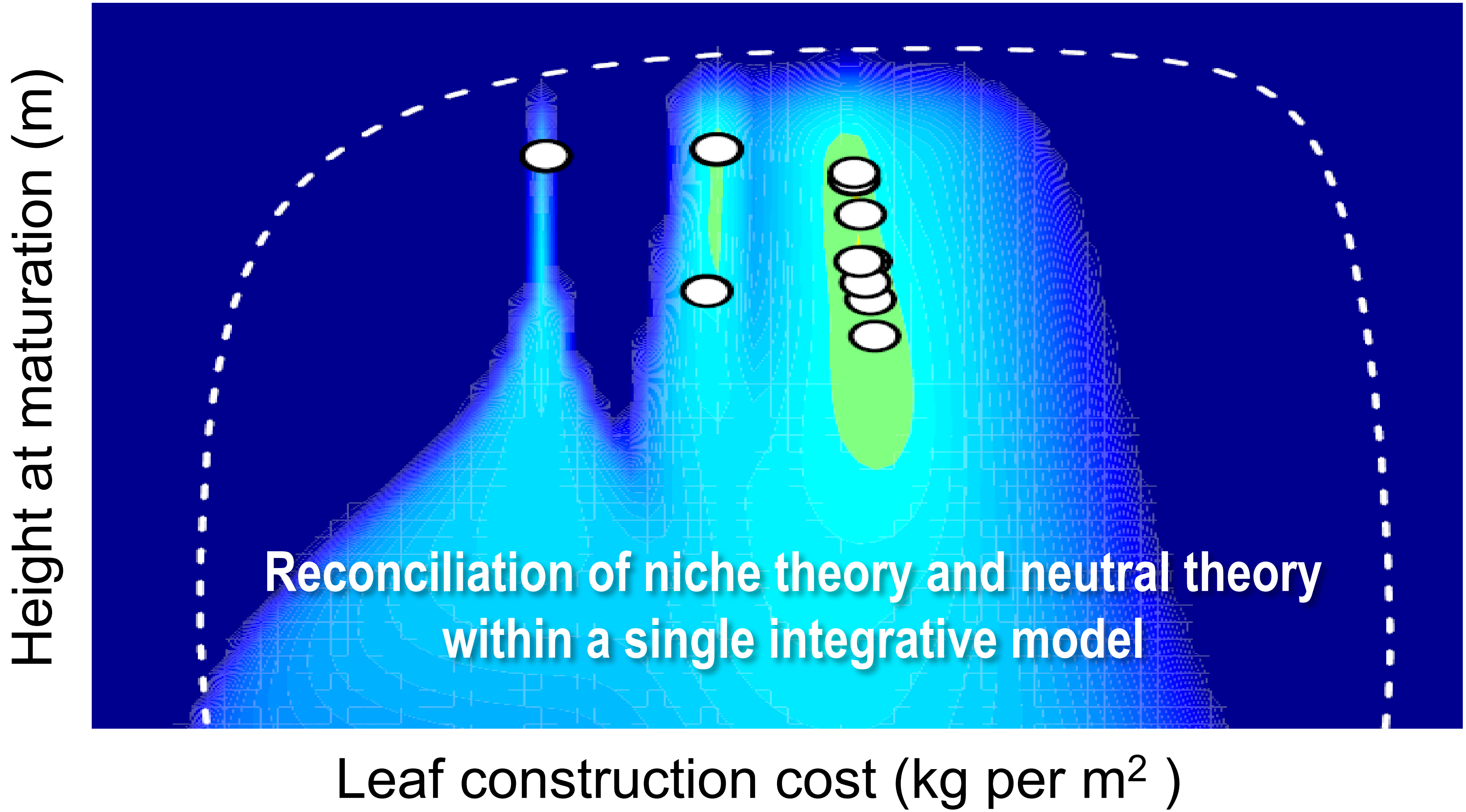


Endogenous Diversification




Leaf area per ground are
0
1
2
3
4
5
Patch survival (%)
0
0.25
0.5
0.75
1
1
5
10
20
40
60
120
180
Time since disturbance (yr)

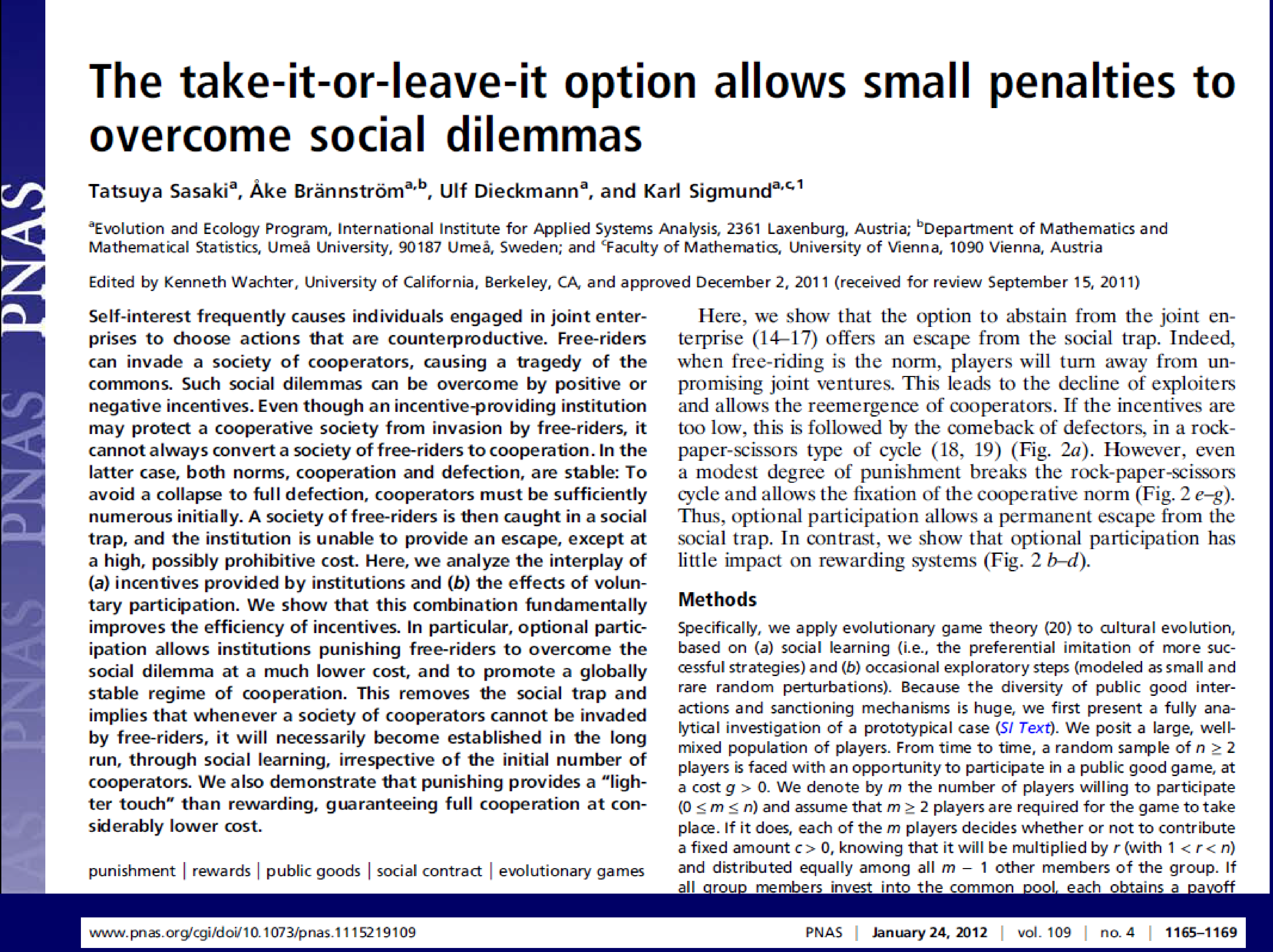
Fitness Landscape of Evolving Vegetation



Reconciliation of niche theory and neutral theory within a single integrative model

4

Tipping Points



The take-it-or-leave-it option allows small penalties to overcome social dilemmas

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Edited by Kenneth Wachter, University of California, Berkeley, CA, and approved December 2, 2011 (received for review September 15, 2011)

Self-interest frequently causes individuals engaged in joint enterprises to choose actions that are counterproductive. Free-riders can invade a society of cooperators, causing a tragedy of the commons. Such social dilemmas can be overcome by positive or negative incentives. Even though an incentive-providing institution may protect a cooperative society from invasion by free-riders, it cannot always convert a society of free-riders to cooperation. In the latter case, both norms, cooperation and defection, are stable: To avoid a collapse to full defection, cooperators must be sufficiently numerous initially. A society of free-riders is then caught in a social trap, and the institution is unable to provide an escape, except at a high, possibly prohibitive cost. Here, we analyze the interplay of (*a*) incentives provided by institutions and (*b*) the effects of voluntary participation. We show that this combination fundamentally improves the efficiency of incentives. In particular, optional participation allows institutions punishing free-riders to overcome the social dilemma at a much lower cost, and to promote a globally stable regime of cooperation. This removes the social trap and implies that whenever a society of cooperators cannot be invaded by free-riders, it will necessarily become established in the long run, through social learning, irrespective of the initial number of cooperators. We also demonstrate that punishing provides a "lighter touch" than rewarding, guaranteeing full cooperation at considerably lower cost.

punishment | rewards | public goods | social contract | evolutionary games

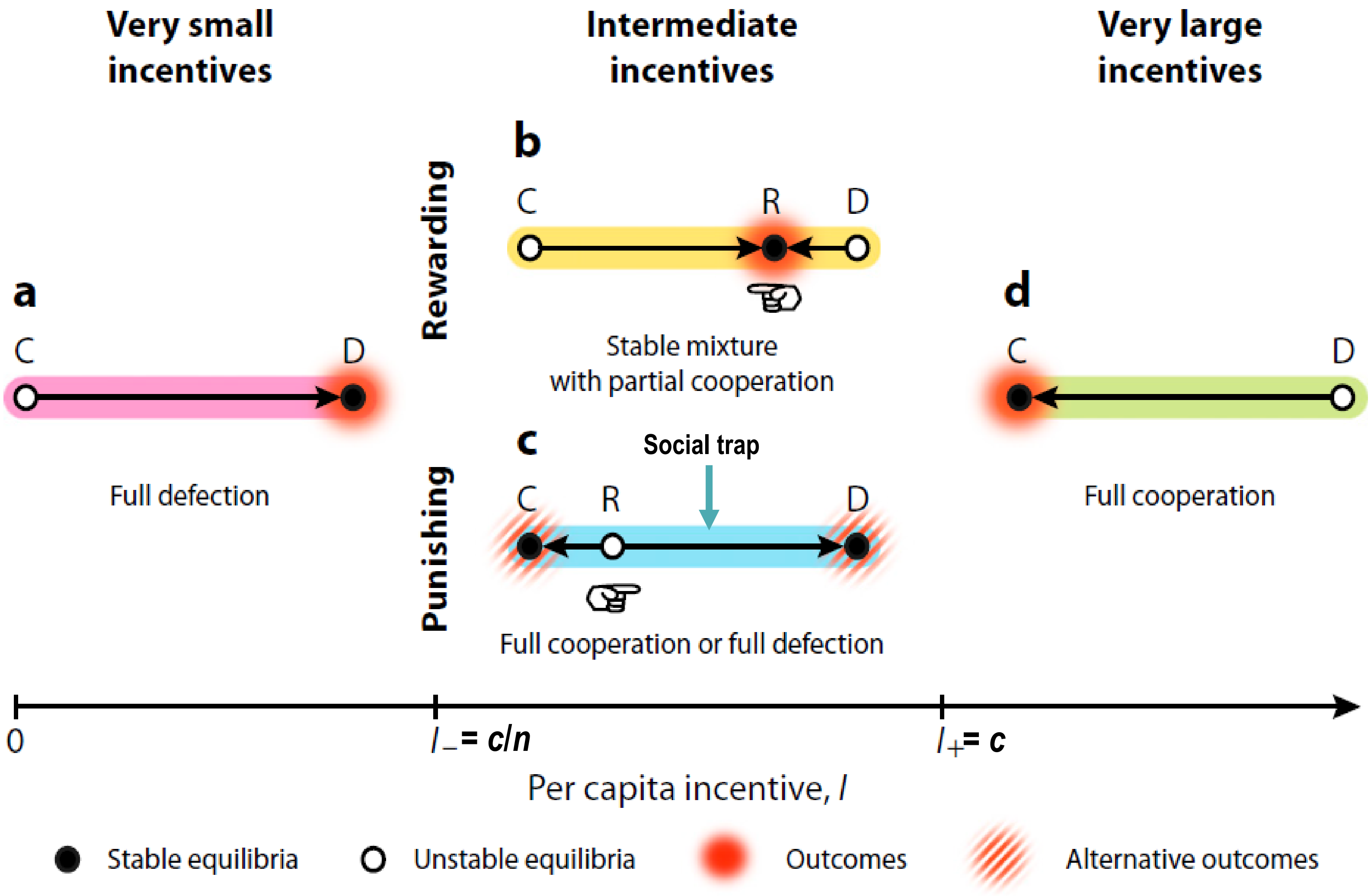
Here, we show that the option to abstain from the joint enterprise (14–17) offers an escape from the social trap. Indeed, when free-riding is the norm, players will turn away from unpromising joint ventures. This leads to the decline of exploiters and allows the reemergence of cooperators. If the incentives are too low, this is followed by the comeback of defectors, in a rock-paper-scissors type of cycle (18, 19) (Fig. 2*a*). However, even a modest degree of punishment breaks the rock-paper-scissors cycle and allows the fixation of the cooperative norm (Fig. 2 *e*–*g*). Thus, optional participation allows a permanent escape from the social trap. In contrast, we show that optional participation has little impact on rewarding systems (Fig. 2 *b*–*d*).

Methods

Specifically, we apply evolutionary game theory (20) to cultural evolution, based on (*a*) social learning (i.e., the preferential imitation of more successful strategies) and (*b*) occasional exploratory steps (modeled as small and rare random perturbations). Because the diversity of public good interactions and sanctioning mechanisms is huge, we first present a fully analytical investigation of a prototypical case (*SI Text*). We posit a large, well-mixed population of players. From time to time, a random sample of $n \geq 2$ players is faced with an opportunity to participate in a public good game, at a cost $g > 0$. We denote by m the number of players willing to participate ($0 \leq m \leq n$) and assume that $m \geq 2$ players are required for the game to take place. If it does, each of the m players decides whether or not to contribute a fixed amount $c > 0$, knowing that it will be multiplied by r (with $1 < r < n$) and distributed equally among all $m - 1$ other members of the group. If all group members invest into the common pool, each obtains a payoff

www.pnas.org/cgi/doi/10.1073/pnas.1115219109 PNAS | January 24, 2012 | vol. 109 | no. 4 | 1165–1169

Compulsory Participation



Very small incentives

Intermediate incentives

Very large incentives

Rewarding

Punishing

a

Full defection

b

Stable mixture with partial cooperation

c

Social trap

Full cooperation or full defection

d

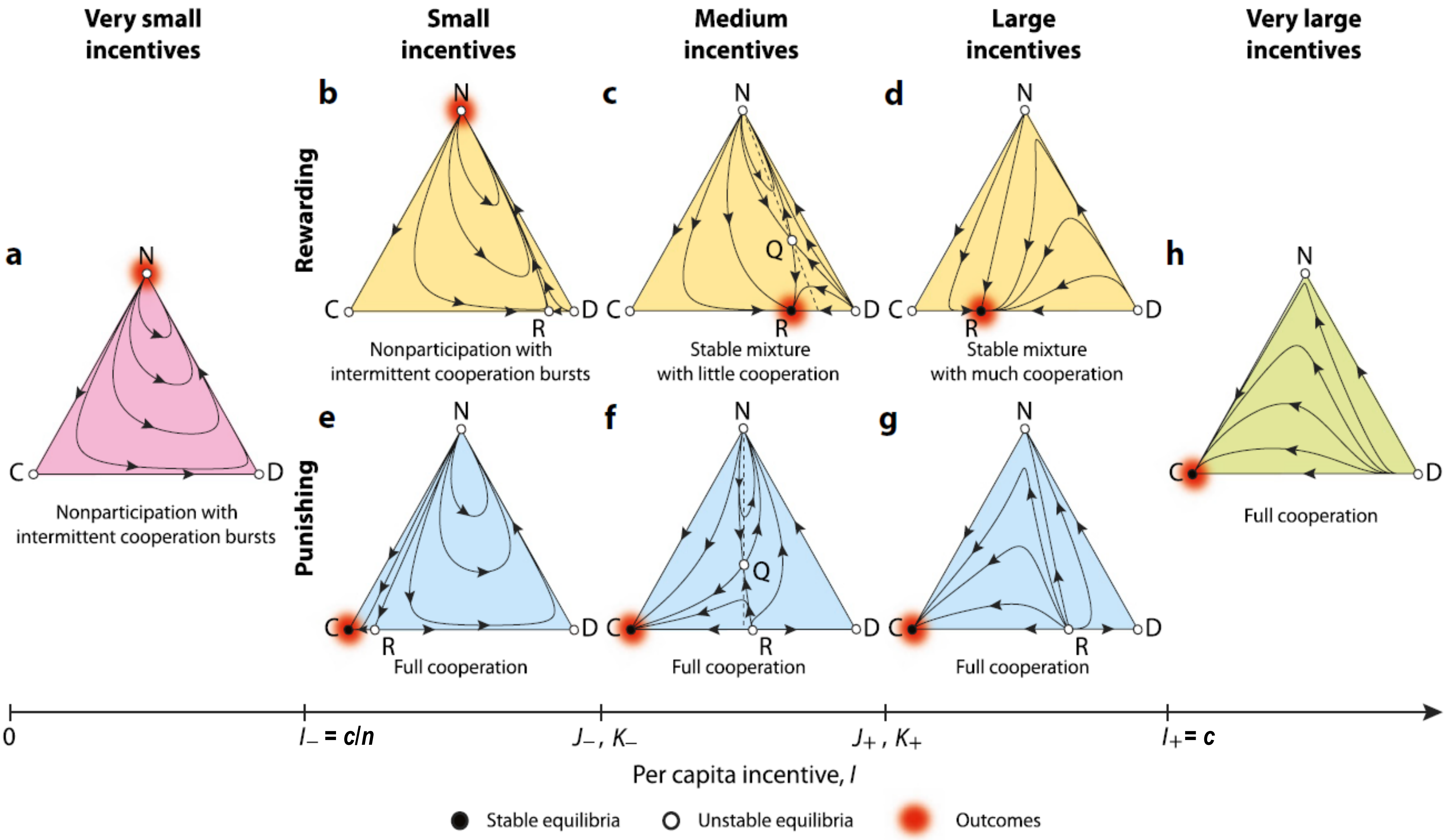
Full cooperation

0 — $I_- = c/n$ — $I_+ = c$

Per capita incentive, I

- ● Stable equilibria
- ○ Unstable equilibria
- Outcomes
- Alternative outcomes

Voluntary Participation



a: Nonparticipation with intermittent cooperation bursts

b: Nonparticipation with intermittent cooperation bursts

c: Stable mixture with little cooperation

d: Stable mixture with much cooperation

e: Full cooperation

f: Full cooperation

g: Full cooperation

h: Full cooperation

5

Self-organized Criticality

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Abrupt community transitions and cyclic evolutionary dynamics in complex food webs[☆]

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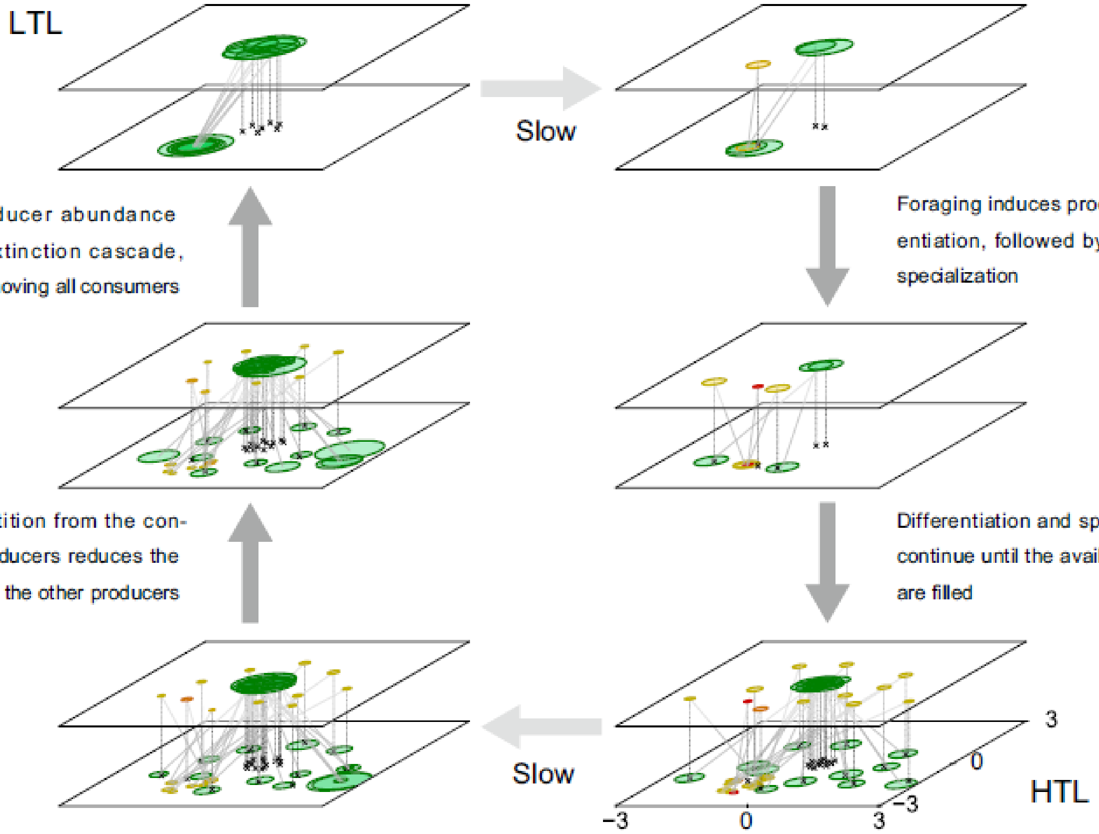
HIGHLIGHTS

- We present the first individual-based model of community evolution in which linear functional responses suffice to enable the emergence of multiple trophic levels.
- Evolving communities stochastically alternate between two states that are either dominated by producers or additionally feature diverse consumers.
- We explain these cyclic transitions by an inexorable evolutionary drive towards particularly fragile community structures that allow extinction cascades causing consumer collapse.
- Our findings are shown to be robust to a wide range of model variations.

Community Assembly and Collapse



A generalist consumer emerges at random, foraging on the producers and itself

Foraging induces producer differentiation, followed by consumer specialization

Differentiation and specialization continue until the available niches are filled

Random extinction of a TL2 consumer increases the abundance of the corresponding producers

Strong competition from the consumer-free producers reduces the abundance of the other producers

Reduced producer abundance triggers an extinction cascade, eventually removing all consumers