Emergence of social inequality in a spatial-ecological public goods game
Jaideep Joshi¹, Åke Brännström²,³, Ulf Dieckmann³

¹ Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, India
² Department of Mathematics and Mathematical Statistics, Umeå University, Umeå, Sweden
³ Evolution and Ecology Program, International Institute for Applied Systems Analysis, Laxenburg, Austria

Abstract

Spatial ecological public goods, such as forests, grasslands, and fish stocks risk being overexploited by selfish consumers, a phenomenon called “the tragedy of commons”. The spatial and ecological dimensions introduce new features absent in non spatio-ecological contexts, such as consumer mobility, incomplete information availability, and rapid evolution by social learning. It is unclear how these different processes interact to influence the harvesting and dispersal strategies of consumers. To answer these questions, we develop and analyze an individual-based, spatially-structured evolutionary model with explicit resource dynamics. We find that, 1) When harvesting efficiency is low, consumers evolve a sedentary harvesting strategy, with which resources are harvested sustainably, but harvesting rates remain far below their maximum sustainable value. 2) As harvesting efficiency increases, consumers adopt a mobile ‘consume-and-disperse’ strategy, which is sustainable, equitable, and allows for maximum sustainable yield. 3) Further increase in harvesting efficiency leads to large-scale overexploitation. 4) If costs of dispersal are significant, increased harvesting efficiency also leads to social inequality between frugal sedentary consumers and overexploitative mobile consumers. Whereas overexploitation can occur without social inequality, social inequality always leads to overexploitation. Thus, we identify four conditions, which are characteristic (and as such positive) features of modern societies resulting from technological progress, but also risk promoting social inequality and unsustainable resource use: high harvesting efficiency, moderately low costs of dispersal, high consumer density, and consumers’ tendency to rapidly adopt new strategies. We also show that access to global information, which is also a feature of modern societies, may help mitigate these risks.

1 Introduction

A public good that is freely accessible to everyone, but limited in quantity, can be optimally used only if everyone cooperates in using no more than their fair share. However, those who consume more than their fair share obtain a greater benefit. This
creates an incentive to overexploit the public good, which threatens to reduce resource availability, leaving everyone worse off. This social dilemma is called the ‘tragedy of the commons’ [1, 2]. The ubiquity of social dilemmas has led to widespread interest in exploring mechanisms that can support cooperation, not only in evolutionary biology but also in economics, cognitive sciences, and social sciences [3–7]. Indeed, research into mechanisms capable of preventing social dilemmas can help inform important policy decisions, such as fisheries regulations, and support treaty negotiations on global commons, such as ozone-layer protection and climate change mitigation [8–17].

Owing to the combined efforts of many scientists, several mechanisms that promote cooperation have been identified [see e.g., 18]. Kin-selection [19], in which cooperative acts are directed towards genetic relatives, and direct reciprocity [20–24], in which individuals cooperate with individuals who return cooperation, are two key mechanisms that promote cooperation. In the case of humans, indirect reciprocity, in which individuals cooperate with those who have a reputation for cooperating [25–27], is also an important mechanism supporting cooperation. Additionally, combinations of positive and negative incentives, such as offering rewards to cooperators and punishing defectors can also be a powerful means of promoting cooperation [28–31]. Such studies are mostly stylized, often based on simple mathematical models and occasionally on experiments.

Most real socio-ecological systems are spatially structured. With some exceptions [e.g., 32], spatial structure is thought to promote cooperation as it both exposes defectors to the consequences of their own selfish acts and allows local clusters of cooperators to form, enabling multilevel selection for cooperation [33–35]. However, space also allows mobility. Mobility can hinder cooperation allowing defectors to escape the consequences of their own acts [36]. Indeed, several studies have considered the effect of fixed mobility and found that cooperation can be sustained when mobility is either low [37] or dependent on local conditions [38, 39]. If mobility incurs no cost, then defectors may invariably evolve high mobility and undermine cooperation. When dispersal is costly, an evolutionary interplay between mobility and cooperation may occur, but thus far only a handful of studies have considered the joint evolution of costly mobility and cooperation [40–44]. A recent study by Mullon et al. [45] found that when dispersal and cooperation coevolve, two coexisting strategies can spontaneously emerge: one benevolent and sessile, the other self-serving and dispersing.

In socio-ecological settings, the ecological dynamics of the resource plays a crucial role in the evolutionary dynamics. First, interactions between individuals are often mediated through the resource, i.e., individuals do not directly interact with other individuals, but respond to changes in the resource caused by others. Second, limited resource availability may lead to the evolution of density-dependent strategies, since per-capita resource extraction is expected to decline with consumer density. Third, ecological public goods, such as renewable resources, have their own ecological time scale of resource replenishment. Most studies assume that evolution is a slow process. However, memetic evolution is not biologically constrained, and can occur on
ecological or even faster timescales. Evolutionary outcomes may be dramatically differ-
ent depending on whether evolution is slow or fast [46]. Furthermore, spatial extent may prevent consumers from having full information about other consumers and the environment, because information may not reach far-off consumers. Such local information may lead to local selection, which is typically expected to benefit defectors. Despite these important gaps, only a few studies have so far considered ecological public goods [2, 47, 48], and even fewer studies explicitly model a renewable resource [e.g., 49].

Here, we move beyond the aforementioned studies, in particular the work by Parvi-
en [44] and Mullon et al. [45], by investigating the role of explicit resource dynamics, fast evolution, and incomplete information about other individuals’ strategies on the evolution of cooperation. Using a socio-ecological model of public-goods utilization, we investigate for the first time the coevolution of resource harvesting and dispersal strategies in realistic socio-ecological settings.

2 Methods summary

We model consumers and resources on a continuous two-dimensional space. We assume that resource growth is logistic with intrinsic growth rate $r$ and carrying capacity $K$. Each consumer $i$ exploits resources in his/her local neighborhood at a harvesting rate $r_{H,i}$. When the local resource falls below a threshold, consumers disperse to new locations drawn from a normal distribution centered at their current position with a mean ‘dispersal radius’ of $\sigma_{D,i}$. The harvested resource $R_i$ yields benefit $bR_i$ and incurs cost $c_{Hr_{H,i}}^2$, while dispersal incurs cost $c_D$ per unit length. The payoff to each individual is the time-averaged utility of resource harvest $(bR_i - c_{Hr_{H,i}}^2)$ minus the cost of total dispersal distance.

To account for evolution by social learning, we assume that at rate $r_I$, individuals imitate the strategies (harvesting rate and dispersal radius) of other individuals with greater payoff. The imitation rate defines the evolutionary timescale: consumers are ‘impatient’ if the imitation rate is much larger than the resource growth rate; such consumers tend to imitate even before the consequences of others’ strategies on the resource become apparent. To account for information availability, we assume that each individual is more likely to choose an individual to imitate within an ‘imitation radius’ $\sigma_I$. A low imitation radius means that consumers are ‘myopic’ and only imitate their neighbors, whereas a very large or infinite imitation radius means that consumers have ‘global information’, and can imitate anyone in the population. In this way, we model the essential characteristics of human behavior to make our model realistic, while leaving out other confounding factors to keep our model minimal.

Without loss of generality, we reduce the number of parameters by carefully choosing our units. Full details of our model and its parameterization are given in Methods. SI-Fig 1 shows a schematic of the system behaviour along with meanings of key parameter
values. Video S5.1 (see https://github.com/jaideep777/jaideep_thesis_videos) shows a representative simulation of consumer behaviour where they exploit local resource and disperse.

An important parameter in our model is the consumer density $\rho$. Additionally, our model has two pairs of key parameters. The first pair are the payoff parameters $b$ and $c_H$ that determine the efficiency $b/c_H$ and utility $(bR_i - c_Hr_{H,i}^2)$ of resource consumption. The second pair are imitation parameters $r_I$ and $\sigma_I$ that determine the spatio-temporal scales of imitation, reflecting impatience and myopia of consumers. See SI-Table 2 for a glossary of terms.

3 Results

To explore the social dynamics of harvesting and dispersal in a realistic environment, we perform simulations of our system for a wide range of parameter values, which correspond to diverse socio-ecological settings. Specifically, we investigate the effect of population density, costs and benefits of harvesting and dispersal, the imitation rate, and imitation radius, on the evolved strategies. We present our key findings below.

3.1 Sedentary and mobile strategies emerge spontaneously

All individuals start with the same harvesting rate and dispersal-kernel size at time $t = 0$. As the interplay of resource and imitation dynamics progresses, individuals diversify into two distinct strategies (Fig. 1). One is a sedentary strategy, with consumers who adopt a low harvesting rate ($r_H = 0.5$) and do not disperse. The second is a mobile strategy, with consumers who adopt a high harvesting rate ($r_H = 6$) and a non-zero dispersal radius ($\sigma_D = 1$ in the outcome shown). At the population level, these strategies coexist over time, although individuals may change their strategy frequently by imitation of other individuals.

To investigate the robustness of this result under more realistic assumptions of intelligent consumers, we allow consumers to ‘explore’ random strategies at a low rate. SI-Fig. 2 shows that with low strategy exploration rates, the system evolves to the same evolutionary endpoints as in Fig. 1.

3.2 Increasing consumer density leads to social inequality

When consumer density is low, all consumers can adopt an ‘affluent’ harvest-intensively-disperse-far strategy. At low consumer density, everyone can harvest at high rates without causing the resource to deplete globally. However, as consumer density increases, harvesting rate and dispersal radius evolve to lower values (Fig. 2). As consumer density increases further, the intensive harvesting strategy is no longer sustainable, because resources begin to deplete. At this stage, instead of lowering their harvesting
rates to adjust to the changed circumstances, some consumers begin to harvest even
more intensely to sustain dispersal, while others adopt a ‘frugal’ harvest-prudently-
don’t-disperse strategy, by accepting lower resource extraction along with reduced
dispersal costs. The proportion of sedentary consumers continues to increase with
consumer density, and finally, when space gets overcrowded, all consumers adopt a
sedentary strategy.

At all consumer densities, the average evolved harvesting rates (white line in Fig. 2) are
higher than the corresponding optimal rates, i.e., the yield-maximizing rate (green) or
the profit-maximizing rate (magenta). Consequently, the average resource extraction
rate is less than the optimal values. Thus, when left to themselves, consumers over-
exploit the resource to some degree and the question arises, when do consumers adapt
a yield-maximizing strategy?

3.3 Mobile consumers achieve maximum yield at the ‘edge of inequality’, unless dispersal is very cheap

When the benefits of harvesting are low, the population is monomorphic (or ‘sedent-
tary’ regime; region S in Fig. 3A,C), and all individuals have a low harvesting rate
(Fig. 3B) and near-zero dispersal (Fig. 3D). The evolved harvesting rates are close
to the yield-maximizing rate for sedentary consumers (see Methods). In this regime,
resource harvesting is inefficient: the harvesting rate is low (Fig. 4A) despite an abun-
dance of resources in the environment (Fig. 4B). This is because high dispersal costs
force consumers to adapt a sedentary lifestyle and prevent them from exploring other
resource rich areas. However, since each consumer only harvests resource from his/her
own location, there is no competition for resource, and resource distribution is equal.

As the harvesting benefits increase and costs of dispersal decrease, dispersal becomes
viable. The population still remains monomorphic, but all consumers now adapt a
mobile (harvest and disperse) strategy (‘mobile’ regime; region M in Fig. 3D). The
harvesting rate and resource extraction rate both increase, until maximum yield is
reached (green band in Fig. 3B and Fig. 4A). At this extraction rate, consumers locally
deplete the resource, but the depletion is temporary and resource extraction is globally
sustainable. Resource distribution is fair, and all consumers harvest the resource at
similar rates. Therefore, resource extraction is efficient as well as fair. However, when
both benefits and costs of harvesting are very high (i.e, equivalently, costs of dispersal
are very low), the temptation to rapidly harvest the resource is strong, and also feasible
as dispersal is cheap. Consequently, consumers begin to overexploit the resource, and
even though the population remains monomorphic (everyone evolves high dispersal),
resource extraction drops below the optimal value as a consequence of the tragedy of
the commons (top right corner in Figs. 3 and 4).

When costs of dispersal are significant, increasing harvesting benefits lead to a diversi-
fication of strategies (‘coexistence’ regime; region S & M). Initially, mobile consumers
tend to harvest at high rates. But as the amount of resource in the environment
reduces because of overexploitation by these consumers, the sedentary strategy also becomes viable. This is because the benefit forgone by a reduction in harvesting rate is balanced by avoiding the cost of dispersal. As some consumers become sedentary, the density of mobile consumers decreases, allowing them to sustain higher harvesting rates. Therefore, prudent sedentary consumers (cooperators) and overexploitative mobile consumers (cheaters) coexist in the population (Fig. 3A,C). This regime is characterized by a social divide, in which the resource distribution is unequal. Low costs of harvesting allow cheaters to greatly increase their harvesting rates (outsets in 3B). A small number of cheaters thrive at the expense of a large fraction of cooperators (SI-Fig. 5). For lower efficiency values, sedentary consumers adapt the profit-maximizing harvesting rate. However, as efficiency increases further, mobile consumers become increasingly overexploitative, destroying even the neighborhoods of sedentary consumers and driving their resource extraction rates to zero (Fig. 4B, outsets). In this regime, resource distribution may be equal on average over a long time period as each consumer adapts either strategy at different times, but in the short term, this regime is inequitable.

3.4 Rapid consumer adaptation and localized information both aggravate social inequality

The imitation of strategies by consumers depends on their knowledge of strategies of other consumers. If information on others’ strategies travels far, each consumer has a larger pool of potential strategies to compare with its own and imitate. So far, we assumed that all individuals can sample the entire population for social learning (\(\sigma_1 \to \infty\)). We now relax this assumption. Figure 5 shows the evolved strategies as a function of the imitation radius and the imitation rate, for payoff parameters from the mobile regime (See SI-Fig. 6 for a similar analysis in the coexistence regime).

For low to moderate imitation rates (region marked ‘M’ in Fig. 5A) the population is monomorphic as in the mobile regime, and the resource extraction rate is high (region ‘M’ in Fig. 6). As the imitation rate increases, i.e., as consumers become ‘impatient’, consumers diversify into mobile and sedentary strategies. Fast imitation causes a strategy to change even before its consequences are reflected in the payoffs. Particularly, it prevents sedentary consumers from realizing the long-term benefits of low harvesting rates, leading to an unsustainable increase in harvesting (outset in Fig. 5 and SI-Fig. 7). For large imitation radius (region I), the difference between the harvesting rates of sedentary and mobile consumers is small (SI-Fig. 7). Since all consumers have high harvesting rates, the resource is overexploited (Fig. 6). As a consequence, the cheaters are only marginally better off than cooperators. The cheater strategy becomes more rewarding when consumers are impatient as well as myopic (region III in Fig. 5A). In this regime, cheaters become extremely overexploitative with very high harvesting rates. However, the proportion of cheaters is low (SI-Fig. 7). Therefore this regime is marked by stark social divide, with a handful of cheaters driving extraction rates of the majority of consumers to zero. Resource extraction
is acutely inefficient, with much of the resource being left unharvested (Fig. 6). For intermediate spatio-temporal scales of imitation (region II), cheaters are less aggressive, but greater in number. Cooperator harvesting rates are close to the sedentary profit-maximizing value. This leads to greater resource extraction, almost entirely by cheaters (Fig. 6, SI-Fig. 7). In other words, this region is most favourable for cheaters.

### 3.5 Effect of parameters and model variations

In SI-Section S3, we investigate the effect of variations in the remaining model parameters as well as some simple model extensions.

### 4 Discussion

#### 4.1 Comparison with previous studies

Spatial public goods games have frequently been used to study the evolution of cooperation. Often, models of spatial public goods rely on additional mechanisms to stabilize cooperation, such as volunteering [34], rewarding cooperators or punishing defectors [28, 50, 51], and conditional strategies [52]. Other models rely on a spatial structure (inherent or emergent) that support clustering of cooperators [35, 53, 54]. In all these studies cooperation has been defined in terms of game-theoretic payoffs, and whether an act is cooperative or defective is independent of the socio-environmental conditions. By contrast, cooperation and defection in our model can only be defined in relation to the resource: cooperation is the strategy that ensures that total resource extraction rate is less than the maximum sustainable yield.

When movement is costly, consumers of a spatial resource may face a ‘milker-killer dilemma’ [55, 56], in which each consumer has a choice to be a milker (like our sedentary consumers) or a killer (like our mobile consumers). Several studies have tried to identify the conditions under which either milker and killer strategies are favored [55, 57, 58]. But none of these studies had found coexistence of milkers and killers. Recently, [45] showed a coexistence of sessile cooperators (like milkers) and mobile defectors (like killers) by allowing the coevolution of cooperation and dispersal. In agreement with their results, we found emergence and coexistence of prudent sedentary consumers and mobile overexploitative consumers. However, in our model, direct interactions between individuals are absent, and payoffs of cooperation and dispersal are realized only through the resource. When cheaters begin to overexploit the resource, the incentive to overexploit diminishes and the sedentary, prudent harvesting strategy becomes equally attractive. Therefore, resource dynamics converts cooperation into a beneficial strategy and allows cooperation to be maintained.

Another recent study by [44] used an infinite island model to study the coevolution of cooperation (in the form of investments to public goods) and dispersal (in the form of the rate of leaving the current patch). They found that both dispersal and cooperation
are favoured if catastrophes wipe out local populations at an intermediate rate. This is because catastrophes reduce local population densities and increase relatedness among the remaining individuals. It would be interesting to examine the effect of catastrophes in our model. On the one hand, catastrophes may prevent strategy diversification, because a decrease in consumer density brought about by a catastrophe may allow all consumers to sustain high harvesting rates. On the other hand, catastrophes may facilitate coexistence due to the well-known competition-colonization tradeoff.

4.2 Extensions and further directions

Our model makes deliberately simple assumptions to capture the essential processes governing strategy evolution. We have assumed that all consumers have the capacity to adapt any strategy they wish. Thus, a sedentary consumer with very low resource extraction rate can switch to an expensive mobile strategy. Because of frequent switching of strategies, all individuals in our population have equal payoffs in the long term, even when two distinct strategies exist at the population level. In real situations however, resource-poor individuals may not be able to afford a strategy switch, forcing them permanently into a low extraction strategy. These effects can be further investigated by incorporating a cost of switching strategies.

Although we have investigated the dependence of evolved strategies on population density, we have kept the population size constant. However, it is well known that increased resource consumption resulting from higher efficiency and better technology leads to a rapid increase in population size. This in turn may necessitate further increase in efficiency. It is possible to incorporate such feedbacks in our model. Exploring the fate of a society in the presence of such feedbacks would be an interesting direction for further research.

5 Conclusion

In conclusion, we have explored how dynamics of a renewable resource influence the harvesting and dispersal strategies of consumers. We found that increased consumer density, increased efficiency of resource harvest, reduced costs of dispersal, rapid adaptation by consumers, and localized information on others, are features that lead to a spontaneous diversification of consumers into prudent sedentary consumers and over-exploitative mobile ones. This social divide is always accompanied by overexploitation of resources. In modern societies, developments such as technological progress have led to an increase in resource harvesting efficiency and reduced costs of dispersal. This has in turn led to an increase in population size. Furthermore, the pace of life has increased, which in our model, reflects in the pace of strategy adaptation. While these are positive developments as such, our model suggests that they may pose a threat to social equality and sustainability of resource. Our model also suggests a way of mitigating these threats: increasing information availability, which is also a character-
istic feature of modern societies. We hope that further work can build on the findings presented here and shed light on the foundations of human and animal behaviour and its changes in response to changing socio-ecological conditions.

6 Acknowledgements

The authors would like to thank Vishwesha Guttal for providing computational facilities (via DST-FIST and DBT-IISc partnership programme). JJ would like to thank TIFAC, Government of India, for providing travel support and stipend for carrying out this work at IIASA, Austria. He would also like to thank MHRD, Government of India, for his PhD scholarship. ÅB gratefully acknowledges support from the Swedish Research Council.

7 Competing interests

We have no competing interests.

8 Author contributions

JJ, ÅB, and UD designed the study; JJ performed the simulations; JJ, ÅB, and UD analysed the results and wrote the paper.
References

[1] Hardin G. The tragedy of the commons. Science. 1968;162(3859):1243–1248.

[2] Hauert C, Wakano JY, Doebeli M. Ecological public goods games: cooperation and bifurcation. Theoretical Population Biology. 2008 Mar;73(2):257–263. Available from: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2276362/.

[3] Bowles S, Gintis H. Origins of human cooperation. Genetic and cultural evolution of cooperation. 2003;2003:429–43. Available from: http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.590.6817&rep=rep1&type=pdf.

[4] Hammerstein P. Genetic and Cultural Evolution of Cooperation. MIT Press; 2003. Google-Books-ID: aVh9jtWbG0wC.

[5] Fehr E, Fischbacher U. Social norms and human cooperation. Trends in Cognitive Sciences. 2004 Apr;8(4):185–190. Available from: http://www.sciencedirect.com/science/article/pii/S1364661304000506.

[6] Tomasello M, Melis AP, Tennie C, Wyman E, Herrmann E. Two Key Steps in the Evolution of Human Cooperation: The Interdependence Hypothesis. Current Anthropology. 2012;53(6):673–692.

[7] Rand DG, Nowak MA. Human cooperation. Trends in Cognitive Sciences. 2013 Aug;17(8):413–425. Available from: http://www.sciencedirect.com/science/article/pii/S1364661313001216.

[8] Ciriacy-Wantrup SV, Bishop RC. Common Property as a Concept in Natural Resources Policy. Natural Resources Journal. 1975;15:713. Available from: http://heinonline.org/HOL/Page?handle=hein.journals/narj15&id=731&div=&collection=.

[9] Feeny D, Berkes F, McCoy BJ, Acheson JM. The Tragedy of the Commons: Twenty-two years later. Human Ecology. 1990 Mar;18(1):1–19.

[10] Bromley DW. The commons, common property, and environmental policy. Environmental and Resource Economics. 1992 Jan;2(1):1–17.

[11] Carraro C, Siniscalco D. Strategies for the international protection of the environment. Journal of Public Economics. 1993 Oct;52(3):309–328. Available from: http://www.sciencedirect.com/science/article/pii/00472729390037T.

[12] Ostrom E, Gardner R, Walker J. Rules, Games, and Common-pool Resources. University of Michigan Press; 1994. Google-Books-ID: DgmLa8gPo4gC.

[13] Conca K, Alberty M, Dabelko GD. Green planet blues: environmental politics from Stockholm to Rio. Westview Press, Inc.; 1995.

[14] Kaul I, Grunberg I, Stern MA, editors. Global public goods: international cooperation in the 21st century. New York: Oxford University Press; 1999.
[15] Dietz T, Ostrom E, Stern PC. The Struggle to Govern the Commons. Science. 2003 Dec;302(5652):1907–1912. Available from: http://science.sciencemag.org/content/302/5652/1907.

[16] Tavoni A, Dannenberg A, Kallis G, Löschel A. Inequality, communication, and the avoidance of disastrous climate change in a public goods game. Proceedings of the National Academy of Sciences. 2011 Jul;108(29):11825–11829. Available from: http://www.pnas.org/content/108/29/11825.

[17] Tavoni A, Levin S. Managing the climate commons at the nexus of ecology, behaviour and economics. Nature Climate Change. 2014 Dec;4(12):1057–1063. Available from: http://www.nature.com/nclimate/journal/v4/n12/full/nclimate2375.html.

[18] Nowak MA. Five Rules for the Evolution of Cooperation. Science. 2006 Dec;314(5805):1560–1563.

[19] Hamilton WD. The genetical evolution of social behaviour. I. Journal of Theoretical Biology. 1964 Jul;7(1):1–16.

[20] Trivers RL. The Evolution of Reciprocal Altruism. The Quarterly Review of Biology. 1971 Mar;46(1):35–57.

[21] Axelrod R, Hamilton WD. The evolution of cooperation. Science. 1981;211(4489):1390–1396.

[22] Keser C, Van Winden F. Conditional Cooperation and Voluntary Contributions to Public Goods. Scandinavian Journal of Economics. 2000 Mar;102(1):23–39.

[23] Fischbacher U, Gächter S, Fehr E. Are people conditionally cooperative? Evidence from a public goods experiment. Economics Letters. 2001 Jun;71(3):397–404. Available from: http://www.sciencedirect.com/science/article/pii/S0165176501003949.

[24] Croson R, Fatas E, Neugebauer T. Reciprocity, matching and conditional cooperation in two public goods games. Economics Letters. 2005 Apr;87(1):95–101. Available from: http://www.sciencedirect.com/science/article/pii/S0165176504003325.

[25] Nowak MA, Sigmund K. Evolution of indirect reciprocity by image scoring. Nature. 1998;393(6685):573–577.

[26] Leimar O, Hammerstein P. Evolution of cooperation through indirect reciprocity. Proceedings of the Royal Society of London B: Biological Sciences. 2001;268(1468):745–753.

[27] Milinski M, Semmann D, Krambeck H. Donors to charity gain in both indirect reciprocity and political reputation. Proceedings of the Royal Society of London B: Biological Sciences. 2002;269(1494):881–883.
[28] Fehr E, Gächter S. Cooperation and Punishment in Public Goods Experiments. Rochester, NY: Social Science Research Network; 1999. ID 203194. Available from: https://papers.ssrn.com/abstract=203194.

[29] Brandt H, Hauert C, Sigmund K. Punishment and reputation in spatial public goods games. Proceedings of the Royal Society of London B: Biological Sciences. 2003 May;270(1519):1099–1104. Available from: http://rspb.royalsocietypublishing.org/content/270/1519/1099.

[30] Cinyabuguma M, Page T, Putterman L. Cooperation under the threat of expulsion in a public goods experiment. Journal of Public Economics. 2005 Aug;89(8):1421–1435. Available from: http://www.sciencedirect.com/science/article/pii/S0047272704001616.

[31] Fowler JH. Altruistic punishment and the origin of cooperation. Proceedings of the National Academy of Sciences of the United States of America. 2005 May;102(19):7047–7049. Available from: http://www.pnas.org/content/102/19/7047.

[32] Hauert C, Doebeli M. Spatial structure often inhibits the evolution of Cooperation in the snowdrift game. Nature. 2004 Apr;428(6983):643–646.

[33] Nowak MA, May RM. The spatial dilemmas of evolution. International Journal of Bifurcation and Chaos. 1993 Feb;03(01):35–78.

[34] Hauert C, Monte SD, Hofbauer J, Sigmund K. Volunteering as Red Queen Mechanism for Cooperation in Public Goods Games. Science. 2002 May;296(5570):1129–1132. Available from: http://science.sciencemag.org/content/296/5570/1129.

[35] Wakano JY. Evolution of cooperation in spatial public goods games with common resource dynamics. Journal of Theoretical Biology. 2007 Aug;247(4):616–622. Available from: http://www.sciencedirect.com/science/article/pii/S0022519307001907.

[36] Enquist M, Leimar O. The evolution of cooperation in mobile organisms. Animal Behaviour. 1993 Apr;45(4):747–757.

[37] Le Galliard JF, Ferrière R, Dieckmann U, Tonsor S. The adaptive dynamics of altruism in spatially heterogeneous populations. Evolution. 2003;57(1):1–17.

[38] Pepper JW, Smuts BB. A Mechanism for the Evolution of Altruism among Nonkin: Positive Assortment through Environmental Feedback. The American Naturalist. 2002 Aug;160(2):205–213. ArticleType: research-article / Full publication date: August 2002 / Copyright © 2002 The University of Chicago.

[39] Aktipis CA. Is cooperation viable in mobile organisms? Simple Walk Away rule favors the evolution of cooperation in groups. Evolution and Human Behavior. 2011 Jul;32(4):263–276.

12
[40] Parvinen K, Dieckmann U, Gyllenberg M, Metz JaJ. Evolution of dispersal in metapopulations with local density dependence and demographic stochasticity. Journal of Evolutionary Biology. 2003 Jan;16(1):143–153.

[41] Le Galliard JF, Ferrière R, Dieckmann U. Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility. The American Naturalist. 2005 Feb;165(2):206–224.

[42] Hochberg ME, Rankin DJ, Taborsky M. The coevolution of cooperation and dispersal in social groups and its implications for the emergence of multicellularity. BMC Evolutionary Biology. 2008;8(1):238.

[43] Purcell J, Brelsford A, Avilés L. Co-evolution between sociality and dispersal: The role of synergistic cooperative benefits. Journal of Theoretical Biology. 2012 Nov;312:44–54. Available from: http://www.sciencedirect.com/science/article/pii/S0022519312003608.

[44] Parvinen K. Joint evolution of altruistic cooperation and dispersal in a metapopulation of small local populations. Theoretical population biology. 2013;85:12–19.

[45] Mullon C, Keller L, Lehmann L. Social polymorphism is favoured by the co-evolution of dispersal with social behaviour. Nature ecology & evolution. 2018;2(1):132.

[46] Cumming G, Cumming DHM, Redman C. Scale Mismatches in Social-Ecological Systems: Causes, Consequences, and Solutions. Ecology and Society. 2006 Mar;11(1). Available from: http://www.ecologyandsociety.org/vol11/iss1/art14/main.html.

[47] Wakano JY, Nowak MA, Hauert C. Spatial dynamics of ecological public goods. Proceedings of the National Academy of Sciences. 2009 May;106(19):7910–7914.

[48] Parvinen K. Adaptive dynamics of cooperation may prevent the coexistence of defectors and cooperators and even cause extinction. Proceedings of the Royal Society of London B: Biological Sciences. 2010;p. rspb20100191.

[49] Weitz JS, Eksin C, Paarporn K, Brown SP, Ratcliff WC. An oscillating tragedy of the commons in replicator dynamics with game-environment feedback. Proceedings of the National Academy of Sciences. 2016 Nov;p. 201604096.

[50] Helbing D, Szolnoki A, Perc M, Szabó G. Punish, but not too hard: how costly punishment spreads in the spatial public goods game. New Journal of Physics. 2010;12(8):083005. Available from: http://stacks.iop.org/1367-2630/12/i=8/a=083005.

[51] Szolnoki A, Perc M. Reward and cooperation in the spatial public goods game. EPL (Europhysics Letters). 2010;92(3):38003. Available from: http://stacks.iop.org/0295-5075/92/i=3/a=38003.
[52] Szolnoki A, Perc M. Conditional strategies and the evolution of cooperation in spatial public goods games. Physical Review E. 2012 Feb;85(2):026104.

[53] Brauchli K, Killingback T, Doebeli M. Evolution of cooperation in spatially structured populations. Journal of Theoretical Biology. 1999;200(4):405–417.

[54] Lion S, Baalen Mv. Self-structuring in spatial evolutionary ecology. Ecology Letters. 2008 Mar;11(3):277–295.

[55] van Baalen M, Sabelis MW. The Milker-Killer Dilemma in Spatially Structured Predator-Prey Interactions. Oikos. 1995 Dec;74(3):391–400. Available from: http://www.jstor.org/stable/3545984.

[56] Pels B, Sabelis MW. Local Dynamics, Overexploitation and Predator Dispersal in an Acarine Predator-Prey System. Oikos. 1999;86(3):573–583. Available from: http://www.jstor.org/stable/3546662.

[57] Sabelis MW, Baalen M, Pels B, Egas M, Janssen A. Evolution of exploitation and defense in tritrophic interactions. Cambridge University Press; 2002. Available from: http://dare.uva.nl/record/1/427698.

[58] Sabelis MW, Janssen A, Diekmann O, Jansen VAA, van Gool E, van Baalen M. Global Persistence Despite Local Extinction in Acarine Predator-Prey Systems: Lessons From Experimental and Mathematical Exercises. In: Advances in Ecological Research. vol. 37. Elsevier; 2005. p. 183–220. Available from: http://linkinghub.elsevier.com/retrieve/pii/S0065250404370066.

[59] Holling CS. The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly1. The Canadian Entomologist. 1959;91(5):293–320.

[60] Torney C, Neufeld Z, Couzin ID, Levin SA. Context-Dependent Interaction Leads to Emergent Search Behavior in Social Aggregates. Proceedings of the National Academy of Sciences of the United States of America. 2009 Dec;106(52):22055–22060.
Sedentary and mobile strategies emerge spontaneously. Distributions of harvesting rate (A), dispersal radius (B), and resource extraction rate (C) in the population over time, shown alongside the time-averaged (evolved) strategy distributions. Brighter colors indicate higher frequency, but note that the color scale is non-linear. The population starts with all individuals having identical strategies. As time progresses, social learning leads to spontaneous emergence of two distinct strategies: a sedentary strategy with a low harvesting rate and zero dispersal, and a mobile strategy with a high harvesting rate and high dispersal. Parameters: $b = 0.059$, $c = 0.68$, $r_1 = 0.1$. Other parameters are as in Table 1.
Figure 2: **Increasing consumer density leads to social inequality.** When consumer density is low, all consumers harvest at high rates and disperse, because available resources suffice for everyone. As consumer density increases, everyone harvesting at high rates becomes unsustainable, leading to diversification of strategies into prudent sedentary consumers and overexploitative mobile consumers (A-B). Average per capita resource extraction rate (% of total carrying capacity of the system) decreases with density (C). However, the average harvesting rate (white line) is higher than the corresponding yield-maximizing (green line) and profit-maximizing (magenta line) rates, leading to overexploitation of resource and suboptimal per capita resource extraction. Parameters: \( b = 0.059, \ c = 0.68, \ r_I = 0.1, \ \sigma_I \rightarrow \infty \). Other parameters are as in Table 1. Each consumer is assumed to ‘occupy’ the space within its exploitation radius, and consumer density is the percentage of total area occupied by all consumers without overlap.)
Figure 3: Three regimes of strategies are observed when varying the costs and benefits of harvesting. The difference between the harvesting rate (A) and dispersal distance (C) of sedentary and mobile consumers; and the average harvesting rate (B) and dispersal distance (D) of the population. In A-B, blue and green represent the sedentary and mobile yield-maximizing strategies, respectively (see Methods). Grey areas are where we could not correctly detect a difference (due to insufficient resolution). We find three regimes of strategies (marked by cyan and blue lines): Sedentary (S), in which all consumers are prudent and sedentary, Mobile (M), in which all consumers are overexploitative and mobile, and Coexistence (S & M). For this regime, outsets show the values separately for sedentary and mobile consumers. Parameters: $r_1 = 0.1$, $\sigma_1 \to \infty$. Other parameters are as in Table 1.
Figure 4: Maximum sustainable resource extraction occurs in the mobile regime. Per capita average resource extraction rate as a fraction of the yield-maximizing rate (A) and the resource left in the environment as a fraction of the carrying capacity (B). The sedentary regime is equitable, but inefficient, because the resource extraction is less than optimal even though there are ample resources in the environment. The mobile regime is both equitable as well as efficient, and the total resource extraction rate reaches its maximum evolved value in this regime. However, for very low dispersal costs, the tragedy of the commons occurs in this regime. The coexistence regime is neither equitable nor efficient. In this regime, the resource extraction rate is suboptimal, and overexploitation by mobile consumers results in the tragedy of the commons.
Figure 5: **Four regimes of strategies are observed when varying the spatio-temporal scales of imitation.** In region M, characterized by low imitation rates, the population is monomorphic with an efficient, mobile strategy. However, as imitation rate increases, the strategy diversifies, taking the system into the coexistence regime (region S & M). We subdivide the S & M region into three regions. In region I, characterized by global information, both sedentary and mobile consumers have high harvesting rates, resulting in the tragedy of the commons. As the imitation radius decreases (region II), (mobile) cheaters become more exploitative, and (sedentary) cooperators harvest at rates close to the sedentary profit-maximizing rate. With even further decrease in imitation radius (region III), cheaters become extremely overexploitative. For more analysis of regions I-III, see SI-Fig. 7. Parameters: $b = 0.02$, $c_H = 0.8$. Other parameters are as in Table 1.
Impatience and myopia among consumers aggravate social inequality. Average resource extraction rate decreases with increasing imitation rate. In region III, this is because only a small fraction of cheaters exploit resource at a high rate, while cooperators, which form a vast majority of the population, get zero resource. In region I, both cooperators and cheaters harvest aggressively and overexploit the resource. Region II allows a substantial number of cheaters to coexist with cooperators. See SI-Fig. 7 for additional analysis of regions I-III.