2. Beckett, M. *House of Commons Hansard Debates, 22 October 2001* 373 (2001) ⟨http://www.parliament.the-stationery-office.co.uk/pa/cm200102/cmhansrd/cm011022/debindx/11022-x.htm⟩.
3. Det Norske Veritas *Assessment of Exposure to BSE Infectivity in the UK Sheep Flock* Report no. C782506 (The Meat and Livestock Commission, London, 1998).
4. Hadlow, W. J., Kennedy, R. C. & Race, R. E. Natural infection of Suffolk sheep with scrapie virus. *J. Infect. Dis.* **146,** 657–664 (1982).
5. van Keulen, L. J. M., Schreuder, B. E. C., Vromans, M. E. W., Langeveld, J. P. M. & Smits, M. A. Scrapie-associated prion protein in the gastrointestinal tract of sheep with natural scrapie. *J. Comp. Pathol.* **121,** 55–63 (1999).
6. van Keulen, L. J. M., Schreuder, B. E. C., Vromans, M. E. W., Langeveld, J. P. M. & Smits, M. A. Pathogenesis of natural scrapie in sheep. *Arch. Virol. Suppl.* **16,** 57–71 (2000).
7. Andreoletti, O. *et al.* Early accumulation of PrP^{Sc} in gut-associated lymphoid and nervous tissues of susceptible sheep from a Romanov flock with natural scrapie. *J. Gen. Virol.* **81,** 3115–3126 (2000).
8. Foster, J. D., Parnham, D. W., Hunter, N. & Bruce, M. Distribution of the prion protein in sheep terminally infected with BSE following experimental oral transmission. *J. Gen. Virol.* **82,** 2319–2326 (2001).
9. Jeffrey, M. *et al.* Oral inoculation of sheep with the agent of bovine spongiform encephalopathy (BSE). 1. Onset and distribution of disease-specific PrP accumulation in brain and viscera. *J. Comp. Pathol.* **124,** 280–289 (2001).
10. Fraser, H., Bruce, M. E., Chree, A., McConnell, I. & Wells, G. A. H. Transmission of bovine spongiform encephalopathy and scrapie to mice. *J. Gen. Virol.* **73,** 1891–1897 (1992).
11. Wells, G. A. H. *et al.* Infectivity in the ileum of cattle challenged orally with bovine spongiform encephalopathy. *Vet. Rec.* **135,** 40–41 (1994).
12. Hart, R. J., Church, P. N., Kempster, A. J. & Matthews, K. R. *Audit of Bovine and Ovine Slaughter and By-products Sector (Ruminant Products Audit)* (Leatherhead Food Research Association, London, 1997).
13. Hunter, N. PrP genetics in sheep and the implications for scrapie and BSE. *Trends Microbiol.* **5,** 331–334 (1997).
14. Hunter, N., Goldmann, W., Marshall, E. & O'Neill, G. Sheep and goats: natural and experimental TSEs and factors influencing incidence of disease. *Arch. Virol. Suppl.* **16,** 181–188 (2000).
15. Jeffrey, M. *et al.* Frequency and tissue distribution of infection-specific PrP in tissues of clinical scrapie and cull sheep obtained from scrapie affected farms in Shetland. *J. Comp. Pathol.* (submitted).
16. Baylis, M., Houston, F., Goldmann, W., Hunter, N. & McLean, A. R. The signature of scrapie: differences in the PrP genotype profile of scrapie-affected and scrapie-free UK sheep flocks. *Proc. R. Soc. Lond. B* **267,** 2029–2035 (2000).
17. Hunter, N. *et al.* Is scrapie solely a genetic disease? *Nature* **386,** 137 (1997).
18. Anderson, R. M. *et al.* Transmission dynamics and epidemiology of BSE in British cattle. *Nature* **382,** 779–788 (1996).
19. Ferguson, N. M., Donnelly, C. A., Woolhouse, M. E. J. & Anderson, R. M. The epidemiology of BSE in cattle herds in Great Britain II: Model construction and analysis of transmission dynamics. *Phil. Trans. R. Soc. Lond. B* **352,** 803–838 (1997).
20. Donnelly, C. A. & Ferguson, N. M. *Statistical Aspects of BSE and vCJD—Models for Epidemics* (Chapman & Hall and CRC, London, 2000).
21. Woolhouse, M. E. J. *et al.* Population dynamics of scrapie in a sheep flock. *Phil. Trans. R. Soc. Lond. B* **354,** 751–756 (1999).
22. Gravenor, M. B., Cox, D. R., Hoinville, L. J., Hoek, A. & McLean, A. R. The flock-to-flock force of infection for scrapie in Britain. *Proc. R. Soc. Lond. B* **268,** 587–592 (2001).
23. Hoinville, L. J. A review of the epidemiology of scrapie in sheep. *Rev. Sci. Techn. Office Int. Epizooties* **15,** 827–852 (1996).
24. Hoinville, L. J., Hoek, A., Gravenor, M. B. & McLean, A. R. Descriptive epidemiology of scrapie in Great Britain: results of a postal survey. *Vet. Rec.* **146,** 455–461 (2000).
25. Ghani, A. C., Ferguson, N. M., Donnelly, C. A. & Anderson, R. M. Predicted vCJD mortality in Great Britain. *Nature* **406,** 583–584 (2000).
26. d'Aignaux, J. N. H., Cousens, S. N. & Smith, P. G. Predictability of the UK variant Creutzfeldt–Jakob disease epidemic. *Science* **294,** 1729–1731; published online 25 October 2001 (10.1126/science.1064748).
27. Valleron, A.-J., Boelle, P.-Y., Will, R. & Cesbron, J.-Y. Estimation of epidemic size and incubation time based on age characteristics of vCJD in the United Kingdom. *Science* **294,** 1726–1728 (2001).
28. Hill, A. F. *et al.* Molecular screening of sheep for bovine spongiform encephalopathy. *Neurosci. Lett.* **255,** 159–162 (1998).
29. Maissen, M., Roeckl, F., Glatzel, M., Goldmann, W. & Aguzzi, A. Plasminogen binds to disease-associated prion protein of multiple species. *Lancet* **357,** 2026–2028 (2001).
30. Hagenaars, T. J., Ferguson, N. M., Donnelly, C. A. & Anderson, R. M. Persistence patterns of scrapie in a sheep flock. *Epidemiol. Infect.* **127,** 157–167 (2001).

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Reputation helps solve the 'tragedy of the commons'

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The problem of sustaining a public resource that everybody is free to overuse—the 'tragedy of the commons'[1–7]—emerges in many social dilemmas, such as our inability to sustain the global climate. Public goods experiments[4], which are used to study this type of problem, usually confirm that the collective benefit will not be produced. Because individuals and countries often participate in several social games simultaneously, the interaction of these games may provide a sophisticated way by which to maintain the public resource. Indirect reciprocity[8], 'give and you shall receive', is built on reputation and can sustain a high level of cooperation, as shown by game theorists[9–11]. Here we show, through alternating rounds of public goods and indirect reciprocity games, that the need to maintain reputation for indirect reciprocity maintains contributions to the public good at an unexpectedly high level. But if rounds of indirect reciprocation are not expected, then contributions to the public good drop quickly to zero. Alternating the games leads to higher profits for all players. As reputation may be a currency that is valid in many social games, our approach could be used to test social dilemmas for their solubility.

Since Hardin[1] first described the 'tragedy of the commons', this type of social dilemma has been studied extensively by political and social scientists, economists and evolutionary theorists (see refs 2–7). Many of the experiments that have been carried out are a variant of the standard design[4]. In this model, four students seated at a table are each given an endowment of £5. They are then told that they can each choose to invest some or all of their £5 in a group project by putting, without discussion, an amount between £0 and £5 in an envelope. The experimenter will collect the 'contributions', total them up, double the amount, and then divide this money among the group.

The economic/game-theory prediction is that no one will ever contribute anything because each £1 contributed yields only £0.50 to its contributor, no matter what the others do. This is a public goods problem because the group would be best off (taking home £10 each) if all contributed £5. But individual self-interest is at odds with group interest. Usually people cooperate more than is predicted by standard economic theory[4]; however, observed cooperation is heterogeneous and declines over time (for example, see ref. 12). It has been shown that direct punishment of non-cooperators can cause a rise in the level of the average contribution to the public good[13–15], and cooperators are even prepared to pay a cost for punishing ('altruistic punishment')[16].

We present an alternative way to maintain potentially a high level of contribution to the public good. It can be achieved through interaction with a second game that promises rewards for those with a good reputation in the public goods game. Theorists have shown that cooperation through indirect reciprocity can evolve[9–11]. For indirect reciprocity, individuals who have helped others are given support, whereby the supporter builds up reputation[8,17] or a positive image score[9,10]. Experimental studies have confirmed that human subjects preferentially help others who have a positive image score[18–20]. As players would risk their reputation if they would not cooperate in a public goods game that is alternated with the indirect reciprocity game, we predicted that alternating rounds of these two games would induce continuous cooperation in the public goods game, in contrast to a situation in which all public goods rounds were played first.

We tested these predictions with 114 first-year students who participated in 19 groups of 6 subjects each in a computerized experiment. The six subjects of each group could see a public screen on which instructions and the actual game was projected. They were told, first, that each person had a starting account of DM 20 (£10) and could gain or lose money dependent on his/her and the participants' decisions; second, that all decisions were anonymous and each player would be assigned a pseudoname (that is, a new identity) for the whole game; and last, that they would play in two different situations, an 'indirect reciprocity game' and a 'public goods game'.

Ten groups played one round of indirect reciprocity in which each subject was a potential donor once and a potential receiver once, and then one round of public goods. This alternating pattern was continued until round 16, thereafter four rounds of public goods were played. Every second group was told in round 17 that from then on only public goods rounds would follow until the end of the game. Nine other groups played eight rounds of public goods, followed by eight rounds of indirect reciprocity, followed by four rounds of public goods. Again, every second group was told in round 17 that from then on only public goods rounds would follow until the end of the game. In each round of an indirect reciprocity game, each potential receiver's history of giving both in the indirect reciprocity and the public goods game was displayed simultaneously for all players.

In groups that started with eight rounds of the public goods game initial cooperation declined as is usual in this type of game from round one to round eight (paired t-test between first and eighth round of public goods game, $n = 9$ groups, $t = 6.958$, $P < 0.0001$; Fig. 1). During the subsequent eight rounds of pairwise indirect reciprocity, cooperation was instantaneously re-established (comparison between eighth round of public goods game and first round of indirect reciprocity: paired t-test, $n = 9$ groups, $t = 2.9$, $P < 0.02$; to avoid pseudoreplication we use each group of six subjects as our statistical unit throughout this paper; all probabilities are two-tailed).

But in groups that started with one round of indirect reciprocity, followed by one round of public goods, and so on until round 16, the initial high cooperation level of the public goods game did not decline during the eight rounds of the public goods game (comparison between the first and the eighth round of public goods game; paired t-test, $n = 10$ groups, $t = 0.897$, $P = 0.40$), and was on average considerably higher than the cooperation level of the nine groups that had started with eight rounds of public goods (unpaired t-test, d.f. = 17, $t = 4.83$, $P < 0.0002$; Fig. 1). When public goods and indirect reciprocity rounds were alternated, the public goods game elicited significantly more cooperation than the indirect reciprocity game (comparison between average cooperation of eight rounds public goods and eight rounds indirect reciprocity; paired t-test, $n = 10$ groups, $t = 3.99$, $P < 0.004$).

The high cooperation level in the public goods game was probably maintained in the following way. Players might have withheld help in the pairwise indirect reciprocity game from players who had refused to give in the preceding public goods round. The probability of receiving 'no' in the indirect reciprocity game was significantly higher for players that had refused to give in the preceding public goods round than for those who had given (Fig. 2a). Similarly, we found a positive correlation between the probability of receiving 'no' in the first round of the indirect reciprocity game and the rate of refused help during the block of eight rounds of the public goods game (mean Spearman's r per group = 0.49; s.e.m. = 0.15; Wilcoxon test against 0, $n = 9$ groups, $z = -2.1$, $P < 0.04$).

The hypothesis that interaction with the indirect reciprocity game keeps up cooperation in the public goods game is directly tested by the four rounds of public goods that groups in both treatments played in rounds 17–20. Every second group was told in round 17 that from then on only public goods rounds would follow until the end of the game. In these groups cooperation declined during the four public goods rounds, whereas cooperation was maintained when the risk of further rounds of indirect reciprocity was not excluded (Fig. 1; comparison of mean cooperation level during four rounds of public goods between five groups 'with' and five groups 'without announcement' after the alternating treatment, d.f. = 8,

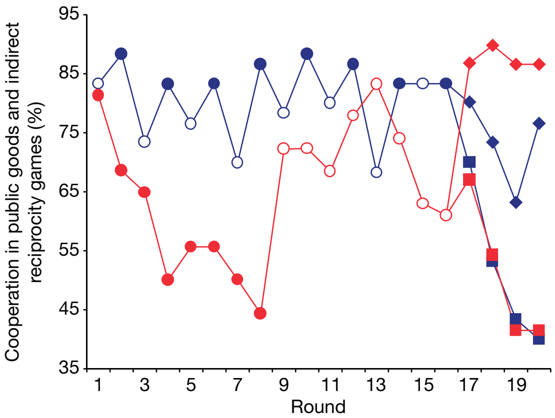

Figure 1 Percentage of cooperation ('yes') per group of six subjects in each round of the public goods game (filled symbols) and in each round of the indirect reciprocity game (open symbols). In one treatment, the groups alternated between rounds of indirect reciprocity and rounds of public goods until round 16 (blue); in the other treatment, groups started with eight consecutive rounds of the public goods game and continued with eight rounds of the indirect reciprocity game (red); in rounds 17–20, groups of both treatments played the public goods game, which was either announced, 'from now on only this type of game until the end' (squares), or not announced (diamonds).

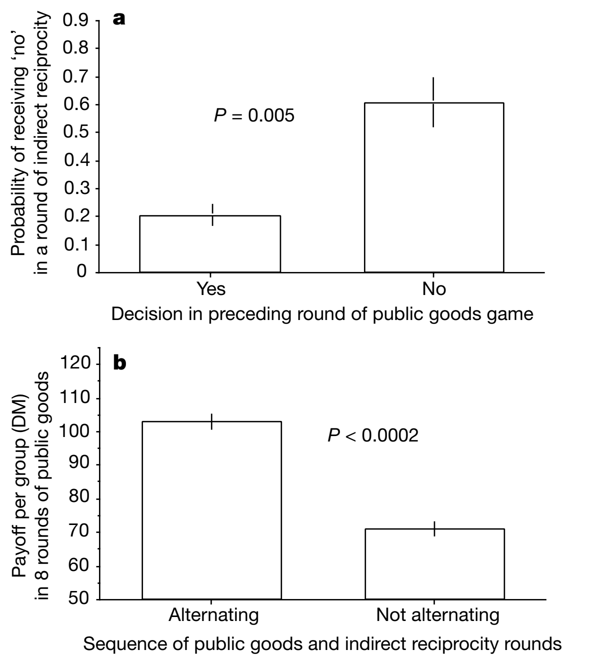

Figure 2 Consequences of cooperation in the public goods game. **a**, Probability of receiving 'no' in a round of the indirect reciprocity game depending on whether a subject had given either 'yes' or 'no' in the preceding round of the public goods game in the alternating treatment. The probability per group is shown (mean ± s.e.m) for both situations; all individual situations were taken to generate one mean value of either type for each group; paired t-test with arcsine-transformed data, $n = 10$ groups, $t = 3.7$, $P = 0.005$. **b**, Payoff (DM) per group (mean ± s.e.m.) in the first 8 rounds of the public goods game of all groups that either alternated the indirect reciprocity and the public goods game during the first 16 rounds or started with 8 consecutive rounds of the public goods game and thereafter played 8 rounds of indirect reciprocity; unpaired t-test, d.f. = 17, $t = 4.83$, $P < 0.0002$.

unpaired t-test, $t = 4.456$, $P = 0.002$, and between five groups 'with' and four groups 'without announcement' after the block treatment, d.f. = 7, unpaired t-test, $t = 6.631$, $P = 0.0003$). Thus, the pending risk of further rounds of indirect reciprocity prevented cooperation in the public goods game from declining at least over four consecutive rounds.

Obviously, refusing to give in the public goods game reduced the reputation of a player to a similar extent as if this person had refused to give in the indirect reciprocity game: his potential donor in the next round of indirect reciprocity just followed the rules for indirect reciprocity and refused to give to someone with a low image score. This is different from punishing because it does not need any special punishing rule or motivation, and the potential donor actually saves money by refusing to give. A recent theoretical analysis[21] suggests that reputation is essential for fostering social behaviour among selfish agents, which is confirmed experimentally here. The inclusion of reputation effects in the corresponding dynamical models leads to the evolution of economically productive behaviour, with agents contributing to the public good and either punishing those who do not or rewarding those who do[21]. Providing help in the indirect reciprocity game is a form of reward.

Cooperation in the public goods game paid off. Groups that alternated rounds of indirect reciprocity and public goods games, and thus were more cooperative in the public goods game, earned significantly more money during the first eight rounds of the public goods game than did groups that played the two games in blocks of eight rounds each (Fig. 2b). This shows that the 'tragedy of the commons' was no longer a tragedy; instead, the commons became productive and could be harvested. Two people usually interact in more than one situation, therefore their actions in one context may influence actions in another[22]. Many social dilemmas are a type of public goods game[6], others have been identified as a type of indirect reciprocity game[4]. It therefore seems likely that the kind of interaction that we have staged experimentally occurs naturally in our society. There might be hidden social dilemmas that would show up only if the interaction with another game were removed. □

Methods

Indirect reciprocity game

Players were anonymous; each subject was assigned a pseudoname by the computer for the whole session of 20 rounds so that at any time, players could make their decisions contingent on the history of the game up to that time; each player knew his/her name but did not know who had been assigned the other names; the subjects were separated by opaque partitions and communicated their decisions with silent (piezo) switches; they knew that they would obtain their money after the game in a way that did not disclose their anonymity.

For the 'indirect reciprocity game'[20], each person was assigned repeatedly as either a potential donor or a potential receiver. For example, a potential donor, say 'Telesto', was asked on the public screen whether he would give to 'Galatea'. Telesto would loose DM 2.50 from his account and Galatea would gain DM 4 on her account if Telesto decided 'yes'. Telesto's decision (yes or no) was displayed for 2 s on the public screen. Everybody knew about the contributions of all players, for example, whether Galatea had given in previous rounds when he/she had been playing as the potential donor. The subjects also knew that there would be no direct reciprocity; if A was the potential donor of B, B would never be the potential donor of A. In each round of the indirect reciprocity game, each of the six players was once a potential donor and once a potential receiver.

Public goods game

For the 'public goods game'[4], all six players were asked simultaneously whether they would contribute DM 2.50 to the public pool, the contents of which would then be doubled and redistributed evenly among all players irrespective of whether they had contributed. After all players had decided, each player's decision (yes or no), his/her contribution (that is, DM 2.50 or 0), and his/her gain (for example, DM 4.17 if all but one had contributed), was displayed below the pseudonames for 20 s.

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1. Hardin, G. The tragedy of the commons. *Science* **162,** 1243–1248 (1968).
2. Dawes, R. Social dilemmas. *Annu. Rev. Psychol.* **31,** 169–193 (1980).
3. Berkes, F., Feeny, D., McCay, B. J. & Acheson, J. M. The benefits of the commons. *Nature* **340,** 91–93 (1989).
4. Ledyard, J. O. in *Handbook of Experimental Economics* (eds Kagel, J. H. & Roth, A. E.) 111–194 (Princeton Univ. Press, Princeton, 1995).
5. Hardin, G. Extensions of "the tragedy of the commons". *Science* **280,** 682–683 (1998).
6. Ostrom, E., Burger, J., Field, C. B., Norgaard, R. B. & Policansky, D. Sustainability—revisiting the commons: local lessons, global challenges. *Science* **284,** 278–282 (1999).
7. Ostrom, E. *Governing the Commons* (Cambridge Univ. Press, Cambridge, 1999).
8. Alexander, R. D. *The Biology of Moral Systems* (de Gruyter, New York, 1987).
9. Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity by image scoring. *Nature* **393,** 573–577 (1998).
10. Nowak, M. A. & Sigmund, K. The dynamics of indirect reciprocity. *J. Theor. Biol.* **194,** 561–574 (1998).
11. Lotem, A., Fishman, M. A. & Stone, L. Evolution of cooperation between individuals. *Nature* **400,** 226–227 (1999).
12. Fischbacher, U., Gächter, S. & Fehr, E. Are people conditionally cooperative? Evidence from a public goods experiment. *Econ. Lett.* **71,** 397–404 (2001).
13. Boyd, R. & Richerson, P. J. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.* **13,** 171–195 (1992).
14. Fehr, E. & Gächter, S. Cooperation and punishment in public goods experiments. *Am. Econ. Rev.* **90,** 980–994 (2000).
15. Gintis, H. *Game Theory Evolving* (Princeton Univ. Press, Princeton, 2000).
16. Fehr, E. & Gächter, S. Altruistic punishment in humans. *Nature* **415,** 137–140 (2002).
17. Zahavi, A. in *Cooperative Breeding in Birds: Long Term Studies in Behaviour and Ecology* (eds Stacey, P. B. & Koenig, W. D.) 105–130 (Cambridge Univ. Press, Cambridge, 1991).
18. Wedekind, C. & Milinski, M. Cooperation through image scoring in humans. *Science* **288,** 850–852 (2000).
19. Seinen, I. & Schram, A. Social status and group norms: indirect reciprocity in a helping experiment. Discussion Paper TI2001-003/1 (Tinbergen Institute, Amsterdam, 2001).
20. Milinski, M., Semmann, D., Bakker, T. C. M. & Krambeck, H.-J. Cooperation through indirect reciprocity: image scoring or standing strategy? *Proc. R. Soc. Lond. B* **268,** 2495–2501 (2001).
21. Sigmund, K., Hauert, C. & Nowak, M. A. Reward and punishment. *Proc. Natl Acad. Sci. USA* **98,** 10757–10762 (2001).
22. Coleman, J. S. *Foundations of Social Theory* (Harvard Univ. Press, Cambridge, MA, 1990).

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Species diversity enhances ecosystem functioning through interspecific facilitation

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Facilitation between species is thought to be a key mechanism by which biodiversity affects the rates of resource use that govern the efficiency and productivity of ecosystems[1–4]; however, there is no direct empirical evidence to support this hypothesis. Here we show that increasing the species diversity of a functional group of aquatic organisms induces facilitative interactions, leading to non-additive changes in resource consumption. We increased the richness and evenness of suspension-feeding caddisfly larvae (Insecta, Trichoptera) in stream mesocosms and found that the increased topographical complexity of the benthic habitat alters patterns of near-bed flow such that the feeding success of individuals is enhanced. Species diversity reduces 'current shading' (that is, the deceleration of flow from upstream to downstream neighbours), allowing diverse assemblages to capture a greater fraction of suspended resources than is caught by any species monoculture. The fundamental nature of this form of hydrodynamic facilitation suggests that it is broadly applicable to freshwater and marine habitats; in addition, it has several analogues in terrestrial ecosystems where fluxes of energy and matter can be

