The evolution of altruism and the serial rediscovery of the role of relatedness - supplementary information

Tomas Kay[1], Laurent Keller[1*], and Laurent Lehmann[1]

[1]*Department of Ecology and Evolution, University of Lausanne, Switzerland*

Literature search results

This supplement comprises six tables. Tables S1 and S2 contain the first hundred results obtained using the Google Scholar search terms "Evolution of altruism" and "Evolution of cooperation" respectively. The tables show (i) whether these papers present formal evolutionary models, and if so; (ii) whether altruism (as defined in the main text) can increase in frequency under selection in any of the models presented in the paper, and if so; (iii) to which mechanism the authors attribute the evolution of altruism; and (iv) whether the authors deny the role of relatedness in their model.

Table S3 evaluates the papers from Tables S1 and S2 which claim that relatedness does not play a role in their model. This table comprises quotes evidencing the claim of unrelatedness, quotes evidencing the presence of relatedness, and an indication as to whether or not kin selection operates.

Table S4 evaluates the papers which attribute the evolution of altruism to a mechanism other than kin selection but do not preclude the operation of relatedness in their models. For these papers we highlight the proposed mechanism, the mode of reproduction and interaction, and again indicate whether kin selection operates.

Table S5 presents search results for "Nowak cooperation", whether the publications constitute primary research in evolutionary theory, whether altruism can evolve, and the mechanism to which the evolution of altruism is attributed. This table was extended until it included ten 'spatial selection' papers.

Table S6 evaluates the claims of seven of the 10 'spatial selection' papers identified in Table S5 (the remaining three already feature in Tables S3 and S4). The reproduction and interaction modes are identified, and whether kin selection operates is indicated.

Table S1: Top 100 google scholar results for "Evolution of Cooperation" on 11/09/2019. Column 3 assesses whether the work constitutes a primary theoretical contribution to evolutionary biology - i.e., is an evolutionary model presented in the paper? Column 4 asks whether it is altruism or cooperation that increases in frequency under selection in the model (i.e., holding $b > 0$, whether c is greater or less than 0). In some cases, depending on the features of the life cycle, the phenotypic effect of alleles could be either cooperative or altruistic for different model parameter values - for these cases we write 'parameter-dependent'. If the entry did not present a formal evolutionary model ('No' in column 3) then we do not assess whether altruism can evolve, and write 'n/a'. Column 5 identifies the mechanism to which the authors attribute the evolution of altruism, if altruism can evolve (otherwise we write 'n/a'). Entries which do not credit relatedness are in boldface and are analysed in Tables S3 and S4. Column 6 indicates whether or not the authors explicitly deny the role of relatedness.

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
1	The evolution of cooperation (Axelrod & Hamilton, 1981)[1]	Yes	Cooperation	n/a	n/a
2	Five rules for the evolution of cooperation (Nowak, 2006)[2]	No - review	n/a	n/a	n/a
3	The evolution of cooperation in strategic alliances: initial conditions or learning processes? (Doz, 2007[3])	No - empirical research	n/a	n/a	n/a
4	The further evolution of cooperation (Axelrod & Dion, 1988)[4]	No - review	n/a	n/a	n/a
5	**A simple rule for the evolution of cooperation on graphs and social networks (Ohtsuki *et al*, 2006)[5]**	**Yes**	**Altruism**	**Spatial position**	**No**
6	Evolution of cooperation without reciprocity (Riolo *et al*, 2001[6])	Yes	Parameter-dependent	Tag-based and relatedness	n/a
7	The evolution of cooperation (Sachs *et al*, 2004)[7]	No - review	n/a	n/a	n/a
8	Punishment allows the evolution of cooperation (or anything else) in sizable groups (Boyd & Richerson, 1992)[8]	Yes	Parameter-dependent	Relatedness and retribution	n/a
9	**Spatial structure often inhibits the evolution of cooperation in the snowdrift game (Hauert & Doebeli, 2004)[9]**	**Yes**	**Parameter-dependent**	**Spatial structure**	**No**
10	**Evolution of cooperation by multilevel selection (Traulsen & Nowak, 2006)[10]**	**Yes**	**Altruism**	**Group selection**	**Yes**
11	**The evolution of strong reciprocity: cooperation in heterogeneous populations (Bowles & Gintis, 2004)[11]**	**Yes**	**Parameter-dependent**	**Group selection**	**Yes**

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
12	Genetic and cultural evolution of cooperation (Hammerstein, 2003)[12]	No - book	n/a	n/a	n/a
13	**Evolution of cooperation through indirect reciprocity (Leimar & Hammerstein, 2001)[13]**	**Yes**	**Parameter-dependent**	**Indirect reciprocity**	**No**
14	Tit for tat in sticklebacks and the evolution of cooperation (Milinski, 1987)[14]	No - empirical research	n/a	n/a	n/a
15	Evolution of cooperation and conflict in experimental bacterial populations (Rainey & Rainey, 2003)[15]	No - empirical research	n/a	n/a	n/a
16	**The evolution of altruistic punishment (Boyd *et al*, 2003)[16]**	**Yes**	**Parameter-dependent**	**Group selection**	**Yes**
17	The evolution of cooperation and altruism – a general framework and a classification of models (Lehmann & Keller, 2006)[17]	Yes	Parameter-dependent	Relatedness	n/a
18	Evolution of indirect reciprocity by image scoring (Nowak & Sigmund, 1998)[18]	Yes	Cooperation	n/a	n/a
19	Why be nice? Psychological constraints on the evolution of cooperation (Stevens & Hauser, 2004)[19]	No - review	n/a	n/a	n/a
20	The evolution of one-shot cooperation: An experiment (Frank *et al*, 1993)[20]	No - empirical research	n/a	n/a	n/a
21	The evolution of cooperation in mobile organisms (Enquist & Leimar, 1993)[21]	Yes	Insufficient information provided*	n/a	n/a
22	**Scale-free networks provide a unifying framework for the emergence of cooperation (Santos & Pacheco, 2005)[22]**	**Yes**	**Altruism**	**Growth and preferential attachment of networks†**	**Yes**

Continued on next page

*The life-cycle assumptions of this model are not stated in the publication

†The meaning of this attribution, along with the meaning of various other attributions (e.g., 'multiplex structure') is not intuitive to biologists. They are verbal descriptions of the distribution of individuals in the models, and how individuals interact. They can be thought of as spatial properties of the model.)

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
23	The emergence of cooperation: national epistemic communities and the international evolution of the idea of nuclear arms control (Adler, 1992)[23]	No - non-evolutionary	n/a	n/a	n/a
24	Evolution of cooperation among tumor cells (Axelrod *et al*, 2006)[24]	Yes	Cooperation	n/a	n/a
25	**Evolution of cooperation in multiplex networks (Gómez-Gardenes *et al*, 2012)[25]**	**Yes**	**Altruism**	**Multiplex structure**	**No**
26	Repression of competition and the evolution of cooperation (Frank, 2003)[26]	Yes	Altruism	Relatedness	n/a
27	Hand of God, mind of man: Punishment and cognition in the evolution of cooperation (Johnson & Bering, 2006)[27]	No - non-evolutionary	n/a	n/a	n/a
28	Sixteen common misconceptions about the evolution of cooperation in humans (West *et al*, 2011)[28]	No - review	n/a	n/a	n/a
29	The evolution of cooperation in infinitely repeated games: Experimental evidence (Dal Bó & Fréchette, 2011)[29]	No - empirical research	n/a	n/a	n/a
30	**Graph topology plays a determinant role in the evolution of cooperation (Santos *et al*, 2006)[30]**	**Yes**	**Altruism**	**Graph topology**	**Yes**
31	The experience and evolution of trust: Implications for cooperation and teamwork (Jones & George, 1998)[31]	No - non-evolutionary	n/a	n/a	n/a
32	**The evolution of cooperation in a lattice-structured population (Nakamaru *et al*, 1997)[32]**	**Yes**	**Parameter-dependent**	**Spatial structure**	**Yes**
33	Evolution of cooperation in a finite homogeneous graph (Taylor *et al*, 2007)[33]	Yes	Altruism	Relatedness	n/a
34	Gift giving and the evolution of cooperation (Carmichael & MacLeod, 1997)[34]	No - non-evolutionary	n/a	n/a	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
35	**Evolution of public cooperation on interdependent networks: The impact of biased utility functions (Wang *et al*, 2012)[35]**	**Yes**	**Parameter-dependent**	**The strength of bias in a utility function linking interdependent networks**	**Yes**
36	Cooperation, punishment, and the evolution of human institutions (Henrich, 2006)[36]	No - perspective	n/a	n/a	n/a
37	The good of wrath: Supernatural punishment and the evolution of cooperation (Johnson & Krüger, 2004)[37]	No - non-evolutionary	n/a	n/a	n/a
38	Intuition, deliberation, and the evolution of cooperation (Bear & Rand, 2016)[38]	Yes	Cooperation	n/a	n/a
39	**A new route to the evolution of cooperation (Santos & Pacheco, 2006)[39]**	**Yes**	**Altruism**	**Network heterogeneity**	**Yes**
40	Emergence of spatial structure in cell groups and the evolution of cooperation (Nadell *et al*, 2010)[40]	Yes	Cooperation	n/a	n/a
41	Cooperation and conflict in the evolution of multicellularity (Michod & Roze, 2001)[41]	No - review	n/a	n/a	n/a
42	Evolution of cooperation between individuals (Lotem *et al*, 1999)[42]	Yes	Cooperation	n/a	n/a
43	More evolution of cooperation (May, 1987)[43]	No - perspective	n/a	n/a	n/a
44	Evolution of cooperation by phenotypic similarity (Antal *et al*, 2009)[44]	Yes	Altruism	Relatedness and phenotype matching	n/a
45	The biological evolution of cooperation and trust (Bateson, 2000)[45]	No - perspective	n/a	n/a	n/a
46	Evolution of cooperation by generalized reciprocity (Pfeiffer *et al*, 2005)[46]	Yes	Parameter-dependent	Relatedness and generalized reciprocity	n/a
47	**Optimal interdependence between networks for the evolution of cooperation (Wang *et al*, 2013)[47]**	**Yes**	**Altruism**	**Strength of network interdependence**	**No**

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
48	Know when to walk away: contingent movement and the evolution of cooperation (Aktipis, 2004)[48]	Yes	Cooperation	n/a	n/a
49	Chaos and the evolution of cooperation (Nowak & Sigmund, 1993)[49]	Yes	Cooperation	n/a	n/a
50	Moral sentiments and material interests: The foundations of cooperation in economic life (Gintis *et al*, 2005)[50]	No - book	n/a	n/a	n/a
51	**Effect of spatial structure on the evolution of cooperation (Roca *et al*, 2009)[51]**	**Yes**	**Altruism**	**Spatial structure**	**No**
52	Emotional expressivity and trustworthiness: The role of nonverbal behavior in the evolution of cooperation (Boone & Buck, 2003)[52]	No - non-evolutionary	n/a	n/a	n/a
53	Supercooperators: Altruism, evolution, and why we need each other to succeed (Nowak & Highfield, 2011)[53]	No - book	n/a	n/a	n/a
54	**The evolution of ethnocentrism (Hammond & Axelrod, 2006)[54]**	**Yes**	**Altruism**	**Ethnocentrism**	**No**
55	**Evolution of cooperation on stochastic dynamical networks (Wu *et al*, 2010)[55]**	**Yes**	**Altruism**	**Strength of interaction between cooperators and non-cooperators**	**No**
56	**Cooperation and competition in the evolution of ATP-producing pathways (Pfeiffer *et al*, 2001)[56]**	**Yes**	**Altruism**	**Spatial structure**	**No**
57	Emergence of cooperation and organization in an evolutionary game (Challet & Zhang, 1997)[57]	Yes	Cooperation	n/a	n/a
58	Evolution of indirect reciprocity (Nowak & Sigmund, 2005)[58]	No - review	n/a	n/a	n/a
59	Group living, competition, and the evolution of cooperation in a sessile invertebrate (Buss, 1981)[59]	No - empirical research	n/a	n/a	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
60	**Evolution of cooperation on scale-free networks subject to error and attack (Perc, 2009)[60]**	**Yes**	**Altruism**	**Network heterogeneity**	**No**
61	Emergence of cooperation and evolutionary stability in finite populations (Nowak *et al*, 2004)[61]	Yes	Cooperation	n/a	n/a
62	Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation (Sinervo & Clobert, 2003)[62]	No - empirical research	n/a	n/a	n/a
63	**Participation costs dismiss the advantage of heterogeneous networks in evolution of cooperation (Masuda, 2007)[63]**	**Yes**	**Altruism**	**Heterogeneity in number of contacts**	**No**
64	The evolution of cooperation within the gut microbiota (Rakoff-Nahoum *et al*, 2016)[64]	No - empirical research	n/a	n/a	n/a
65	**Degree mixing in multilayer networks impedes the evolution of cooperation (Wang *et al*, 2014)[65]**	**Yes**	**Altruism**	**Assortative mixing**	**No**
66	Enforcement and the Evolution of Cooperation (Downs, 1997)[66]	No - review	n/a	n/a	n/a
67	**Social diversity promotes the emergence of cooperation in public goods games (Santos *et al*, 2008)[67]**	**Yes**	**Altruism**	**Social diversity**	**No**
68	Evolutionary cycles of cooperation and defection (Imhof *et al*, 2005)[68]	Yes	Cooperation	n/a	n/a
69	Twenty years on: The evolution of cooperation revisited (Hoffmann, 2000)[69]	No - review	n/a	n/a	n/a
70	**The role of diversity in the evolution of cooperation (Santos *et al*, 2012)[70]**	**Yes**	**Altruism**	**Heterogeneity**	**No**
71	Coordinated punishment of defectors sustains cooperation and can proliferate when rare (Boyd *et al*, 2010)[71]	Yes	Parameter-dependent	Relatedness and group selection	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
72	Co-evolution of behaviour and social network structure promotes human cooperation (Fehl *et al*, 2011)[72]	No - empirical research	n/a	n/a	n/a
73	**Evolution of cooperation in spatially structured populations (Brauchli *et al*, 1999)[73]**	**Yes**	**Parameter-dependent**	**Spatial structure**	**No**
74	**Social diversity and promotion of cooperation in the spatial prisoner's dilemma game (Perc & Szolnoki, 2008)[74]**	**Yes**	**Altruism**	**Social diversity**	**No**
75	**Social dilemmas in an online social network: the structure and evolution of cooperation (Fu *et al*, 2007)[75]**	**Yes**	**Altruism**	**Network heterogeneity**	**Yes**
76	Uncertainty and the evolution of cooperation (Bendor, 1993)[76]	Yes	Cooperation	n/a	n/a
77	Evolution of cooperation under N-person snowdrift games (Souza *et al*, 2009)[77]	Yes	Cooperation	n/a	n/a
78	The algebra of assortative encounters and the evolution of cooperation (Bergstrom, 2003)[78]	Yes	Altruism	Relatedness and assortativity	n/a
79	Origins of human cooperation (Bowles & Gintis, 2003)[79]	No - book chapter	n/a	n/a	n/a
80	**Inferring reputation promotes the evolution of cooperation in spatial social dilemma games (Wang *et al*, 2012)[80]**	**Yes**	**Parameter-dependent**	**Spatial reciprocity**	**Yes**
81	The evolution of mutualisms: exploring the paths between conflict and cooperation (Herre *et al*, 1999)[81]	No - review	n/a	n/a	n/a
82	**If players are sparse social dilemmas are too: Importance of percolation for evolution of cooperation (Wang *et al*, 2012)[82]**	**Yes**	**Parameter-dependent**	**Spatial reciprocity**	**No**
83	Culture and the evolution of human cooperation (Boyd & Richerson, 2009)[83]	No - perspective	n/a	n/a	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
84	**Behavior-dependent contexts for repeated plays of the Prisoner's Dilemma II: Dynamical aspects of the evolution of cooperation (Feldman & Thomas, 1987)[84]**	**Yes**	**Parameter-dependent**	**Clustering**	**No**
85	**Evolution of contingent altruism when cooperation is expensive (Hammond & Axelrod, 2006)[85]**	**Yes**	**Parameter-dependent**	**Viscosity and tabs**	**No**
86	**Anti-social punishment can prevent the co-evolution of punishment and cooperation (Rand *et al*, 2010)[86]**	**Yes**	**Parameter-dependent**	**Punishment and spatial structure**	**No**
87	Evolution of cooperation and control of cheating in a social microbe (Strassmann & Queller, 2011)[87]	No - review	n/a	n/a	n/a
88	**Impact of aging on the evolution of cooperation in the spatial prisoner's dilemma game (Szolnoki *et al*, 2009)[88]**	**Yes**	**Altruism**	**Spatial structure and heterogeneity**	**No**
89	A functional imaging study of cooperation in two-person reciprocal exchange (McCabe *et al*, 2001)[89]	No - empirical research	n/a	n/a	n/a
90	Evolution of cooperation by reciprocation within structured demes (Joshi, 1987)[90]	Yes	Cooperation	n/a	n/a
91	Kin competition and the evolution of cooperation (Platt & Bever, 2009)[91]	Yes	Altruism	Relatedness	n/a
92	Cooperation and nonlinear dynamics: an ecological perspective on the evolution of sociality (Avilés 1999)[92]	Yes	Cooperation	n/a	n/a
93	Anarchy, egoism, and third images: The Evolution of Cooperation and international relations (Gowa, 1986)[93]	No - book review	n/a	n/a	n/a
94	**Coevolution of teaching activity promotes cooperation (Szolnoki & Perc, 2008)[94]**	**Yes**	**Altruism**	**Level of teaching activity**	**No**
95	The evolution of cooperation (Dugatkin, 1997)[95]	No -review	n/a	n/a	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
96	**Evolution of cooperation in a spatial prisoner's dilemma (Schweitzer *et al*, 2002)[96]**	**Yes**	**Altruism**	**Spatial structure**	**No**
97	Importance of cooperation and affiliation in the evolution of primate sociality (Sussman *et al*, 2005)[97]	No - perspective	n/a	n/a	n/a
98	**Conditional strategies and the evolution of cooperation in spatial public goods games (Szolnoki & Perc, 2012)[98]**	**Yes**	**Altruism**	**Pattern formation**	**Yes**
99	The evolution of cooperation through imitation (Levine & Pesendorfer, 2007)[99]	No - non-evolutionary	n/a	n/a	n/a
100	The evolution of degrees of cooperation (Frean, 1996)[100]	Yes	Cooperation	n/a	n/a

23

Table S2: Top 100 papers for "Evolution of Altruism" on 11/09/2019. This table follows the same structure as Table S1; see Table S1 legend for details.

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
1	The evolution of altruistic behavior (Hamilton, 1963)[101]	Yes	Altruism	Relatedness	n/a
2	**Group competition, reproductive leveling, and the evolution of human altruism (Bowles, 2006)[102]**	**Yes**	**Parameter-dependent**	**Intergroup competition**	**Yes**
3	Reliability in communication systems and the evolution of altruism (Zahavi, 1977)[103]	No - book chapter	n/a	n/a	n/a
4	A simple and general explanation for the evolution of altruism (Fletcher & Doebeli, 2008)[104]	No - perspective	n/a	n/a	n/a
5	The unit of selection in viscous populations and the evolution of altruism (van Baalen & Rand, 1998)[105]	Yes	Altruism	Relatedness and cluster structure	n/a
6	Population viscosity and the evolution of altruism (Mitteldorf & Wilson, 2000)[106]	Yes	Altruism	Relatedness and spatial structure	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
7	Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding (Brown, 2015)[107]	No - empirical research	n/a	n/a	n/a
8	Genetics of mutualism: the evolution of altruism between species (Frank, 1994)[108]	Yes	Cooperation	n/a	n/a
9	Conditions for the evolution of altruism under Darwinian selection (Matessi & Jayakar)[109]	Yes	Cooperation	n/a	n/a
10	The evolution of reciprocal altruism (Trivers, 1971)[110]	Yes	Cooperation	n/a	n/a
11	Evolution and altruism: Combining psychological mediators with naturally selected tendencies (Kruger, 2003)[111]	No - empirical research	n/a	n/a	n/a
12	Contextual analysis of models of group selection, soft selection, hard selection, and the evolution of altruism (Goodnight *et al*, 1992)[112]	Yes	Altruism	Relatedness	n/a
13	Restricted migration and the evolution of altruism (Kelly, 1992)[113]	Yes	Altruism	Relatedness	n/a
14	**Interdemic selection and the evolution of altruism: a computer simulation study (Levin & Kilmer, 1974)[114]**	**Yes**	**Parameter-dependent**	**Interdemic selection**	**Yes**
15	**Evolution of contingent altruism when cooperation is expensive (Hammond & Axelrod, 2006)[85]**	**Yes**	**Parameter-dependent**	**Viscosity and tags**	**No**
16	The evolution of altruism in humans (Kurzban *et al*, 2015)[115]	No - review	n/a	n/a	n/a
17	Evolution of indirect reciprocity by social information: the role of trust and reputation in evolution of altruism (Mohtashemi & Mui, 2003)[116]	Yes	Cooperation	n/a	n/a
18	Kin selection is the key to altruism (Foster *et al*, 2006)[117]	No - review	n/a	n/a	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
19	Parental manipulation, kin selection, and the evolution of altruism (Craig, 1979)[118]	Yes	Altriusm	Relatedness	n/a
20	Altruism in viscous populations—an inclusive fitness model (Taylor, 1992)[119]	Yes	Altruism	Relatedness	n/a
21	The evolution of altruism and the ordering of love (Pope, 1994)[120]	No - book	n/a	n/a	n/a
22	A note on the evolution of altruism in structured demes (Charlesworth, 1979)[121]	Yes	Cooperation	n/a	n/a
23	Adaptive evolution of social traits: origin, trajectories, and correlations of altruism and mobility (Le Galliard *et al*, 2005)[122]	Yes	Altruism	Relatedness	n/a
24	Altruism through beard chromodynamics (Jansen & Van Baalen, 2006)[123]	Yes	Parameter-dependent	Relatedness	n/a
25	The evolution of altruism: Correlation, cost, and benefit (Sober, 1992)[124]	Yes	Altruism	Relatedness and reciprocity	n/a
26	A mechanism for the evolution of altruism among nonkin: positive assortment through environmental feedback (Pepper & Smuts, 2002)[125]	Yes	Altruism	Relatedness (positive assortment of genotypes)	n/a
27	Evolution of altruism in stepping-stone populations with overlapping generations (Irwin & Taylor, 2001)[126]	Yes	Altruism	Relatedness and spatial structure	n/a
28	Can altruism evolve in purely viscous populations? (Wilson *et al*, 1992)[127]	Yes	Parameter-dependent	Relatedness and space	n/a
29	A quantitative test of Hamilton's rule for the evolution of altruism (Waibel *et al*, 2011)[128]	Yes	Altruism	Relatedness	n/a
30	The evolution of altruism: game theory in multilevel selection and inclusive fitness (Fletcher & Zwick, 2007)[129]	No - review	n/a	n/a	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
31	Group selection, altruism, reinforcement, and throwing in human evolution (Darlington Jr, 1975) [130]	No - review	n/a	n/a	n/a
32	Putting the altruism back into altruism: the evolution of empathy (De Waal, 2008) [131]	No - review	n/a	n/a	n/a
33	Altruism as a handicap: the limitations of kin selection and reciprocity (Zahavi, 1995) [132]	No - perspective	n/a	n/a	n/a
34	Enforced altruism in insect societies (Wenseleers & Ratnieks, 2006) [133]	No - empirical research	n/a	n/a	n/a
35	The evolution of altruism by costly punishment in lattice-structured populations: score-dependent viability versus score-dependent fertility (Nakamaru & Iwasa, 2005) [134]	Yes	Parameter-dependent	Relatedness, punishment and group selection	n/a
36	Kin recognition and the evolution of altruism (Agrawal, 2001) [135]	Yes	Altruism	Relatedness	n/a
37	Kindness in a cruel world: The evolution of altruism (Barber, 2004) [136]	No - book	n/a	n/a	n/a
38	Altruism, spite, and greenbeards (West & Gardner, 2010) [137]	No - review	n/a	n/a	n/a
39	Darwinian selection and "altruism" (Cavalli-Sforza & Feldman, 1978) [138]	Yes	Altruism	Relatedness and other mechanisms	n/a
40	Altruism: Its characteristics and evolution (Darlington Jr, 1978) [139]	No - review	n/a	n/a	n/a
41	Models of the evolution of altruism (Maynard Smith, 1980) [140]	Yes	Altruism	Relatedness	n/a
42	Evolution of altruism under group selection in large and small populations in fluctuating environments (Uyenoyama, 1979) [141]	Yes	Cooperation	n/a	n/a
43	What is altruism? (Kerr *et al*, 2004) [142]	No - review	n/a	n/a	n/a
44	Evolution of altruism in kin-structured and random subdivided populations (Fix, 1985) [143]	Yes	Parameter-dependent	Relatedness	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
45	Inbreeding and the evolution of altruism under kin selection: effects on relatedness and group structure (Uyenoyama, 1984)[144]	Yes	Altruism	Relatedness	n/a
46	Genetic relatedness and the evolution of altruism (Okasha, 2002)[145]	No - perspective	n/a	n/a	n/a
47	Origins of altruism and cooperation (Sussman & Cloninger, 2011)[146]	No - book	n/a	n/a	n/a
48	Experimental evolution: concepts, methods, and applications of selection experiments (Garland & Rose, 2009)[147]	No - book	n/a	n/a	n/a
49	Sex-biased dispersal of adults mediates the evolution of altruism among juveniles (Gardner, 2010)[148]	Yes	Altruism	Relatedness	n/a
50	Inclusive fitness in evolution (Ferriere & Michod, 2011)[149]	No - perspective	n/a	n/a	n/a
51	Gene-culture coevolution: models for the evolution of altruism with cultural transmission (Feldman *et al*, 1985)[150]	Yes	Altruism	Relatedness	n/a
52	Group selection, altruism, and structured-deme models (Nunney, 1985)[151]	Yes	Altruism	Relatedness and group selection	n/a
53	Friendship and the banker's paradox: Other pathways to the evolution of adaptations for altruism (Tooby & Cosmides, 1996)[152]	No - perspective	n/a	n/a	n/a
54	The evolution of cooperation and altruism – a general framework and a classification of models (Lehmann & Keller, 2006)[17]	Yes	Parameter-dependent	Relatedness	Gray
55	"Runaway" social evolution: reinforcing selection for inbreeding and altruism (Breden & Wade, 1991)[153]	Yes	Altruism	Relatedness	n/a
56	Biological altruism (Okasha, 2003)[154]	No - book chapter	n/a	n/a	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
57	Moral origins: The evolution of virtue, altruism, and shame (Boehm, 2012)[155]	No - book	n/a	n/a	n/a
58	Altruism researchers must cooperate (Okasha, 2010)[156]	No - perspective	n/a	n/a	n/a
59	Selfishness as second-order altruism (Eldakar & Wilson, 2008)[157]	Yes	Cooperation	n/a	n/a
60	On the evolution of altruism by kin selection (Matessi & Karlin, 1984)[158]	Yes	Yes	Relatedness	n/a
61	The generalized exchange perspective on the evolution of altruism (Takagi, 1996)[159]	No - book chapter	n/a	n/a	n/a
62	Sex-ratio conflicts, kin selection, and the evolution of altruism (Alonso & Schuck-Paim, 2002)[160]	No - perspective	n/a	n/a	n/a
63	Demography, altruism, and the benefits of budding (Gardner & West, 2006)[161]	Yes	Altruism	Relatedness	n/a
64	Supercooperators: Altruism, evolution, and why we need each other to succeed (Nowak & Highfield, 2011)[53]	No - book	n/a	n/a	n/a
65	Evolution of indirect reciprocity (Nowak & Sigmund, 2005)[58]	No - review	n/a	n/a	n/a
66	Altruism and organism: Disentangling the themes of multilevel selection theory (Wilson, 1997)[162]	No - review	n/a	n/a	n/a
67	**The spatial spread of altruism versus the evolutionary response of egoists (Koella, 2000)[163]**	**Yes**	**Altruism**	**Population viscosity**	**No**
68	**Group selection and the evolution of altruism (Cooper & Wallace, 2004)[164]**	**Yes**	**Altruism**	**Group selection**	**No**
69	Life history, habitat saturation and the evolution of fecundity and survival altruism (Lion & Gandon, 2010)[165]	Yes	Altruism	Relatedness	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
70	Altruism in Mendelian populations derived from sibling groups: the haystack model revisited (Wilson, 1987)[166]	Yes	Altruism	Relatedness and group structure	n/a
71	Genetic stability and territorial structure facilitate the evolution of tag-mediated altruism (Spector & Klein, 2006)[167]	Yes	Altruism	Relatedness	n/a
72	**The coevolution of parochial altruism and war (Choi & Bowles, 2007)[168]**	**Yes**	**Parameter-dependent**	**Intergroup conflict**	**Yes**
73	Altruism in forest chimpanzees: the case of adoption (Boesch *et al*, 2010)[169]	No - empirical	n/a	n/a	n/a
74	Evolution of mutualism through spatial effects (Yamamura *et al*, 2004)[170]	Yes	Cooperation	n/a	n/a
75	Ultimate causes and the evolution of altruism (Marshall, 2011)[171]	No - perspective	n/a	n/a	n/a
76	The adaptive dynamics of altruism in spatially heterogeneous populations (Le Galliard *et al*, 2003)[172]	Yes	Altruism	Relatedness	n/a
77	The evolution of human altruism (Kitcher, 1993)[173]	Yes	Cooperation	n/a	n/a
78	Problems with altruism (Bertram, 1982)[174]	No - book chapter	n/a	n/a	n/a
79	Neoproterozoic 'snowball Earth' glaciations and the evolution of altruism (Boyle *et al*, 2007)[175]	Yes	Altruism	Relatedness	n/a
80	The evolution of cheating and selfish behavior (Wade & Breden, 1980)[176]	Yes	Altruism	Relatedness and group structure	n/a
81	Questioning the cultural evolution of altruism (André & Morin, 2011)[177]	No - review	n/a	n/a	n/a
82	**The evolution of eusociality (Nowak *et al*, 2010)[178]**	**Yes**	**Altruism**	**Group selection**	**Yes**
83	**The coevolution of altruism and punishment: role of the selfish punisher (Nakamaru & Iwasa, 2006)[179]**	**Yes**	**Parameter-dependent**	**Punishment**	**Yes**

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
84	Social evolution in structured populations (Débarre *et al*, 2014) [180]	Yes	Altruism	Relatedness and assortment	n/a
85	**The evolution of altruism in spatially structured populations (Németh & Takács, 2007) [181]**	**Yes**	**Parameter-dependent**	**Social distance**	**Yes**
86	The evolution of alarm calls: altruism or manipulation? (Charnov & Krebs, 1975) [182]	Yes	Cooperation	n/a	n/a
87	Is altruism evolutionarily stable? (Bester & Güth, 1994) [183]	Yes	Cooperaiton	n/a	n/a
88	An adaptation for altruism: The social causes, social effects, and social evolution of gratitude (McCullough *et al*, 2008) [184]	No - non-evolutionary	n/a	n/a	n/a
89	Ecological symmetry breaking can favour the evolution of altruism in an action-response game (Di Paolo, 2000) [185]	Yes	Insufficient information provided	n/a	n/a
90	How altruism evolves: assortment and synergy (Fletcher & Doebeli, 2006) [186]	No - perspective	n/a	n/a	n/a
91	**Deterministic group selection model for the evolution of altruism (Silva & Fontanari, 1999) [187]**	**Yes**	**Parameter-dependent**	**Group selection**	**No**
92	Pathogen resistance as the origin of kin altruism (Lewis, 1998) [188]	No - perspective	n/a	n/a	n/a
93	**A simple rule for the evolution of cooperation on graphs and social networks (Ohtsuki *et al*, 2006) [5]**	**Yes**	**Altruism**	**Spatial position**	**No**
94	The evolution of social behavior — A classification of models (Maynard Smith, 1982) [189]	No - book chapter	n/a	n/a	n/a
95	Some models of the evolution of altruistic behaviour between siblings (Charlesworth, 1978) [190]	Yes	Altruism	Relatedness	n/a
96	On the relationship between evolutionary and psychological definitions of altruism and selfishness (Wilson, 1992) [191]	No - perspective	n/a	n/a	n/a

Continued on next page

Index	Publication	Formal evolutionary model?	Phenotype	Attribution	Denies relatedness?
97	An inclusive fitness analysis of altruism on a cyclical network (Grafen, 2007)[192]	Yes	Altruism	Relatedness	n/a
98	Genes underlying altruism (Thompson *et al*, 2013)[193]	No - perspective	n/a	n/a	n/a
99	Strong altruism can evolve in randomly formed groups (Fletcher & Zwick, 2004)[194]	Yes	Cooperation	n/a	n/a
100	The genetical evolution of social behaviour. II (Hamilton, 1964)[195]	Yes	Altruism	Relatedness	n/a

Table S3: Papers where the authors explicitly deny that their models entail relatedness (quotes taken from the papers are shown in column 2). But their models do entail relatedness (as shown by quotes from the same papers in column 3), and kin selection therefore operates (i.e., $rb > 0$) on genetic and/or cultural variants (column 4)

Publication	Claim of unrelatedness	Mode of reproduction	Mode of interaction	Kin selection operates
Traulsen and Nowak, 2006[10]	"Groups consist of genetically unrelated individuals"	"In any one time step, a single individual from the entire population is chosen for reproduction... The offspring is added to the same group."	"Interactions occur between members of the same group."	Yes, on genes
Bowles and Gintis, 2004[11]	"Our results do not require that group members be related"	"Parents pass on their type to their offspring... Selfish agents inherit the estimate of $s > 0$ (the cost of being ostracized) from their parents... We assume an ostracized agent works alone for a period of time before being readmitted to a group. "	"Agents can also work cooperatively in a group, each producing an amount b at cost c (all benefits and costs are in fitness units). We assume that output of the group is shared equally by the agents, so if all group members work, each has a net group fitness benefit $b - c > 0$".	Yes, on genes
Boyd *et al*, 2003[16]	"This behavior is puzzling from an evolutionary perspective because cooperating individuals incur individual costs to confer benefits on unrelated group members"	"An individual i who encounters an individual j imitates j with probability $W_j/(W_j + W_i$, where W_x is the payoff of individual x in the game"	"After the second stage, individuals encounter another individual from their own group"	Yes, on memes
Santos and Pacheco, 2005[22]	"prisoner's dilemma and snowdrift game as metaphors of cooperation between unrelated individuals."	"Whenever a site x is updated, a neighbor y is drawn at random among all k_x neighbors"	"In each generation, all pairs of individuals x and y, directly connected, engage in a single round of a given game"	Yes, on genes

Continued on next page

Publication	Claim of unrelatedness	Mode of reproduction	Mode of interaction	Kin selection operates
Santos *et al*, 2006[30]	"prisoner's dilemma (PD) as a metaphor for studying cooperation between unrelated individuals"	"To update a strategy located in vertex x, a neighbour y is drawn at random among all k_x neighbours"‡	"During each generation (which constitutes our unit of discrete evolutionary time), all pairs of directly connected individuals, x and y, engage in a single round of the game"	Yes, on memes
Nakamaru *et al*, 1997[32]	"The evolution of cooperation among unrelated individuals is studied in a lattice-structured habitat"	"After the death of an individual, the site is replaced immediately by a copy of a randomly chosen neighbor."	"individuals using either TFT or AD play the iterated Prisoners Dilemma game with its neighbors"	Yes, on genes
Wang *et al*, 2012[35]	"The study of evolutionary games on networks and graphs ... has proven very gratifying in terms of improving our understanding of the emergence and sustenance of cooperation among selfish and unrelated individuals."	"strategy invasions are attempted between nearest neighbors"§	"in each group cooperators contribute 1 to the public good while defectors contribute nothing."	Yes, on memes
Santos and Pacheco, 2006[39]	"Prisoner's Dilemma (PD) as a metaphor for studying cooperation between unrelated individuals".	"whether the strategy located in a given vertex will be replicated to the next generation or, instead, will be replaced by the strategy of a better fit neighbour."	"agents will have an accumulated payoff resulting from their one-round interactions with each of their immediate neighbours"	Yes, on memes
Fu *et al*, 2007[75]	"evolutionary game theory provides a systematic framework for investigating the emergence and maintenance of cooperative behavior among unrelated and selfish individuals"	"players are allowed to adopt the strategies of their neighbors after each round"	"Each individual plays the PDG/SG with its immediate "neighbors""	Yes, on memes
Wang *et al*, 2012[80]	"various specific mechanisms have been proposed ... to promote the evolution of cooperation among unrelated individuals... Here we propose an approach that ..."	"After the neighbor j is chosen, player i adopts the strategy s_j of the selected player j"	First, player i acquires its payoff P_i by playing the game with all its neighbors.	Yes, on memes

Continued on next page

‡In this and other cultural models, strategies are equivalent to phenotypes in genetic clonal models to which they compare. When one strategy is chosen to update a given vertex, this is equivalent to the death of an individual with a particular phenotype, and subsequent replacement by the offspring of a neighbour (i.e., reproduction under local dispersal).

§'strategy invasions' are equivalent to 'strategy updates' (see previous footnote), and are also equivalent to 'strategy replacement', 'strategy adoption', and 'strategy enforcement' (in the following table entries). In all of these cases, memes spread locally and so are likely to interact with memes with which they share a recent common ancestor.

Publication	Claim of unrelatedness	Mode of reproduction	Mode of interaction	Kin selection operates
Szolnoki and Perc, 2012[98]	"new ways by means of which the successful evolution of cooperation among selfish and unrelated individuals can be understood..."	"Each Monte Carlo step (MCS) gives a chance for every player to enforce its strategy onto one of its neighbors"	"A randomly selected player x plays the public goods game with its $G-1$ partners as a member of all the g groups, whereby its overall payoff P_{s_x} is thus the sum of all the payoffs acquired in the five groups. Next, player x chooses one of its nearest neighbors at random, and the chosen coplayer y also acquires its payoff P_{s_y} in the same way"	Yes, on memes
Bowles, 2006[102]	"The left-hand term, like Hamilton's degree of relatedness (r), is a measure of positive assortment; but here assortment arises solely from between-deme differences in the prevalence of A's"	"Consider a large metapopulation of individuals living in partially isolated subpopulations (called demes)... Reproduction is asexual"¶	"Altruists (A's) take an action costing c that confers a benefit b on an individual randomly selected from the n members of the deme"	Yes, on genes
Levin and Kilmer, 1974[114]	"Interdemic selection requires subdivided populations, but does not require associations among related individuals."	"demes are connected by migration... reproduction and Mendelian selection is completed in all demes"	"After flow migration, the probability of survival for each deme is computed from the formula: $PS_i = a + bq_i^e$ where a, b and c are constants and q_i is the post-migration frequency of the A allele in that deme."	Yes, on genes
Choi and Bowles, 2007[168]	"Preferential assortment with close genetic kin is not involved"	"members of each group are paired randomly with members of their group to produce offspring... With probability $(1-m)$, the nonmutational replication above takes place"	"We model the evolution of genetically transmitted behavioral types in a population of foragers who engage in both within- and between-group interactions."	Yes, on genes
Nowak *et al*, 2010[178]	"In our model relatedness does not drive the evolution of eusociality"	"We assume that the dispersal behaviour can be affected by genetic mutations. We postulate a mutant allele, a, which induces daughters to stay with the nest."	"*AA* and *Aa* daughters leave the nest, whereas *aa* stay at the nest with probability q, and become workers"	Yes, on genes

Continued on next page

¶This quote makes explicit that the model is an 'isolation-by-distance' model, but the same is true for all other models in this table. Wherever neighbours interact with neighbours (local interaction) and offspring are placed into the same neighbourhood as the parents (local dispersal) then the population will exhibit isolation-by-distance, and individuals/ strategies will be positively related to the individuals/ strategies with which they interact.

Publication	Claim of unrelatedness	Mode of reproduction	Mode of interaction	Kin selection operates
Nakamaru and Iwasa, 2006[179]	"Punishment is an important mechanism promoting the evolution of altruism among non-relatives. We investigate..."	"After the death of an individual, the site becomes empty, and one of the four nearest neighbors colonizes"	"players using the same strategy make clusters in the lattice"	Yes, on genes
Németh and Takács, 2007[181]	"Helping other individuals is often kinship-based or reciprocal. Several examples show, however, that ... people are willing to support unrelated others even when this is at a cost and they receive nothing in exchange. Here we examine the evolution of this "pure" altruism"	"we have a "viscous" population in which reproduction and interaction takes place locally"	"we have a "viscous" population in which reproduction and interaction takes place locally"	Yes, on genes

25

Table S4: Impactful papers presenting evolutionary models where altruism evolves, and the authors attribute the evolution of altruism to a mechanism other then kin selection (column 1). In all cases, the benefits of altruism are accrued by relatives (columns 2 and 3), and kin selection operates on genetic and/or cultural variants (column 4)

Publication	Proposed mechanism	Reproduction mode	Interaction mode	Kin selection operates
Ohtsuki *et al*, 2006[5]	"cooperation can evolve as a consequence of 'social viscosity'"	"at each time step, a random individual is chosen to die… subsequently the neighbours compete for the empty site"	"Interactions occur between members of the same group"	Yes, on genes
Hauert and Doebeli, 2004[9]	"spatial structure can promote persistence of cooperation"	"Whenever a site is updated, the present occupant and its nearest neighbours compete to populate the site with their offspring"	"individuals interact only within a limited local neighbourhood"	Yes, on genes
Leimar and Hammerstein, 2001[13]	"How can cooperation through indirect reciprocity evolve and what would it be like?"	"A new generation is formed by asexual reproduction... A new individual is locally derived with probability p"‖	"Two individuals are randomly chosen from the group in each round of interaction"*	Yes, on genes
Gómez-Gardenes *et al*, 2012[25]	"multiplex structure enhances the resilience of cooperation to defection"	"Each of the players, say i, chooses... a neighbor j... agent i will take the strategy of j"	"After round t... an individual has played once with its k_i^l neighbors"	Yes, on memes

Continued on next page

‖ 'new individuals' being 'locally derived' equates to limited dispersal and isolation-by-distance. Under these conditions, individuals will generally be surrounded by individuals with whom they share recent common ancestors (i.e., relatives).

*The crucial words here are 'from the group'; the population is a structured one, comprising multiple groups, and individuals are more likely to interact with other individuals from their group (with whom they are, on average, positively related) than with individuals from other groups.

Publication	Proposed mechanism	Reproduction mode	Interaction mode	Kin selection operates
Wang *et al*, 2013[47]	"Network reciprocity is amongst the most well-known mechanisms that may sustain cooperation in evolutionary games"	"one randomly chosen neighbor of x within the same network, denoted by y... player x attempts to adopt the strategy s_y from player y with a probability"	"player x acquires its utility U_x by playing the game with all its nearest neighbors"	Yes, on memes
Roca *et al*, 2009[51]	"Several mechanisms have been proposed to explain the appearance and survival of cooperation… the structure of the population being one of them"	"With the replicator rule one neighbor $j \in N_i$ is chosen at random. The probability of player i adopting the strategy of player j"	"each individual only plays with her neighbors"	Yes, on memes
Hammond and Axelrod, 2006[54]	"ethnocentrism itself can be necessary to sustain cooperation"	"Reproduction consists of creating an offspring in an adjacent empty site, if there is one"	"Each pair of neighbors then interacts in a one-move prisoner's dilemma"	Yes, on genes
Wu *et al*, 2010[55]	"Cooperative behavior that increases the fitness of others at a cost to oneself can be promoted by ... population structure, which can lead to clustering of cooperating agents"	"Individuals... update their strategies by imitating their partners"	"The payoff of each individual is obtained by playing the PD game with all of its immediate neighbors"	Yes, on memes
Pfeiffer *et al*, 2001[56]	"a form of cooperative resource use and may evolve in spatially structured environments"	"spatial model including diffusion of cells"[†]	"spatial model including diffusion of ... resource"[‡]	Yes, on genes
Perc, 2009[60]	"The decline of cooperation can be directly linked to the decrease of heterogeneity of scale-free networks"	"one randomly chosen neighbor of x, denoted by y, also acquires its payoff p_y by playing the game with all its k_y neighbors. Lastly, if $p_x > p_y$ player x tries to enforce its strategy s_x on player y"	"a randomly selected player x acquires its payoff p_x by playing the game with all its k_x neighbors"	Yes, on memes
Masuda, 2007[63]	"In the Prisoner's Dilemma, altruism is also promoted by the viscosity of populations"	"Each player tends to copy successful strategies in their neighbourhood"[§]	"everybody participates in the two-person game with all the neighbours"	Yes, on memes
Wang *et al*, 2014[65]	"If interactions among players are structured rather than well mixed, the clustering of cooperators is more likely to be stable"	"players seek for neighbors to potentially update their strategy"	"a randomly selected player x acquires its payoff P_x by playing the game with all its neighbors on the interaction network"	Yes, on memes

Continued on next page

[†]The exact structure of this model is rather opaque, however the fact that the cells diffuse in a spatial model implies that reproduction occurs locally and that neighbouring cells are likely to share a recent common ancestor.

[‡]A locally dispersing resource implies that interactions predominantly occur locally.

[§]The 'strategy copying' described here is the same process as 'strategy update' (i.e., equivalent to birth and death).

Publication	Proposed mechanism	Reproduction mode	Interaction mode	Kin selection operates
Santos *et al*, 2008[67]	"We introduce social diversity by means of heterogeneous graphs and show that cooperation is promoted by the diversity associated with the number and size of the public goods game in which each individual participates and with the individual contribution to each such game"	"When a site x with a payoff P_x is selected for update, a neighbour y (with a payoff P_y) is drawn at random between all k_x neighbours. If $P_x > P_y$, no update occurs. If $P_x < P_y$, x will adopt y's strategy with a probability given by $(P_y - P_x)/M$"	"individuals occupy the vertices of the graph, and social interactions proceed along the edges"¶	Yes, on memes
Santos *et al*, 2012[70]	"topological heterogeneity... holds back the invasion of free riders"	"We consider that each individual i adopts the strategy of a randomly selected (social) neighbor j"	"'defectors' success is contingent on the number of $\boldsymbol{C}$'s in the neighborhood"	Yes, on memes
Brauchli *et al*, 1999[73]	"spatial structure greatly influences the evolution of cooperation"	"all individuals of the nxn lattice play an IPD game against their eight nearest neighbours"	"the individual on each cell is replaced by an offspring of the highest scoring individual among the former site holder and its eight nearest neighbours"	Yes, on memes
Perc and Szolnoki, 2008[74]	"The facilitation of the cooperative strategy relies mostly on the inhomogeneous social state of players, resulting in the formation of cooperative clusters which are ruled by socially high-ranking players that are able to prevail against the defectors"	"The performance of player i is compared with that of a randomly chosen neighbor j and the probability that its strategy changes to s_j is given by ..."	"Each individual is allowed to interact only with its four nearest neighbors"	Yes, on memes
Wang *et al*, 2012[82]	"Spatial reciprocity is a well known tour de force of cooperation promotion"	"one randomly chosen neighbor, denoted by y, also acquires its payoff p_y by playing the game with its four neighbors. Lastly, player x tries to enforce its strategy s_x on player y"	"player x acquires its payoff p_x by playing the game with its k neighbors"	Yes, on memes
Feldman and Thomas, 1987[84]	"The tendency for clustering among like strategists to enhance their initial increase when rare is also explored dynamically"	"The constitution of the next generation, $t+1$, is the result of competition between TFT and all-D"	"p_a and p_b are the respective probabilities that TFT and all-D assort"	Yes, on genes

Continued on next page

¶On a graph, edges connect neighbouring vertices, so interactions proceeding along edges' translates as individuals interacting locally.

Publication	Proposed mechanism	Reproduction mode	Interaction mode	Kin selection operates
Rand *et al*, 2010[86]	"Theoretical models have revealed that spatial structure can favor the coevolution of punishment and cooperation... our results demonstrate serious restrictions on the ability of costly punishment to allow the evolution of cooperation in spatially structured populations."	"Each player interacts with the four players in her von Neumann neighbourhood"	"In each generation a random player is given a chance to update her strategy... With probability ... she abandons her current strategy (i.e. dies) and randomly adopts the strategy of one of the z players she just interacted with."	Yes, on memes
Szolnoki *et al*, 2009[88]	"Prominently, spatial structure may foster the formation of cooperative clusters on the grid"	"one randomly chosen neighbor denoted by y also acquires its payoff p_y by playing the game with its four neighbors. Lastly, player x tries to enforce its strategy s_x on player y"	"player x acquires its payoff p_x by playing the game with its nearest neighbors"	Yes, on memes
Szolnoki and Perc, 2008[94]	"this simple mechanism spontaneously creates relevant inhomogeneities in the teaching activities that support the maintenance of cooperation"	"one randomly chosen neighbor, denoted by y, also acquires its payoff P_y by playing the game with its four neighbors. Lastly, player x tries to enforce its strategy s_x on player y"	"player x acquires its payoff P_x by playing the game with its four nearest neighbors"	Yes, on memes
Schweitzer *et al*, 2002[96]	"space indeed plays a definite role in the evolution of cooperation, because a spatially restricted interaction may lead to a global cooperation"	"if one of its neighbors j has received the higher payoff, then agent i will adopt the behavior of the respective agent"	"each agent only locally interacts with his neighbors"	Yes, on memes
Hammond and Axelrod, 2006 b[85]	"a new mechanism that combines both lines of work to show when and how favoritism toward apparently similar others can evolve in the first place. The mechanism is the joint operation of viscosity and of tags..."	"offspring are created only if they can be placed in an empty site adjacent to the parent"	"each pair of adjacent agents interacts"	Yes, on genes
Koella, 2000[163]	"altruism can spread in viscous populations"	"The offspring are successful only if they find an empty site within dispersal distance of their parent"	"An individual's probability of reproducing, however, is determined by its own strategy and by its neighbourhood"	Yes, on genes

Continued on next page

Publication	Proposed mechanism	Reproduction mode	Interaction mode	Kin selection operates
Cooper and Wallace, 2004[164]	"The smaller the group size, or the larger the benefit-to-cost ratio, the higher the survival chances of altruism. Additionally, for altruism to survive, the number of generations spent in isolated groups must be neither too big nor too small."	"Having played the game and received their associated payoffs the new proportion of altruists within each group is calculated"	"agents interact only with other members of their group"	Yes, on genes
Silva and Fontanari, 1999[187]	"we compare our standard group selection model with a recently proposed alternative model for the evolution of altruistic traits"	"The metapopulation is composed of an infinite number of demes, each of which is composed of N haploid, asexually reproducing individuals... The reproduction process described here takes place inside the demes"	"The alleles A or B at a single locus determine whether a given individual is altruist or non-altruist, respectively. The fitness or reproductive rate of the individuals is determined solely by this trait"	Yes, on genes

26

Table S5: Top papers for "Nowak cooperation" on 28/10/2019. This table follows the same structure as Table S1 (though does not ask whether the presence of relatedness is explicitly denied); see Table S1 legend for details.

Index	Publication	Formal evolutionary model?	Phenotype	Attribution
1	Five rules for the evolution of cooperation (Nowak, 2006)[2]	No - review	n/a	n/a
2	**Evolutionary games and spatial chaos (Nowak & May, 1992)[196]**	**Yes**	**Altruism**	**Spatial pattern**
3	Evolution of indirect reciprocity by image scoring (Nowak & Sigmund, 1998)[18]	Yes	Cooperation	n/a
4	Evolution of indirect reciprocity (Nowak & Sigmund, 2005)[58]	No - review	n/a	n/a
5	A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game (Nowak & Sigmund, 1993)[197]	Yes	Cooperation	n/a
6	**A simple rule for the evolution of cooperation on graphs and social networks (Ohtsuki *et al*, 2006)[5]**	**Yes**	**Altruism**	**Spatial position**‖

Continued on next page

‖The wording of the attributions is taken from the publications, and the plethora of terms ('spatial pattern', 'spatial position', 'population structure',

Index	Publication	Novel evolutionary model?	Altruism evolves?	Attribution
7	Emergence of cooperation and evolutionary stability in finite populations (Nowak *et al*, 2004)[61]	Yes	Cooperation	n/a
8	**The evolution of eusociality (Nowak *et al*, 2010)[178]**	**Yes**	**Altruism**	**Population structure**
9	Tit for tat in heterogeneous populations (Nowak & Sigmund 1992b[198]	Yes	Cooperation	n/a
10	**Evolutionary dynamics on graphs (Lieberman *et al*, 2005)[199]**	**Yes**	**Parameter-dependent**	**Graph arrangement**
11	Spontaneous giving and calculated greed (Rand *et al*, 2012)[200]	No - empirical research	n/a	n/a
12	Evolutionary dynamics of biological games (Nowak & Sigmund, 2004)[201]	No - review	n/a	n/a
13	Fairness versus reason in the ultimatum game (Nowak *et al*, 2000)[202]	Yes	Cooperation	n/a
14	**The spatial dilemmas of evolution (Nowak & May, 1993)[203]**	**Yes**	**Altruism**	**Spatial effects**
15	Human cooperation (Rand & Nowak, 2013)[204]	No - review	n/a	n/a
16	SuperCooperators: Altruism, Evolution, and why we need each other to succeed (Nowak & Highfield, 2011)[53]	No - book	n/a	n/a
17	**Evolution of cooperation by multilevel selection (Traulsen & Nowak, 2006)[10]**	**Yes**	**Altruism**	**Group selection**
19	Winners don't punish (Dreber *et al*, 2008)[205]	No - empirical research	n/a	n/a
20	Via freedom to coercion: the emergence of costly punishment (Hauert *et al*, 2007)[206]	Yes	Cooperation	n/a

Continued on next page

'graph arrangement', 'spatial effects', 'spatial parameters' *etc*.) are all variations around the same theme: where populations have spatial structure, and individuals disperse and interact locally, then positive relatedness among interacting individuals emerges from the spatial structure of the population.

Index	Publication	Novel evolutionary model?	Altruism evolves?	Attribution
21	The dynamics of indirect reciprocity (Nowak & Sigmund, 1998b)[207]	Yes	Cooperation	n/a
22	Positive interactions promote public cooperation (Rand *et al*, 2009)[208]	No - empirical research	n/a	n/a
23	Coevolution of strategy and structure in complex networks with dynamical linking (Pacheco *et al*, 2006)[209]	Yes	Cooperation	n/a
24	Social heuristics shape intuitive cooperation (Rand *et al*, 2014)[210]	No - empirical research	n/a	n/a
25	Reward and punishment (Sigmund *et al*, 2001)[211]	Yes	Cooperation	n/a
26	**Spatial games and the maintenance of cooperation (Nowak *et al*, 1994)[212]**	**Yes**	**Altruism**	**Spatial parameters**
27	Stochastic dynamics of invasion and fixation (Traulsen *et al*, 2006)[213]	Yes	Cooperation	n/a
28	Reputation-based partner choice promotes cooperation in social networks (Fu *et al*, 2008)[214]	Yes	Cooperation	n/a
29	Evolutionary game dynamics in finite populations (Taylor *et al*, 2004)[215]	Yes	Cooperation	n/a
30	**Evolutionary dynamics in structured populations (Nowak *et al*, 2010b)[216]**	**Yes**	**Altruism**	**Spatial selection**
31	The arithmetics of mutual help (Nowak *et al*, 2001)[217]	No - review	n/a	n/a
32	Evolutionary cycles of cooperation and defection (Imhof *et al*, 2005)[68]	Yes	Cooperation	n/a
33	**More spatial games (Nowak *et al*, 1994b)[218]**	**Yes**	**Altruism**	**Spatial arrays**

Continued on next page

Index	Publication	Novel evolutionary model?	Altruism evolves?	Attribution
34	**The replicator equation on graphs (Ohtsuki & Nowak, 2006)[219]**	**Yes**	**Altruism**	**Population structure**

Table S6: 'Spatial selection' papers authored by Martin Nowak and colleagues. In all cases, levels of relatedness are high, dispersal is limited (column 2), interactions are local (column 3), and kin selection therefore operates on genetic and/or cultural variants (column 4)

Publication	Reproduction mode	Interaction mode	Kin selection operates
Nowak and May, 1992[196]	"At the start of the next generation, each lattice-site is occupied by the player with the highest score among the previous owner and the immediate neighbours"	"each round every individual 'plays the game' with the immediate neighbours"	Yes, on genes
Lieberman *et al*, 2005[199]	"players arranged on a directed cycle... with player i placing its offspring into $i+1$"	"the payoff of any individual comes from an interaction with one of its neighbours"	Yes, on genes
Nowak and May, 1993[203]	"After this, each site is occupied by either its original owner or by one of the neighbours"	"In each round every individual "play the game" with its immediate neighbours"	Yes, on genes
Nowak *et al*, 1994[212]	"...After this, each site is occupied either by its original owner or by one of the neighbors"	"players... interact with neighbors in some spatial array"	Yes, on genes
Nowak *et al*, 2010[216]	"one individual is chosen at random to die; the neighbours compete for the empty site"	"Each individual interacts with all of its neighbours"	Yes, on genes
Nowak *et al*, 1994b[218]	"a cell is always given to its most successful neighbour"**	"Another possibility is to study spatial games in three dimensions... Here interaction is with the six nearest neighbours"	Yes, on genes
Ohtsuki and Nowak, 2006[219]	"the offspring of this individual replaces a randomly chosen neighbor"	"the fitness of an individual is locally determined from interactions with all adjacent individuals"	Yes, on genes and memes

References

[1] Axelrod, R. & Hamilton, W. D. The evolution of cooperation. *Science* **211**, 1390–1396 (1981).

[2] Nowak, M. A. Five rules for the evolution of cooperation. *Science* **314**, 1560–1563 (2006).

[3] Doz, Y. L. The evolution of cooperation in strategic alliances: initial conditions or learning processes? *Strategic Management Journal* **17**, 55–83 (1996).

[4] Axelrod, R. & Dion, D. The further evolution of cooperation. *Science* **242**, 1385–1390 (1988).

[5] Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M. A. A simple rule for the evolution of cooperation on graphs and social networks. *Nature* **441**, 502 (2006).

[6] Riolo, R. L., Cohen, M. D. & Axelrod, R. Evolution of cooperation without reciprocity. *Nature* **414**, 441 (2001).

**This entry is one of Nowak's earlier papers mentioned in Box 2, where the model is deterministic. Note that a cell is *always* given to the most successful neighbour. This means that with a single altruist, altruism could never spread. For the models to give interesting results, they are seeded with multiple altruists. Since these are created simultaneously, they share no common ancestry, and are 'identical by state'. However, because reproduction is local in the models, the offspring of the founders interact with relatives, and so kin selection plays a role in the propagation and maintenance of altruism. The determinism also results in symmetrical distributions of selfish individuals and altruists at the population level (when the model is initiated with a symmetrical distribution). Together these factors made Nowak's models appear different from the concurrent kin selection models despite the fact that the mechanism driving the evolution of altruism was the same.

[7] Sachs, J. L., Mueller, U. G., Wilcox, T. P. & Bull, J. J. The evolution of cooperation. *The Quarterly Review of Biology* **79**, 135–160 (2004).
[8] Boyd, R. & Richerson, P. J. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* **13**, 171–195 (1992).
[9] Hauert, C. & Doebeli, M. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature* **428**, 643 (2004).
[10] Traulsen, A. & Nowak, M. A. Evolution of cooperation by multilevel selection. *Proceedings of the National Academy of Sciences* **103**, 10952–10955 (2006).
[11] Bowles, S. & Gintis, H. The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theoretical Population Biology* **65**, 17–28 (2004).
[12] Hammerstein, P. *Genetic and cultural evolution of cooperation* (MIT press, 2003).
[13] Leimar, O. & Hammerstein, P. Evolution of cooperation through indirect reciprocity. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**, 745–753 (2001).
[14] Milinski, M. Tit for tat in sticklebacks and the evolution of cooperation. *Nature* **325**, 433–435 (1987).
[15] Rainey, P. B. & Rainey, K. Evolution of cooperation and conflict in experimental bacterial populations. *Nature* **425**, 72–74 (2003).
[16] Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences* **100**, 3531–3535 (2003).
[17] Lehmann, L. & Keller, L. The evolution of cooperation and altruism–a general framework and a classification of models. *Journal of Evolutionary Biology* **19**, 1365–1376 (2006).
[18] Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity by image scoring. *Nature* **393**, 573–577 (1998).
[19] Stevens, J. R. & Hauser, M. D. Why be nice? psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences* **8**, 60–65 (2004).
[20] Frank, R. H., Gilovich, T. & Regan, D. T. The evolution of one-shot cooperation: An experiment. *Ethology and Sociobiology* **14**, 247–256 (1993).
[21] Enquist, M. & Leimar, O. The evolution of cooperation in mobile organisms. *Animal Behaviour* **45**, 747–757 (1993).
[22] Santos, F. C. & Pacheco, J. M. Scale-free networks provide a unifying framework for the emergence of cooperation. *Physical Review Letters* **95**, 098104 (2005).
[23] Adler, E. The emergence of cooperation: national epistemic communities and the international evolution of the idea of nuclear arms control. *International Organization* **46**, 101–145 (1992).
[24] Axelrod, R., Axelrod, D. E. & Pienta, K. J. Evolution of cooperation among tumor cells. *Proceedings of the National Academy of Sciences* **103**, 13474–13479 (2006).
[25] Gómez-Gardenes, J., Reinares, I., Arenas, A. & Floría, L. M. Evolution of cooperation in multiplex networks. *Scientific Reports* **2**, 620 (2012).
[26] Frank, S. A. Repression of competition and the evolution of cooperation. *Evolution* **57**, 693–705 (2003).
[27] Johnson, D. & Bering, J. Hand of god, mind of man: Punishment and cognition in the evolution of cooperation. *Evolutionary Psychology* **4**, 147470490600400119 (2006).
[28] West, S. A., El Mouden, C. & Gardner, A. Sixteen common misconceptions about the evolution of cooperation in humans. *Evolution and Human Behavior* **32**, 231–262 (2011).
[29] Dal Bó, P. & Fréchette, G. R. The evolution of cooperation in infinitely repeated games: Experimental evidence. *American Economic Review* **101**, 411–29 (2011).
[30] Santos, F. C., Rodrigues, J. & Pacheco, J. Graph topology plays a determinant role in the evolution of cooperation. *Proceedings of the Royal Society B: Biological Sciences* **273**, 51–55 (2005).
[31] Jones, G. R. & George, J. M. The experience and evolution of trust: Implications for cooperation and teamwork. *Academy of Management Review* **23**, 531–546 (1998).
[32] Nakamaru, M., Matsuda, H. & Iwasa, Y. The evolution of cooperation in a lattice-structured population. *Journal of Theoretical Biology* **184**, 65–81 (1997).
[33] Taylor, P. D., Day, T. & Wild, G. Evolution of cooperation in a finite homogeneous graph. *Nature* **447**, 469–472 (2007).
[34] Carmichael, H. L. & MacLeod, W. B. Gift giving and the evolution of cooperation. *International Economic Review* 485–509 (1997).
[35] Wang, Z., Szolnoki, A. & Perc, M. Evolution of public cooperation on interdependent networks: The impact of biased utility functions. *EPL (Europhysics Letters)* **97**, 48001 (2012).
[36] Henrich, J. Cooperation, punishment, and the evolution of human institutions. *Science* **312**, 60–61 (2006).
[37] Johnson, D. & Krüger, O. The good of wrath: Supernatural punishment and the evolution of cooperation. *Political Theology* **5**, 159–176 (2004).
[38] Bear, A. & Rand, D. G. Intuition, deliberation, and the evolution of cooperation. *Proceedings of the National Academy of Sciences* **113**, 936–941 (2016).
[39] Santos, F. C. & Pacheco, J. M. A new route to the evolution of cooperation. *Journal of Evolutionary Biology* **19**, 726–733 (2006).

[40] Nadell, C. D., Foster, K. R. & Xavier, J. B. Emergence of spatial structure in cell groups and the evolution of cooperation. *PLoS Computational Biology* **6** (2010).
[41] Michod, R. E. & Roze, D. Cooperation and conflict in the evolution of multicellularity. *Heredity* **86**, 1–7 (2001).
[42] Lotem, A., Fishman, M. A. & Stone, L. Evolution of cooperation between individuals. *Nature* **400**, 226 (1999).
[43] May, R. M. More evolution of cooperation. *Nature* **327**, 15–17 (1987).
[44] Antal, T., Ohtsuki, H., Wakeley, J., Taylor, P. D. & Nowak, M. A. Evolution of cooperation by phenotypic similarity. *Proceedings of the National Academy of Sciences* **106**, 8597–8600 (2009).
[45] Bateson, P. The biological evolution of cooperation and trust. *Trust: Making and Breaking Cooperative Relations* 14–30 (2000).
[46] Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Bonhoeffer, S. Evolution of cooperation by generalized reciprocity. *Proceedings of the Royal Society B: Biological Sciences* **272**, 1115–1120 (2005).
[47] Wang, Z., Szolnoki, A. & Perc, M. Optimal interdependence between networks for the evolution of cooperation. *Scientific Reports* **3**, 2470 (2013).
[48] Aktipis, C. A. Know when to walk away: contingent movement and the evolution of cooperation. *Journal of Theoretical Biology* **231**, 249–260 (2004).
[49] Nowak, M. & Sigmund, K. Chaos and the evolution of cooperation. *Proceedings of the National Academy of Sciences* **90**, 5091–5094 (1993).
[50] Gintis, H., Bowles, S., Boyd, R. T., Fehr, E. *et al. Moral sentiments and material interests: The foundations of cooperation in economic life*, vol. 6 (MIT press, 2005).
[51] Roca, C. P., Cuesta, J. A. & Sánchez, A. Effect of spatial structure on the evolution of cooperation. *Physical Review E* **80**, 046106 (2009).
[52] Boone, R. T. & Buck, R. Emotional expressivity and trustworthiness: The role of nonverbal behavior in the evolution of cooperation. *Journal of Nonverbal Behavior* **27**, 163–182 (2003).
[53] Nowak, M. & Highfield, R. *Supercooperators: Altruism, evolution, and why we need each other to succeed* (Simon and Schuster, 2011).
[54] Hammond, R. A. & Axelrod, R. The evolution of ethnocentrism. *Journal of conflict resolution* **50**, 926–936 (2006).
[55] Wu, B. *et al.* Evolution of cooperation on stochastic dynamical networks. *PLoS One* **5**, e11187 (2010).
[56] Pfeiffer, T., Schuster, S. & Bonhoeffer, S. Cooperation and competition in the evolution of atp-producing pathways. *Science* **292**, 504–507 (2001).
[57] Challet, D. & Zhang, Y.-C. Emergence of cooperation and organization in an evolutionary game. *Physica A: Statistical Mechanics and its Applications* **246**, 407–418 (1997).
[58] Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity. *Nature* **437**, 1291–1298 (2005).
[59] Buss, L. W. Group living, competition, and the evolution of cooperation in a sessile invertebrate. *Science* **213**, 1012–1014 (1981).
[60] Perc, M. Evolution of cooperation on scale-free networks subject to error and attack. *New Journal of Physics* **11**, 033027 (2009).
[61] Nowak, M. A., Sasaki, A., Taylor, C. & Fudenberg, D. Emergence of cooperation and evolutionary stability in finite populations. *Nature* **428**, 646–650 (2004).
[62] Sinervo, B. & Clobert, J. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science* **300**, 1949–1951 (2003).
[63] Masuda, N. Participation costs dismiss the advantage of heterogeneous networks in evolution of cooperation. *Proceedings of the Royal Society B: Biological Sciences* **274**, 1815–1821 (2007).
[64] Rakoff-Nahoum, S., Foster, K. R. & Comstock, L. E. The evolution of cooperation within the gut microbiota. *Nature* **533**, 255–259 (2016).
[65] Wang, Z., Wang, L. & Perc, M. Degree mixing in multilayer networks impedes the evolution of cooperation. *Physical Review E* **89**, 052813 (2014).
[66] Downs, G. W. Enforcement and the evolution of cooperation. *Michigan Journal of International Law* **19**, 319 (1997).
[67] Santos, F. C., Santos, M. D. & Pacheco, J. M. Social diversity promotes the emergence of cooperation in public goods games. *Nature* **454**, 213 (2008).
[68] Imhof, L. A., Fudenberg, D. & Nowak, M. A. Evolutionary cycles of cooperation and defection. *Proceedings of the National Academy of Sciences* **102**, 10797–10800 (2005).
[69] Hoffmann, R. Twenty years on: The evolution of cooperation revisited. *Journal of Artificial Societies and Social Simulation* **3**, 1390–1396 (2000).
[70] Santos, F. C., Pinheiro, F. L., Lenaerts, T. & Pacheco, J. M. The role of diversity in the evolution of cooperation. *Journal of Theoretical Biology* **299**, 88–96 (2012).
[71] Boyd, R., Gintis, H. & Bowles, S. Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science* **328**, 617–620 (2010).
[72] Fehl, K., van der Post, D. J. & Semmann, D. Co-evolution of behaviour and social network structure promotes human cooperation. *Ecology Letters* **14**, 546–551 (2011).
[73] Brauchli, K., Killingback, T. & Doebeli, M. Evolution of cooperation in spatially structured populations. *Journal*

of Theoretical Biology **200**, 405–417 (1999).
[74] Perc, M. & Szolnoki, A. Social diversity and promotion of cooperation in the spatial prisoner's dilemma game. *Physical Review E* **77**, 011904 (2008).
[75] Fu, F., Chen, X., Liu, L. & Wang, L. Social dilemmas in an online social network: the structure and evolution of cooperation. *Physics Letters A* **371**, 58–64 (2007).
[76] Bendor, J. Uncertainty and the evolution of cooperation. *Journal of Conflict Resolution* **37**, 709–734 (1993).
[77] Souza, M. O., Pacheco, J. M. & Santos, F. C. Evolution of cooperation under n-person snowdrift games. *Journal of Theoretical Biology* **260**, 581–588 (2009).
[78] Bergstrom, T. C. The algebra of assortative encounters and the evolution of cooperation. *International Game Theory Review* **5**, 211–228 (2003).
[79] Bowles, S. & Gintis, H. Origins of human cooperation. *Genetic and Cultural Evolution of Cooperation* 429–43 (2003).
[80] Wang, Z., Wang, L., Yin, Z.-Y. & Xia, C.-Y. Inferring reputation promotes the evolution of cooperation in spatial social dilemma games. *PLoS One* **7**, e40218 (2012).
[81] Herre, E. A., Knowlton, N., Mueller, U. G. & Rehner, S. A. The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends in Ecology & Evolution* **14**, 49–53 (1999).
[82] Wang, Z., Szolnoki, A. & Perc, M. If players are sparse social dilemmas are too: Importance of percolation for evolution of cooperation. *Scientific Reports* **2**, 369 (2012).
[83] Boyd, R. & Richerson, P. J. Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 3281–3288 (2009).
[84] Feldman, M. W. & Thomas, E. A. Behavior-dependent contexts for repeated plays of the prisoner's dilemma ii: Dynamical aspects of the evolution of cooperation. *Journal of Theoretical Biology* **128**, 297–315 (1987).
[85] Hammond, R. A. & Axelrod, R. Evolution of contingent altruism when cooperation is expensive. *Theoretical Population Biology* **69**, 333–338 (2006).
[86] Rand, D. G., Armao IV, J. J., Nakamaru, M. & Ohtsuki, H. Anti-social punishment can prevent the co-evolution of punishment and cooperation. *Journal of Theoretical Biology* **265**, 624–632 (2010).
[87] Strassmann, J. E. & Queller, D. C. Evolution of cooperation and control of cheating in a social microbe. *Proceedings of the National Academy of Sciences* **108**, 10855–10862 (2011).
[88] Szolnoki, A., Perc, M., Szabó, G. & Stark, H.-U. Impact of aging on the evolution of cooperation in the spatial prisoner's dilemma game. *Physical Review E* **80**, 021901 (2009).
[89] McCabe, K., Houser, D., Ryan, L., Smith, V. & Trouard, T. A functional imaging study of cooperation in two-person reciprocal exchange. *Proceedings of the National Academy of Sciences* **98**, 11832–11835 (2001).
[90] Joshi, N. Evolution of cooperation by reciprocation within structured demes. *Journal of Genetics* **66**, 69–84 (1987).
[91] Platt, T. G. & Bever, J. D. Kin competition and the evolution of cooperation. *Trends in Ecology & Evolution* **24**, 370–377 (2009).
[92] Avilés, L. Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. *Evolutionary Ecology Research* **1**, 459–477 (1999).
[93] Gowa, J. Anarchy, egoism, and third images: The evolution of cooperation and international relations-robert axelrod. the evolution of cooperation. new york: Basic, 1984. *International Organization* **40**, 167–186 (1986).
[94] Szolnoki, A. & Perc, M. Coevolution of teaching activity promotes cooperation. *New Journal of Physics* **10**, 043036 (2008).
[95] Dugatkin, L. A. The evolution of cooperation. *Bioscience* **47**, 355–362 (1997).
[96] Schweitzer, F., Behera, L. & Mühlenbein, H. Evolution of cooperation in a spatial prisoner's dilemma. *Advances in Complex Systems* **5**, 269–299 (2002).
[97] Sussman, R. W., Garber, P. A. & Cheverud, J. M. Importance of cooperation and affiliation in the evolution of primate sociality. *American Journal of Physical Anthropology* **128**, 84–97 (2005).
[98] Szolnoki, A. & Perc, M. Conditional strategies and the evolution of cooperation in spatial public goods games. *Physical Review E* **85**, 026104 (2012).
[99] Levine, D. K. & Pesendorfer, W. The evolution of cooperation through imitation. *Games and Economic Behavior* **58**, 293–315 (2007).
[100] Frean, M. The evolution of degrees of cooperation. *Journal of Theoretical Biology* **182**, 549–559 (1996).
[101] Hamilton, W. D. The evolution of altruistic behavior. *The American Naturalist* **97**, 354–356 (1963).
[102] Bowles, S. Group competition, reproductive leveling, and the evolution of human altruism. *Science* **314**, 1569–1572 (2006).
[103] Zahavi, A. Reliability in communication systems and the evolution of altruism. In *Evolutionary Ecology*, 253–259 (Springer, 1977).
[104] Fletcher, J. A. & Doebeli, M. A simple and general explanation for the evolution of altruism. *Proceedings of the Royal Society B: Biological Sciences* **276**, 13–19 (2009).
[105] Van Baalen, M. & Rand, D. A. The unit of selection in viscous populations and the evolution of altruism. *Journal of Theoretical Biology* **193**, 631–648 (1998).
[106] Mitteldorf, J. & Wilson, D. S. Population viscosity and the evolution of altruism. *Journal of Theoretical Biology*

204, 481–496 (2000).
[107] Brown, J. L. Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. *American Zoologist* **14**, 63–80 (1974).
[108] Frank, S. A. Genetics of mutualism: the evolution of altruism between species. *Journal of Theoretical Biology* **170**, 393–400 (1994).
[109] Matessi, C. & Jayakar, S. Conditions for the evolution of altruism under darwinian selection. *Theoretical Population Biology* **9**, 360–387 (1976).
[110] Trivers, R. L. The evolution of reciprocal altruism. *The Quarterly Review of Biology* **46**, 35–57 (1971).
[111] Kruger, D. J. Evolution and altruism: Combining psychological mediators with naturally selected tendencies. *Evolution and Human Behavior* **24**, 118–125 (2003).
[112] Goodnight, C. J., Schwartz, J. M. & Stevens, L. Contextual analysis of models of group selection, soft selection, hard selection, and the evolution of altruism. *The American Naturalist* **140**, 743–761 (1992).
[113] Kelly, J. K. Restricted migration and the evolution of altruism. *Evolution* **46**, 1492–1495 (1992).
[114] Levin, B. R. & Kilmer, W. L. Interdemic selection and the evolution of altruism: a computer simulation study. *Evolution* 527–545 (1974).
[115] Kurzban, R., Burton-Chellew, M. N. & West, S. A. The evolution of altruism in humans. *Annual Review of Psychology* **66**, 575–599 (2015).
[116] Mohtashemi, M. & Mui, L. Evolution of indirect reciprocity by social information: the role of trust and reputation in evolution of altruism. *Journal of Theoretical Biology* **223**, 523–531 (2003).
[117] Foster, K. R., Wenseleers, T. & Ratnieks, F. L. Kin selection is the key to altruism. *Trends in Ecology & Evolution* **21**, 57–60 (2006).
[118] Craig, R. Parental manipulation, kin selection, and the evolution of altruism. *Evolution* 319–334 (1979).
[119] Taylor, P. D. Altruism in viscous populations—an inclusive fitness model. *Evolutionary Ecology* **6**, 352–356 (1992).
[120] Pope, S. J. *The evolution of altruism and the ordering of love* (Georgetown University Press, 1995).
[121] Charlesworth, B. A note on the evolution of altruism in structured demes. *The American Naturalist* **113**, 601–605 (1979).
[122] Le Galliard, J.-F., Ferriere, R. & Dieckmann, U. Adaptive evolution of social traits: origin, trajectories, and correlations of altruism and mobility. *The American Naturalist* **165**, 206–224 (2005).
[123] Jansen, V. A. & Van Baalen, M. Altruism through beard chromodynamics. *Nature* **440**, 663–666 (2006).
[124] Sober, E. The evolution of altruism: Correlation, cost, and benefit. *Biology and Philosophy* **7**, 177–187 (1992).
[125] Pepper, J. W. & Smuts, B. B. A mechanism for the evolution of altruism among nonkin: positive assortment through environmental feedback. *The American Naturalist* **160**, 205–213 (2002).
[126] Irwin, A. J. & Taylor, P. D. Evolution of altruism in stepping-stone populations with overlapping generations. *Theoretical Population Biology* **60**, 315–325 (2001).
[127] Wilson, D. S., Pollock, G. B. & Dugatkin, L. A. Can altruism evolve in purely viscous populations? *Evolutionary Ecology* **6**, 331–341 (1992).
[128] Waibel, M., Floreano, D. & Keller, L. A quantitative test of hamilton's rule for the evolution of altruism. *PLoS Biology* **9** (2011).
[129] Fletcher, J. A. & Zwick, M. The evolution of altruism: game theory in multilevel selection and inclusive fitness. *Journal of Theoretical Biology* **245**, 26–36 (2007).
[130] Darlington, P. J. Group selection, altruism, reinforcement, and throwing in human evolution. *Proceedings of the National Academy of Sciences* **72**, 3748–3752 (1975).
[131] De Waal, F. B. Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology* **59**, 279–300 (2008).
[132] Zahavi, A. Altruism as a handicap: the limitations of kin selection and reciprocity. *Journal of Avian Biology* **26**, 1–3 (1995).
[133] Wenseleers, T. & Ratnieks, F. L. Enforced altruism in insect societies. *Nature* **444**, 50–50 (2006).
[134] Nakamaru, M. & Iwasa, Y. The evolution of altruism by costly punishment in lattice-structured populations: score-dependent viability versus score-dependent fertility. *Evolutionary Ecology Research* **7**, 853–870 (2005).
[135] Agrawal, A. Kin recognition and the evolution of altruism. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**, 1099–1104 (2001).
[136] Barber, N. *Kindness in a cruel world: The evolution of altruism* (Prometheus Books, 2010).
[137] West, S. A. & Gardner, A. Altruism, spite, and greenbeards. *Science* **327**, 1341–1344 (2010).
[138] Cavalli-Sforza, L. L. & Feldman, M. W. Darwinian selection and "altruism". *Theoretical Population Biology* **14**, 268–280 (1978).
[139] Darlington, P. J. Altruism: Its characteristics and evolution. *Proceedings of the National Academy of Sciences* **75**, 385–389 (1978).
[140] Smith, J. M. Models of the evolution of altruism. *Theoretical Population Biology* **18**, 151–159 (1980).
[141] Uyenoyama, M. K. Evolution of altruism under group selection in large and small populations in fluctuating environments. *Theoretical Population Biology* **15**, 58–85 (1979).

[142] Kerr, B., Godfrey-Smith, P. & Feldman, M. W. What is altruism? *Trends in Ecology & Evolution* **19**, 135–140 (2004).
[143] Fix, A. G. Evolution of altruism in kin-structured and random subdivided populations. *Evolution* **39**, 928–939 (1985).
[144] Uyenoyama, M. K. Inbreeding and the evolution of altruism under kin selection: effects on relatedness and group structure. *Evolution* 778–795 (1984).
[145] Okasha, S. Genetic relatedness and the evolution of altruism. *Philosophy of Science* **69**, 138–149 (2002).
[146] Sussman, R. W. & Cloninger, C. R. *Origins of altruism and cooperation* (Springer, 2011).
[147] Garland, T. & Rose, M. R. *Experimental evolution: concepts, methods, and applications of selection experiments* (University of California Press Berkeley, CA, 2009).
[148] Gardner, A. Sex-biased dispersal of adults mediates the evolution of altruism among juveniles. *Journal of Theoretical Biology* **262**, 339–345 (2010).
[149] Ferriere, R. & Michod, R. E. Inclusive fitness in evolution. *Nature* **471**, E6 (2011).
[150] Feldman, M. W., Cavalli-Sforza, L. L. & Peck, J. R. Gene-culture coevolution: models for the evolution of altruism with cultural transmission. *Proceedings of the National Academy of Sciences* **82**, 5814–5818 (1985).
[151] Nunney, L. Group selection, altruism, and structured-deme models. *The American Naturalist* **126**, 212–230 (1985).
[152] Tooby, J., Cosmides, L. *et al.* Friendship and the banker's paradox: Other pathways to the evolution of adaptations for altruism. In *Proceedings-British Academy*, vol. 88, 119–144 (OXFORD UNIVERSITY PRESS INC., 1996).
[153] Breden, F. & Wade, M. J. "runaway" social evolution: reinforcing selection for inbreeding and altruism. *Journal of Theoretical Biology* **153**, 323–337 (1991).
[154] Okasha, S. Biological altruism. In *The Stanford Encyclopedia of Philosophy* (Metaphysics Research Lab, Stanford University, 2013), fall 2013 edn.
[155] Boehm, C. *Moral origins: The evolution of virtue, altruism, and shame* (Soft Skull Press, 2012).
[156] Okasha, S. Altruism researchers must cooperate. *Nature* **467**, 653–655 (2010).
[157] Eldakar, O. T. & Wilson, D. S. Selfishness as second-order altruism. *Proceedings of the National Academy of Sciences* **105**, 6982–6986 (2008).
[158] Matessi, C. & Karlin, S. On the evolution of altruism by kin selection. *Proceedings of the National Academy of Sciences* **81**, 1754–1758 (1984).
[159] Takagi, E. The generalized exchange perspective on the evolution of altruism. In *Frontiers in Social Dilemmas Research*, 311–336 (Springer, 1996).
[160] Alonso, W. J. & Schuck-Paim, C. Sex-ratio conflicts, kin selection, and the evolution of altruism. *Proceedings of the National Academy of Sciences* **99**, 6843–6847 (2002).
[161] Gardner, A. & West, S. Demography, altruism, and the benefits of budding. *Journal of Evolutionary Biology* **19**, 1707–1716 (2006).
[162] Wilson, D. S. Altruism and organism: Disentangling the themes of multilevel selection theory. *The American Naturalist* **150**, s122–S134 (1997).
[163] Koella, J. C. The spatial spread of altruism versus the evolutionary response of egoists. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **267**, 1979–1985 (2000).
[164] Cooper, B. & Wallace, C. Group selection and the evolution of altruism. *Oxford Economic Papers* **56**, 307–330 (2004).
[165] Lion, S. & Gandon, S. Life history, habitat saturation and the evolution of fecundity and survival altruism. *Evolution: International Journal of Organic Evolution* **64**, 1594–1606 (2010).
[166] Wilson, D. S. Altruism in mendelian populations derived from sibling groups: the haystack model revisited. *Evolution* **41**, 1059–1070 (1987).
[167] Spector, L. & Klein, J. Genetic stability and territorial structure facilitate the evolution of tag-mediated altruism. *Artificial Life* **12**, 553–560 (2006).
[168] Choi, J.-K. & Bowles, S. The coevolution of parochial altruism and war. *Science* **318**, 636–640 (2007).
[169] Boesch, C., Bole, C., Eckhardt, N. & Boesch, H. Altruism in forest chimpanzees: the case of adoption. *PLoS One* **5** (2010).
[170] Yamamura, N., Higashi, M., Behera, N. & Wakano, J. Y. Evolution of mutualism through spatial effects. *Journal of Theoretical Biology* **226**, 421–428 (2004).
[171] Marshall, J. A. Ultimate causes and the evolution of altruism. *Behavioral Ecology and Sociobiology* **65**, 503–512 (2011).
[172] Le Galliard, J.-F., Ferrière, R. & Dieckmann, U. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution* **57**, 1–17 (2003).
[173] Kitcher, P. The evolution of human altruism. *The Journal of Philosophy* **90**, 497–516 (1993).
[174] Bertram, B. C. *et al.* Problems with altruism. *Current Problems in Sociobiology* 251–267 (1982).
[175] Boyle, R. A., Lenton, T. M. & Williams, H. T. Neoproterozoic 'snowball earth'glaciations and the evolution of altruism. *Geobiology* **5**, 337–349 (2007).
[176] Wade, M. J. & Breden, F. The evolution of cheating and selfish behavior. *Behavioral Ecology and Sociobiology* **7**, 167–172 (1980).

[177] André, J.-B. & Morin, O. Questioning the cultural evolution of altruism. *Journal of Evolutionary Biology* **24**, 2531–2542 (2011).
[178] Nowak, M. A., Tarnita, C. E. & Wilson, E. O. The evolution of eusociality. *Nature* **466**, 1057 (2010).
[179] Nakamaru, M. & Iwasa, Y. The coevolution of altruism and punishment: role of the selfish punisher. *Journal of Theoretical Biology* **240**, 475–488 (2006).
[180] Débarre, F., Hauert, C. & Doebeli, M. Social evolution in structured populations. *Nature Communications* **5**, 3409 (2014).
[181] Németh, A. & Takács, K. The evolution of altruism in spatially structured populations. *Journal of Artificial Societies and Social Simulation* **10**, 4 (2007).
[182] Charnov, E. L. & Krebs, J. R. The evolution of alarm calls: altruism or manipulation? *The American Naturalist* **109**, 107–112 (1975).
[183] Bester, H. & Güth, W. Is altruism evolutionarily stable? *Journal of Economic Behavior & Organization* **34**, 193–209 (1998).
[184] McCullough, M. E., Kimeldorf, M. B. & Cohen, A. D. An adaptation for altruism: The social causes, social effects, and social evolution of gratitude. *Current Directions in Psychological Science* **17**, 281–285 (2008).
[185] Di Paolo, E. A. Ecological symmetry breaking can favour the evolution of altruism in an action-response game. *Journal of Theoretical Biology* **203**, 135–152 (2000).
[186] Fletcher, J. A. & Doebeli, M. How altruism evolves: assortment and synergy. *Journal of Evolutionary Biology* **19**, 1389–1393 (2006).
[187] Silva, A. & Fontanari, J. Deterministic group selection model for the evolution of altruism. *The European Physical Journal B-Condensed Matter and Complex Systems* **7**, 385–392 (1999).
[188] Lewis, K. Pathogen resistance as the origin of kin altruism. *Journal of Theoretical Biology* **193**, 359–363 (1998).
[189] Smith, J. M. The evolution of social behavior—a classification of models. In *Current Problems in Sociobiology*, 28–44 (Cambridge University Press Cambridge, 1982).
[190] Charlesworth, B. Some models of the evolution of altruistic behaviour between siblings. *Journal of Theoretical Biology* **72**, 297–319 (1978).
[191] Wilson, D. S. On the relationship between evolutionary and psychological definitions of altruism and selfishness. *Biology and Philosophy* **7**, 61–68 (1992).
[192] Grafen, A. An inclusive fitness analysis of altruism on a cyclical network. *Journal of Evolutionary Biology* **20**, 2278–2283 (2007).
[193] Thompson, G. J., Hurd, P. L. & Crespi, B. J. Genes underlying altruism. *Biology Letters* **9**, 20130395 (2013).
[194] Fletcher, J. A. & Zwick, M. Strong altruism can evolve in randomly formed groups. *Journal of Theoretical Biology* **228**, 303–313 (2004).
[195] Hamilton, W. D. The genetical evolution of social behaviour. ii. *Journal of Theoretical Biology* **7**, 17–52 (1964).
[196] Nowak, M. A. & May, R. M. Evolutionary games and spatial chaos. *Nature* **359**, 826 (1992).
[197] Nowak, M. & Sigmund, K. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the prisoner's dilemma game. *Nature* **364**, 56–58 (1993).
[198] Nowak, M. A. & Sigmund, K. Tit for tat in heterogeneous populations. *Nature* **355**, 250–253 (1992).
[199] Lieberman, E., Hauert, C. & Nowak, M. A. Evolutionary dynamics on graphs. *Nature* **433**, 312 (2005).
[200] Rand, D. G., Greene, J. D. & Nowak, M. A. Spontaneous giving and calculated greed. *Nature* **489**, 427–430 (2012).
[201] Nowak, M. A. & Sigmund, K. Evolutionary dynamics of biological games. *Science* **303**, 793–799 (2004).
[202] Nowak, M. A., Page, K. M. & Sigmund, K. Fairness versus reason in the ultimatum game. *Science* **289**, 1773–1775 (2000).
[203] Nowak, M. A. & May, R. M. The spatial dilemmas of evolution. *International Journal of Bifurcation and Chaos* **3**, 35–78 (1993).
[204] Rand, D. G. & Nowak, M. A. Human cooperation. *Trends in Cognitive Sciences* **17**, 413–425 (2013).
[205] Dreber, A., Rand, D. G., Fudenberg, D. & Nowak, M. A. Winners don't punish. *Nature* **452**, 348–351 (2008).
[206] Hauert, C., Traulsen, A., Brandt, H., Nowak, M. A. & Sigmund, K. Via freedom to coercion: the emergence of costly punishment. *Science* **316**, 1905–1907 (2007).
[207] Nowak, M. A. & Sigmund, K. The dynamics of indirect reciprocity. *Journal of Theoretical Biology* **194**, 561–574 (1998).
[208] Rand, D. G., Dreber, A., Ellingsen, T., Fudenberg, D. & Nowak, M. A. Positive interactions promote public cooperation. *Science* **325**, 1272–1275 (2009).
[209] Pacheco, J. M., Traulsen, A. & Nowak, M. A. Coevolution of strategy and structure in complex networks with dynamical linking. *Physical Review Letters* **97**, 258103 (2006).
[210] Rand, D. G. *et al.* Social heuristics shape intuitive cooperation. *Nature Communications* **5**, 1–12 (2014).
[211] Sigmund, K., Hauert, C. & Nowak, M. A. Reward and punishment. *Proceedings of the National Academy of Sciences* **98**, 10757–10762 (2001).
[212] Nowak, M. A., Bonhoeffer, S. & May, R. M. Spatial games and the maintenance of cooperation. *Proceedings of the National Academy of Sciences* **91**, 4877–4881 (1994).

[213] Traulsen, A., Nowak, M. A. & Pacheco, J. M. Stochastic dynamics of invasion and fixation. *Physical Review E* **74**, 011909 (2006).

[214] Fu, F., Hauert, C., Nowak, M. A. & Wang, L. Reputation-based partner choice promotes cooperation in social networks. *Physical Review E* **78**, 026117 (2008).

[215] Taylor, C., Fudenberg, D., Sasaki, A. & Nowak, M. A. Evolutionary game dynamics in finite populations. *Bulletin of Mathematical Biology* **66**, 1621–1644 (2004).

[216] Nowak, M. A., Tarnita, C. E. & Antal, T. Evolutionary dynamics in structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 19–30 (2010).

[217] Nowak, M. A., May, R. M. & Sigmund, K. The arithmetics of mutual help. *Scientific American* **272**, 76–81 (1995).

[218] Nowak, M. A., Bonhoeffer, S. & May, R. M. More spatial games. *International Journal of Bifurcation and Chaos* **4**, 33–56 (1994).

[219] Ohtsuki, H. & Nowak, M. A. The replicator equation on graphs. *Journal of Theoretical Biology* **243**, 86–97 (2006).