



The evolution of altruism and the serial rediscovery of the role of relatedness

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The genetic evolution of altruism (i.e., a behavior resulting in a net reduction of the survival and/or reproduction of an actor to benefit a recipient) once perplexed biologists because it seemed paradoxical in a Darwinian world. More than half a century ago, W. D. Hamilton explained that when interacting individuals are genetically related, alleles for altruism can be favored by selection because they are carried by individuals more likely to interact with other individuals carrying the alleles for altruism than random individuals in the population (“kin selection”). In recent decades, a substantial number of supposedly alternative pathways to altruism have been published, leading to controversies surrounding explanations for the evolution of altruism. Here, we systematically review the 200 most impactful papers published on the evolution of altruism and identify 43 evolutionary models in which altruism evolves and where the authors attribute the evolution of altruism to a pathway other than kin selection and/or deny the role of relatedness. An analysis of these models reveals that in every case the life cycle assumptions entail local reproduction and local interactions, thereby leading to interacting individuals being genetically related. Thus, contrary to the authors’ claims, Hamilton’s relatedness drives the evolution to altruism in their models. The fact that several decades of investigating the evolution to altruism have resulted in the systematic and unwitting rediscovery of the same mechanism is testament to the fundamental importance of positive relatedness between actor and recipient for explaining the evolution of altruism.

evolution | kin selection | altruism | Hamilton’s rule | rediscovery

Academic discoveries are often made simultaneously and independently by multiple scientists (1–3). In the 17th century, Newton and Leibniz independently developed calculus. The theory of evolution by natural selection was discovered independently by Charles Darwin (1858) and Alfred Wallace (1858). There are also instances of the same discovery being made many years apart. The heliocentric solar system was first discovered by the Ancient Greek astronomer Aristarchos of Samos (~310 to 230 BC), but received little attention until it was independently rediscovered 18 centuries later by the Renaissance mathematician Nicolaus Copernicus. Such asynchronous rediscoveries have become rare in a globalized world of communication between distant regions and accessible online information. However, over the past few decades a striking exception has unfolded in the evolutionary sciences, where many researchers have repeatedly rediscovered that interactions between relatives favor the evolution of altruistic traits, despite this mechanism having been uncovered and mathematically described more than half a century ago by W. D. Hamilton (4–6). What is more, unlike previous cases, this rediscovery does not seem to have resulted from ignorance of the existence of previous work, but from a failure to recognize the equivalence between the processes underlying the models.

The question of the genetic evolution of altruism—defined here as a behavior decreasing the expected survival and/or reproduction (fitness) of the actor while increasing the fitness of the recipient—rose to prominence because altruism seemed paradoxical in a Darwinian world. In 1963, Hamilton showed that to

understand the genetic evolution of altruism, and more generally of any trait, it is crucial to consider the average fitness of all individuals bearing a given allele responsible for producing a change in that trait. In particular, in a population of homogeneous individuals, an altruism-inducing allele will increase in frequency when $rb - c > 0$, where $-c$ is the average effect of the altruism-inducing allele on the fitness of its bearer, b is the average effect on the fitness of recipients, and r is the genetic relatedness between the actor and the recipients (7).

Relatedness r is a regression coefficient measuring how the alleles in a particular individual covary in frequency with those of individuals with whom the individual interacts (8, 9). Relatedness is thus a measure of the extent to which the recipient of altruism is more likely than a random individual in the population to carry the altruism-inducing allele present in the actor. Usually, such assortment results from actor and recipient having inherited identical alleles from a recent common ancestor (i.e., alleles in actor and recipient are identical by descent; see Box 1 for more complex situations). For example, family structure results in particular relatedness patterns: In diploid species where mating occurs randomly in the population, siblings have a relatedness of 1/2 (i.e., they have a 50% chance of having inherited the same allele from their parents at any given locus) and the relatedness between aunt and nephew is 1/4. Because the best-known cases of altruism occur between highly related individuals, John Maynard Smith coined the term kin selection to describe the operation of natural selection in a context where interactions occur among genetically related individuals (10, 11). Unfortunately, this has sometimes given the incorrect impression that kin selection operates only within structured families. In reality, kin selection operates as soon as there is limited genetic mixing and interacting group size is not infinite, as in the “viscous,” “island,” and “stepping-stone” models of spatial population structure described in Fig. 1. In these models, dispersal is limited and locally interacting individuals are likely to share

Significance

The canonical explanation for the evolution of altruism (“kin selection”)—which was mathematically derived in the 1960s by W. D. Hamilton—emphasizes the importance of genetic relatedness. Over the past three decades, numerous authors claim to have discovered alternative explanations. We systematically analyze the models substantiating these claims and reveal that in every model the interacting individuals are genetically related and that the authors have therefore unwittingly rediscovered Hamilton’s insight.

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Box 1: Relatedness and Green Beard Models.

Relatedness is a measure of assortment of alleles between actor and recipient, where assortment means that actor and recipient share more alleles that are identical by state than the population average. And assortment, whereby individuals bearing altruistic alleles preferentially benefit from the altruism of other individuals bearing altruistic alleles, is a necessary condition for genetic altruism to be favored by kin selection (4, 12, 17). As explained in the main text, in family-structured populations and under limited dispersal, assortment results from actor and recipient sharing identical-by-state alleles that are identical by descent, so that interacting individuals are positively related. While identity by descent is the main mechanism generating assortment, identical-by-state assortment can also occur without identity by descent. One such scenario is where the same altruistic allele arises frequently through mutation and recognizes replicate copies in other individuals. This is the “green beard effect” (42, 43), a mechanism for the evolution of altruism discussed (but not investigated formally) by Hamilton (6) and Dawkins (42). While the green beard mechanism it is an intriguing thought experiment, it is unlikely that it could drive the genetic evolution of altruism independent of kin selection. First, its requirements are very stringent: A single Mendelian element must encode a signal, the ability to discriminate among others on the basis of that signal, and an altruistic phenotype. Second, if these requirements are met, modeling shows that the process is generally unstable (44). Finally, even when green beard models entail interactions among relatives, where one would expect them to be more stable, without a near perfect association between signal and altruistic phenotype, the evolutionary dynamics tend to remain unstable (45).

alleles from a common ancestor who lived in the same spatial neighborhood in previous generations. Under limited dispersal, the genetic components of evolving traits expressed by an actor therefore affect the reproduction and survival of others who share alleles identical by descent with the actor at the loci determining the trait. This is the defining condition for kin selection to operate (12, 13). Since most if not all populations are likely to exhibit some form of limited genetic mixing (14), hence most if not all social traits are likely to be shaped by kin selection to at least some extent (15). Importantly, limited genetic mixing also implies that interactions occur locally and hence that related individuals are more likely to compete against each other than are individuals sampled at random from the population. This leads to the occurrence of “kin competition.” Under certain situations, kin competition can cancel out the indirect benefits of altruism and prevent the evolution of phenotypes increasing the survival and reproduction of neighbors (13, 16). Yet, even in this context, phenotypic evolution is shaped by kin selection.

Despite the fact that kin selection is known to operate under limited dispersal, mathematical and simulation models employing the population structures described in Fig. 1 often claim to have found new mechanisms to account for the evolution of altruism. A number of previous studies have taken particular such models and mathematically proved that relatedness is positive among interacting individuals and that altruism would not evolve without it (22–27). However, these efforts have enjoyed little success in curbing false claims about the novelty of the mechanism driving the evolution of altruism. And, while a core of evolutionary biologists working on altruism remain confident about the central role of relatedness, the larger circle of evolutionists and laypeople who follow this literature now believe

that the issue remains unsolved. Here we therefore take a different approach. We broadly survey the literature to identify papers claiming alternative mechanisms and then analyze the life cycle assumptions of these models (i.e., the demographic, behavioral, and genetic assumptions underlying all events faced by organisms in an evolving population) to investigate whether they allow the evolution of altruism without positive relatedness between interacting individuals (i.e., whether altruism can evolve without kin selection).

Results and Discussion

The claims of novel mechanisms to account for the evolution of altruism are too numerous to review comprehensively. Therefore, we identified the most prominent examples by selecting the top 100 Google Scholar search results for each of “evolution of cooperation” and “evolution of altruism” (*SI Appendix, Tables S1 and S2*; total = 195 papers; 5 appeared under both). Seventy-six of these papers do not present formal evolutionary models. We scrutinized the life cycles of the remaining 119 papers, which do present formal evolutionary models. These models investigate the dynamics of either genetic variants (alleles) or cultural variants (memes) with most considering only two competing variants (one “altruistic” and one “selfish”). In many of the models, whether the expression of a particular allele (or meme) results in altruism (i.e., $c > 0$ and $b > 0$) or merely cooperation—defined as a behavior increasing the fitness of both actor and recipient (i.e., $c < 0$ and $b > 0$)—depends on the parameter values determining the life cycle. This parameter dependence arises because the costs and benefits are defined operationally as the lifetime fitness effects of an actor on

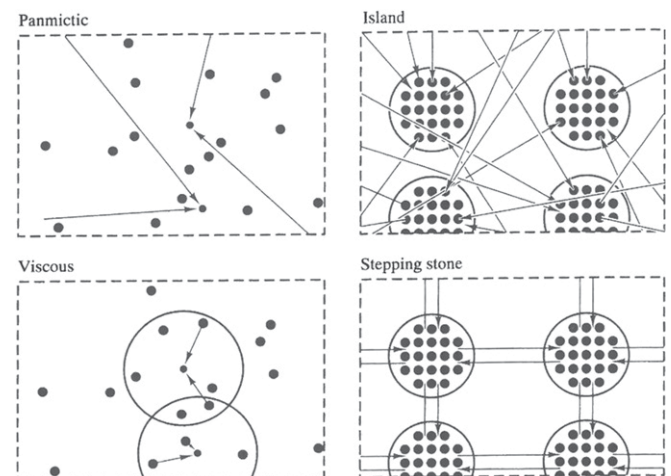


Fig. 1. Population structure and relatedness, reproduced from Hamilton (17), who discussed how limited dispersal induced by various population structures influences patterns of relatedness and thereby affects the evolution of social behavior. In the panmictic and viscous models, smaller dots indicate younger individuals, and arrows indicate parenthood. In the island and stepping-stone models, younger individuals are not shown because reproduction occurs within groups. Arrows indicate dispersal between groups. For the viscous, island, and stepping-stone models, locally interacting individuals are positively related under limited dispersal, and the local relatedness structure has been explored in the field of population genetics (13, 18–21). The viscous model with continuous space is the most challenging to analyze and remains the least explored, yet it is probably the most realistic model for plant populations. Most of the papers rediscovering kin selection use either the island model (using groups of size > 1 and with interactions occurring within groups) or the stepping-stone model (using “groups” composed of a single individual, represented as the node of a lattice structure; since migration links nodes, the population becomes a network with interactions occurring between neighboring nodes). Reprinted with permission from ref. 17.

recipients and are therefore complex functions of all life cycle features. In particular, since costs and benefits are affected by kin competition, they depend on parameters defining the spatial structure of the evolving population (equation 7.13 in ref. 13, equations 5–7 in ref. 24, and figures 1 and 2 in ref. 28), and since they are affected by the type of interaction and the likelihood of repeated interaction, they depend on parameters defining the behavioral interactions between individuals (equation 5 in ref. 29 and equations 8 and 9 in ref. 26). These (lifetime) fitness costs c and benefits b are therefore nontrivial to calculate and essentially never correspond directly to the proximate costs and benefits of the prisoner's dilemma stage game matrix to which they may be naively equated (the exception being a panmictic population with one-shot interactions). Further, for a given situation, the cost c may change sign, from altruism (positive) to cooperation (negative), as a function of the model's parameter values, such as dispersal rate and group size (see figures 1 and 2 in ref. 28 for illustrative examples). Since quantitatively calculating c and b can be very demanding for a given model, we here qualitatively infer whether c is expected to be positive or negative as this can often be done on examination of the life cycle assumptions. Overall, altruism evolved under some parameter values in models presented in 89 of these papers. Among the remaining 30 papers, cooperation evolved in 28 cases, and we were unable to assess whether altruism or cooperation evolved in the remaining 2 cases (marked as “insufficient information” in *SI Appendix, Tables S1 and S2*).

Among the 89 altruism models, 46 adopted Hamilton's conceptual framework, attributing the evolution of altruism to positive relatedness. The remaining 43 all claimed alternative mechanisms. To evaluate the veracity of their claims, we first subdivided these 43 papers into those where the role of relatedness was denied (17 cases; *SI Appendix, Table S3*), and those which made little or no mention of relatedness (26 cases; *SI Appendix, Table S4*).

Among the 17 papers where the presence/role of relatedness was denied (*SI Appendix, Table S3*), our analysis of the life cycles of the models showed that the proposed scenario led to positive relatedness between interacting agents in every case. Moreover, in most of these models, agents reproduced clonally (e.g., “parents pass on their type to their offspring”) with interactions occurring among nearest neighbors, as in the stepping-stone model of Fig. 1, with only one individual per node/group. This represents the tritest instance of kin selection. Relatedness coefficients equal 1 between parent and offspring and between siblings, and dispersal is limited to neighboring nodes so parents place offspring therein and subsequently interact with them. While many of these models are framed in terms of the transmission of cultural variants (or memes) and are often called “strategies” (with strategies with higher payoffs being more frequently “imitated”), from a conceptual evolutionary dynamics perspective these models are indistinguishable from genetic models, since they both investigate the differential proliferation of different variants in a population. Different modes of cultural transmission (e.g., payoff-biased learning, vertical transmission, one to many transmission such as following a leader) (30) will affect the level of relatedness between interacting individuals as well as the amount of (cultural) kin competition between them, and this can result in higher or lower selection pressure on altruism than under genetic transmission (31). However, no other mechanism has been discovered, since selection still acts on the social trait according to relatedness (and competition) because traits are inherited and subject to differential proliferation. Thus, altruism spreads via cultural transmission when altruistic actors preferentially help individuals to whom they are positively culturally related. Hence, these models represent an advance only insofar as Hamilton never applied his framework to cultural evolution [this was pioneered in the 1990s (32)

and has been applied concretely to the calculation of cultural relatedness in the “island model” of Fig. 1 (31) and reviewed (33)]. The inconsistency between the novelty claims of these publications and their content is difficult to explain. One likely contributing factor is the nonbiological framing of the models; terms such as “site update” and “strategy invasion” replace birth and death, and “players” and “neighbors” replace organisms, siblings, and offspring. This semantic divergence obfuscates the relation between these models and the established theory.

The 26 papers which make little or no mention of relatedness attribute the evolution of altruism to diverse alternative mechanisms including “social diversity,” “social viscosity,” “topological heterogeneity,” “network heterogeneity,” “network reciprocity,” “spatial reciprocity,” “spatial structure,” and “multiplex structure” (*SI Appendix, Table S4*). Analysis of these models revealed that in every case interacting individuals are related, relatives benefit from each other's altruism, and kin selection therefore operates. This occurs through limited dispersal (or limited cultural mixing) and local interaction as in the island and stepping-stone models of Fig. 1. Again, the framing of these models obscures the underlying role of relatedness. For example, Szolnoki et al. (ref. 34, p. 2) write, “First, a randomly selected player x acquires its payoff p_x by playing the game with its nearest neighbors. Next, 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 in accordance with the probability, $W(s_x \rightarrow s_y) = w_x / (1 + \exp[(p_y - p_x)/K])$, where K denotes the amplitude of noise.” For a biologist, this translates as follows: Individuals are randomly killed and tend to be replaced by the clonal offspring of their most fecund neighbors. In this situation, individuals will interact preferentially with clonal relatives, and interactions are likely to occur between parents and offspring and siblings owing to the stepping-stone structure (Fig. 1) of the model. Altruistic alleles (or memes) therefore spread through genetic (or cultural) kin selection.

The most commonly cited alternative mechanism to kin selection is “spatial selection.” This mechanism was pioneered by Martin Nowak, who has been uniquely vocal in attempting to differentiate it from kin selection [e.g., “it is clear that kin selection is different from group selection and different from spatial selection” (ref. 35, p. 26)] despite his claims being repeatedly and formally dismissed (22–27). Using Google Scholar we therefore identified his 10 most impactful spatial selection papers (*SI Appendix, Table S5*). All of these papers use models where individuals interact with relatives and where kin selection affects the evolution of altruism. Three of these Nowak papers already feature in *SI Appendix, Table S3* [Traulsen and Nowak (36) and Nowak et al. (37)] and *SI Appendix, Table S4* [Ohtsuki et al. (38)]. The remaining seven constitute *SI Appendix, Table S6*. The models are of various types but all use lattice or graph population structures, which are akin to the stepping-stone model of Fig. 1. The occurrence of such clear-cut rediscovery is easier to understand when considering the chronological development of the separate literatures. While Nowak's earlier models adopted rather different assumptions from those of the more biologically oriented concurrent/earlier kin selection literature, they converged to them over time (Box 2).

The claims that spatial structure affects the evolution of altruism are not incorrect per se. As Hamilton himself emphasized (17), limited dispersal and local interaction lead to positive relatedness among interacting individuals, which may promote altruism under certain biological scenarios, as long as kin competition is not too strong. Hence, the finding that spatial selection favors altruism is not novel, and the emphasis on space can be misleading; space is merely a proxy for relatedness patterns and in itself not sufficient to explain altruism. Space provides

Box 2: Evolution of Theoretical Evolution Models.

We here briefly explore the “rediscovery” history of the spatial selection literature. This is useful as through understanding this history, one can better understand how such large-scale rediscovery could have occurred. The broad assumptions of Martin Nowak and colleagues’ models differed from those of “typical” kin selection models initially [in the 1990s; reviewed in 2004 (13)] and converged to them only over time. Unlike typical kin selection models, the simulations of Nowak and May (46, 47) do not allow for any chance effects in reproduction (i.e., genetic drift). The models are therefore fully deterministic, meaning that altruism can never spread when rare, since a single altruistic mutant will be immediately eliminated as it would be surrounded on all sides by nonaltruists receiving higher payoffs. This means that relatedness can never build up. But, when the simulations are initiated with multiple altruists so that interacting individuals experience identical-by-state assortment, then altruism can be maintained but undergoes chaotic temporal dynamics [e.g., Nowak and May (47)]. While the initial altruists are identical by state, and not related, their offspring are identical by descent (related) and likely to interact, since there is limited genetic mixing. Kin selection therefore plays a role in the evolutionary dynamics of altruism [as acknowledged by Nowak and May (ref. 47, p. 76)]. In the simulations of Nowak et al. (48, 49) chance effects in reproduction are allowed, meaning that local genetic drift allows relatedness to build up and altruistic alleles increase in frequency when rare, so that kin selection can operate at all allele frequencies. Finally, Ohtsuki et al. (38) provide mathematical solutions to the spread of altruism in stepping-stone-like models under weak selection. This paper makes the same assumptions as previous kin selection models and analyzing the model with Hamilton’s rule yields identical results (22, 24). Over time, the spatial selection models thus became more biologically realistic as they converged to typical previous kin selection models.

no detailed information about the fitness cost c and benefit b , depending on which the same spatial arrangement may favor altruism and/or intensify kin competition. Moreover, to focus on such a proxy is unhelpful as it is difficult to intuit how the evolution of altruism will respond to different biological assumptions. Consider mating systems. It is clear that polyandry (where females mate with multiple males) will result in decreased relatedness among interacting individuals relative to monoandry (where females mate with only one male) (39); relatedness also decreases with migration, group size, and environmental disturbance, while it tends to increase with survival and variance in reproductive success (13). In other words, how life cycle factors affect relatedness has been extensively worked out and is often intuitively clear, allowing empiricists to make and test predictions across diverse biological systems (40). It is unclear, however, how different biological assumptions (e.g., a change in the mating system or group composition) would interact with spatial selection. Consequently, these models do not provide testable predictions for biological scenarios beyond their authors’ many and highly specific assumptions.

While it remains surprising that so many specific models not tightly connected to the preceding literature are published, we envisage at least three reasons for the serial rediscovery of the role of relatedness. First, these models are often presented by people with strong formal training, but who are not evolutionary biologists (e.g., physicists, economists, mathematicians), and who have a limited understanding of genetics. Hamilton’s rule

is a population genetics theory result, and population genetics itself is an application of dynamical system and stochastic process theories. Yet, while these latter theories are well known to formally trained scientists, nonbiologists tend to approach the problem of the evolution of altruism from a textbook dynamical systems perspective, thereby narrowly focusing on the iconic replicator equation while eschewing well-established and important population genetic results. Second, Hamilton’s rule seems so intuitively clear to evolutionary biologists that they often do not engage with it as a formal population genetic theory and are not always rigorous in providing hard proofs to substantiate models of the evolution of social traits. This is exemplified by the fact that it took four decades to formally integrate Hamilton’s rule into the wider context of evolutionary game theory and adaptive dynamics. The basis of a conceptually transparent and wide-ranging kin selection theory was obtained only at the turn of the 20th century (41), while it was treated as such long before. Finally, some authors simply do not engage at all with the extensive kin selection theory literature, aware that doing so would cost considerable time and effort and could limit the boldness of the originality claims that they felt able to make “in good faith.” This has proved particularly true for some evolutionists from nonbiological backgrounds who have been highly successful in publishing studies dramatically overselling the novelty of their findings.

Conclusion

The field of evolutionary science has become replete with claims of novel mechanisms for the evolution of altruism. Previous papers have reanalyzed specific “novel” models to show their exact equivalence to results from preceding kin selection models (22–27) and thus their redundancy with established knowledge. Here, we have conducted a broader-scale analysis of these claims to reveal how and why these authors have unconsciously constructed situations in which kin selection operates. While we examined only the most prominent papers, we are not aware of any other paper that provides a biologically relevant explanation for the evolution of altruism by a mechanism other than positive relatedness between actor and recipient, as originally outlined by Hamilton (4–6, 17). The fact that researchers from diverse fields across the social and natural sciences have systematically reached similar conclusions is testament to the stricture of Hamilton’s ideas.

Materials and Methods

To systematically evaluate the claims that altruism could evolve by mechanisms other than kin selection, we selected the first 100 Google Scholar search results for each of evolution of altruism (*SI Appendix, Table S1*) and evolution of cooperation (*SI Appendix, Table S2*). In Google Scholar, papers are ranked according to their relevance to the search terms as well as the number of citations, meaning that our results will feature the most relevant and impactful papers, with a bias toward older papers. For each search result, we proceeded as follows:

- 1) We assessed whether a formal evolutionary model was presented. The search results come from fields as diverse as law, economics, physics, and biology and range in substance from theoretical research to empirical research, to reviews, books, and philosophical treatises.
- 2) For papers which presented a formal evolutionary model, we qualitatively evaluated whether altruism or cooperation increases in frequency under selection in the models presented in the paper; that is, whether $b > 0$ and $c > 0$. All models have $b > 0$ because all consider a situation where individuals increase the survival or reproduction of others (i.e., helping behavior). Whether $c > 0$ depends on the models’ assumptions and population state. For instance, when interactions are modeled as a one-shot prisoner’s dilemma game under panmixia, the action “defect” always results in a higher payoff than the action “cooperate,” and $c > 0$. But, for various more complicated scenarios (e.g., other types of game, repeated interaction, small interactive group sizes), actors may derive direct benefits from their action, in which case the sign of c depends on specific parameter settings (13, 24, 26, 28, 29), as well as on the

frequency of traits, alleles, or memes in the population. We therefore classified these papers according to whether the evolved trait is “altruism,” “cooperation,” or “parameter dependent” (*SI Appendix, Tables S1, S2, and S5*).

- 3) If altruism could evolve in at least one model presented in a given paper, we next identified the mechanism to which the authors attributed the evolution of altruism and subdivided the papers which attribute the evolution of altruism to an evolutionary process other than kin selection into two categories: those which deny the role of relatedness in their models (*SI Appendix, Table S3*, where quotes denying relatedness are provided) and those which make no mention of relatedness (*SI Appendix, Table S4*, where the proposed alternative mechanism is identified). For both of these categories we examined the life cycle assumptions model, in particular the modes of reproduction (e.g., the dispersal kernel) and interactions (e.g., the group size within which individuals interact), to evaluate whether the model is expected to lead to positive relatedness between interacting individuals. If relatedness is expected to be nonzero

on the basis of this qualitative analysis, we then stated that kin selection operates.

In addition to these analyses, we focused on the most frequently cited alternative mechanism to kin selection: spatial selection, pioneered by Martin Nowak. We used the search term “Nowak cooperation” to identify his 10 most impactful spatial selection papers (*SI Appendix, Table S5*). We categorized all search results according to the scheme described above and then, again, analyzed the life cycle assumptions of these models to identify the modes of interaction and reproduction. Based on these, we indicated whether or not kin selection will operate (*SI Appendix, Table S6*).

Data Availability. All study data are included in this article and *SI Appendix*.

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

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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 <i>et al</i>, 2006)⁵	Yes	Altruism	Spatial position	No
6	Evolution of cooperation without reciprocity (Riolo <i>et al</i> , 2001) ⁶	Yes	Parameter-dependent	Tag-based and relatedness	n/a
7	The evolution of cooperation (Sachs <i>et al</i> , 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 <i>et al.</i>, 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 <i>et al.</i> , 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 co-operation: 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 <i>et al.</i> , 2006) ²⁴	Yes	Cooperation	n/a	n/a
25	Evolution of cooperation in multiplex networks (Gómez-Gardenes <i>et al.</i>, 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 <i>et al.</i> , 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 <i>et al.</i>, 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 <i>et al.</i>, 1997)³²	Yes	Parameter-dependent	Spatial structure	Yes
33	Evolution of cooperation in a finite homogeneous graph (Taylor <i>et al.</i> , 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 <i>et al</i>, 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 2005) ⁴⁶	Yes	Parameter-dependent	Relatedness and generalized reciprocity	n/a
47	Optimal interdependence between networks for the evolution of cooperation (Wang <i>et al</i>, 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 <i>et al.</i> , 2005) ⁵⁰	No - book	n/a	n/a	n/a
51	Effect of spatial structure on the evolution of cooperation (Roca <i>et al.</i>, 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 <i>et al.</i>, 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 <i>et al.</i>, 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 <i>et al</i> , 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 <i>et al</i> , 2016) ⁶⁴	No - empirical research	n/a	n/a	n/a
65	Degree mixing in multilayer networks impedes the evolution of cooperation (Wang <i>et al</i>, 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 <i>et al</i>, 2008) ⁶⁷	Yes	Altruism	Social diversity	No
68	Evolutionary cycles of cooperation and defection (Imhof <i>et al</i> , 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 <i>et al</i>, 2012) ⁷⁰	Yes	Altruism	Heterogeneity	No
71	Coordinated punishment of defectors sustains cooperation and can proliferate when rare (Boyd <i>et al</i> , 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 <i>et al.</i> , 2011) ⁷²	No - empirical research	n/a	n/a	n/a
73	Evolution of cooperation in spatially structured populations (Brauchli <i>et al.</i>, 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 <i>et al.</i>, 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 snow-drift games (Souza <i>et al.</i> , 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 <i>et al.</i>, 2012)⁸⁰	Yes	Parameter-dependent	Spatial reciprocity	Yes
81	The evolution of mutualisms: exploring the paths between conflict and cooperation (Herre <i>et al.</i> , 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 <i>et al.</i>, 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 <i>et al</i>, 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 <i>et al</i>, 2009)⁸⁸	Yes	Altruism	Spatial structure and heterogeneity	No
89	A functional imaging study of cooperation in two-person reciprocal exchange (McCabe <i>et al</i> , 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 non-linear 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 <i>et al</i>, 2002)⁹⁶	Yes	Altruism	Spatial structure	No
97	Importance of cooperation and affiliation in the evolution of primate sociality (Sussman <i>et al</i> , 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

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 <i>et al.</i> , 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 <i>et al.</i> , 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 <i>et al.</i> , 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	Altruism	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 <i>et al.</i> , 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 <i>et al.</i> , 1992) ¹²⁷	Yes	Parameter-dependent	Relatedness and space	n/a
29	A quantitative test of Hamilton's rule for the evolution of altruism (Waibel <i>et al.</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 2010) ¹⁶⁹	No - empirical	n/a	n/a	n/a
74	Evolution of mutualism through spatial effects (Yamamura <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i>, 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i>, 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

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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 <i>et al</i> , 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 <i>et al</i> , 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

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Publication	Claim of unrelatedness	Mode of reproduction	Mode of interaction	Kin selection operates
Santos <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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

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[‡]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 <i>et al.</i> , 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

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[¶]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

Table S4: Impactful papers presenting evolutionary models where altruism evolves, and the authors attribute the evolution of altruism to a mechanism other than 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 <i>et al</i> , 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 <i>et al</i> , 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^t neighbors”	Yes, on memes

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^{||} ‘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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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

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[†]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 <i>et al</i> , 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 <i>et al</i> , 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 C 's in the neighborhood”	Yes, on memes
Brauchli <i>et al</i> , 1999 ⁷³	“spatial structure greatly influences the evolution of cooperation”	“all individuals of the $n \times n$ 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 <i>et al</i> , 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

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[¶]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 <i>et al</i> , 2010 ⁸⁶	“Theoretical models have revealed that spatial structure can favor the co-evolution 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 <i>et al</i> , 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 <i>et al</i> , 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

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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

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 <i>et al</i>, 2006)⁵	Yes	Altruism	Spatial position

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^{||}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 <i>et al</i> , 2004) ⁶¹	Yes	Cooperation	n/a
8	The evolution of eusociality (Nowak <i>et al</i>, 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 <i>et al</i>, 2005)¹⁹⁹	Yes	Parameter-dependent	Graph arrangement
11	Spontaneous giving and calculated greed (Rand <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 2008) ²⁰⁵	No - empirical research	n/a	n/a
20	Via freedom to coercion: the emergence of costly punishment (Hauert <i>et al</i> , 2007) ²⁰⁶	Yes	Cooperation	n/a

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

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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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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 <i>et al</i> , 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

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^{***}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.

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