Banking on cooperation: An evolutionary analysis of microfinance loan repayment behaviour

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Abstract (200 words):

Microfinance is an economic development intervention that provides loans to low-income borrowers to stimulate economic growth and reduce financial hardship. Lenders typically require joint liability, where multiple borrowers share the responsibility of repaying a group loan. We propose that this lending practice creates a cooperation dilemma similar to that faced by humans and other organisms in nature across many domains. This could offer a real-world test case for evolutionary theories of cooperation from the biological sciences. In turn, such theories could provide new insights into loan repayment behaviour. We first hypothesise how group loan repayment efficacy should be affected by mechanisms of assortment from the evolutionary literature on cooperation, i.e. common ancestry (kin selection), prior interaction (reciprocity), partner choice, similarity of tags, social learning, and ecology and demography. We then assess selected hypotheses by reviewing 40 studies from 31 countries on micro-borrowers' loan repayment, evaluating which characteristics of borrowers are associated with credit repayment behaviour. Surprisingly, we find that kinship is mostly negatively associated with repayment efficacy, but prior interaction and partner choice are both more positively associated. Our work highlights the scope of evolutionary theory to provide systematic insight into how humans respond to novel economic institutions and interventions.

Keywords: *Assortment; Evolution of Cooperation; Group Lending; Joint Liability; Kin Selection; Microcredit; Partner Choice; Reciprocity; Social capital; Social Dilemma.*

1. Introduction

Microfinance is a globally widespread economic development tool that aims to provide financial services to people from low income backgrounds. One of its cornerstones is the provision of small, short-term loans which enable borrowers to invest in new income-generating activities (Armendáriz and Morduch, 2010; Brau and Woller, 2004; Cull and Morduch, 2018). Conventional lending by banks requires loan-takers to provide material collateral, such as a house or land, that the bank holds as a guarantee and will confiscate if the borrower fails to repay the initial loan. In contrast, microfinance institutions (MFIs) offer loans to individuals who cannot obtain loans from mainstream banking services because they cannot provide the required securities and have no formal credit rating.

A common feature of MFIs is to provide loans to a group of borrowers who are jointly liable to repay it. This has been called joint liability lending (JLL): borrowers are mutually responsible for each other's repayment and must collectively make up any shortfall in repayment if other group members are unable or unwilling to repay. Typically, if the group does not achieve repayment, all group members are barred access to future loans from the micro-lending programme. The typical economic rationale is that JLL can exploit local social networks and "peer pressure" to boost repayment (Besley and Coate, 1995; Ghatak and Guinnane, 1999).

This interdependence in JLL creates a cooperative dilemma, because the responsibility of collective loan repayment to the lender, as well as the potential benefit of loan renewal in case of success, is shared by all group members. Here we build on Lamba (2014) and propose that group-based lending provides a model system to test the extent to which evolutionary theories on cooperation from the biological sciences apply to contemporary human societies. Conversely, evolutionary theories of cooperation from the biological sciences can potentially explain patterns of repayment observed in the microfinance sector.

In this paper, we identify theoretical links between the evolution of cooperation literature and microfinance, thereby connecting literatures from development economics and the evolutionary sciences that have to date developed separately. We describe the cooperative dilemma of joint liability lending (Section 2), outline several evolutionary mechanisms of cooperation and generate specific hypotheses relating to microfinance (Section 3), review empirical studies on microloan repayment to empirically assess whether their findings are qualitatively consistent with the evolutionary literature on cooperation (Section 4) and discuss the results of the review and our approach more generally (Section 5).

2. Microfinance and the cooperative dilemma in joint liability lending

Microfinance describes a bundle of financial services of which the most common is microcredit, the aim of which is to provide loans to small-scale entrepreneurs to reduce financial poverty and spur

economic growth. In recent decades, microfinance has grown and spread across the globe (Armendáriz and Morduch, 2010; Brau and Woller, 2004; Cull and Morduch, 2018). Today, there are estimated to be over 200 million recipients of microfinance worldwide, three quarters of whom are women, served by more than 3,000 microfinance institutions (MFIs), which include NGOs, commercial banks and other financial institutions (Microcredit Summit Campaign, 2015). More than half of microfinance clients are living in "extreme poverty" as defined by international poverty lines or the relative income position in their home country. Despite years of enthusiasm and success stories among practitioners and observers, rigorous evaluations of the impact of microcredit provision have at best shown modest causal effects on business and income growth (A. Banerjee et al., 2015; Duvendack et al., 2011; Meager, 2019) and debates about the evidence continue (Dahal and Fiala, 2020). Nevertheless, many scholars suggest that microfinance helps in "managing the ups and downs of lives in poverty and near-poverty, even when poverty persists" (Cull and Morduch, 2018, p. 551) by improving household finances and smoothing consumption. This contributes to the well-being of borrowers, albeit not triggering transformative economic growth (although others point towards the potential harmful social consequences of microcredit, e.g., Banerjee and Jackson, 2017; Hulme, 2000).

The microfinance movement in its current form as an entrepreneur-targeted development intervention was initiated in the 1970s by the Grameen Bank in Bangladesh. One of the major innovations was the introduction of JLL in small groups, which is still central to many MFIs and often seen as key to their success (Armendáriz and Morduch, 2010; Hermes and Lensink, 2007). In the JLL model, individuals receive loans in groups and are liable for repayment as a collective: only when the group loan is fully repaid will the individual group members have access to future loans and avoid other penalties. This allows lending to customers who have little material collateral and lack formal records of creditworthiness. By allocating repayment responsibilities to a group rather than an individual, the JLL contract creates an incentive for group members to look after each other's financial investments and activities in order to maintain their own access to future loans. Consequently, information and enforcement duties of mainstream lenders are transferred to the borrowers themselves (Besley and Coate, 1995; Ghatak and Guinnane, 1999; Stiglitz, 1990), replacing material collateral with social collateral. As Armendáriz and Morduch (2010, p. 13) write, "the classic Grameen contract takes advantage of clients' close ties within their communities". However, this shared responsibility for repaying a collective loan creates a cooperative dilemma. Each borrower is better off not repaying their share of the loan and letting other group members repay it. Yet if all borrowers do not repay their share, then the group will fail to repay the collective loan and will face penalties including being blocked from future loans. Therefore, in order to repay the collective loan, it is essential for group members to cooperate, for example by paying in full their own share or take diligent loan investment decisions that make it more likely to be able to repay.

74 Figure 1 sketches the stylized timeline of a typical loan cycle and Table 1 describes the decisions
75 taken by group members at each step. These decisions all feed into the cooperative dilemma
76 underlying JLL as there is conflict between the group goal (group's repayment) and the individual
77 goal (maximise own income). For example, the decision of a borrower regarding how to spend the
78 loan, whether to monitor others' investments, how many group meetings to attend or whether to
79 truthfully report the outcomes of one's own project, can all affect whether the loan is fully repaid at
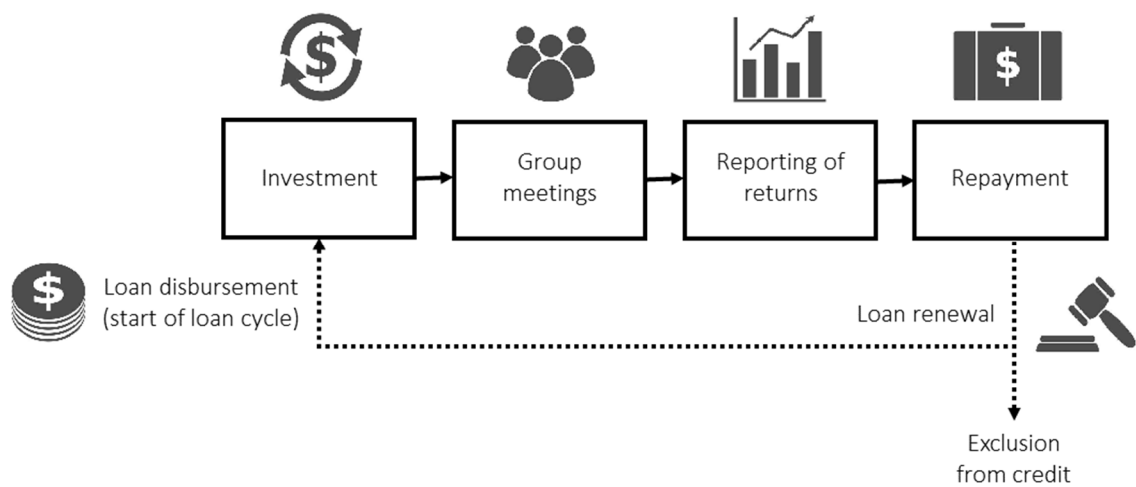80 the end of the loan cycle.

81

82

83 **Figure 1.** The stylized timeline of a typical joint liability loan cycle from loan disbursement by the microfinance institution
84 to the decision of the microfinance institution about loan renewal or exclusion from credit, which is conditional on
85 borrowers' repayment behaviour. At each stage framed by a rectangle, borrowers can be thought of as taking an action and
86 this action can affect the group's repayment outcome (see Table 1).

87   **Table 1.** Description of typical stages of a microfinance loan cycle with joint liability lending (see Figure 1) and how group
88   members' decisions at these stages affect the cooperative dilemma.

Stage	Description	Decision from borrower's perspective	How the decision affects the cooperative dilemma of JLL
Loan disbursement	Credit money is given to group members.	-	-
Investment	Group members invest their share of the loan in projects of their choice.	How to invest the loan and whether to monitor others' investment	Temptation for short-term consumption of the loan money, poor project choice or low entrepreneurial effort can reduce the likelihood of successful group repayment, but can be in the immediate self-interest of the borrower
Group meetings	Group members participate in regular meetings to discuss loan-related issues and repay small instalments.	Whether to attend group meetings and monitor other group members	Meetings confer multiple benefits to the loan group by providing opportunities for mutual monitoring, exchange of business-related information and training. Attendance can increase the likelihood of successful group repayment, but is individually costly (opportunity costs, travelling, being audited by lender, monitoring others). There is also an incentive to free-ride on the monitoring efforts of others.
Reporting of returns	Members disclose the returns from their projects.	Whether to be honest about investments and returns	Investment outcomes are reported in order to determine the ability to repay. Reporting lower returns than realised can increase individual income, especially if it is costly for the lender or other group members to verify. This benefits the individual but decreases the likelihood of group repayment.
Repayment	Group members contribute their monetary share to repay the group's loan.	Whether and how much to contribute to loan repayment and whether to sanction other non-contributors	Not contributing can increase own income when others help out and repay one's missing share. Social sanctions may prevent this, but if sanctions are costly to impose, there is an incentive to free-ride on the sanctioning efforts of others.
Loan renewal / Exclusion from credit	The group is either in default and excluded from future loans by the lender, or repays and becomes eligible to enter another loan cycle, often with improved conditions like larger loans.	-	-

89   Despite the cooperative dilemma at the heart of JLL, repayment rates of Grameen Bank and other
90   MFIs employing the JLL model have been high, often above 95% (Armendáriz and Morduch, 2010;
91   Brau and Woller, 2004; Cull and Morduch, 2018; Hossain, 1988). Yet there is considerable variation
92   in repayment rates across time and space. For example, JLL credit defaults temporarily rose from
93   around 2% to 90% in the 2010 Indian microfinance crisis (Haldar and Stiglitz, 2016). There is also
94   variation in the reported success of the JLL model relative to individual liability micro-lending. In
95   some contexts, empirical studies report that JLL leads to better loan repayment than when individuals
96   are solely liable for the loan (Carpena et al., 2013; Gomez and Santor, 2008; Khandker, 2012;
97   Mahmud, 2019), while in others there is no difference (Attanasio et al., 2015; Giné and Karlan, 2014).
98   This variation in repayment rates and the variable success of the JLL model remain largely
99   unexplained.

100   We suggest that variation in repayment rates and therefore the success of JLL may be linked to
101   whether individuals can solve the cooperative dilemma underlying it. If this is the case, then we
102   expect that factors facilitating cooperation amongst group members should have a positive outcome
103   on repayment efficacy. Here we propose and test whether these factors may be the same as those
104   proposed to facilitate the evolution of cooperation in nature as identified in the biological sciences.

105   The notion that repayment under JLL is a cooperative dilemma requiring collective action has long
106   been recognised by social scientists (Anthony, 2005; Guttman, 2007; Sabin and Reed-Tsochas, 2018;
107   van Bastelaer and Leathers, 2006), but it is not always treated explicitly as such in group lending
108   models. For example, the seminal economic model of group lending by Besley and Coate (1995)
109   assumes that borrowers employ sanctions to oblige other group members to repay their shares, making
110   repayment the self-interested choice. However, while sanctions are assumed to be caused by the
111   "social connectedness" of group members, how this social connectedness arises is not addressed.
112   Similarly, peer punishment or "social capital" – the ability to trust and cooperate with peers due to
113   some social structure, relations or norms (Coleman, 1988) – are widely cited reasons for the success
114   of group lending (e.g., Hermes and Lensink, 2007), but how and why certain social structures solve
115   the cooperative dilemma inherent to JLL is unspecified. We propose that evolutionary theories of
116   cooperation provide a tractable and measurable framework for understanding concepts like social
117   capital and social connectedness at a deeper level and may help to unify the currently diverse and
118   disconnected findings in the literature on JLL.

119   **3. Evolutionary theories of cooperation and predictions for microfinance loan repayment**

120   **3.1 The puzzle of cooperation and a general solution**

121   In evolutionary biology, cooperation is defined as a behaviour that is beneficial to the recipient of the
122   act, often (but not necessarily) at a cost to the actor (West et al., 2007a). The existence of costly
123   cooperation presents a puzzle to evolutionary biologists. The problem arises because cooperators

interact with selfish individuals (i.e. 'defectors') who benefit from the acts of cooperators but never bear the costs of cooperating themselves. Over the long term, selfish individuals should outcompete cooperators because selfish individuals accrue benefits while cooperators accumulate costs.

A general solution to this puzzle is to ensure that cooperators preferentially interact with other cooperators in the population (Fletcher and Doebeli, 2009; Fletcher and Zwick, 2006; Queller, 1985). This allows cooperators to share and accumulate the benefits of cooperation amongst themselves and prevents selfish individuals from free-riding on these benefits. Hence, the evolution of cooperation requires mechanisms of (positive) assortment that ensure that the average interaction group of cooperators contains more cooperators than the average interaction group of defectors (Fletcher and Doebeli, 2009). Then, cooperators profit more from other cooperators than they pay costs for their own behavior.

The following frequently used mathematical formalisation popularly known as "Hamilton's rule" (Hamilton, 1964a) specifies the conditions under which cooperative behaviour is favoured:

$$br > c \tag{1}$$

Cooperative behaviour is favoured when the benefit b of cooperation to the recipient, scaled by the degree of "relatedness" r between the actor and the recipient, is greater than the cost c of cooperation to the actor. In Hamilton's original formulation (Hamilton, 1964a), r was interpreted as the degree of genetic similarity between the actor and the recipient. However, r can be more broadly interpreted as the degree to which cooperators in the population interact preferentially with other cooperators (Fletcher and Doebeli, 2009, 2010; Fletcher and Zwick, 2006; Queller, 1992), as it is the statistical association between like types (Hamilton, 1975). Hence, r is a measure of assortment.

3.2 Assortment mechanisms and evolutionary hypotheses for loan repayment

Over the last half-century, several mechanisms that produce assortment have been discussed that support the evolution of cooperation (for reviews, see Lehmann and Keller, 2006; Nowak, 2006; Sachs et al., 2004; West et al., 2007b), some with a special emphasis on human cooperation (e.g., Apicella and Silk, 2019; Hammerstein, 2003; N. Henrich and Henrich, 2007; Powers et al., 2019; Rand and Nowak, 2013). Here, we describe a subset that we consider important in the context of microfinance. For each assortment mechanism, we derive hypotheses for loan repayment, some of which we then test in Section 4. As argued in Section 2, the basis for our predictions is the assumption that higher repayment efficacy in JLL groups, i.e., lower likelihood of credit default or loan delinquency, constitutes a higher degree of cooperation among group members.

3.2.1 Common ancestry

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Cooperation can be maintained when it is preferentially directed towards genetic relatives of the actor (Hamilton, 1964a, 1964b). Here, the mechanism of assortment is genetic. The likelihood of two individuals sharing a gene that makes them behave cooperatively increases with increasing genetic relatedness (Grafen, 2007, 2009). For example, a gene for cooperation is more likely to be shared by identical twins than fraternal twins. Thus, common ancestry is a reliable indicator that the recipient of cooperation is also likely to be cooperative and pass on the benefits of received cooperation to future generations of kin. This process by which cooperation evolves due to the actor and the recipient sharing ancestry is called "kin selection" (Maynard Smith, 1964). Interacting preferentially with kin is a heuristic that allows the assortment of cooperators and can lead to an accumulation of the benefits of cooperation across generations. The strength of kin-directed cooperation is therefore affected by the degree of genetic relatedness between the actor and recipient. For example, siblings, who on average share 50% of unique genetic variation, should be more likely to help one another than cousins, who share 12.5%.

Kin selection requires the availability of information about common ancestry which can be gained from cues and psychological short-cuts that identify kin (Bressan and Kramer, 2015; Lacy and Sherman, 1983). It leads to the evolution of emotions and motivations to care for kin (Ko et al., 2019). There is ample evidence that people bias help towards close kin for many different types of interaction such as food sharing (Gurven et al., 2002; Kaplan et al., 1985), cooperative hunting (Morgan, 1979), monetary giving (Bowles and Posel, 2005) and child care (Anderson et al., 1999).

Hypothesis for microfinance research: JLL groups comprising individuals who are more closely related via common ancestry (i.e., genetic kin) should have higher repayment efficacy than those comprising non-kin.

3.2.2 Prior interaction

Cooperation can be maintained when the actor's decision to cooperate or defect depends on the previous cooperative behaviours of the recipient. This is called reciprocity and can either be based on prior interactions with the same partner (direct reciprocity; Axelrod, 1984; Axelrod and Hamilton, 1981; Trivers, 1971) or on the basis of one's partner's reputation from her prior interactions with other partners (indirect reciprocity; Alexander, 1987; Leimar and Hammerstein, 2001; Nowak and Sigmund, 2005; Panchanathan and Boyd, 2003). Assortment arises because individuals direct cooperation to others who are known to have cooperated in the past. In this case, the effectiveness of assortment increases with the time horizon of repeated interactions or with more reliable information on the behaviour of others (Nowak, 2006). Direct reciprocity requires cognitive and psychological mechanisms such as memory to identify suitable long-term partners or emotions such as affinity and friendship to maintain reciprocal relationships (Fessler and Haley, 2003; Seyfarth and Cheney, 2012). Indirect reciprocity in humans is likely supported by our capacity for language to pass on information

(Nowak and Sigmund, 2005), inclinations to spread gossip (N. Henrich and Henrich, 2007), concern with reputation (D. Karlan and McConnell, 2014; Milinski, 2016) and sympathy for people who do good to others (Bereczkei et al., 2007). There is evidence from laboratory experiments and field studies that humans reciprocate directly (Dal Bó and Fréchette, 2018; Fischbacher et al., 2001; Gurven, 2006; Kasper and Borgerhoff Mulder, 2015) and indirectly (Diekmann et al., 2014; Seinen and Schram, 2006; Wedekind and Braithwaite, 2002).

Hypotheses for microfinance research: JLL groups with the opportunity for direct reciprocity between group members, such as when the group participates in repeated loan cycles (Che, 2002) should have higher repayment efficacy. Opportunities for mutual exchange outside the JLL group, such as when members have personal and business relations with each other (Anthony, 2005; de Quidt et al., 2016), should be associated with higher repayment efficacy. JLL groups with the opportunity for indirect reciprocity, such as when members share mutual acquaintances within a larger social network (Postelnicu et al., 2019), or engage in many social activities outside the group, should have higher repayment efficacy as this may provide a means to acquire and spread reputational information.

3.2.3 Partner choice

Cooperation can be maintained when actors are able to select their interaction partners. Assortment occurs because individuals can choose to interact with known cooperators and avoid interacting with defectors from the outset (Bull and Rice, 1991; Enquist and Leimar, 1993; Gintis et al., 2001; Hammerstein and Noë, 2016; Roberts, 1998). This is different to, but can work alongside, other mechanisms such as reciprocity (Section 3.2.2), in which individuals do not actively choose their interaction partners or "walk away" from them, but can only choose whether or not to cooperate with an encountered partner (partner choice vs. partner control, see Schino and Aureli, 2017). Partner choice requires the ability to identify and choose cooperative partners using signals of their likelihood of being a cooperator. Signals of likely cooperation should be costly, and thereby "honest", so that defectors cannot fool cooperators by faking such signals (Bowles and Hammerstein, 2003). Honest signals might include an individual's past cooperative behaviour (Guido et al., 2019; Sylwester and Roberts, 2010), costly cultural practices such as holding extravagant feasts (Barker et al., 2019), or facial or other physical characteristics (although evidence on humans' capacity to detect cheaters by biological markers alone is mixed (Aamodt and Custer, 2006; Fetchenhauer et al., 2010).

Hypotheses for microfinance research: JLL groups which form via the selection of group members by other members, e.g., by being able to choose who is admitted to your group, should have higher repayment efficacy than groups where membership is not controlled by group members. Note that self-formation of groups is a traditional feature of the Grameen Bank, with economists suggesting that this allows peers to screen each other for the riskiness of their business project (Armendáriz and Morduch, 2010; Ghatak and Guinnane, 1999; Van Tassel, 1999). We expand this idea by suggesting

226   that borrowers might screen for cooperativeness in general (as in biological market theory, see
227   Hammerstein and Noë, 2016).

3.2.4 Similarity of tags

229   Cooperation can be maintained when it is directed only towards interaction partners that are similar to
230   the actor in an arbitrary observable character or tag if that tag is a reliable indicator that the recipient
231   of cooperation is also a cooperator (Antal et al., 2009; Gardner and West, 2010; Hales, 2005;
232   Hammond and Axelrod, 2006; Riolo et al., 2001). In this case, interacting based on this tag leads to
233   assortment. Tag-based cooperators of this type have sometimes been referred to as "greenbeards",
234   after a thought experiment in which green beards act as tags of cooperation (Dawkins, 1976; Gardner
235   and West, 2010). Assortment via tags is threatened when defectors can fake the cooperators' tags and
236   thus requires, and increases with, the reliability of tags as indicators of behaviour (Hales, 2005), for
237   example by using signals that non-cooperators cannot easily fake. Like prior interaction, tag-based
238   cooperation is different to partner choice (Section 3.2.3) as individuals cannot actively choose their
239   interaction partners, but can only choose whether or not to cooperate with an encountered interaction
240   partner. In humans, tag-based cooperation depends on a psychological inclination to cooperate
241   preferentially with others who appear similar in certain ways (Fu et al., 2012). Such tags might
242   include accents (Cohen and Haun, 2013), facial resemblance (DeBruine, 2002), expressions of
243   cultural and social identity like clothing, humour, sports or music preferences (Smaldino, 2017) or
244   other arbitrary markers of groups (Tajfel and Turner, 1986).

245   *Hypotheses for microfinance research:* Repayment efficacy may be structured by observable
246   biological or socio-cultural tags (e.g. accents, facial resemblance, clothing), after controlling for other
247   differences between groups. Assuming that the tag is a known and reliable indicator of cooperation, a
248   more specific prediction is that homogenous JLL groups whose members share this tag should have
249   higher repayment efficacy than heterogenous groups whose members have different tags, after
250   controlling for other differences between groups.

3.2.5 Social learning

252   Cooperation can be maintained when cooperative behaviour is transmitted between individuals via
253   social learning mechanisms such as imitation and conformity (Boyd and Richerson, 1985; J. Henrich
254   and Boyd, 2001; N. Henrich and Henrich, 2007). Socially learned rules or norms of behaviour can
255   make individuals in an interacting group more similar to each other (Apicella and Silk, 2019; Boyd
256   and Richerson, 2009). Hence, the assortment of cooperators can be achieved via social learning.
257   Tendencies to conform to others' behaviour and adopt local institutions can generate behavioural
258   variation between interaction groups, with some groups in the population being more cooperative than
259   others (Chudek and Henrich, 2011). Competition between these groups enables the evolution of

cooperation, as the costs borne by the individuals of a more cooperative group are outweighed by the benefits they receive when their group outcompetes the other. This process can lead to norms and institutions that favour cooperation and has been called cultural group selection (Handley and Mathew, 2020; J. Henrich, 2004; Richerson et al., 2016; Waring et al., 2015). Here, the degree of assortment increases with the tendency of individuals to socially learn and exhibit the behaviour of the group they are in, compared to other groups. Note that any type of assortment mechanism, including the ones mentioned in previous sections, can be conceptualized as resulting in group selection because assortment leads to "groups" (e.g. kin groups, groups of reciprocators) in which individuals preferentially bestow benefits on each other (see (Birch, 2019; Wilson and Dugatkin, 1997; Wilson and Sober, 1994)). Cultural group selection depends on socially learned norms sustained by conformity or punishment. While there is evidence of variation in cooperation across human populations which is consistent with assortment via social learning of cooperation (e.g., Gächter et al., 2010; J. Henrich et al., 2005; Richerson et al., 2016), the degree to which such variation is caused by the cultural transmission of behavioural norms rather than other factors, like en masse individual responses to shared ecological and demographic factors which can also create behavioural uniformity, is debated (Lamba and Mace, 2011).

Hypotheses for microfinance research: Repayment efficacy may be structured by socio-cultural group if there are socially learned rules of cooperation associated with these socio-cultural group boundaries. Repayment efficacy may be structured at any level at which behaviour may be socially transmitted, i.e. community, village, ethno-linguistic group, any other kind of interaction group. Specifically, JLL groups of the same socio-cultural group should have more similar repayment rates to groups from a different socio-cultural group, after controlling for other differences.

3.2.6 Ecology and demography

Cooperation can be maintained when ecological factors and demographic processes create and maintain behavioural similarity between individuals (Smaldino et al., 2013; Wilson, 1977). Assortment due to ecology may arise because individuals' environments vary with respect to the costs and benefits associated with cooperation. For example, the challenge of long-term survival in harsh ecologies may favour cooperation compared to groups living in less harsh (Smaldino et al., 2013) and ecological disturbances can alter the population structure (Foster and Xavier, 2007). A substantial body of theory in evolutionary biology predicts that demographic characteristics of populations, such as their size and patterns of migration, are important drivers of cooperation and competition (Doebeli et al., 1997; Johnstone and Cant, 2008; Platt and Bever, 2009; West et al., 2002). Demography affects the stability of the various mechanisms of assortment described above, as well as the costs and benefits of cooperation. For example, high rates of migration in a population can destabilize cooperation by breaking down the assortment generated by common ancestry, prior interaction or

partner choice. Similarly, cooperation via prior interaction can be destabilized in large populations as it may become harder to keep track of and remember past interactions and reputations (Boyd and Richerson, 1988; Milinski et al., 2001). There is empirical evidence that demographic and ecological factors, such as household organization, population size and age structure, geography, and environmental productivity affect cooperation across human populations (Blurton Jones, 2016; Gurven et al., 2002; Lamba and Mace, 2011, 2013)

Hypotheses for microfinance research: Repayment efficacy may be structured by socio-cultural group if there are similarities in ecology and demography associated with these socio-cultural group boundaries. Repayment efficacy may be structured at any level at which ecology and demography are shared, i.e. community, village, ethno-linguistic group, any other kind of interaction group. Specifically, JLL groups of the same socio-cultural group (e.g., whose members were born or live in the same area) should have more similar repayment rates to groups from a different socio-cultural group, after controlling for other differences. Additionally, demographic factors such as population size and rates of migration might be associated with repayment efficacy. For example, repayment efficacy might be higher in smaller populations and populations with less migration (e.g. rural rather than urban populations).

3.3 Summary and clarifying comments

In the previous sections we have described several evolutionary mechanisms by which cooperators may preferentially assort (common ancestry, prior interaction, partner choice, similarity of tags, social learning, and ecology and demography), thus leading to the maintenance of cooperation. For each of these, we have specified hypotheses for how the mechanism may affect repayment efficacy in JLL-based microfinance loan groups. Before testing some of these hypotheses in the existing microfinance literature in Section 4, we offer some clarifications of these hypotheses, as well as of evolutionary approaches to human behaviour more generally, with a social science audience in mind.

First, it is important to keep in mind that these mechanisms may not be mutually exclusive (Sachs et al., 2004), i.e., multiple mechanisms may operate simultaneously in the same loan group. For example, people may select loan group members (partner choice) partly based on their reputation (prior interaction).

Second, while some of these mechanisms rely on a genetic basis for cooperative behaviour (e.g. common ancestry, see Section 3.2.1), other mechanisms assume that behaviour is acquired and transmitted non-genetically (e.g. via social learning, see Section 3.2.5). Therefore, an evolutionary approach does not require that cooperative behaviour itself is entirely genetically determined, rather genetically evolved cognitive or psychological faculties such as memory or language may facilitate the ability to use these assortment mechanisms.

Third, we can therefore make a distinction between the assortment mechanism that is ultimately supporting the maintenance of cooperation (e.g. common ancestry) and the proximate physiological, developmental and psychological processes (e.g. kin recognition) by which that mechanism operates. This distinction between *ultimate* and *proximate* causes of behaviour (Tinbergen, 1963) is sometimes blurred in the social science literature particularly relating to human cooperation (Alexander, 1987; West et al., 2007a). Proximate motivations and emotions among group lenders like fear (Dube and Kamath, 2018), trust (van Bastelaer and Leathers, 2006) or a "preference" for others' payoffs (Carpenter and Williams, 2014) do not distinguish between the ultimate assortment mechanisms at play. For example, people may "trust" both their kin and repeated interaction partners, but this does not explain why trust is directed towards these particular categories of people. Identifying the ultimate assortment mechanisms underlying human cooperation can allow us to make novel predictions about what characteristics of individuals and groups are likely to be associated with repayment efficacy.

Finally, evolutionary theory does not require that individuals are consciously aware of the ultimate evolutionary reason why they are performing a particular behaviour (Nettle et al., 2013). Indeed, people might more often cite proximate motivations and emotions such as fear, trust or love for why they may or may not cooperate with another person. Consequently, people's actual behaviour provides the appropriate data for testing our hypotheses rather than their self-reported motivations.

4. Empirical review: Do predictors of loan repayment correspond to evolutionary mechanisms of cooperation?

In this section we attempt to test the first three assortment mechanisms presented in Section 3.2, common ancestry, prior interaction and partner choice. At this stage, we do not explicitly test the other three mechanisms – similarity of tags, social learning, and ecology and demography. Disentangling these mechanisms requires the examination of patterns of relative variation in a multilevel dataset, for example with borrowers nested within loan groups, nested within MFIs, nested within socio-cultural groups, nested within regions etc. (see, e.g., Lamba and Mace, 2011). Furthermore, these latter three mechanisms overlap in their predictions. For example, all three mechanisms predict that repayment efficacy may be structured by socio-cultural group boundaries or tags. A multilevel dataset is essential to distinguish between them. This analytical approach is beyond the scope of this initial review. Here, we simply assess whether the empirical MFI literature contains predictors that can be related to evolutionary assortment mechanisms and conduct a rough assessment of the evidence for only the first three (common ancestry, prior interaction and partner choice).

Economists and other social scientists have conducted multiple empirical studies exploring the factors linked to the repayment efficacy of microfinance groups. Their aim is typically to assess what mitigates the incentive problems inherent in microfinance, such as the temptation to dishonestly misuse the loan ("moral hazard") or to evade the repayment obligation that is difficult to enforce.

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364 These studies usually compare multiple loan groups from the same MFI to examine whether certain
365 characteristics of loan groups or borrowers are associated with higher or lower repayment efficacy.
366 Our first step was to review the MFI literature to identify factors that had been tested by economists
367 and other social scientists for their association with repayment efficacy of JLL groups and that could
368 plausibly be linked to our evolutionary mechanisms specified in Section 3.2, especially common
369 ancestry, prior interaction and partner choice. Since these studies originally were not guided by an
370 evolutionary framework, they do not consistently and precisely measure the evolutionary factors that
371 we predict to be associated with cooperation and generally vary in how they measure certain concepts.
372 Consequently, we grouped predictors from the literature into categories that themselves fell under the
373 first three assortment mechanisms. For example, several authors measured associations between some
374 form of geographical proximity between loan group members and repayment efficacy. We therefore
375 created a category "geographical proximity" to include these associations, which, among potentially
376 others, is likely to reflect the assortment mechanism of prior interaction.

377 We conduct a qualitative "vote count" of findings within each category based on statistical
378 significance (Koricheva et al., 2013). We count the number of associations that were in line with the
379 evolutionary hypothesis ("positive"), not in line ("negative") and that showed no statistical
380 significance ("non-significant"). We acknowledge that the "vote-counting" methodology has clear
381 weaknesses compared to a formal meta-analysis: it does not properly account for the size and
382 uncertainty of effects, relies on results from error-prone statistical null hypothesis testing, and weighs
383 equally studies with different sample sizes, methods and quality (Koricheva et al., 2013). Further,
384 despite our systematic approach, we cannot claim that this review is exhaustive or unbiased, since the
385 collection of literature and effects involved multiple steps that were exploratory. Nevertheless, it
386 provides a first systematic overview of the MFI literature within an evolutionary framework. A more
387 rigorous quantitative meta-analysis would be the next step, but is challenging given the heterogeneity
388 of the microfinance literature (Duvendack et al., 2011). Therefore, here we first assess the feasibility
389 of pursuing this research agenda.

390 **4.1 Review methodology**

391 **4.1 Literature search**

392 We searched Google Scholar for various combinations of the terms: "microfinance", "microcredit",
393 "group lending", "joint liability", "repayment", "default", "delinquency", "arrears", "cooperation",
394 "social capital", "factors", "determinants", "predictors". We first screened for studies in the peer-
395 reviewed and grey literature (dissertations, working papers, preprints) that (i) analysed factors
396 associated with a measure of repayment efficacy (e.g., timeliness of repayment, proportion of loan
397 repaid at due date, full loan repaid yes/no, occurrence of repayment problems yes/no) in groups that
398 take out loans and have some degree of joint liability, (ii) were quantitative, and (iii) reported methods

399   and results sufficiently. We further screened the resulting papers to exclude studies that (i) reported

400   aggregate data at the level of an entire country or MFI rather than at the level of individual borrowers

401   or loan groups, (ii) used lab or lab-in-the-field experiments (Harrison and List, 2004) on MFIs instead

402   of data from real MFIs, and (iii) did not report results for a predictor that links to the evolutionary

403   hypotheses we set out to examine (Section 3.2). Thus, we built a database of predictors examined in

404   the MFI literature that link to the evolutionary hypotheses we wish to test (Section 3.2). Building on

405   Lamba (2014), we focus on a set of predictors which is by no means an exhaustive list of all

406   predictors occurring in the literature. Since no other previous work has been guided by similar

407   hypotheses, we invite readers to examine our choices in the Supplementary Material 1 (SM1) and

408   build upon them. We also scanned the bibliographies of all included work to find additional relevant

409   studies. Based on this, predictors from a set of 40 studies were included in this review, with the vast

410   majority from the economics discipline, but also few from sociology.

411   **4.1.2 Extraction of effects of predictors on repayment efficacy from reviewed literature**

412   For each predictor variable included in our database we qualitatively recorded whether their

413   association with repayment efficacy was statistically positive, negative or nonsignificant. We then

414   recoded the predictors used in the original studies such that a positive association is in line with the

415   evolutionary hypothesis, i.e. supports the hypothesis of a positive relationship between the

416   evolutionary predictor and repayment efficacy, and negative associations are contrary to the

417   evolutionary prediction, i.e. in the opposite direction. For example, we predict a *positive* relationship

418   between geographical *proximity* and repayment efficacy (see Section 3.2.2). If a study reported a

419   statistically significant *positive* association between 'geographical *distance* between group members'

420   and repayment efficacy, we recoded the predictor as 'geographical *proximity*', and consequently

421   recoded its relationship with repayment efficacy as *negative*. Therefore, since in this case

422   'geographical *proximity*' has a negative association with repayment efficacy, it is recorded as not in

423   line with our evolutionary hypothesis. Note that repayment efficacy was sometimes measured

424   inversely (e.g., credit default or repayment delay, see SM1). Non-significant associations were not

425   altered and always coded as non-significant.

426   The microfinance literature includes both characteristics of borrowers and characteristics of loan

427   groups as predictors of repayment efficacy. We have specified in our database in SM1 the level at

428   which the predictor was measured, when possible, by referring to borrower or loan group as

429   appropriate in the description of the predictor.

430   We did not include predictor variables measuring psychological states such as trust, anger, a

431   willingness to exert pressure on others, or self-reported motives for repayment (e.g., Dube and

432   Kamath, 2018; Griffin and Husted, 2015), because these do not directly capture assortment

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mechanisms for the evolution of cooperation. Rather, these represent proximate psychological motivations (see Section 3.3) which were not the focus of this study.

When multiple analyses were reported for the same predictors in one study (e.g., various types of models and/or varying sets of covariates were reported), we only extracted *one association per predictor per study*. We selected only the analysis explicitly favoured by the original authors, except if there was a regression model with even more predictors included simultaneously, i.e., a "full model", including all control covariates. In that case, we selected the association reported in the larger model. In rare cases, when the analysis favoured by the original authors was not judged appropriate for the purpose of this review, the most suitable analysis was chosen by the first author (SG). For example, Griffin and Husted (2015) aggregated different questionnaire items into one latent variable, but the raw correlation between the questionnaire item of interest with repayment efficacy was seen as more suitable. When multiple measures for repayment efficacy were reported, we always selected whichever was most conservative in classifying repayment as low. For example, when both repayment problems within the loan group, i.e., individual borrowers not paying their shares ("internal delinquency"), and repayment problems between the loan group and the MFI, i.e., the loan group not repaying its collective amount of loans ("external delinquency"), were reported, we used the latter. We invite readers to assess our choices of extracted variables, models and effects reported in SM1. We report associations as positive, negative or non-significant in accordance with the original authors' own most permissive significance cut-offs ($p<0.1$ in the majority of studies; SM1). In all studies, only monotonic relationships between predictors and repayment efficacy were analysed, except for two studies (Kolstad et al., 2017; Sabin and Reed-Tsochas, 2018), which reported an inverted U-shaped relationship between a predictor and repayment efficacy. Thus, in the results, "Inverted U" is reported as an extra category.

4.1.3 Categorisation of predictors

Based on the empirical microfinance literature, we generated 13 categories into which predictors were grouped to capture their similarities and provide an overview of which evolutionary hypotheses find support. This was necessary because different authors measured the same concept in different ways. For example, the predictors "Number of family members in group" (Carpenter and Williams, 2014) and "Proportion of group members who have a close relative in the group" (Ahlin and Townsend, 2007) from two different studies were are both classified as "Family members in group". Each predictor was only included in one category. The 13 categories are displayed in Figure 2 and SM1 provides the original definition of all underlying predictor and outcome variables included in each category.

Finally, as shown in Figure 2, we link 10 of these 13 categories to one of the three assortment mechanisms (common ancestry, prior interaction, partner choice) that we test, and grouped the final 3

categories as "Other / multiple mechanisms" because these categories relate to and overlap across the three assortment mechanisms (similarity of tags, social learning, ecology and demography) that we do not explicitly test.

4.2 Results

In total, 139 associations from 40 studies covering 31 countries were included and classified into 13 broader categories, shown in Figure 2. We find 45 (32.4%) positive associations of the predictor and repayment, meaning that the evolutionary hypothesis is supported in these cases. Two associations (1.4%) are initially positive for low values of the predictor, but then turn negative (inverted U-shaped, fit via a quadratic function). 29 associations (20.9%) are negative. There are 63 (45.3%) non-significant associations. Thus, just under half of the associations are non-significant, about one third are positive, and one fifth are negative. Proportions of positive, negative and non-significant associations for each of the 13 categories separately are reported in SM2.

The 30 studies that reported loan group size report a mean group size of 9.83 borrowers, median group size of 9.15 borrowers, and range 2.6-35 borrowers. The assessed predictor variables, outcome variables, types of analysis and other study characteristics are presented in SM1.
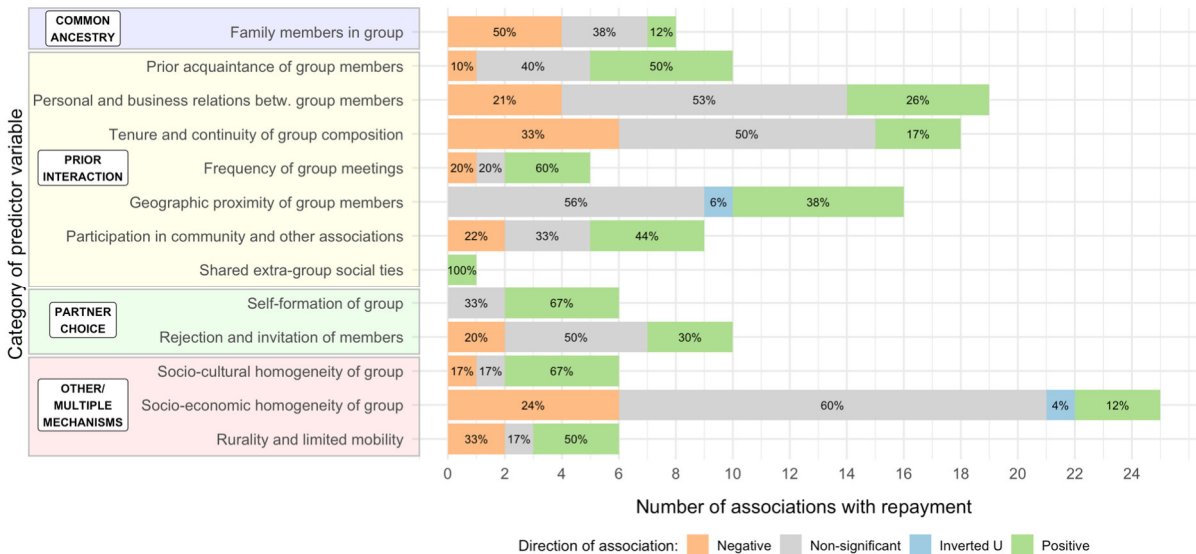

Figure 2. Number and qualitative directions of associations between predictor categories and repayment efficacy of JLL borrowers reported in the literature. Predictors are grouped into 13 categories based on the concept they are measuring. Coloured boxes further group these 13 categories into the evolutionary assortment mechanisms (see Section 4.1.3 for details). Associations are reported qualitatively as negative (orange), non-significant (grey), inverted U-shaped (blue) or positive (green) as per the original study (see Section 4.1.2 for details) with percentages of each type of association shown. Note that some bars do not add up exactly to 100% due to rounding errors. The figure is based on a total of 139 associations from 40 empirical studies spanning 31 countries. See SM1 for details and references for every association extracted from the literature and SM2 for a table with the data underlying this figure. Within the group of categories labelled 'Prior interaction', the first 6 categories relate to direct reciprocity, and the last 3 to indirect reciprocity, with 2 categories relating to both direct

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493 or indirect reciprocity, specifically 'Geographic proximity of group members' and 'Participation in community and other
494 associations'. 'Geographic proximity of group members' may also relate to the 'Other / multiple mechanisms' grouping.

5. Discussion

5.1 Summary of findings

497 In this paper, we assess whether the empirical literature on repayment efficacy among microcredit
498 loan groups contains predictors that can be related to evolutionary assortment mechanisms that enable
499 the evolution of cooperation: common ancestry, prior interaction, partner choice, similarity of tags,
500 social learning, and ecology and demography. Given the cooperation problem inherent in loan groups
501 that share their repayment burden, we expect predictors related to these mechanisms to affect
502 repayment efficacy. We conduct a rough assessment of the evidence for three of these (common
503 ancestry, prior interaction, partner choice). Overall, the majority of associations are statistically non-
504 significant, about one third are positive (in line with our evolutionary hypotheses), about one fifth are
505 negative (not in line with our evolutionary hypotheses), and two associations take an inverted-U
506 shape.

507 For the three mechanisms that we explicitly test, we find different levels of support. For common
508 ancestry, most of the studies show either negative or no associations between kin and repayment
509 efficacy, meaning that this evolutionary mechanism of assortment finds little support. For prior
510 interaction, a majority of associations are positive for three categories of predictors (prior
511 acquaintance of group members, frequency of group meetings and shared extra-group social ties),
512 meaning that these categories show some support for this assortment mechanism. On the other hand, a
513 majority of associations are negative or non-significant for four categories (personal and business
514 relations between group members, tenure and continuity of group composition, geographic proximity
515 of group members, and participation in community and other associations), although for the latter two
516 categories at least one third of the associations is positive and these outnumber the negative
517 associations. Consequently, these categories show mixed support for the mechanism of prior
518 interaction. For partner choice, a majority of associations are positive for one category of predictors
519 (self-formation of group) with no negative associations at all. A majority of associations are negative
520 or non-significant for the other category (rejection and invitation of members), although 30% are
521 positive and outnumber the negative associations. Consequently, both categories together show some
522 support for this assortment mechanism. Of the three assortment mechanisms that we explicitly
523 examine, we find little support for common ancestry, and some support for prior interaction and
524 partner choice.

525 For the three mechanisms that we do not explicitly test (similarity of tags, social learning, ecology and
526 demography), we nonetheless find predictors in the MFI literature to which they may be related, and
527 which we grouped into three categories (socio-cultural homogeneity of group, socio-economic

528   homogeneity of group, and rurality and limited mobility). We find broad support for two of these

529   categories (socio-cultural homogeneity of group, and rurality and limited mobility), with a majority of

530   associations positive and the number of positive associations equal to or greater than a half of all

531   associations. For the category socio-economic homogeneity of group, we find a large number of

532   associations, indicating the popularity of these predictors in the economic literature, but also the fact

533   that this category was quite diverse. There is limited support for socio-economic homogeneity, with a

534   majority of associations negative or non-significant, and more negative than positive associations.

535   However, as discussed in Section 4, it is unclear how to link these categories of predictors to our

536   evolutionary mechanisms given that all three mechanisms make predictions that overlap across these

537   categories. In any case, these simple predictor-outcome associations cannot be used to test these

538   mechanisms and multilevel data are required. Furthermore, these categories lump together many

539   different kinds of homogeneity, and in many cases this homogeneity is measured in the original study

540   using a composite index that combines several characteristics of borrowers. For example, similarity of

541   ethnic markers, religion or caste are included in the category socio-cultural homogeneity of the loan

542   group and similarity of occupation, gender, age, income and education are included in the category

543   socio-economic homogeneity of the loan group. Therefore, these associations are difficult to interpret.

544   5.2 The negative effect of common ancestry

545   The finding that the majority of associations between kin and repayment efficacy are negative (i.e. not

546   in line with our evolutionary hypothesis) is surprising given that many evolutionary studies in humans

547   (Kurzban et al., 2015) and other species (Strassmann et al., 2011) have shown that help is

548   preferentially directed towards kin. It is possible that the evolutionary theory of kin selection fails to

549   explain repayment behaviour in the context of microfinance. Alternatively, there are at least three

550   potential reasons for this unexpected finding which are in fact consistent with the theory.

551   First, economists have suggested that enforcement of loan repayment may be difficult among relatives

552   and that it is easier for relatives to collude against the MFI (Ahlin and Townsend, 2007; Hermes and

553   Lensink, 2007; Sharma and Zeller, 1997). This may nevertheless be consistent with kin selection if

554   group members who are relatives do not want to impose costs on their kin by punishing them for non-

555   repayment or are more lenient in giving them more time to repay their loans, and if they are willing to

556   bear the penalties of non-repayment imposed by the lender. In fact, some MFIs like Akhuwat in

557   Pakistan have entirely banned family members from joining the same group (Mahmud, 2019).

558   Second, if the loan group is embedded in a wider social network such that individuals have kin

559   outside the loan group as well as inside, then the relationships between kin outside the loan group may

560   influence the relationships between kin inside the loan group. For example, if one has lots of close

561   relatives within one's village but one forms a loan group with more distant relatives, then if one's

562   close kin in the village need help, one may help them at the expense of being able to repay one's share

563 of the loan on time. In this case, although one is defaulting on kin within the loan group, it is to help
564 closer kin outside the loan group, consistent with kin selection. For example, Cieslik et al., (2019)
565 report how borrowers from Burundi are breaking rules of the MFI as a side-effect of deepening
566 existing social bonds and securing the social status of the family.

567 Third, if the density of kin in the wider social network is high, then upon forming a loan group with
568 some of these kin, one may prioritise one's own earnings over the earnings of one's kin because one is
569 also in economic competition with those kin. For example, a borrower living in a small village and
570 forming a loan group with her sister, both of which own shops which compete for the same business,
571 may invest in her own business at the expense of repaying her share of the loan, tolerating the
572 negative consequences for her sister. This phenomenon, where cooperation between kin is
573 undermined by competition between them, has been described by evolutionary biologists as kin
574 competition and results when assortment due to common ancestry is small due to a high relatedness in
575 the whole population (Taylor, 1992; West et al., 2002). Interestingly, one of the studies in our dataset
576 could provide potential evidence for this: when splitting up their sample, Ahlin and Townsend (2007)
577 find a negative effect of kinship on loan repayment only in the more rural region of Thailand, where
578 people might reside, and hence compete, more in extended families.

579 To summarise, two out of three reasons why kin has a negative effect on repayment may actually be
580 in line with kin selection, while the third is consistent with another theory from evolutionary biology,
581 kin competition. Thus, MFI loan groups demonstrate that kin selection need not always result in a
582 positive association between kin and cooperation within an interaction group, for example when the
583 wider social context is taken into account or when enforcement towards kin is necessary for
584 cooperation.

585 The observation that kinship can generate collusion (i.e., cooperation) within the loan group against
586 the MFI suggests that other factors which increase within-group cohesion may similarly reduce
587 repayment efficacy. For example, a decrease in repayment was observed in a microcredit program in
588 Sierra Leone when groups were "too cohesive", measured by their geographical proximity (Sabin and
589 Reed-Tsochas, 2018). When penalties by the lender are too small, cooperation for repayment at the
590 loan-group level may be less relevant than cooperation at other levels, such as the household,
591 neighbourhood, community or dyad. Frameworks of "linked games" (Spagnolo, 1999) and multi-level
592 selection (J. Henrich, 2004; Richerson et al., 2016; Waring et al., 2015) which address interconnected
593 and nested social dilemmas can potentially help to understand these phenomena.

594 ## 5.3 Limitations

595 The reviewed studies are diverse in the country/regions where they were conducted, in the
596 methodology used, in the measurement of variables and in the level of empirical investigation
597 (individual borrowers versus loan groups). Some authors interviewed multiple group members, others

598 just one. Sometimes the repayment outcome was a more direct measure from administrative records
599 (e.g., % of loan value not repaid at a certain date), while other studies measured more indirect
600 outcomes via self-report (e.g., whether group members reported experiencing repayment difficulties).
601 The same variables were measured in different ways across studies. Sample sizes and sizes of loan
602 groups varied widely (SM1). We expect some false positives, due to the multiple analyses run and
603 variables tested within the same paper, and false negatives, due to low statistical power in many
604 studies, in addition to potential publication bias or questionable research practices. A quantitative
605 meta-analysis with more rigorous inclusion criteria is an important next step.

606 Most of the associations in our database are cross-sectional and correlational, casting doubt on the
607 causal relationship between predictor and repayment efficacy. For example, borrower groups formed
608 via self-selection will likely include members that have stronger reciprocal ties than groups that were
609 formed exogenously. Mahmud (2019) found that the more time people had to form their groups in one
610 Pakistani MFI, the more the groups were composed of people who knew each other previously. This
611 confounds prior interaction and partner choice which we have presented as separate mechanisms in
612 Section 3.2. Selection bias may limit findings in cases where loans are only offered to, or taken up by
613 particular kinds of individuals (e.g. women). Reversed causality may occur, for example when
614 repayment outcomes affect the social ties between borrowers, or when groups show more discipline in
615 attending group meetings because they have less repayment difficulties, rather than vice versa
616 (discussed by van Bastelaer and Leathers, 2006). Encouragingly, the few studies that attempt to
617 explicitly test causality by using quasi-experimental approaches (see SM1 for details) find effects that
618 are in line with our hypotheses: repeated interactions in group meetings (Dalla Pellegrina et al., 2017),
619 and geographical proximity (D. S. Karlan, 2007), both led to higher repayment efficacy. In the future,
620 exploiting natural experiments and longitudinal data could provide a broader empirical basis for tests
621 of our evolutionary hypotheses.

622 Some positives associations in our review might plausibly be explained by factors other than
623 assortment. As outlined in the introduction (Section 3.1) the evolution of cooperation also depends on
624 the relative costs and benefits. For example, longer tenure of a group might increase assortment by
625 facilitating repeated interactions among members (Section 3.2.2), but it may also improve the
626 borrowers finances, or cause borrowers to exhaust productive business opportunities to invest their
627 loan (Guttman, 2007), thereby reducing the need for a microloan. This reduces the individual benefits
628 of disciplined repayment and loan renewal. In terms of Hamilton's rule (Section 3.1), in this case
629 though r may increase, b may simultaneously decrease. This could explain why this category of
630 predictors ("tenure and continuity of group composition", Figure 2) has fewer positive associations
631 with repayment than other proxies for prior interaction.

5.4 Implications for evolutionary biology and economic research

633   We end by noting some general implications of our study. First, our unexpected finding that kin in the
634   loan group are negatively associated with repayment efficacy highlights the need for evolutionary
635   biologists and evolutionary human scientists to go beyond simplistic applications of evolutionary
636   theory that make general claims that cooperation should always be preferentially directed towards kin,
637   and test more nuanced predictions that arise from kin selection theory. Conversely, this also offer
638   novel avenues of investigation for economists and social scientists studying microfinance. For
639   example, the direction of the effect of kin on repayment efficacy may depend on the degree of kinship
640   not only within the loan group, but also outside the group in the wider population. Typically, only the
641   former is measured in economic or sociological studies.

642   Second, it is important to think about the overall structure of the cooperative dilemma ("game") that
643   joint liability borrowers face as cooperative dilemmas come in different forms (Archetti and
644   Scheuring, 2011, 2012). Once this is more clearly defined, predictions for different levels of
645   assortment on the evolution of cooperation in this particular dilemma can be derived more precisely.
646   A plausible model of JLL is a threshold public goods game: if a group's credit is fully repaid (i.e.,
647   repayment is above a threshold), all group members are rewarded with a new, larger loan, but under a
648   strict implementation of JLL the lender is indifferent to who repays. Such dilemmas have been
649   theoretically examined in economics (e.g., Palfrey and Rosenthal, 1984) and have been studied under
650   the name of the "volunteer's dilemma" in sociology (Diekmann, 1985) and biology (Archetti, 2009).
651   Indeed, theoretical work suggests that it is easier to maintain cooperation in a threshold public goods
652   game than in a linear public goods game, and that the role of assortment is less crucial (Archetti,
653   2009; Archetti and Scheuring, 2011). This is generally consistent with the high repayment efficacy
654   among group lending programmes globally.

655   Third, economists acknowledge the important role of different forms of "social capital" for loan
656   repayment in the microfinance literature (Armendáriz and Morduch, 2010; Cassar et al., 2007;
657   Hermes and Lensink, 2007). (Coleman, 1988) defines social capital as social structure which
658   facilitates particular actions of actors within that structure. In his definition, Coleman specifically
659   highlights the roles of mutual obligation, expectations, trustworthiness, social norms, social sanctions
660   and the transmission of information. In the context of JLL, social capital thus defined appears to
661   comprise mechanisms that facilitate cooperators to selectively interact with each other. We propose
662   that these are assortment mechanisms as described in Section 3.2, leading to the maintenance of
663   cooperation. Therefore r, i.e., the degree of assortment in Hamilton's equation (Section 3.1), can be
664   interpreted as a general measure of the effects of social capital. However, whereas the evolutionary
665   biology literature distinguishes between ultimate causes of behaviour and the proximate motivations
666   and preferences that support them (Section 3.3), the term social capital as used and measured by
667   economists does not make this distinction. By distinguishing the two, an evolutionary approach allows
668   us to identify the ultimate reasons why a behaviour or relationship occurs. For example, it allows us to

669 explain *why* trust is directed at certain individuals or *why* certain peer networks are more or less
670 conducive to successful repayment. This unpacking of social capital may lead to new insights and
671 novel predictions also in economic research. The concept of social capital emphasises not just the
672 relations between actors but also the social structure in which they are embedded. This may serve as a
673 reminder to the evolutionary sciences that measurements of r might benefit from taking account of not
674 only the relatedness or degree of assortments of individuals within an interaction group but also the
675 relative degrees of assortment within and between groups (see discussion Section 5.2).

676 In conclusion, we hope to have demonstrated the feasibility of using group-based microfinance as a
677 real-world test case for theories of the evolution of cooperation, and conversely that evolutionary
678 theory may provide a unifying framework for organising existing findings on microfinance and
679 generating new predictions regarding loan repayment under joint liability.

Conflict of interest

692 The authors declare no conflicts of interest.

Author contributions

694 SG, AM and SL designed the study. SG and SL reviewed the literature. SG collated studies, extracted
695 data, and conducted the analysis. AM and SL error checked a sub-sample of extracted data. SG, AM
696 and SL co-wrote the paper.

Data availability

700   R code and results data from the literature review to reproduce Figure 2 and Table SM2 are available

701   at: https://github.com/stefgehrig/bankingoncooperation.

702 **References**

703 Aamodt, M. G., and Custer, H. (2006). Who can best catch a liar?: A meta-analysis of individual

704   differences in detecting deception. *The Forensic Examiner*, *15*(1), 6–11.

705 Ahlin, C., and Townsend, R. M. (2007). Using Repayment Data to Test Across Models of Joint

706   Liability Lending. *The Economic Journal*, *117*(517), F11–F51. https://doi.org/10.1111/j.1468-

707   0297.2007.02014.x

708 Alexander, R. D. (1987). *The biology of moral systems*. Aldine de Gruyter.

709 Anderson, K. G., Kaplan, H., Lam, D., and Lancaster, J. (1999). Paternal Care by Genetic Fathers and

710   Stepfathers II: Reports by Xhosa High School Students. *Evolution and Human Behavior*,

711   *20*(6), 433–451. https://doi.org/10.1016/S1090-5138(99)00022-7

712 Antal, T., Ohtsuki, H., Wakeley, J., Taylor, P. D., and Nowak, M. A. (2009). Evolution of cooperation

713   by phenotypic similarity. *Proceedings of the National Academy of Sciences*, *106*(21), 8597–

714   8600. https://doi.org/10.1073/pnas.0902528106

715 Anthony, D. (2005). Cooperation in Microcredit Borrowing Groups: Identity, Sanctions, and

716   Reciprocity in the Production of Collective Goods. *American Sociological Review*, *70*(3),

717   496–515. https://doi.org/10.1177/000312240507000307

718 Apicella, C. L., and Silk, J. B. (2019). The evolution of human cooperation. *Current Biology*, *29*(11),

719   R447–R450. https://doi.org/10.1016/j.cub.2019.03.036

720 Archetti, M. (2009). Cooperation as a volunteer's dilemma and the strategy of conflict in public goods

721   games. *Journal of Evolutionary Biology*, *22*(11), 2192–2200. https://doi.org/10.1111/j.1420-

722   9101.2009.01835.x

723 Archetti, M., and Scheuring, I. (2011). Coexistence of cooperation and defection in public goods

724   games. *Evolution*, *65*(4), 1140–1148. https://doi.org/10.1111/j.1558-5646.2010.01185.x

725 Archetti, M., and Scheuring, I. (2012). Review: Game theory of public goods in one-shot social

726   dilemmas without assortment. *Journal of Theoretical Biology*, *299*, 9–20.

727   https://doi.org/10.1016/j.jtbi.2011.06.018

728 Armendáriz, B., and Morduch, J. (2010). *The Economics of Microfinance* (2nd ed.). MIT Press.

729   Attanasio, O., Augsburg, B., De Haas, R., Fitzsimons, E., and Harmgart, H. (2015). The Impacts of

730   Microfinance: Evidence from Joint-Liability Lending in Mongolia. *American Economic*

731   *Journal: Applied Economics*, *7*(1), 90–122. https://doi.org/10.1257/app.20130489

732   Axelrod, R. (1984). *The evolution of cooperation*. Basic Books.

733   Axelrod, R., and Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*(4489), 1390–

734   1396. https://doi.org/10.1126/science.7466396

735   Banerjee, A., Karlan, D., and Zinman, J. (2015). Six Randomized Evaluations of Microcredit:

736   Introduction and Further Steps. *American Economic Journal: Applied Economics*, *7*(1), 1–21.

737   https://doi.org/10.1257/app.20140287

738   Banerjee, S. B., and Jackson, L. (2017). Microfinance and the business of poverty reduction: Critical

739   perspectives from rural Bangladesh. *Human Relations*, *70*(1), 63–91.

740   https://doi.org/10.1177/0018726716640865

741   Barker, J. L., Power, E. A., Heap, S., Puurtinen, M., and Sosis, R. (2019). Content, cost, and context:

742   A framework for understanding human signaling systems. *Evolutionary Anthropology: Issues,*

743   *News, and Reviews*, *28*(2), 86–99. https://doi.org/10.1002/evan.21768

744   Bereczkei, T., Birkas, B., and Kerekes, Z. (2007). Public charity offer as a proximate factor of

745   evolved reputation-building strategy: An experimental analysis of a real-life situation.

746   *Evolution and Human Behavior*, *28*(4), 277–284.

747   https://doi.org/10.1016/j.evolhumbehav.2007.04.002

748   Besley, T., and Coate, S. (1995). Group lending, repayment incentives and social collateral. *Journal*

749   *of Development Economics*, *46*(1), 1–18. https://doi.org/10.1016/0304-3878(94)00045-E

750   Birch, J. (2019). Are kin and group selection rivals or friends? *Current Biology*, *29*(11), R433–R438.

751   https://doi.org/10.1016/j.cub.2019.01.065

752   Blurton Jones, N. (2016). *Demography and Evolutionary Ecology of Hadza Hunter-Gatherers*.

753   Cambridge University Press.

754   Bowles, S., and Hammerstein, P. (2003). Does Market Theory Apply to Biology? *Santa Fe Institute*

755   *Working Paper*.

756   Bowles, S., and Posel, D. (2005). Genetic relatedness predicts South African migrant workers'

757   remittances to their families. *Nature*, *434*(7031), 380–383.

758   https://doi.org/10.1038/nature03420

759   Boyd, R., and Richerson, P. J. (1985). *Culture and the evolutionary process*. University of Chicago

760   press.

761   Boyd, R., and Richerson, P. J. (1988). The evolution of reciprocity in sizable groups. *Journal of*

762   *Theoretical Biology*, *132*(3), 337–356.

763   Boyd, R., and Richerson, P. J. (2009). Culture and the evolution of human cooperation. *Philosophical*

764   *Transactions of the Royal Society B: Biological Sciences*, *364*(1533), 3281–3288.

765   https://doi.org/10.1098/rstb.2009.0134

766   Brau, J., and Woller, G. (2004). Microfinance: A Comprehensive Review of the Existing Literature.

767   *The Journal of Entrepreneurial Finance*, *9*(1), 1–28.

768   Bressan, P., and Kramer, P. (2015). Human kin detection. *Wiley Interdisciplinary Reviews: Cognitive*

769   *Science*, *6*(3), 299–311. https://doi.org/10.1002/wcs.1347

770   Bull, J. J., and Rice, W. R. (1991). Distinguishing mechanisms for the evolution of co-operation.

771   *Journal of Theoretical Biology*, *149*(1), 63–74. https://doi.org/10.1016/S0022-

772   5193(05)80072-4

773   Carpena, F., Cole, S., Shapiro, J., and Zia, B. (2013). Liability Structure in Small-Scale Finance:

774   Evidence from a Natural Experiment. *The World Bank Economic Review*, *27*(3), 437–469.

775   https://doi.org/10.1093/wber/lhs031

776   Carpenter, J., and Williams, T. (2014). Peer Monitoring and Microcredit: Field Experimental

777   Evidence from Paraguay. *Oxford Development Studies*, *42*(1), 111–135.

778   https://doi.org/10.1080/13600818.2014.887061

779   Cassar, A., Crowley, L., and Wydick, B. (2007). The Effect of Social Capital on Group Loan

780   Repayment: Evidence from Field Experiments. *The Economic Journal*, *117*(517), F85–F106.

781   https://doi.org/10.1111/j.1468-0297.2007.02016.x

782   Che, Y.-K. (2002). Joint Liability and Peer Monitoring under Group Lending. *Contributions in*

783   *Theoretical Economics*, *2*(1). https://doi.org/10.2202/1534-5971.1016

784   Chudek, M., and Henrich, J. (2011). Culture–gene coevolution, norm-psychology and the emergence

785   of human prosociality. *Trends in Cognitive Sciences*, *15*(5), 218–226.

786   https://doi.org/10.1016/j.tics.2011.03.003

787   Cieslik, K., Hudon, M., and Verwimp, P. (2019). Unruly entrepreneurs – investigating value creation

788   by microfinance clients in rural Burundi. *Oxford Development Studies*, *0*(0), 1–18.

789   https://doi.org/10.1080/13600818.2019.1597034

790   Cohen, E., and Haun, D. (2013). The development of tag-based cooperation via a socially acquired

791   trait. *Evolution and Human Behavior*, *34*(3), 230–235.

792   https://doi.org/10.1016/j.evolhumbehav.2013.02.001

793   Coleman, J. S. (1988). Social Capital in the Creation of Human Capital. *American Journal of

794   Sociology*, *94*, S95–S120.

795   Cull, R., and Morduch, J. (2018). Microfinance and economic development. *Handbook of Finance

796   and Development*.

797   https://www.elgaronline.com/view/edcoll/9781785360503/9781785360503.00030.xml

798   Dahal, M., and Fiala, N. (2020). What do we know about the impact of microfinance? The problems

799   of statistical power and precision. *World Development*, *128*, 104773.

800   https://doi.org/10.1016/j.worlddev.2019.104773

801   Dal Bó, P., and Fréchette, G. R. (2018). On the Determinants of Cooperation in Infinitely Repeated

802   Games: A Survey. *Journal of Economic Literature*, *56*(1), 60–114.

803   https://doi.org/10.1257/jel.20160980

804   Dalla Pellegrina, L., De Michele, A., Di Maio, G., Landoni, P., and Parravicini, S. (2017). Group

805   Meeting Frequency and Borrowers' Repayment Performance in Microfinance: Evidence from

806   a Quasi-Natural Experiment in South Africa. *University of Milan Bicocca Department of

807   Economics, Management and Statistics Working Paper No. 374*.

808   http://dx.doi.org/10.2139/ssrn.3080201

809   Dawkins, R. (1976). *The selfish gene*. Oxford University Press.

810   de Quidt, J., Fetzer, T., and Ghatak, M. (2016). Group lending without joint liability. *Journal of

811   Development Economics*, *121*, 217–236. https://doi.org/10.1016/j.jdeveco.2014.11.006

812   DeBruine, L. M. (2002). Facial resemblance enhances trust. *Proceedings of the Royal Society of*

813   *London. Series B: Biological Sciences*, *269*(1498), 1307–1312.

814   https://doi.org/10.1098/rspb.2002.2034

815   Diekmann, A. (1985). Volunteer's Dilemma. *Journal of Conflict Resolution*, *29*(4), 605–610.

816   https://doi.org/10.1177/0022002785029004003

817   Diekmann, A., Jann, B., Przepiorka, W., and Wehrli, S. (2014). Reputation Formation and the

818   Evolution of Cooperation in Anonymous Online Markets. *American Sociological Review*,

819   *79*(1), 65–85. https://doi.org/10.1177/0003122413512316

820   Doebeli, M., Blarer, A., and Ackermann, M. (1997). Population dynamics, demographic stochasticity,

821   and the evolution of cooperation. *Proceedings of the National Academy of Sciences*, *94*(10),

822   5167–5171. https://doi.org/10.1073/pnas.94.10.5167

823   Dube, A., and Kamath, R. (2018). Microfinance Group Processes and Crises: Responses to Economic

824   and Psychological Threats. *The Journal of Development Studies*, 1–13.

825   Duvendack, M., Palmer-Jones, R., Copestake, J. G., Hooper, L., Loke, Y., and Rao, N. (2011). *What*

826   *is the evidence of the impact of microfinance on the well-being of poor people?* EPPI-Centre,

827   Social Science Research Unit, Institute of Education, University of London.

828   Enquist, M., and Leimar, O. (1993). The evolution of cooperation in mobile organisms. *Animal*

829   *Behaviour*, *45*(4), 747–757. https://doi.org/10.1006/anbe.1993.1089

830   Fessler, D. M. T., and Haley, K. J. (2003). The strategy of affect: Emotions in human cooperation. In

831   *Genetic and Cultural Evolution of Cooperation* (pp. 7–36). MIT Press.

832   Fetchenhauer, D., Groothuis, T., and Pradel, J. (2010). Not only states but traits—Humans can

833   identify permanent altruistic dispositions in 20 s. *Evolution and Human Behavior*, *31*(2), 80–

834   86. https://doi.org/10.1016/j.evolhumbehav.2009.06.009

835   Fischbacher, U., Gächter, S., and Fehr, E. (2001). Are people conditionally cooperative? Evidence

836   from a public goods experiment. *Economics Letters*, *71*(3), 397–404.

837   Fletcher, J. A., and Doebeli, M. (2009). A simple and general explanation for the evolution of

838   altruism. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1654), 13–19.

839   https://doi.org/10.1098/rspb.2008.0829

840   Fletcher, J. A., and Doebeli, M. (2010). Assortment is a more fundamental explanation for the

841   evolution of altruism than inclusive fitness or multilevel selection: Reply to Bijma and Aanen.

842   *Proceedings of the Royal Society B: Biological Sciences*, *277*(1682), 677–678.

843   https://doi.org/10.1098/rspb.2009.1722

844   Fletcher, J. A., and Zwick, M. (2006). Unifying the Theories of Inclusive Fitness and Reciprocal

845   Altruism. *The American Naturalist*, *168*(2), 252–262. https://doi.org/10.1086/506529

846   Foster, K. R., and Xavier, J. B. (2007). Cooperation: Bridging ecology and sociobiology. *Current*

847   *Biology: CB*, *17*(9), R319-321. https://doi.org/10.1016/j.cub.2007.03.005

848   Fu, F., Nowak, M. A., Christakis, N. A., and Fowler, J. H. (2012). The Evolution of Homophily.

849   *Scientific Reports*, *2*, 845. https://doi.org/10.1038/srep00845

850   Gächter, S., Herrmann, B., and Thöni, C. (2010). Culture and cooperation. *Philosophical*

851   *Transactions of the Royal Society B: Biological Sciences*, *365*(1553), 2651–2661.

852   https://doi.org/10.1098/rstb.2010.0135

853   Gardner, A., and West, S. A. (2010). Greenbeards. *Evolution*, *64*(1), 25–38.

854   https://doi.org/10.1111/j.1558-5646.2009.00842.x

855   Ghatak, M., and Guinnane, T. W. (1999). The economics of lending with joint liability: Theory and

856   practice. *Journal of Development Economics*, *60*(1), 195–228. https://doi.org/10.1016/S0304-

857   3878(99)00041-3

858   Giné, X., and Karlan, D. S. (2014). Group versus individual liability: Short and long term evidence

859   from Philippine microcredit lending groups. *Journal of Development Economics*, *107*, 65–83.

860   https://doi.org/10.1016/j.jdeveco.2013.11.003

861   Gintis, H., Smith, E. A., and Bowles, S. (2001). Costly Signaling and Cooperation. *Journal of*

862   *Theoretical Biology*, *213*(1), 103–119. https://doi.org/10.1006/jtbi.2001.2406

863   Gomez, R., and Santor, E. (2008). Does the Microfinance Lending Model Actually Work. *Whitehead*

864   *Journal of Diplomacy and International Relations*, *9*, 37.

865   Grafen, A. (2007). Detecting kin selection at work using inclusive fitness. *Proceedings. Biological*

866   *Sciences*, *274*(1610), 713–719. https://doi.org/10.1098/rspb.2006.0140

867   Grafen, A. (2009). Formalizing Darwinism and inclusive fitness theory. *Philosophical Transactions of*

868   *the Royal Society B: Biological Sciences*, *364*(1533), 3135–3141.

869   https://doi.org/10.1098/rstb.2009.0056

870   Griffin, D., and Husted, B. W. (2015). Social sanctions or social relations? Microfinance in Mexico.

871   *Journal of Business Research*, *68*(12), 2579–2587.

872   https://doi.org/10.1016/j.jbusres.2015.06.023

873   Guido, A., Robbett, A., and Romaniuc, R. (2019). Group formation and cooperation in social

874   dilemmas: A survey and meta-analytic evidence. *Journal of Economic Behavior &*

875   *Organization*, *159*, 192–209. https://doi.org/10.1016/j.jebo.2019.02.009

876   Gurven, M. (2006). The Evolution of Contingent Cooperation. *Current Anthropology*, *47*(1), 185–

877   192. https://doi.org/10.1086/499552

878   Gurven, M., Hill, K., and Kaplan, H. (2002). From Forest to Reservation: Transitions in Food-Sharing

879   Behavior among the Ache of Paraguay. *Journal of Anthropological Research*, *58*(1), 93–120.

880   https://doi.org/10.1086/jar.58.1.3631070

881   Guttman, J. M. (2007). Repayment Performance in Microcredit Programs: Theory and Evidence.

882   *Networks Financial Institute Working Paper*, *2007-WP-11*.

883   https://www.indstate.edu/business/sites/business.indstate.edu/files/Docs/2007-WP-

884   11_Guttman.pdf

885   Haldar, A., and Stiglitz, J. E. (2016). Group Lending, Joint Liability, and Social Capital: Insights

886   From the Indian Microfinance Crisis. *Politics & Society*, *44*(4), 459–497.

887   https://doi.org/10.1177/0032329216674001

888   Hales, D. (2005). Change Your Tags Fast! – A Necessary Condition for Cooperation? In P.

889   Davidsson, B. Logan, and K. Takadama (Eds.), *Multi-Agent and Multi-Agent-Based*

890   *Simulation* (pp. 89–98). Springer Berlin Heidelberg.

891   Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical*

892   *Biology*, *7*(1), 1–16. https://doi.org/10.1016/0022-5193(64)90038-4

893   Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical*

894   *Biology*, *7*(1), 17–52. https://doi.org/10.1016/0022-5193(64)90039-6

895   Hamilton, W. D. (1975). Innate social aptitudes of man: An approach from evolutionary genetics.

896   *Biosocial Anthropology*, *53*, 133–155.

897   Hammerstein, P. (2003). *Genetic and Cultural Evolution of Cooperation*. MIT Press.

898   Hammerstein, P., and Noë, R. (2016). Biological trade and markets. *Philosophical Transactions of the*

899   *Royal Society B: Biological Sciences*, *371*(1687), 20150101.

900   https://doi.org/10.1098/rstb.2015.0101

901   Hammond, R. A., and Axelrod, R. (2006). The Evolution of Ethnocentrism. *Journal of Conflict*

902   *Resolution*, *50*(6), 926–936. https://doi.org/10.1177/0022002706293470

903   Handley, C., and Mathew, S. (2020). Human large-scale cooperation as a product of competition

904   between cultural groups. *Nature Communications*, *11*(1), 1–9. https://doi.org/10.1038/s41467-

905   020-14416-8

906   Harrison, G. W., and List, J. A. (2004). Field experiments. *Journal of Economic Literature*, *42*(4),

907   1009–1055.

908   Henrich, J. (2004). Cultural group selection, coevolutionary processes and large-scale cooperation.

909   *Journal of Economic Behavior & Organization*, *53*(1), 3–35.

910   Henrich, J., and Boyd, R. (2001). Why people punish defectors: Weak conformist transmission can

911   stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical*

912   *Biology*, *208*(1), 79–89.

913   Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., McElreath, R., Alvard, M., Barr,

914   A., Ensminger, J., Henrich, N. S., Hill, K., Gil-White, F., Gurven, M., Marlowe, F. W.,

915   Patton, J. Q., and Tracer, D. (2005). 'Economic man' in cross-cultural perspective: Behavioral

916   experiments in 15 small-scale societies. *The Behavioral and Brain Sciences*, *28*(6), 795–815;

917   discussion 815-855. https://doi.org/10.1017/S0140525X05000142

918   Henrich, N., and Henrich, J. (2007). *Why Humans Cooperate: A Cultural and Evolutionary*

919   *Explanation*. Oxford University Press.

920   Hermes, N., and Lensink, R. (2007). The empirics of microfinance: What do we know? *The Economic*

921   *Journal*, *117*(517), F1–F10. https://doi.org/10.1111/j.1468-0297.2007.02013.x

922   Hossain, M. (1988). *Credit for alleviation of rural poverty: The Grameen Bank in Bangladesh*.

923   International Food Policy Research Institute (IFPRI).

924   https://EconPapers.repec.org/RePEc:fpr:resrep:65

925   Hulme, D. (2000). Is microdebt good for poor people? A note on the dark side of microfinance. *Small*

926   *Enterprise Development*, *11*(1), 26–28. https://doi.org/10.3362/0957-1329.2000.006

927   Johnstone, R. A., and Cant, M. A. (2008). Sex Differences in Dispersal and the Evolution of Helping

928   and Harming. *The American Naturalist*, *172*(3), 318–330. https://doi.org/10.1086/589899

929   Kaplan, H., Hill, K., Cadeliña, R. V., Hayden, B., Hyndman, D. C., Preston, R. J., Smith, E. A.,

930   Stuart, D. E., and Yesner, D. R. (1985). Food Sharing Among Ache Foragers: Tests of

931   Explanatory Hypotheses [and Comments and Reply]. *Current Anthropology*, *26*(2), 223–246.

932   https://doi.org/10.1086/203251

933   Karlan, D., and McConnell, M. A. (2014). Hey look at me: The effect of giving circles on giving.

934   *Journal of Economic Behavior & Organization*, *106*, 402–412.

935   Karlan, D. S. (2007). Social connections and group banking. *The Economic Journal*, *117*(517), F52–

936   F84. https://doi.org/10.1111/j.1468-0297.2007.02015.x

937   Kasper, C., and Borgerhoff Mulder, M. (2015). Who Helps and Why?: Cooperative Networks in

938   Mpimbwe. *Current Anthropology*, *56*(5), 701–732. https://doi.org/10.1086/683024

939   Khandker, S. R. (2012). *Grameen Bank Lending: Does Group Liability Matter?* The World Bank.

940   https://doi.org/10.1596/1813-9450-6204

941   Ko, A., Pick, C. M., Kwon, J. Y., Barlev, M., Krems, J. A., Varnum, M. E. W., Neel, R., Peysha, M.,

942   Boonyasiriwat, W., Brandstätter, E., Cruz Vasquez, J. E., Galindo, O., David, D., Pereira de

943   Felipe, R., Crispim, A. C., Fetvadijev, V. H., Fischer, R., Karl, J., Galdi, S., … Kenrick, D. T.

944   (2019). Family matters: Rethinking the psychology of human social motivation. *Perspectives*

945   *on Psychological Science*. https://kar.kent.ac.uk/75338/

946   Kolstad, I., Pires, A. J. G., and Wiig, A. (2017). Within-group heterogeneity and group dynamics:

947   Analyzing exit of microcredit groups in Angola. *Oxford Development Studies*, *45*(3), 338–

948   351. https://doi.org/10.1080/13600818.2016.1243237

949   Koricheva, J., Gurevitch, J., and Mengersen, K. (2013). *Handbook of Meta-analysis in Ecology and*

950   *Evolution*. Princeton University Press.

951   Kurzban, R., Burton-Chellew, M. N., and West, S. A. (2015). The Evolution of Altruism in Humans.

952   *Annual Review of Psychology*, *66*(1), 575–599. https://doi.org/10.1146/annurev-psych-

953   010814-015355

954   Lacy, R. C., and Sherman, P. W. (1983). Kin Recognition by Phenotype Matching. *The American*

955   *Naturalist*, *121*(4), 489–512. https://doi.org/10.1086/284078

956   Lamba, S. (2014). A Comparison of the Economic Literature on Microfinance and the Evolutionary

957   Literature on Cooperation. In M. A. Gibson and D. W. Lawson (Eds.), *Applied Evolutionary*

958   *Anthropology: Darwinian Approaches to Contemporary World Issues* (pp. 39–57). Springer

959   New York. https://doi.org/10.1007/978-1-4939-0280-4_3

960   Lamba, S., and Mace, R. (2011). Demography and ecology drive variation in cooperation across

961   human populations. *Proceedings of the National Academy of Sciences*, *108*(35), 14426–

962   14430. https://doi.org/10.1073/pnas.1105186108

963   Lamba, S., and Mace, R. (2013). The evolution of fairness: Explaining variation in bargaining

964   behaviour. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1750), 20122028.

965   https://doi.org/10.1098/rspb.2012.2028

966   Lehmann, L., and Keller, L. (2006). The evolution of cooperation and altruism – a general framework

967   and a classification of models. *Journal of Evolutionary Biology*, *19*(5), 1365–1376.

968   https://doi.org/10.1111/j.1420-9101.2006.01119.x

969   Leimar, O., and Hammerstein, P. (2001). Evolution of cooperation through indirect reciprocity.

970   *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1468), 745–

971   753. https://doi.org/10.1098/rspb.2000.1573

972   Mahmud, M. (2019). Repaying Microcredit Loans: A Natural Experiment on Liability Structure. *The*

973   *Journal of Development Studies*, *0*(0), 1–16. https://doi.org/10.1080/00220388.2019.1632432

974   Maynard Smith, J. (1964). Group Selection and Kin Selection. *Nature*, *201*(4924), 1145–1147.

975   https://doi.org/10.1038/2011145a0

976 Meager, R. (2019). Understanding the Average Impact of Microcredit Expansions: A Bayesian

977   Hierarchical Analysis of Seven Randomized Experiments. *American Economic Journal:*

978   *Applied Economics*, *11*(1), 57–91. https://doi.org/10.1257/app.20170299

979 Microcredit Summit Campaign. (2015). Mapping Pathways out of Poverty. *The State of the*

980   *Microcredit Summit Campaign Report*.

981 Milinski, M. (2016). Reputation, a universal currency for human social interactions. *Philosophical*

982   *Transactions of the Royal Society B: Biological Sciences*, *371*(1687), 20150100.

983   https://doi.org/10.1098/rstb.2015.0100

984 Milinski, M., Semmann, D., Bakker, T. C. M., and Krambeck, H.-J. (2001). Cooperation through

985   indirect reciprocity: Image scoring or standing strategy? *Proceedings of the Royal Society of*

986   *London. Series B: Biological Sciences*, *268*(1484), 2495–2501.

987   https://doi.org/10.1098/rspb.2001.1809

988 Morgan, C. J. (1979). Eskimo hunting groups, social kinship, and the possibility of kin selection in

989   humans. *Ethology and Sociobiology*, *1*(1), 83–86. https://doi.org/10.1016/0162-

990   3095(79)90008-6

991 Nettle, D., Gibson, M. A., Lawson, D. W., and Sear, R. (2013). Human behavioral ecology: Current

992   research and future prospects. *Behavioral Ecology*, *24*(5), 1031–1040.

993 Nowak, M. A. (2006). Five Rules for the Evolution of Cooperation. *Science*, *314*(5805), 1560–1563.

994   https://doi.org/10.1126/science.1133755

995 Nowak, M. A., and Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, *437*(7063), 1291–

996   1298. https://doi.org/10.1038/nature04131

997 Palfrey, T., and Rosenthal, H. (1984). Participation and the provision of discrete public goods: A

998   strategic analysis. *Journal of Public Economics*, *24*(2), 171–193.

999 Panchanathan, K., and Boyd, R. (2003). A tale of two defectors: The importance of standing for

1000   evolution of indirect reciprocity. *Journal of Theoretical Biology*, *224*(1), 115–126.

1001   https://doi.org/10.1016/S0022-5193(03)00154-1

1002 Platt, T. G., and Bever, J. D. (2009). Kin competition and the evolution of cooperation. *Trends in*

1003   *Ecology & Evolution*, *24*(7), 370–377. https://doi.org/10.1016/j.tree.2009.02.009

Postelnicu, L., Hermes, N., and Servin, R. (2019). External Social Ties and Loan Repayment of

Group Lending Members: A Case Study of Pro Mujer Mexico. *The Journal of Development

Studies*, *55*(8), 1784–1798. https://doi.org/10.1080/00220388.2018.1464148

Powers, S. T., van Schaik, C. P., and Lehmann, L. (2019). *Cooperation in large-scale human societies

– What, if anything, makes it unique, and how did it evolve?* OSF Preprints.

https://doi.org/10.31219/osf.io/v47ap

Queller, D. C. (1985). Kinship, reciprocity and synergism in the evolution of social behaviour.

Nature, *318*(6044), 366–367. https://doi.org/10.1038/318366a0

Queller, D. C. (1992). A General Model for Kin Selection. *Evolution*, *46*(2), 376–380.

https://doi.org/10.1111/j.1558-5646.1992.tb02045.x

Rand, D. G., and Nowak, M. A. (2013). Human cooperation. *Trends in Cognitive Sciences*, *17*(8),

413–425. https://doi.org/10.1016/j.tics.2013.06.003

Richerson, P., Baldini, R., Bell, A. V., Demps, K., Frost, K., Hillis, V., Mathew, S., Newton, E. K.,

Naar, N., Newson, L., Ross, C., Smaldino, P. E., Waring, T. M., and Zefferman, M. (2016).

Cultural group selection plays an essential role in explaining human cooperation: A sketch of

the evidence. *The Behavioral and Brain Sciences*, *39*, e30.

https://doi.org/10.1017/S0140525X1400106X

Riolo, R. L., Cohen, M. D., and Axelrod, R. (2001). Evolution of cooperation without reciprocity.

Nature, *414*(6862), 441–443. https://doi.org/10.1038/35106555

Roberts, G. (1998). Competitive altruism: From reciprocity to the handicap principle. *Proceedings of

the Royal Society of London. Series B: Biological Sciences*, *265*(1394), 427–431.

https://doi.org/10.1098/rspb.1998.0312

Sabin, N., and Reed-Tsochas, F. (2018). *Able but Unwilling to Enforce: Cooperative Dilemmas in

Group Lending* (SSRN Scholarly Paper ID 3275526). Social Science Research Network.

https://papers.ssrn.com/abstract=3275526

Sachs, J. L., Mueller, U. G., Wilcox, T. P., and Bull, J. J. (2004). The Evolution of Cooperation. *The

Quarterly Review of Biology*, *79*(2), 135–160. https://doi.org/10.1086/383541

1031   Schino, G., and Aureli, F. (2017). Reciprocity in group-living animals: Partner control versus partner

1032   choice. *Biological Reviews*, *92*(2), 665–672. https://doi.org/10.1111/brv.12248

1033   Seinen, I., and Schram, A. (2006). Social status and group norms: Indirect reciprocity in a repeated

1034   helping experiment. *European Economic Review*, *50*(3), 581–602.

1035   Seyfarth, R. M., and Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of*

1036   *Psychology*, *63*, 153–177. https://doi.org/10.1146/annurev-psych-120710-100337

1037   Sharma, M., and Zeller, M. (1997). Repayment performance in group-based credit programs in

1038   Bangladesh: An empirical analysis. *World Development*, *25*(10), 1731–1742.

1039   https://doi.org/10.1016/S0305-750X(97)00063-6

1040   Smaldino, P. E. (2017). Social identity and cooperation in cultural evolution. *Behavioural Processes*,

1041   *161*, 108–116. https://doi.org/10.1016/j.beproc.2017.11.015

1042   Smaldino, P. E., Schank, J. C., and McElreath, R. (2013). Increased costs of cooperation help

1043   cooperators in the long run. *The American Naturalist*, *181*(4), 451–463.

1044   https://doi.org/10.1086/669615

1045   Spagnolo, G. (1999). Social relations and cooperation in organizations. *Journal of Economic Behavior*

1046   *& Organization*, *38*(1), 1–25. https://doi.org/10.1016/S0167-2681(98)00119-X

1047   Stiglitz, J. E. (1990). Peer Monitoring and Credit Markets. *The World Bank Economic Review*, *4*(3),

1048   351–366. https://doi.org/10.1093/wber/4.3.351

1049   Strassmann, J. E., Page, R. E., Robinson, G. E., and Seeley, T. D. (2011). Kin selection and

1050   eusociality. *Nature*, *471*(7339), E5–E6. https://doi.org/10.1038/nature09833

1051   Sylwester, K., and Roberts, G. (2010). Cooperators benefit through reputation-based partner choice in

1052   economic games. *Biology Letters*, *6*(5), 659–662. https://doi.org/10.1098/rsbl.2010.0209

1053   Tajfel, H., and Turner, J. C. (1986). The social identity theory of intergroup behavior. *Psychology of*

1054   *Intergroup Relations*, *5*, 7–24.

1055   Taylor, P. D. (1992). Altruism in viscous populations—An inclusive fitness model. *Evolutionary*

1056   *Ecology*, *6*(4), 352–356. https://doi.org/10.1007/BF02270971

1057   Tinbergen, N. (1963). On aims and methods of Ethology. *Zeitschrift Für Tierpsychologie*, *20*(4), 410–

1058   433. https://doi.org/10.1111/j.1439-0310.1963.tb01161.x

1059   Trivers, R. L. (1971). The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology*, *46*(1),

1060   35–57. https://doi.org/10.1086/406755

1061   van Bastelaer, T., and Leathers, H. (2006). Trust in Lending: Social Capital and Joint Liability Seed

1062   Loans in Southern Zambia. *World Development*, *34*(10), 1788–1807.

1063   Van Tassel, E. (1999). Group lending under asymmetric information. *Journal of Development*

1064   *Economics*, *60*(1), 3–25. https://doi.org/10.1016/S0304-3878(99)00034-6

1065   Waring, T. M., Kline, M. A., Brooks, J., Goff, S., Gowdy, J., Jansen, M., Smaldino, P., and Jacquet, J.

1066   (2015). A multilevel evolutionary framework for sustainability analysis. *Ecology and Science*,

1067   *20*(2). https://doi.org/DOI:10.5751/ES-07634-200234

1068   Wedekind, C., and Braithwaite, V. A. (2002). The Long-Term Benefits of Human Generosity in

1069   Indirect Reciprocity. *Current Biology*, *12*(12), 1012–1015. https://doi.org/10.1016/S0960-

1070   9822(02)00890-4

1071   West, S. A., Griffin, A. S., and Gardner, A. (2007a). Social semantics: Altruism, cooperation,

1072   mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, *20*(2),

1073   415–432. https://doi.org/10.1111/j.1420-9101.2006.01258.x

1074   West, S. A., Griffin, A. S., and Gardner, A. (2007b). Evolutionary Explanations for Cooperation.

1075   *Current Biology*, *17*(16), R661–R672. https://doi.org/10.1016/j.cub.2007.06.004

1076   West, S. A., Pen, I., and Griffin, A. S. (2002). Cooperation and competition between relatives. *Science*

1077   *(New York, N.Y.)*, *296*(5565), 72–75. https://doi.org/10.1126/science.1065507

1078   Wilson, D. S. (1977). Structured Demes and the Evolution of Group-Advantageous Traits. *The*

1079   *American Naturalist*, *111*(977), 157–185. JSTOR.

1080   Wilson, D. S., and Dugatkin, L. A. (1997). Group Selection and Assortative Interactions. *The*

1081   *American Naturalist*, *149*(2), 336–351. https://doi.org/10.1086/285993

1082   Wilson, D. S., and Sober, E. (1994). Reintroducing group selection to the human behavioral sciences.

1083   *Behavioral and Brain Sciences*, *17*(4), 585–607.

1084