# Modeling relatedness and demography in social evolution

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**With any theoretical model, the modeler must decide what kinds of detail to include and which simplifying assumptions to make. It could be assumed that models that include more detail are better, or more correct. However, no model is a perfect description of reality and the relative advantage of different levels of detail depends on the model's empirical purpose. We consider the specific case of how relatedness is modeled in the field of social evolution. Different types of model either leave relatedness as an independent parameter (open models), or include detail for how demography and life cycle determine relatedness (closed models). We exploit the social evolution literature, especially work on the evolution of cooperation, to analyze how useful these different approaches have been in explaining the natural world. We find that each approach has been successful in different areas of research, and that more demographic detail is not always the most empirically useful strategy.**

Theoretical models are often used to help explain how organisms behave in the natural world (Westneat and Fox 2010; Davies et al. 2012). In the field of social evolution, we use theoretical models to make predictions about and to ultimately understand behaviors that affect the fitness of individuals other than the actor (Hamilton 1964; Frank 1998; Bourke 2011). For example, we use models to predict when it is advantageous for individuals to cooperate; we use models to uncover the factors that contribute to the origin of selfish, altruistic, and even spiteful behaviors; and we use models to account for variation in the tendency to help both within and between species.

Perhaps the most influential model in social evolution was proposed by Hamilton (1964) and showed that genetic relatedness can be a key factor in explaining the adaptive value of social behaviors. Genetic relatedness is the probability that a social partner shares the same gene at a given locus relative to that of a random individual sampled from the population (Hamilton 1964, 1970; Grafen 1985). In large outbreeding populations, full siblings are related by ½, half-sibs by ¼, and so on (Grafen 1985). Individuals are favored to help relatives as this provides an indirect opportunity to further spread identical copies of their genes into the next generation. Over the last 50 years, relatedness has proven to be a fundamental concept for explaining social behavior across the tree of life, and theoretical models employing genetic relatedness have formed a cornerstone of social evolution (Frank 1998; Rousset 2004; West 2009; Bourke 2011).

The way in which relatedness is captured in theoretical models can be divided into two approaches, termed "open" and "closed" models (Box 1) (Taylor and Frank 1996; Frank 1998; Rousset 2004; Gardner and West 2006; Lion et al. 2011). In an open model, relatedness is left as an independent parameter that can be directly tuned by the theoretician without affecting the other features of the model. In a closed model, the modeler goes an extra step, to make specific assumptions about how population structure and life cycle determine relatedness. For example, the modeler might specify how model parameters, such as dispersal from the natal patch, the extent to which generations overlap, or

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the degree of monogamous mating impact relatedness from one generation to the next.

A potential problem with open models is that relatedness is not necessarily an independent variable (Taylor 1992a, 1992b). The factors that determine relatedness can influence other important factors. For example, patterns of dispersal and whether generations overlap can affect both relatedness and the relative marginal costs and benefits of social traits. Consequently, assuming that relatedness is an independent parameter in an open model could give misleading predictions. In contrast, closed models can take account of how different parameters are correlated, and so could be argued to be more correct or internally consistent. Closed modeling has become the most common approach in the field of social evolution, and has been suggested as the preferable method (Lehman and Rousset 2010; Lion et al. 2011). This raises the question of whether open models should be used.

Our aim is to critically analyse the utility of both open and closed approaches. Our starting point is two propositions, which we presume are widely agreed upon: (1) All models are wrong, in that they are not an exact representation of the natural world. (2) The usefulness of any model is determined by its ability to help explain the natural world. These two points are trivially true, but there has been little guidance in the literature for empirically minded theoreticians on when to develop one type of model over the other. We first examine the theoretical trade-offs of each approach and consider how they may be appropriate for different empirical questions. We then consider a few areas where open and closed models have been developed, including cooperation, sex allocation, and dispersal. We evaluate the success of each approach in explaining empirical patterns in these areas, to see if any lessons can be drawn for future research.

## BOX 1: Open and closed: A toy model

We develop a simple model of public goods, first with an open and then a closed approach, to illustrate the two methods. We model the most general form of a public good, following Hamilton (1964), Taylor (1992a, 1992b), and Frank (2010). We take an inclusive fitness approach because the fitness derivations are simpler in this case, though an equivalent direct (neighbor modulated) fitness approach can be found in Taylor et al. (2007) and Levin and West (2017b).

*Open Model:* Some organism, such as a microbe, produces some costly public good, the benefits of which are shared between its social partners and itself. Examples in nature of public goods include the production and release of molecules by bacteria that scavenge for iron or digest protein (Griffin et al 2004; Diggle et al 2007). Because the production of the

public good is costly to the individual, we might expect natural selection to favor individuals that do not incur the cost of production, but reap the benefits of good-producing social partners. Thus, we are interested in the conditions that would favor the evolution of the public good producing trait.

We assume an infinite population of individuals subdivided into social groups of size N (the infinite island model). Individuals can produce the public good at some private fecundity cost, c, which provides some fecundity benefit, b, to all individuals on the patch (including the focal individual). Hamilton (1964, 1970) showed that a trait will spread if its inclusive fitness effect, $W_{IF}$, is greater than $0$ ($W_{IF} > 0$), where the inclusive fitness effect of an actor's trait is its effect on all individuals in the population, weighted by relatedness of the actor to those affected individuals (including the actor itself), or "recipients." In this case, the trait has a negative cost to the actor (with relatedness 1), and the relatedness to recipients is *r*, the average whole group relatedness in a social group (as opposed to others-only relatedness). Thus, the trait will spread if:

$$rb - c > 0,$$

which is a simple form of Hamilton's (1964) rule with b and c as simple additive fitness effects, as opposed to the general, regression form of Hamilton's rule (Gardner et al. 2011b). This is an open model, in which the mechanism by which *r* is generated is undefined. Positive relatedness in this model could come about through limited dispersal, kin recognition, partner choice, or any other process that generates genetic correlations within social groups. However, if *r* is correlated with the other model parameters (*b* and *c*), the predictions of this model might not be very useful for explaining variation in nature.

*Closed Model:* We might, for example, be interested in the case in which relatedness is generated through limited dispersal. We can capture this by incorporating a new parameter, *d*, which measures the proportion of offspring that disperse from their natal social group (with a fraction *(1-d)* remaining in the group). Following Taylor (1992a), we must now take into account not only the offspring produced as a direct result of public goods production, but also those offspring indirectly displaced as a result of the cooperative trait. An individual that expresses the public good trait incurs a fecundity cost, *c*, with relatedness 1, and provides a fecundity benefit, *b*, to recipients whose average relatedness is *r*. These extra *(b − c)* offspring remain in the social group with probability *(1 − d)*, in which case the individuals they displace are also native with probability *(1 − d)*, and therefore have relatedness r. The overall inclusive fitness effect, then, is

$$W_{IF} = rb - c - r(1 - d)^2(b - c).$$

The above is still an open model, assuming independence between relatedness and model parameters. This illustrates that in principle, up until this point open and closed models can incorporate the same amount of demographic detail (though in practice, open models often do not). Taylor (1988, 1992a) showed how we can close the model by making additional assumptions. Specifically, he calculated relatedness in terms of the demographic parameters of the model ($d$ & $N$). We can do this by writing the following population genetic recursion for the change in relatedness in a social group from one generation to the next:

$$r_{t+1} = 1/N + r_t(1 - d)^2(N - 1)/N.$$

Where the first term is the chance that two randomly sampled individuals on the patch are the same individual, and have relatedness one, and the second term is the chance they are different individuals both native to the patch, and therefore have the relatedness from the previous generation. Solving for the equilibrium value of relatedness, and plugging into the inclusive fitness effect above, we find the condition for the trait to spread is:

$$b/N > c.$$

This is Taylor's classic result—that the dispersal rate has no impact on whether the trait will spread.

*Extensions:* we can extend this closed model a number of ways to look at the impact of different life histories and explicit demographic parameters (Table 2). We do this by rewriting the fitness function and recalculating our estimate of relatedness accordingly. As one example, Taylor and Irwin (2000) allowed for overlapping generations by including a parameter $s$, the probability that a parent survives into the next generation. The inclusive fitness effect becomes:

$$W_{IF} = (1 - s)[(rb - c) - r(1 - d)^2(b - c)].$$

Plugging in the equilibrium relatedness value, calculated in terms of $s$, $d$, and $N$, the condition for the public good trait to evolve becomes:

$$b/c > N - (N - 1)[(2s(1 - d))/((2-d)(1 + s))].$$

**The Scale of Competition**

Open models can be used to provide an alternate way to look at the factors that arise in closed models (Frank 1998, Gardner and West 2006). For example, Frank (1998) developed a model for incorporating competition into an open model, by subsuming the scale of competition into benefit term of Hamilton's rule:

$$RB - C > 0$$

Where $R = r$, C = c, and B = b − a(b − c), and $a$ is the proportion of competition that happens locally.

Queller (1994) developed a similar approach in which competition is subsumed into the relatedness parameter:

$$RB - C > 0$$

Where B = b, C = c, and $R = (r - ar)/(1 - ar)$, and therefore relatedness is not to an average member of the population but to an average competitor. Both the Queller (1994) and Frank (1998) approaches recover Taylor's (1992a) result as a specific case (see Gardner and West (2006) for further discussion).

## The Trade-offs of Open and Closed Models

Open and closed modeling approaches differ in how they treat relatedness. Across nature, there is a wide diversity of life cycles and demographic structures that can generate relatedness between interacting individuals (Hamilton 1964; Frank 1998; Rousset 2004). Some well-characterized examples include:

1. Kin discrimination–if individuals can somehow distinguish relatives from nonrelatives and preferentially direct cooperation toward them, then this can generate positive relatedness between actor and recipient (Sharp et al. 2005; Mehdiabadi et al. 2006).
2. Dispersal patterns–limited dispersal, or dispersing as groups of relatives, can keep relatives together and hence generate positive relatedness between interacting individuals, in the absence of any kin discrimination (Hamilton 1964).
3. Mating patterns–monogamy or lower levels of polyandry can increase the relatedness between interacting siblings (Boomsma 2007; Hughes et al. 2008; Cornwallis et al. 2010, 2017; Lukas and Clutton-Brock 2012a).

### OPEN MODELS

An open model is agnostic about which of the above factors (or others) are responsible for the generation of relatedness between individuals. Instead, relatedness is deliberately left as an independent factor that can be tuned directly by the modeler. The benefit of this approach is that it can generate predictions that should hold across many systems, regardless of which specific demographic processes are responsible for relatedness between interacting individuals. Thus, if the model predicts that investment in a public good will increase for higher relatedness, then this should hold just as well in systems that employ kin discrimination, limited dispersal or monogamous mating in the generation of relatedness.

The downside of an open approach is that relatedness is not necessarily independent of other factors. For example, relatedness can be an important driver of the evolution of dispersal, but relatedness also crucially depends upon dispersal (Taylor 1988; Frank 1998). Open models miss such feedbacks (West et al. 2002; Lehmann and Rousset 2010). Consequently, open models may gain widespread applicability, but at a cost of demographic precision.

## CLOSED MODELS

### Closed models

In contrast, a closed model specifies the precise way in which population dynamical processes generate genetic relatedness (Table 2). In doing so, concrete assumptions must be made about the exact life cycle and demography of the system and how these factors contribute to the relatedness of interacting individuals.

The benefit of a closed-model approach is that it allows a specific question to be answered about a characterized system, in which the processes that generate relatedness are known. Any feedback effects between parameters or traits of the model with the underlying genotypic assortment in the population are captured by the model. Furthermore, because the population-genetic assumptions about relatedness are clearer, closed models lend themselves to tweaking and altering assumptions or parameters in a way that allows theoreticians to build a family of related models, for which the intermodel relationships are apparent (Table 2).

However, the final step of closing a model involves determining precisely how a specific demography generates relatedness. Consequently, any conclusions drawn might only be applicable to that or a limited number of scenarios. This gives a precise solution, but it might be precisely irrelevant to what occurs in the real world. In fact, the way that relatedness arises in natural systems is frequently not well understood, arising from a convoluted combination of factors and processes. As such, the additional demographic assumptions that make closed models solvable are sometimes so idealized that they may add less realism to the model than might otherwise be expected (Taylor 1992a, 1992b; Gardner and West 2006; Lehman and Rousset 2010; Table 2). Consequently, closed models gain precise demographic detail, but at a cost of broader applicability.

## OPEN VERSUS CLOSED

The differences between open and closed models can be illustrated graphically. Figure 1 graphs the relatedness ($R$) between interacting individuals versus the extent to which density dependent competition is at the scale of the local patch ($a$; Frank 1998). An open model can allow both these parameters to vary independently (the entire parameter space). A closed model determines how these parameters are related for a specified demography (one line on the figure). There are many different possible demographic scenarios and corresponding closed models (different lines on the figure). We provide some examples, which illustrate how different demographic assumptions can qualitatively change whether and how $R$ and $a$ are linked. This figure also illustrates how an open model can be used as a "meta-model" to examine how different closed models work and relate to each other (Frank 1998).

While there is a rough correlation between "open and closed" and "simple and complex," this is not always the case. In principle, closed models are nested within open models–up until the
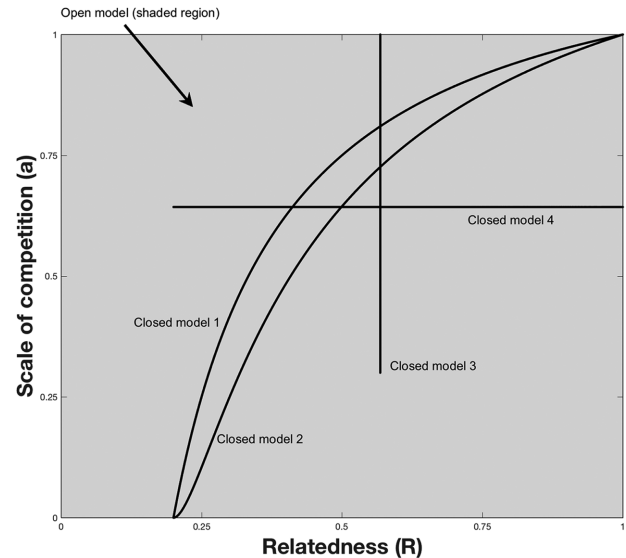


**Figure 1.** The relation between open and closed models. Frank (1998) developed an open model to show how local competition could reduce selection for cooperation between relatives. He used a parameter "*a*" to measure the scale at which density-dependent competition occurs, which can range from completely global (a = 0) to completely local (a = 1). In this figure, *a* is plotted against relatedness (*R*). Frank allowed these two variables to vary independently, and so his model encompasses the entire plane (shaded gray). In a closed model, we assume a specific demography and life history, and this causes *a* and *R* to be correlated in a specific way, leading to a particular curve in the plane (dark lines). For example, Closed model 1 is Taylor's 1992a model, closed model 2 is Taylor and Irwin's (2000) overlapping generations model, and closed models 3 and 4 are Gardner and West's 2006 budding dispersal model, for a fixed budding dispersal rate and range of migration rates, and a fixed migration rate and range of budding dispersal rates, respectively. Adapted from Gardner and West (2006).

point of specifying relatedness, a closed model is open (Box 1). However, in practice, not all open models are one step away from being a closed model as the demography that determines relatedness and is required to close the model may not be specified at all (Wild 2011). Open models may instead include other ecological factors or otherwise unlinked demographic details and thus can be arbitrarily complex. Furthermore, in closed models, the interplay between different factors can sometimes lead to simpler predictions, as some parameters drop out of the analysis (Pen and Weissing 2000). Consequently, the difference between open and closed models may often be less of a distinction in complexity rather than a differing emphasis in the kinds of details that are included.

The above is a conceptual discussion of the relative trade-offs of open and closed modeling. However, the utility of different theoretical approaches is not a philosophical question, it is something that needs to be empirically tested. What matters is the interplay

between theory and data. Luckily, such an analysis is possible, via the extensive theoretical and empirical literature on the evolution of cooperation.

## The Evolution of Cooperation: An Illustrative Example

A behavior or trait is defined as cooperation if it provides a benefit to another individual, and has evolved at least partially because of this benefit (West et al. 2007b). Cooperation poses an evolutionary problem because, all else being equal, it would reduce the relative fitness of the co-operator, and hence be selected against. There is a rich theoretical and empirical literature explaining the factors that can favor cooperation (Sachs et al. 2004; West et al. 2007a; Bourke 2011).

### OPEN MODELS OF COOPERATION

A potential explanation for cooperation is that it is directed toward relatives, who also carry the gene for cooperation. By helping a relative reproduce, an individual is still passing copies of its genes to the next generation, just indirectly. This process, which is usually termed kin selection, was first modeled by Hamilton (1964) (Box 1). Hamilton showed that an altruistic cooperative trait will evolve if the fitness cost to the cooperator (C) is smaller than the fitness benefit (B) to the recipient, where the benefit to the recipient is weighted by the relatedness (R) of the cooperator to the recipient: $RB – C > 0$.

This result, known as Hamilton's rule, is an open model. Relatedness is a parameter ($R$) that is treated as independent of the other parameters of the model. There is no specification of how a positive $R$ arises. As such, there are a number of population—and individual-level mechanisms that could generate a given $R$ value.

Hamilton's rule has been employed to explain a wide range of traits across the tree of life (Table 1). It has been used to explain behavior, and variation in behavior, across diverse taxa, including bacteria, slime moulds, insects, birds, and mammals. The behaviors considered include many different forms of cooperation, policing, division of labor, dispersal, and harming behaviors such as killing or cannibalism. Furthermore, this includes cases where positive relatedness, or variation in relatedness, arises from a variety of factors, including limited dispersal, level of polyandry (promiscuity), kin discrimination and how groups are formed. In many cases, open models for more specific traits have also been developed (Table 1).

### Closed models of cooperation

The open models discussed above black-boxed the mechanism that generated relatedness, and implicitly assumed that relatedness was independent of other model parameters. Over the last 30 years, many modelers interested in cooperation have instead employed closed models (Table 2).

Hamilton (1964) recognized that population viscosity via limited dispersal is a key mechanism for generating the positive relatedness values that can favor cooperation in Hamilton's rule. At the same time, however, limited dispersal can also increase competition between relatives, which reduces the relative benefit of helping relatives (Hamilton 1971, 1975). It is possible to put this local competition into an open model by adding an extra independent parameter or parameters (Grafen 1984; Frank 1998; Grafen and Archetti 2008). For example, $RB-C-R_2D_2$, where $R_2$ is the average relatedness between the actor and the individuals that suffer from increased competition and $D_2$ is the cost to these individuals (Grafen 1984). However, when parameters such as R and $R_2$ or B and $D_2$ are determined by the same factors, they will be correlated. Consequently, keeping them as independent parameters could give misleading predictions. For example, if limited dispersal increases both R and $R_2$, then we might not expect a higher relatedness (R) to lead to higher cooperation.

Taylor (1992a) developed a closed model of cooperation that considered the explicit effects of social group size and dispersal rates. He then estimated the value of relatedness as generated by the specific life-history details of the model. In a landmark result, he found that the dispersal rate had no influence on the evolution of cooperation. In Taylor's model, the effect of increased relatedness and competition exactly cancel. As such, Taylor's closed model predicted that a decrease in dispersal (and therefore an increase in relatedness) would not favor cooperation as predicted by the simple form of Hamilton's rule. As well as this specific result, for that exact life history, Taylor's model makes a general point about how we need to consider both cooperation and competition between relatives.

Taylor's model has since been expanded into a number of other closed models that tweak the life history in some manner (Table 2). In many of these cases, the specific life cycle allows limited dispersal to increase relatedness ($R$), without being exactly cancelled by a decreased benefit to relatives ($B$). Consequently, in these models, limited dispersal can favor cooperation. For example, Taylor and Irwin (2000) found that overlapping generations increase relatedness without inflating the costs of competition. This happens because there is a population-level mechanism (parent survival) for genetic associations to accrue in the absence of extra offspring remaining on the patch and competing (Box 1).

However, these closed models have had relatively little impact on our empirical understanding of specific biological cases. There is only one empirical example from the natural world where the data suggests that the influence of dispersal rates on relatedness and competition exactly cancel out–competition for mates between male fig wasps (West et al. 2001). The closed models stimulated experimental evolution studies in bacteria,

**Table 1.** Examples of some of the phenomena where an open model approach (Hamilton's rule) has helped us understand biological phenomena.

| Taxa | Trait/Phenomena explained | Cause of variation in $R$ | Empirical approach | More specific open models |
|---|---|---|---|---|
| Bacteria | Public goods (extracellular factors) | Dispersal pattern | Experimental evolution (Griffin et al. 2004) | Brown 1999; West and Buckling 2003; Dionisio and Gordo 2006; Frank 2010 |
| Bacteria | Quorum sensing | Dispersal pattern | Experimental evolution (Diggle et al. 2007; Rumbaugh et al. 2012; Pollitt et al. 2014; Popat et al. 2015) | Brown and Jonstone 2001 |
| Bacteria | Killing (bacteriocins) | Kin discrimination, dispersal pattern | Experimental (Inglis et al. 2009) | Gardner et al. 2004 |
| Bacteria | Symbiotic benefit | Dispersal pattern (transmission) | Comparative (Fisher et al. 2017) | Frank 1996a |
| Birds and mammals | Cooperative breeding | Level of polyandry | Comparative (Cornwallis et al. 2010; 2017; Lukas and Clutton-Brock 2012a, 2012b) | Charnov 1981 |
| Birds and mammals | Cooperation | Kin discrimination | Observational, experimental, comparative (Komdeur 1994; Russell and Hatchwell 2001; Griffin and West 2003; Komdeur et al. 2004; Sharp et al. 2005; Cornwallis et al 2009) | – |
| Fungus | Cooperation | Group formation, kin discrimination | Experimental evolution (Bastians et al. 2016) | – |
| Insects | Eusociality | Level of polyandry | Comparative (Hughes et al. 2008) | Charnov 1978, 1981; Gardner et al. 2011a; Alpedrinha et al. 2013, 2014; Rautiala et al. 2014; Liao et al. 2015, |
| Insects | Policing | Level of polyandry | Experimental, Comparative (Wenseleers and Ratnieks 2006a, 2006b; Ratnieks et al. 2006) | Ratnieks 1988; Wenseleers et al. 2004a, 2004b |
| Insects | Killing | Haplodiploidy, dispersal pattern, kin discrimination | Observational, experimental (Grbic et al. 1992; Giron et al. 2004a, 2004b) | – |
| Insects | Reproductive restraint | Level of polyandry | Observational, comparative (Wensellers and Ratnieks 2004) | Wenseleers et al. 2003, 2004a |
| Salamanders | Cannibalism | Kin discrimination | Experimental (Pfennig and Collins 1993; Pfennig et al. 1994, 1999) | – |

(*Continued*)

**Table 1.** Continued.

| Taxa | Trait/Phenomena explained | Cause of variation in $R$ | Empirical approach | More specific open models |
|---|---|---|---|---|
| Slime moulds | Fruiting bodies | Dispersal pattern, kin discrimination | Observational, experimental evolution, genomic (Mehdiabadi et al. 2006; Gilbert et al. 2007; Kuzdzal-Fick et al. 2011; Ostrowski et al. 2015; Noh et al. 2018) | – |
| Social groups of cells (across taxa) | Division of labor, sterile cells | Dispersal pattern | Comparative (Fisher et al. 2013) | Cooper and West 2018 |

Our list is illustrative, not exhaustive, and we provide examples of the consequences of variation in only a single parameter (*R*). More specific open models are often constructed for specific traits. In many cases, some form of Hamilton's rule emerges as a prediction and is useful for interpreting these models (Taylor and Frank 1996; Frank 1998). For some other traits, such as sex allocation, the results are still interpreted with kin selection, but Hamilton's rule per se is less useful for interpretation. Studies focusing on the consequences of variation in other parameters (B, C), and whether Hamilton's rule is satisfied, are reviewed elsewhere (Bourke 2011, 2014).

examining how patterns of dispersal can influence both relatedness and competition (Griffin et al. 2004, Kümmerli et al. 2009). However, these studies can be seen as "wet simulations" that validate theory, but do not actually measure the consequences of competition in nature. Further, the role of demographic details has been discussed but rarely tested in a number of taxa, including RNA replicators, birds, and killer whales (Hatchwell 2009; Johnstone and Cant 2010; Croft et al. 2017; Levin and West 2017a).

**OPEN VERSUS CLOSED**

Why have open models been more useful for explaining specific empirical examples of cooperation? We suggest seven, nonmutually exclusive possibilities: (i) a closed model specifies a certain demography, narrowing the organisms to which it can be applied; (ii) closed models include an additional layer of demographic detail, which can make them more complex, and harder for empiricists to apply (or at least, they appear to); (iii) open models can offer intuitive heuristics, like Hamilton's rule, which can be applied broadly, generate simple predictions, and facilitate interpretation of results; (iv) open models make predictions in terms of $R$, which will often be a relatively easy parameter to measure; (v) open models disentangle causal effects in similar way to experiments that try to manipulate single factors while keeping everything else fixed; (vi) open models can focus on other biological details of potential interest, rather than demography (e.g., partner sanctions, or how cooperative benefits are shared; West et. all 2002; Cooper and West 2018); and (vii) there may not be enough two-way interactions between those developing the theory and those collecting the data.

The utility of the different approaches can also be illustrated by imagining a hypothetical scenario in which theoretical work on cooperation had started with Taylor's (1992a) closed model. In this case, we would have been left with the prediction that limited dispersal (higher relatedness) does not favor cooperation. Empirically this is clearly not the case, as limited dispersal appears to play a key role in favoring cooperation in a broad range of taxa (Table 1). But, at the same time, Taylor's model has been incredibly influential in its own right. The point is that Taylor's closed model was useful when discussed against an open model (Hamilton's rule). Hamilton's rule said relatedness matters, and it clearly does (Table 1). Taylor's model showed that, in certain cases, things could be more complicated as competition can reduce selection or even negate selection for cooperation between relatives. This helped us explain the data from fig wasps and stimulated experiments on bacteria (West et al. 2001; Griffin et al. 2004; Kümmerli et al. 2009), and led to a large body of theoretical work (Lehmann and Rousset 2010; Van Cleve and Lehman 2013; Van Cleve 2015; Peña et al. 2015). Furthermore, the combination of open and closed models in this area also spurred work on how local competition can favor spiteful harming behaviors (Gardner and West 2004; Gardner et al. 2004; 2007; Lehmann et al. 2006).

## Beyond Cooperation

How useful have open and closed models been more generally? Another area of social evolution where there has been productive interplay between theory and data is the study of how organisms allocate resources to male and female offspring, termed sex

**Table 2.** Examples of the ways that Taylor's (1992a) model has been extended to incorporate additional biological details (nonexhaustive).

| Theoretical models | Process modeled | When does limited dispersal favours cooperation? |
|---|---|---|
| Taylor 1992a | Patch elasticity | Always |
| Taylor and Irwin 2000, Irwin and Taylor 2001, Levin and West 2017b | Overlapping generations | When generations overlap |
| Gardner and West 2006, Lehmann et al. 2006, Lehmann et al. 2007, Traulsen and Nowak 2006 | Budding dispersal | When individuals are more likely to disperse together than singly (budding). |
| Rogers 1990 | Selective emigration | If altruists are more likely to emigrate |
| Gardner 2010, Johnstone and Cant 2008 | Sex-specific dispersal | When the sex with higher variance in fitness is (slightly) more likely to disperse |
| Lehmann et al. 2008, Johnstone 2008 | Caste-specific dispersal | When different castes (e.g. queen and worker) have different dispersal rates, reproductive values, and dispersal timings |
| Alizon and Taylor 2008 | Empty sites | When there are empty sites on patches |
| El Mouden and Gardner 2008 | Conditional helping | When co-operators adjust their behaviour conditional on whether they disperse |
| Taylor 1992b, Kelly 1992, Queller 1994, Gardner and West 2006 | Various timings of cooperation and competition | Under some but not all demographic timing schemes |
| Yeh and Gardner 2012 | Different ploidies | Under some but not all ploidies |
| Rodrigues and Gardner 2012, 2013a, b | Heterogeneity in patch quality, group size, and individual quality | When patches vary spatially and temporally in patch quality and group size, and (under some circumstances) when individuals vary in quality |
| Perrin and Lehmann 2001 | Kin discrimination | When individuals can actively discriminate kin |

We focus here on analytical models (rather than simulations), as these allow us to the see the explicit role of different parameters. We focus on island models, as opposed to spatially explicit models (e.g., lattice or stepping stone), as the added mathematical complexity of these models makes it harder to interpret parameter relationships, without necessarily revealing patterns that can't already be identified in simpler island models (Lehmann and Rousset 2010). A number of other models have used different approaches (e.g., lattice models, cellular automata, evolution on graphs) to identify a number of other factors that can alleviate the effects of local competition (e.g., van Baalen and Rand 1998; Mitteldorf and Wilson 2000; Ohtsuki et al. 2006; Lehmann et al. 2006; Grafen 2007; Taylor et al. 2007; Lion and Gandon 2009).

allocation (West 2009). Within this area, the two relevant success stories are: (1) local mate competition (LMC)–how population structuring, with competition for mates between related males, selects for female biased sex ratios (Hamilton 1967); (2) sex allocation driven by relatedness asymmetries in haplodiploid social insects (Trivers and Hare 1976; Boomsma and Grafen 1991). Closed and open models have driven research in these two areas respectively, demonstrating that, in different fields, one approach has sometimes been more useful than the other.

Hamilton (1967) showed that if $n$ diploid females lay eggs on a patch, if mating then occurs on this patch, and if only the females disperse to compete globally, then the evolutionarily stable strategy is to invest a fraction $(n-1)/2n$ of resources into female offspring. The beauty of this closed model is that it is an excellent approximation of the life history of many species, and leads to a prediction in terms of one parameter that is often relatively easy to measure ($n$). A closed model works so well here, because clear morphological features, such as nondispersing wingless males, enforce life-history features that facilitate mathematical simplifications. Hamilton's LMC model has proved extremely useful for explaining variation in sex allocation, both within and between species (West 2009). Furthermore, theory has been extended in numerous directions to account for life history and demographic details relevant to certain species (West 2009). Alternative open formulations of Hamilton's LMC equation are possible, which focus on the relatedness between male and female offspring on a patch, but these can be less easy to apply (Frank 1998; Nee et al. 2002).

Boomsma and Grafen (1991) showed that, in haplodiploid social insects, workers are favored to adjust the colony sex allocation in response to the relatedness structure within their colony. They

produced an open model, and outlined how relatedness structure could be determined by a number of demographic factors, including queen mating rate, queen number, worker reproduction and queen replacement. Their model is able to explain considerable variation in sex allocation, between colonies (split sex ratios), in response to these factors (West 2009). A single open model could be applied across, and therefore unify, a number of different scenarios, where different features of the demography drive "split sex ratios." Together, these examples from sex allocation highlight that, for distinct empirical questions, different approaches have been more useful.

There are other areas where open or closed models have been more important for the development of theory. For example, closed models have dominated theoretical work on the evolution of dispersal, because the dispersal rate is both the trait under selection and the determinant of relatedness (Taylor 1988; Frank 1998; Gandon 1999; Gandon and Michalakis 1999; Gandon and Rousset 1999; Rousset 2004). Another example is the evolution of virulence, where early models tended to be open whereas later models are predominately closed (Frank 1996b; Gandon and Michalakis 2000; Wild et al. 2009; Alizon and Lion 2011; Lion 2013). However, neither of these fields has led to a similar interplay between theory and data, possibly because most of the theory was not developed to address specific empirical patterns (Crespi and Taylor 1990; Innocent et al. 2010).

Finally, there are also parameters other than relatedness that could be left open or closed. For example, in models where populations are structured into different classes—such as age, sex, or size—reproductive values are usually treated as closed. However, open models could be developed in these cases by employing a conservation of reproductive value criterion. Because total reproductive value of the population is constant, an increase in the reproductive value of one individual necessitates exact compensatory changes in the reproductive value of others, allowing the modeler to keep this as an open parameter (e.g., Wild and West 2007). Exactly how our analysis extends to these other questions remains unclear.

## Guidelines

An obvious take home is that the different approaches have different utilities. But this is a bit vague and obvious. Can a summary of our above discussion provide more specific guidelines?

Open models have proved more useful when we want to consider cases where multiple demographic and life-history details can influence relatedness. For example, how limited dispersal, kin discrimination, and female mating rate influence the evolution of cooperation, or how queen mating rate, queen number, and queen replacement influence the evolution of split sex ratios (Hamilton 1964; Boomsma and Grafen 1991). In these cases, an open model

can be applied broadly across diverse taxa, with very different life cycles. In addition, open models have been useful for providing conceptual unification, and intuitive heuristics for guiding empirical work.

Closed models have proved particularly useful when a single demographic factor is more universally important. For example, how the number of females laying eggs per patch influences sex allocation (Hamilton 1967). In such cases, a closed model can be applied broadly across different taxa, which share this key aspect of their life cycle. In addition, closed models have been useful conceptually for disentangling the roles of different demographic parameters.

More generally, with all these considerations, the emphasis should always be on the interplay between theory and data, and how the theory will be used to help us explain the natural world. When developing theory, there are a number of empirically motivated questions to be asked. What aspect of the empirical data can't be explained by existing theory and needs a new model? What are the parameters that empirical work suggests need more attention? Do we want to make broad predictions across species with different life cycles, or for a single species with a specific life cycle? The advantage of more empirically minded development of theory is clearly illustrated by the success of closed models developed to examine sex allocation (local mate competition), compared to those for cooperation and dispersal. In particular, the extensions of basic local mate competition theory have proven very useful precisely because their development was driven by cases where the data and/or life-history assumptions did not fit existing theory (West 2009).

## Conclusions

To conclude, open and closed models are complementary and not competing approaches. Ultimately, we must ask what the modeler is prepared to give up, and what they want to gain, which will depend on the modeler's empirical aim. Sylvain Gandon pointed out to us that an analogy here can be made with the analysis of statistical data. If the addition of an extra variable does not significantly improve the explanation of the data, then the more detailed model, with that extra variable, can be a less good model, as judged by statistical measures such as AIC. An important goal should be to develop a model with the minimal level of detail required to answer a specific biological question (May 2004). Evaluating whether to use an open or closed model is then simply a matter of determining where that minimal level of detail falls with respect to demography and population structure.

Finally, this debate touches on a recurring theme in behavioral and evolutionary ecology, where there are numerous examples of different potential approaches. Some examples include

population genetics versus game theory, general versus specific models in game theory, or experimental studies on a specific species versus across species comparative studies (Harvey and Purvis 1991; Parker and Maynard Smith 1990; Davies et al. 2012). All of these cases have generated arguments that one approach is "better" or "more correct" than the other whereas, in reality, the different methodologies have different strengths and weaknesses and are each appropriate in different scenarios.

## AUTHOR CONTRIBUTIONS

All authors contributed to the manuscript equally.

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