Using inclusive fitness and eco-evolutionary theory to model cultural evolution

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Abstract

Baumard and André (2025) have suggested that cultural dynamics can be studied as a form of ecology. This provides a simpler unified approach to explaining cultural evolution, within the context of human behavioiur being shaped by natural selection. We briefly expand on two points: (1) why inclusive fitness represents our most general answer to what organisms are selected to maximise; (2) the potential for using existing eco-evolutionary theory methods to model cultural evolution.

1 A simpler unified approach to understanding cultural evolution

Baumard and André (2025) have tackled a very important problem: research on cultural evolution is a bit of a mess. Rather than a single unified theory, several different approaches have been used to model or conceptualise cultural evolution. Different methods can give contrasting predictions, even when they seem to be based on the same assumptions. Similarly, the conclusions from empirical data can vary widely. Consequently, fundamental questions remain unanswered. Can cultural evolution be explained with 'standard' evolutionary theory, or do we need something new and special, such as dual inheritance theory or an extended evolutionary synthesis? Can we have a single unified theory? Have proximate and ultimate factors been mixed up? Is human culture unique, requiring a special theory?

Baumard and André (2025) argue that one theory suffices to explain cultural evolution: ecological theory. They argue that any aspects of culture can be regarded as ecology, by drawing a number of examples comparing cultural and ecological phenomena. Thus, cultural dynamics can be handily modelled by the existing ecological theory. For example, aspects of culture such as fashions change at a faster timescale than evolutionary gene-frequency change. Culture mediates information-processing among individuals. Individuals construct cultural architectures that influence the decision making of individuals in subsequent generations. All of these are interchangeably interpreted as culture or ecology.

The idea of linking ecology to culture per se is not new. Steward (1955) coined the term "cultural ecology" to refer to the study of the cultural aspects of human interaction with the environment. More recently, Sutton and Anderson's (2013) monograph synthesises Steward's idea. However, this previous work was relatively informal: it lacked the theoretical framework or modeling approach of cultural dynamics. We therefore have long missed the key idea of Baumard and André's to use theoretical ecology methods to study cultural dynamics. This lack is in stark contrast to the disciplines of ecology and evolution, where researchers routinely use mathematical models and describe them with equations. Such models are based on a relatively common theoretical framework, in particular, inclusive fitness theory and eco-evolutionary theory. These existing theories provide a useful tool, which have not been fully integrated into cultural dynamical theory as such.

In this commentary we focus on two areas where additional information may be useful. First, we discuss the basis of inclusive fitness theory, which Baumard and André, 2025 put at their centre of their approach, but did not have space to fully justify. Second, we discuss how eco-evolutionary theory may offer useful methodologies for modelling cultural evolution.

2 Inclusive fitness and adaptation

Baumard and André (2025) base their framework on inclusive fitness theory, but space limitations meant that they could not go into how and why inclusive fitness theory was developed. Inclusive fitness theory is often misunderstood and so we wanted to briefly review its links to evolutionary theory more generally, to summarise why inclusive fitness provides our most general theory for explaining adaptation.

Individual organisms appear designed or adapted for the environments in which they live. The theory of natural selection provided an explanation for this empirical pattern of adaptation. Darwin (1859) pointed out that heritable characters that are associated with greater ability to survive and reproduce will tend to accumulate in biological populations. Natural selection is therefore an improving process. Given a sufficiently long period of time, this will lead to organisms that appear as if they were designed to survive and reproduce in their environments. Fisher (1930) formalised this idea with population genetic theory, using the term 'fitness' to describe the ability of an individual to pass genes to future generations. He showed that natural selection would lead to organism that were designed to maximise their fitness. Furthermore, that in the special case with no social interactions, where all offspring are equal, and the population size is roughly constant, fitness is equal to the total number of offspring produced in a lifetime (reproductive success). Consequently, in this case, we should expect organisms to appear and behave as if they had been designed to maximise their reproductive success.

Hamilton (1964) pointed out that this previous understanding of natural selection could only explain traits that were beneficial to the individual performing them, by increasing reproductive success (fitness). Consequently, previous theory could not explain altruistic helping behaviours that were costly but benefitted others, with an extreme example provided by the sterile workers in social insect colonies. Or more generally that previous theory would make incorrect predictions if there were any type of social interaction between relatives that influenced reproductive success. The problem is that Fisher had deliberately focused on only the direct transmission of genes via offspring, ignoring how individuals could also influence the transmission of their genes by altering the reproductive success of other individuals who shared those genes (relatives; Fig 1A).

We can rephrase the problem here in several alternate ways. What feature of individuals does natural selection maximise? In what way should we expect organisms to be designed? What form should we expect adaptation to take? What is fitness? An individual maximising its reproductive success would not perform an altruistic behaviour, and so reproductive success cannot be our most general answer to these questions.

Hamilton, (1970, 1964) showed that the most general answer to these questions was inclusive fitness. Inclusive fitness sums the consequences of a trait for the actor (direct fitness) and for the recipients (indirect fitness) of that trait. Inclusive fitness is the property that is maximised by natural selection (maximand) because it satisfies two criteria: (i) natural selection favours genes which increase inclusive fitness (inclusive fitness is a 'target' of natural selection); (ii) inclusive fitness is under an organisms control, meaning that it is determined only by the traits of that organism (i.e. it is something that can be maximised at the level of the individual; Grafen, 1991 West and Gardner 2013). Inclusive fitness isn't just a modelling framework for social interactions. It is our most general answer to what organisms are selected to maximise. It is incorrect to draw a sharp distinction between population genetics and inclusive fitness theory. Inclusive fitness maximisation is a result from population genetics about the form we expect adaptation to take at the level of the individual organism (Grafen, 2006). The maximisation of reproductive success in scenarios without social interactions is an important special case of inclusive fitness theory. Inclusive fitness theory is not in conflict with other approaches such as multi-level selection – those alternate approaches also lead to the prediction of inclusive fitness maximization (Hamilton, 1975; Frank, 1986; Grafen, 1984; Queller, 1992). We conclude by noting that our above summary is deliberately simple. The interested reader is pointed elsewhere for research that clarifies links with different areas of evolutionary theory and facilitates the modelling of different biological scenarios (Taylor and Frank, 1996; Frank, 1998; Rousset, 2004; Gardner et al., 2006; Grafen, 2006; Taylor et al., 2007; Gardner et al., 2011; Lehmann and Rousset, 2020) .

3 Cultural evolutionary theory from an "eco-evolutionary" perspective

Baumard and André (2025) suggest modelling culture as an ecological system. We take their key insight, although implicit there, as using the existing theory of eco-evolutionary dynamics. Eco-evolutionary dynamics describe the interdependence between ecological and evolutionary processes. Consequently, this represents a parsimonious approach to formulate even seemingly complex cultural dynamics.

By linking cultural dynamics with eco-evolutionary dynamics, Baumard and André's (2025) argument on the inclusive fitness theory sensu cultura becomes even clearer (Fig 1A, B). Inclusive fitness theory is based on the transmission of a focal individual's genes to future generations either directly, through the impact of those genes on the reproductive success of the actor, or indirectly via their effect on the reproductive success of related individuals. In eco-evolutionary feedback theory, evolutionary dynamics changes ecology (e.g., density), while the ecology influences evolutionary dynamics (e.g., the direction of selection). In cultural dynamics, members make actions that influence their culture (or ecology), which in turn changes the members' behaviors plastically (or evolutionarily, respectively). The key feature in the cultural dynamics is a dynamic interplay among systems, allows for information exchange. Baumard and André's Tables 1 and 2 provide a nice summary of such links, each item of which is fully consistent with the eco-evolutionary feedback theory. We finally point

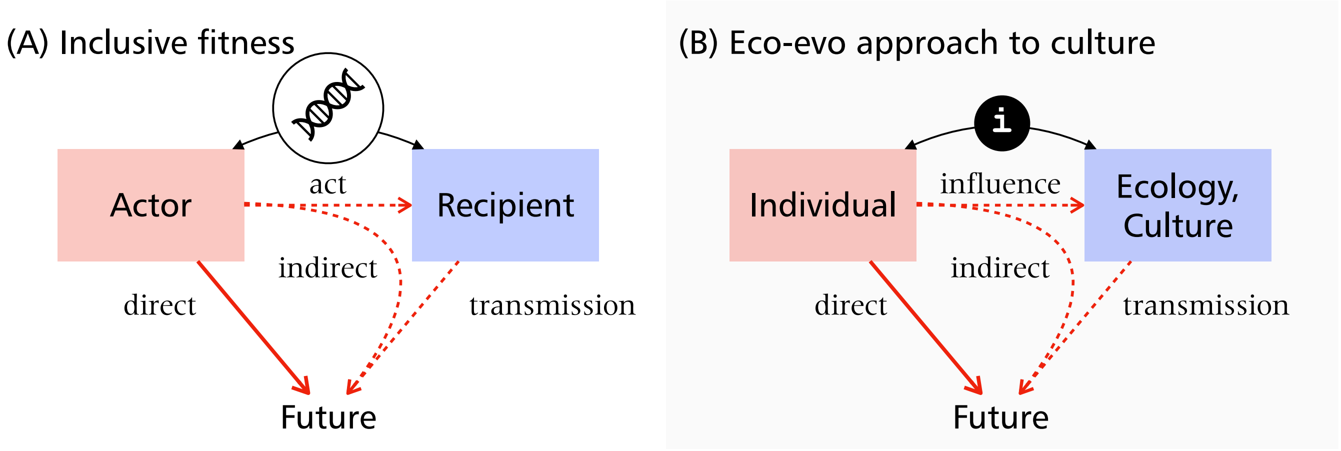

Figure 1: Inclusive fitness and an eco-evo approach to culture. (A) Inclusive fitness. An actor performs an action to influence the recipient's gene transmission to future populations, either directly or indirectly (via other individuals - recipients). Actor and recipients share genetic information (genome; black arrows). (B) Ecological approach to culture, based on eco-evolutionary feedback theory. Individuals contribute to ecology and culture, which influences how likely the individual can (not only directly but also) indirectly change the future state of the population in, e.g., ecology, environment, or culture. Individual(s) and ecology/culture share the same information (e.g., knowledge, technology, trend) due to their mutual influences. Note, some of the arrows are not shown (e.g. from ecology/culture to individual) to avoid double-counting.

out a useful theoretical advantage of Baumard and André's (2025) conceptualization. Inclusive fitness focuses on the fitness of an actor (actor-centred view of fitness; Fig 1A). Similarly, the eco-evo approach focuses on the direct effect of individual's behavior and its indirect effect via culture on future states (cultural feedback; Fig 1B). However, the roles of actor and recipient are exchangeable (Taylor et al., 2007). If we "mirror" all the arrows in Fig 1 (and replace the "future" with "past"; Lehmann, 2007; Iritani et al., 2021), we arrive at a recipient-centered view of fitness, also called neighbour-modulated fitness (Hamilton, 1964). Distinguishing the two fitness concepts, albeit mathematically equivalent in terms of predictions made, is important, as neighbour-modulated fitness allows a powerful method to develop biology based models, while inclusive fitness facilitates intuitive interpretation (Grafen, 1982; Taylor et al., 2007; Levin et al., 2019) . Similarly, the roles of individual and ecology/culture are also exchangeable, which leads to a culture-centred view. Whereas the two pathways of cultural transmission (direct and indirect) are prone to the double-counting of cultural fitness (Taylor et al., 2007; Taylor and Frank, 1996), using the eco-evo theoretical framework automatically solves this problem: we can make use of established dynamical framework (e.g., the evolutionary invasion analysis of adaptive dynamics; Dieckmann and Law, 1996; Metz et al., 1992; Geritz et al., 1998). Readers may therefore refer to these theoretically well backed-up tools, which allows for rigorous formulation of cultural dynamics. Once the correct formulation is done, any disagreement is due merely to modelling assumptions (which can be solved), or misconceptions (which can be resolved).

To conclude, Baumard and André's framework offers an exciting potential to advance research on cultural evolution. A crucial next step will be to apply this framework to specific behaviours, such as cooperation, to see if it can turn messy disagreement into order and unification.

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