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### Title

How (not) to review papers on inclusive fitness

### Permalink

<https://escholarship.org/uc/item/1423243g>

### Journal

Trends in Ecology & Evolution, 30(5)

### ISSN

0169-5347

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### Publication Date

2015-05-01

### DOI

10.1016/j.tree.2015.02.007

Peer reviewed

continue to be so. However, our planning focus needs to shift from place to process.

Cowling *et al.* defined pattern and process as separate elements in systematic conservation planning [3]. Pattern was the distribution of species across a landscape, resulting in unique assemblages at each place. Process included evolution and shifting geomorphology. Why do we see present pattern as static when we understand so well that patterns continually change – that in fact what we are studying is not a pattern, but a moment in dynamic process? It is likely to do with our preoccupation with place, our place-centric terminology and the inherent difficulty in grasping change that unfolds on timescales that are long relative to a human lifespan.

Now, human-induced climate change is speeding up the game, making it impossible to pretend that pattern and place are synonymous. It is clear that modern conservation planning needs a paradigm focused on process, not pattern.

Microrefugia are the last gasp of place-based conservation planning. We now know that microscale processes are important and that they have macroscale implications. However, if we think that means there are small places that do not change, we are surely mistaken – they simply change at different rates. We still must plan for process.

Precedents exist. In fire management, the historical range of variability (HRV) in fire characteristics (sizes, frequencies, intensities, and seasonalities), their complex effects, and landscape-scale vegetation composition has long been used in understanding the role of wildfire as a crucial natural disturbance in a given ecosystem [4–6]. Conservation in fire-prone environments may thus depend as much on wildfire as a process, incorporating factors that control ongoing fire regimes and avoiding critical thresholds [7], as on protecting a particular piece of landscape. Conservation planning for climate change needs an analogous paradigm. Understanding the relative importance of climate shifts and their conservation implications will hinge on an understanding of the processes in question.

Conservation planners have begun to embrace this challenge, developing conservation planning tools that explicitly address change. For example, conservation planning tools are available that explicitly incorporate

simulated range movements of species with climate change [8,9]. Dynamic vegetation models, Earth System Models, physiological models and others focus on the dynamics of change, although not all have been fully integrated into conservation planning. Terms such as ‘topographic buffering’ are emerging, which emphasize process over place.

Conservation planning for climate change is not about place; it is about dynamics. However, these dynamics can lead us to places in which our traditional place-based conservation tool, protected areas, can make a difference in a dynamic world. Partial solutions that skip the dynamics by ‘conserving the stage’, banking on microrefugia that do not change or ignoring climate change altogether, will not be robust throughout the rest of this century. Conservation planning for climate change will be effective when dynamic planning tools are widely used and incorporate fine-grain effects, empowering conservationists to move from a paradigm focused on places to one focused on dynamics.

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# How (not) to review papers on inclusive fitness

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Evolutionary fitness of traits or behaviors is inclusive [1] of their ‘direct’ effects on the trait bearers’ reproduction and

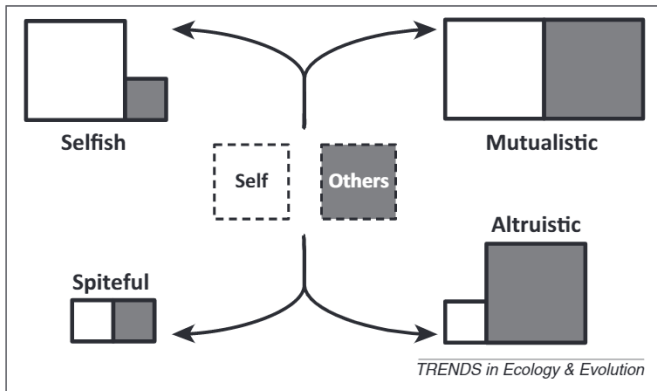
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Keywords: inclusive fitness; reviewing.

0169-5347/

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their ‘indirect’ effects on others’ reproduction (Figure 1). Inclusive fitness models lay bare that traits can be selectively advantageous even when they negatively impact direct fitness. A capstone of this approach is that Darwin’s dilemma of sterile workers and nonreproductive helpers seems neatly solved by the simplicity of Hamilton’s Rule ( $rb - c > 0$ ). Workers work and helpers help to maximize



**Figure 1.** Inclusive fitness and four categories of traits. A trait's effect on an ancestral organism's fitness is inclusive of the direct effects on the organism's own reproduction (broken white box) and the indirect effect on the reproduction of others (broken gray box), presented here for illustrative purposes only as being equal in magnitude. Depending on whether the further evolution of a trait increases or decreases the relative sizes of the direct and indirect fitness 'boxes', organisms can evolve to be more Selfish, Mutualistic, Altruistic, or Spiteful. Evolution of mutualism and altruism becomes more likely when Others are genetic kin, while selfishness and spite become more likely when the Others are non-kin. Thus, for many the term 'kin selection' is synonymous with the evolution of altruism, where gains in indirect fitness offset losses in direct fitness.

their inclusive fitness. Recently, however, the inclusive fitness approach has been severely criticized for both its mathematics and the lack of critical tests of this fundamental prediction [2,3]. This marshaled a robust defense from hundreds (including an author of this response) [4,5] and a rebuttal review listing 12 studies that test whether indirect fitness gains can explain reproductive altruism [6]. Several of the reviewed studies had methodological limitations, however, and five suggested that gains in indirect fitness alone could not explain cooperation. Given thousands of published papers on inclusive fitness since Hamilton's seminal work [4], such a paucity of explicit tests may indeed buttress E.O. Wilson's pronouncement that empirical advances have been 'meagre'.

We believe from our own experience and conversations with colleagues that more datasets testing the central prediction are available but languish unpublished. The surprising main reason is not that such manuscripts are negatively reviewed by inclusive fitness critics, but more often, that they are shot down by Hamilton's putative supporters. In short, there is a consensus that inclusive fitness 'works', but none regarding how to explicitly measure and test it. Obviously this does nothing but strengthen the case of those who look askance at the mathematics of inclusive fitness theory [3,7,8].

A main objection that we believe often prevents the publication of datasets directly testing the parameters of Hamilton's Rule centers on measuring inclusive fitness. Many reviewers are absolutely certain about the correct method, but rarely do two reviewers agree. A major issue is the infamous 'double-accounting' problem that occurs when calculating the inclusive fitness of both helpers and helped. To avoid double scoring, the extra offspring produced as a result of helping are considered to contribute to the inclusive fitness of the helper but not the helpee (often the helper's parent). Yet, the helpee produced these extra offspring and was positively selected to receive help (or even to manipulate

the helper). Its direct fitness must also have been increased by receiving help. Especially for research focusing on eusocial insects, a charge of double accounting is enough to sink any manuscript comparing direct and indirect fitness components of helpers and helpees.

One reasonable solution to the methodological variety in calculating inclusive fitness is to use multiple points of view [9]. In our experience, this approach is also insufficient for some reviewers and sometimes leads to quite unreasonable requirements for publication, such as a claim that inclusive fitness alternatives can be properly compared only by observing outcomes when the same individuals cooperated and when they did not. Requirements such as these, which ignore the actual behavior of the animals being studied, truly make predictions based on inclusive fitness completely untestable.

We are not advocating an outright dismissal of concern over calculating inclusive fitness, but instead are illustrating the inordinate difficulties valuable datasets encounter in review. Our proposed solution is a simple admonition to reviewers: 'Reflective, not reflexive critique, please!' First, tests of Hamilton's Rule are scientifically legitimate and do not in and of themselves constitute an attack on Hamiltonian logic. Second, it has long been understood that in testing Hamilton's Rule, assessing benefit and cost is the great difficulty [6] – the priority should be to publish datasets that allow this. For both reviewing and in the published form, authors must provide their raw data and explicitly describe their inclusive fitness calculation methods. Thus reviewers and readers can check the results or apply their own preferred calculations. We take heart that some tests of the capstone prediction are starting to see the light of day. Interestingly, the results are strongly suggestive of multiple paths to cooperation. In one species, indirect fitness gains may indeed account for worker behavior [10]. In a second, working can produce direct fitness gains [11]. In a third, only maternal manipulation is consistent with observed patterns of worker behavior [9] and in a fourth working results from neither inclusive fitness gains nor maternal manipulation but apparently as a byproduct of philopatric dispersal behavior [12]. Clearly more work is needed to generate a consensus about the correct way to both calculate inclusive fitness and advance our understanding of the diversity in social evolution. We urge reviewers to be constructive, not obstructive, in this process.

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## Specimens as primary data: museums and 'open science'

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In 1977, Eugene Odum advocated a synthetic approach if ecology were to rise above the level of explanation afforded by independent, individual studies [1]. Today, Odum's wish is being fulfilled, and important advances are being made by synthesising data derived from great numbers of studies, either by scaling up temporally or geographically [2]. However, to allow effective, creative, and reproducible integration of ecological and environmental results, the methods and data used need to be made freely accessible and combinable. Only then can integrated ecology become a field where the ideals of 'open science' [3] fully come to fruition. Indeed, although great challenges remain [4,5], open access to ecological data, methods, and analysis is rapidly improving [6,7]. Nonetheless, we here call attention to what we perceive as one important obstacle to open data in biodiversity studies.

The 'raw data' in biodiversity research consist not of tabulations of numbers of individuals of species sampled at a particular date and place, but of the properly-labelled specimens themselves; occurrence records associated with specimens are metadata. We feel it is insufficiently appreciated that each assignment of a specimen to a particular taxon (whether a formally described species or a pragmatic 'morphospecies' [8]), is a researcher's interpretation, and therefore not a primary datum.

Because the scholarship of biodiversity includes scrutinising earlier work, evaluating what was written before, and adding new information and insight, it should always be possible to return to those specimens. They are the primary evidence for the information presented. The ability of researchers to re-examine the primary data and question the conclusions of previous work is a crucial part of what makes this a scientific activity. Especially in groups where the taxonomy is in flux, this is essential to ensure long-term comparability and vitality of data.

Unfortunately, in our experience, the accessibility of specimens sampled during biodiversity studies is problematic for two reasons. First, after publishing their results, many researchers and institutes do not systematically archive the samples of specimens that form the basis for the analyses. Specimens are either discarded or only a small reference collection is saved, leaving no way to verify the metadata. Even if specimens are stored, material from separate plots or dates are often pooled to reduce storage space [9], rendering valuable information irretrievable.

We therefore suggest that it become accepted policy in ecological research that full, unadulterated collections of all specimens from a study be deposited in a natural history collection. This is common practice in other areas of specimen-based biological research, such as taxonomy and palaeontology. Public natural history collections increasingly make the content of their collections databases available through the Global Biodiversity Information Facility (GBIF), which should facilitate retrieval and verification of specimens as well as reuse of the associated metadata [10]. Moreover, the specimens would then be available for obtaining additional information (such as genetic and morphometric data, and sometimes even information about ecological interactions [11]).

The second reason for the inaccessibility of specimens, however, lies with those same publicly-accessible collections. Natural history museums often appear unable or reluctant to assume a custodian's role as repositories for bulk samples from ecological studies. This is understandable in view of the traditional focus of natural history museums on systematics and biogeography, which gives rise to a desire to maximise the information density of their holdings by giving priority to previously unrepresented species or localities. Given the universal features of species-abundance distributions, however, biodiversity research will yield samples that are dominated by common and widespread species. Faced with space limitations, and a lack of funding and staff to be able to curate and maintain large ecological collections,

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0169-5347/

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