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BOOK REVIEW

Microbial communities as interactors

S. Andrew Inkpen and W. Ford Doolittle: Can microbial communities regenerate? Uniting ecology and evolutionary biology. Chicago: University of Chicago Press, 2022, 182 pp, $20.00 PB

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Regeneration as a conceptual issue has stubbornly persisted through the history of biological and related philosophical thinking. The issue has seemingly spanned all levels of biological organization to include developmental regeneration of organismal parts, the reconstitution of species, recurrence of multi-species communities, and the resilience of ecosystems or whole-world Gaia. More recently, the bounds of the regeneration problem have been pushed with technological advances in microbiology which have allowed easy study of microbial communities. Bacteria in particular have vexed many canonical assumptions in standard formulations of evolutionary theory. As interesting phenomena in their own right in the milieu of biological regeneration, analysis of microbial community regeneration has the potential to inform ongoing debates on the structure of evolutionary and ecological theory.

To address the issue of regeneration broadly and its framing in contemporary research, the Marine Biological Laboratory has sponsored a series of books on the regeneration problem. This includes a succinct book by Inkpen and Doolittle presenting a laudable attempt to make sense and provide a unified explanatory basis and conceptual analysis of regeneration in microbial community ecology and evolution. Inkpen and Doolittle make a compelling case for a familiar proposal that builds on the hard core of evolutionary theory. Indeed, the book leverages both empirical examples and philosophical analyses to complete this task, all while having the ambitious goal of informing a diverse target audience of laypeople, scientists, and policymakers.

Inkpen and Doolittle start by providing definitional clarification of ‘community regeneration’ through the example of ecologist Frederic Clements’s theory of succession. This example (1) has them discussing community regeneration as “backward-looking, in that regeneration involves something from the past reemerging” (9) and (2) provides a clarification of ‘ecological community’ for bacteria. As Inkpen

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and Doolittle state, and clarify, bacterial community definitions are confounded by either taxonomic or functional approaches to what bacterial ‘species’ are. The next definitional task that they turn to is what counts as ‘microbial’. They point out the intertwined nature between microbial and macrobial (e.g., holobionts) and how they should be considered in discussions of regeneration as applied to biodiversity conservation and human health. In dealing with regeneration questions related to conservation and health, Inkpen and Doolittle end their introduction by reasserting their task: solving the regeneration problem applied to microbial communities. Specifically, to “offer a way of *explaining* microbial community regeneration” (17). To this end, Inkpen and Doolittle introduce the proximate/ultimate distinction of explanation as a way to tackle the overarching regeneration problem. For them, proximate explanations appeal to the sequence of causes that produce a given phenomena and are addressed through the lens of community ecology (Chapter 2) whereas ultimate explanations appeal to an overarching function or purpose and are addressed through an evolutionary lens (Chapters 3–4). Lastly, Inkpen and Doolittle point out that microbial community regeneration might also be addressed through a human-centric engineering lens, having a different ultimate explanation (Chapter 5).

In Chapter 2, *Ecology*, Inkpen and Doolittle engage proximate explanations of microbial community regeneration through an ecological perspective. They start by engaging a classic case study of community regeneration in the Georgia Piedmont. This case study elicits questions pertaining to the predictability of transitions and the role of external effectors on predictability and path convergence. They then return to Clements and explore the applicability of his six causes, five as causes serving proximate explanations (nudation, migration, ecesis, reaction, and competition) and one as an Aristotelian final cause serving as an ultimate explanation (stabilization). Relatedly, they discuss Clements’s final cause in the context of dissent by Clements’s contemporary, the ecologist Henry Gleason. Inkpen and Doolittle frame this debate as differing visions—a conclusion that aids in the tractability of their proposal. Community change is then discussed from the contemporary perspective of Mark Velland and his four processes (selection, drift, speciation, and dispersal), which draws on evolutionary causes often invoked in population genetics. Velland’s processes are taken and modified for an emphasis on microbes and the associated phenomenon of lateral gene transfer (LGT). As the discussion in this chapter largely focuses on the previously introduced proximate explanations to ‘how questions’, Inkpen and Doolittle end with related ‘why questions’. This sets the stage for discussing an ultimate explanation for community selection in their next chapters.

In Chapters 3 and 4, *Evolution* and *Interactors*, Inkpen and Doolittle “take stock of traditional Darwinian thinking about community evolution and regeneration” (51) and assess whether microbial community and organismal regeneration are similar in their ultimate explanations. They explore this by starting with traditional Darwinian evolution following Lewontin’s recipe, natural selection by heritable variation in fitness. This mode of explanation, even expanded to canonical multi-level selection, is shown not to work for microbial communities as they do not reproduce. As Lewontin’s formulation cannot adequately explain community regeneration as the result of selection targeted to communities, Inkpen and Doolittle claim that modification should be considered. Indeed, they double-down on their assertion that there is a need for an ultimate explanation of microbial community regeneration and more broadly, collective processes that affect the regenerative abilities of communities. As ‘standard evolutionary theory’ cannot fit communities and their emergent functional properties due to no reproduction, the impetus arises for Inkpen and Doolittle’s how-possibly explanation. Two major problems for a community-selection account of evolution are therefore: (1) communities do not exhibit canonical reproduction, a problem shorthanded as NO-REPRODUCTION; and (2) what counts as community regeneration is often functional and not taxonomic, shorthanded as SONG-NOT-SINGERS.

NO-REPRODUCTION is examined with two examples. The first is the holobiont concept, where Inkpen and Doolittle conclude that outside of rare exceptions such as aphid-*Buchnera* reproduction, most holobionts do not ‘reproduce’ as a single unit with vertical transmission of their associated microbiota. The other example used to address the issue of NO-REPRODUCTION among communities is the Gaia hypothesis. These examples effectively show that canonical multi-level selection theory does not work at the level of communities or above, and that notions of community and organismal regeneration are only analogous with no shared ultimate explanation. As Inkpen and Doolittle aim to provide a unified ultimate explanation of regeneration, they argue that this failure motivates new theory. They offer a solution in the form of the replicator–interactor distinction of David Hull.

In invoking the replicator–interactor distinction, Inkpen and Doolittle first address the SONG-NOT-SINGERS problem previously discussed, and double-down on their emphasis of function over taxonomy. They also emphasize the importance of LGT in that different functions can be swapped between species. Importantly, they state: “It may ultimately be genes and the functions they determine, rather than the species that house them, that really matter when it comes to how natural selection affects microbial community structure and change” (93). Inkpen and Doolittle then return to the NO-REPRODUCTION problem for bacterial communities and build on ‘standard’ evolutionary theory using Hull’s replicator–interactor framework. This move gets them out of the NO-REPRODUCTION dilemma and allows microbial communities to regenerate in a manner that has the same ultimate explanation to ‘why questions’ as limb regeneration in a salamander. Replicators are used for bookkeeping whereas interactors are the targets of selection. Communities can therefore be the target of selection, but this is not where the bookkeeping happens. Inkpen and Doolittle go on to combine this move with canonical multi-level selection theory. They insist that the replicator–interactor separation is acceptable and that selection can occur without reproduction, as long as there is “re-production” (103) (e.g., ecological assembly). They state this clearly: “Interactors can become better adapted to their environments without needing to be selected on the basis of their own differential reproduction” (104).

The final substantive chapter of the text, Chapter 5, *Engineering*, closely aligns to Chapters 3 and 4 in that ultimate explanations to the ‘why question’ of regeneration are addressed—albeit from the view of human normative goals. The natural-artificial distinction is used to show that artificial microbial community engineering necessitates a different ultimate explanation from the evolutionary one previously discussed. Inkpen and Doolittle state that when systems are “engineered by humans for a particular purpose or function, an ultimate explanation is also warranted, one aligned with the human designer's intent" (110). On Inkpen and Doolittle's account, a unique class of ultimate explanations are needed in microbial engineering applications, where specific communities are desired for health or conservation.

Inkpen and Doolittle end the book by stating that conservation efforts may have an additional implication in that community interactors have their own intrinsic moral standing. This is perhaps an overstated claim that risks subsuming organismal agency but is nonetheless an interesting direction for future work.

To summarize, Inkpen and Doolittle's book results in another useful way of thinking about the problem of community regeneration. This includes their proposal of a common ultimate explanation of regeneration using the replicator–interactor framework. Not addressed, however, is how to account for macroevolutionary novelties and possibilities, which may be important when considering SONG repertoires of different taxa, the asymmetric extinction of possibilities, and functional regeneration with 'new stuff'. These are outstanding questions that have bearing on the regeneration problem and would need to be addressed in either (i) Inkpen and Doolittle's proposed framework, (ii) a differing account of selective evolution, or (iii) an altogether different evolutionary theory such as biological structuralism. The goal to revise and improve evolutionary theory is certainly ongoing, and this book undoubtedly helps.

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