is Joel L. Sachs' chapter "The exploitation of mutualisms," where he posits that mutualisms are not as beset by conflicts of interest as the models often assume. Based on the empirical evidence, Sachs suggests most cases of exploitation in mutualisms are caused by parasites of mutualisms and not by evolved cheater mutants. Examples of cheaters tend to be found only in obligate mutualisms, while the majority of mutualisms are more diffuse. We might lack the datasets needed to detect the presence of cheater mutants, or perhaps exploited partners have more options from which to choose when engaged in diffuse mutualisms. Another example of a relatively fresh outlook is found in the chapter on "Mutualism in a community context" by Todd M. Palmer, Elizabeth G. Pringle, Adrian Stier, and Robert D. Holt. This chapter nicely highlights how mutualisms are never simple interactions between two species, and instead are usually composed of multiple mutualistic partners, embedded in a complex community. I greatly enjoyed the chapter, but was surprised to see it did not cite a paper on the same topic (Michelle E. Afkami, Jennifer A. Rudgers, and John J. Stachowicz. 2014. Multiple mutualist effects: conflict and synergy in multispecies mutualisms. *Ecology* 95:833–844).

Although never explicitly stated, the book's content suggests that different contributing authors have conflicting opinions on certain topics. I count this as one of the volume's strengths. A well-rounded view does not emerge from one perspective, but instead from the discussion and synthesis of different opinions and ideas.

In its entirety, *Mutualism* holds a wealth of information from diverse scientists and is an excellent resource for the study of mutualism. This is a field that is rapidly changing, in part because of the many new technologies that enable us to investigate myriad mutualists at multiple levels of analysis. The volume may well end up being a snapshot of our current time. But if so, it will be a thorough and useful snapshot, filled with complex ideas and exciting glimpses of the future. We have come a long way since Robert M. May described how mutualism tended to be neglected in ecological treatments because it was less common (or more subtle to appreciate) in temperate habitats, and because it suffered from the theoretical difficulty that simple Lotka-Volterra ecological models of mutualism "lead to both populations undergoing unbounded exponential growth, in an orgy of reciprocal benefaction" (Robert M. May. 1982. Mutualistic interactions among species. Nature 296: 803–804).

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# Understanding macroevolution through the origin of higher taxa

T. S. Kemp. 2015. **The origin of higher taxa: palaeobiological, developmental, and ecological perspectives**. The University of Chicago Press, Chicago, Illinois, USA. 320 p. $120.00 (cloth), ISBN: 978-0-2263-3581-0; 320 p. $49.00 (paper), ISBN: 978-0-2263-3595-7; 320 p. $39.00 (e-book), ISBN: 979-0-2263-3600-8.

*Key words: character identity networks; developmental evolution; epistemology; macroevolutionary lags; ontology; phenotypic traits; speciation.*

Higher taxa originate often enough that the major phases of the geologic timescale can be quantified by their turnover. But the origination of new higher taxa is rare relative to the origin of new species. Only a subset of speciation events are associated with the origin of one or more novel traits and with the occupation of new ecologies that lead to new higher taxa. This confluence of developmental and ecological novelty leads to innovation, and the proliferation of these traits makes it important and interesting to study the origin of higher taxa.

Tom Kemp (Oxford University) in his new book *The origin of higher taxa* makes an argument for just how important it is for us to understand their origin. In this book, Kemp summarizes and synthesizes what we currently know about the origin of higher taxa. Because ecological, phenotypic, and developmental attributes of organisms all change during the origin of higher taxa, Kemp pulls evidence from the fields of ecology, developmental biology, and paleontology to buttress his arguments that there really is an interesting scientific question here.

And the origin of higher taxa really is interesting, even if the interesting questions are constantly nagged by the possibility that higher taxa may not be real. For some, the reality of higher taxa is important, because if they lack realness, then why bother studying them? I don't share that cynical view, but it is commonly held. For some, higher taxa are arbitrary products of our work to classify organisms, so to study their origins is nothing more than studying the act of classification rather than the evolution of organisms—more an act of philosophy than an act of science. But that cynical attitude misses the point. The origins of higher taxa are inherently interesting because, as Kemp points out, the confluence of changes that occur there represent discontinuities in the macroevolution of lineages. The confluence of changes associated with the origins of higher taxa are observed phenomena. How and why that confluence occurs is an interesting question, even if higher taxa that arise out of that confluence are not themselves real.

The struggle between ontology and epistemology is a theme throughout the book. Each line of evidence comes from a scientific discipline that provides insights but never the whole picture. Kemp spends a lot of time delineating the limits of each possible view on the origins of higher taxa. The paleontological evidence is particularly tricky because the fossil record samples past life in non-random ways. The hope that the fossil record will preserve ancestral forms and allow the easy study of higher taxa is dashed by the fact that ancestors are somewhat rare. Nevertheless, the fossil record is critical because it gives us real examples. It shows that the origins of higher taxa share some similarities and also show some important differences. In some groups, such as irregular echinoids (Hopkins and Smith 2015), their radiation happens close to their time of origin. Yet in other groups, such as grasses, there is a protracted lag between the origin of the group and their subsequent radiation (Strömberg 2011).

The existence of macroevolutionary lags means that the developmental, phenotypic, and ecological changes that occur during the origin of higher taxa don't always happen together. In the evolution of grasses, the ecological opportunity for grasslands significantly postdates the origin of grasses themselves. This lag is due to complex interactions between different higher taxa (various herbivorous mammal groups and other plant groups that compete for space with grasses) and climate changes.

The structure and evolutionary potential of organisms provides the foundation of Kemp's thoughts on the origin of higher taxa. The phenotypic traits of organisms interact with each other functionally and developmentally. Kemp argues that phenotypic traits evolve as an ensemble within populations of organisms by the correlated progression model. This is a model of developmental evolution that he contrasts with the atomistic and modular models. Each of these three models differ only in how the phenotypic traits are connected by a network of interactions. The atomistic model has few connections, the modular model has strong connections within modules and weak between. His correlated progression model hits in-between these, with all traits having a more even distribution of interactions. For Kemp, this model of developmental evolution provides the only route for the suite of phenotypic changes that occur during the origin of higher taxa. However, I'm not sure we need to restrict ourselves to a single model of developmental evolution. Recent theoretical work by Sean Rice (Rice 2004*a*, *b*, 2008) provides an alternative way of understanding developmental evolution that includes all possible interactions networks. Rice's approach produces a phenotypic landscape that is the result of a set of variously underlying factors (genetic, developmental, and environmental), and the path of multivariate phenotypic evolution is described by the structure of that landscape.

Thinking about developmental evolution from the theoretical distance that Rice takes makes it clear that there is another aspect of it important for the origins of higher taxa—phenotypic novelty. The origin of novel traits, those autapomorphies that characterize higher taxa, are a critical part of the story. Novelties are the source of the phenotypic discontinuities between higher taxa, and so understanding how they arise is critical to understand the origin of higher taxa. I am not sure how Kemp's correlated progression model deals with novelty. Wagner (2014) provides a powerful way to think about novelty and its role in developmental evolution through the evolution of homologous traits. According to Wagner, homologues arise when recursive character identity networks (ChINs) are added to the developmental pathway that produces a phenotypic trait. The addition of novel ChINs into the development of an organism is sufficient to provide a discontinuity in overall phenotypes, because part of the phenotype did not exist prior to the origin of the ChIN.

The evolution of irregular echinoids from regular echinoids (Hopkins and Smith 2015) is good example of how complicated the origin of higher taxa can be and yet still be understood. The origin of irregular echinoids involves major shifts in development and ecology and can be seen as a large jump in morphospace. In their study, Hopkins and Smith (2015) show that the paraphyletic regular echinoids are phenotypically contained prior to the divergence of irregulars and that they remain similarly constrained after the split. Irregulars immediately show higher rates of morphological evolution as they occupy new areas of morphospace associated with feeding structures and a new ecology. This shift requires that the developmental capacity of irregulars evolve together with their ecological innovations.

Kemp's book is a good introduction to the ontological and epistemological issues inherent in the study of the origins of higher taxa. I suspect that this is the path that will lead to a new evolutionary synthesis because it focuses our attention on the mechanisms that produce phenotypic and ecological discontinuities. Those higher taxa that show a macroevolutionary lag between the developmental novelties at their origin, and ecological innovations that proliferate when they become successful, are the most promising cases for teasing apart how it all works. If ecological interactions between higher taxa are important factors in the duration of macroevolutionary lags, as Van Valen (1976) suggests, then we might have to embrace the reality and evolutionary significance of higher taxa.

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### Literature Cited

Hopkins, M. J., and A. B. Smith. 2015. Dynamic evolutionary change in post-Paleozoic echinoids and the importance of scale when interpreting changes in rates of evolution. Proceedings of the National Academy of Sciences 112:3758–3763.

Rice, S. H. 2004*a*. Developmental associations between traits: covariance and beyond. Genetics 166:513–526.

Rice, S. H. 2004*b*. Evolutionary theory: mathematical and conceptual foundations. Sinauer Associates, Sunderland, Massachusetts, USA.

Rice, S. H. 2008. Theoretical approaches to the evolution of development and genetic architecture. Annals of the New York Academy of Sciences 1133:67–86.

Strömberg, C. A. 2011. Evolution of grasses and grassland ecosystems. Annual Review of Earth and Planetary Sciences 39:517–544.

Van Valen, L. 1976. Energy and evolution. Evolutionary Theory 1:179–229.

Wagner, G. P. 2014. Homology, genes, and evolutionary innovation. Princeton University Press, Princeton, New Jersey, USA.

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## The Shack revisited: a Sand County memoir

Estella B. Leopold 2016. **Stories from the Leopold Shack: Sand County Almanac revisited**. Oxford University Press, New York, New York. xvi + 325 p $27.95 (hardcover), ISBN: 978-0-19-046322-9; $18.99 (e-book), ASIN: B01G7A8AVM.

*Key words: botany; ecological restoration; ecology; glaciation; land ethic; land health; palynology; phenology; wildlife.*

Aldo Leopold, one of the most influential 20th century ecologists, has left an enduring legacy. The science of ecology today is a direct outgrowth of his prescient ideas about the complexity of ecological communities, the value of predators and disturbances such as fire, and the impacts of a burgeoning human population. His land ethic philosophy, "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise," (Leopold, A. 1948. *A Sand County almanac: and sketches here and there.* Oxford University Press, Oxford) resulted from a lifetime afield, collaboration with seminal ecologists Sir Charles Elton and Olaus Murie, and others, and painful, life-changing lessons learned from his own mistakes. Many books have been published about Leopold's life and evolution as a wildlife ecologist, including outstanding volumes by Curt Meine, Julianne Lutz Warren, Susan Flader, J. Baird Callicott, and Richard Knight. These books delve deeply into the land ethic and the relevance of Leopold's ideas in today's world. Indeed, one could say that this ground has been thoroughly plowed.

*Stories from the Leopold Shack: Sand County revisited* by Estella B. Leopold, Aldo Leopold's youngest child, in her own right an eminent ecologist who initially worked as a palynologist at the US Geological Survey and subsequently became a professor at the University of Washington, where she taught forestry and botany, uniquely complements the formidable Leopoldian literature mentioned above. It provides a plain-spoken, intimate memoir of life at the ecologically-impoverished, Central Wisconsin farmland her family acquired in 1935 and dubbed simply the "Shack."

"This book is about two things: familiarity with nature and togetherness," writes Estella. Focusing on the Shack, which was little more than a dilapidated shed on degraded agricultural land when the family purchased it, she explains how her parents saw this property as a "land of opportunities" for them. Intended to be a hunting retreat, the Shack was restored by the Leopolds to improve wildlife habitat. To do so, they worked diligently across the arc of the seasons and span of the years in what was essentially a labor of love, planting pines, oaks and native plants. However, Estella notes that just as they restored the land, the land restored them. Their father forged his land ethic philosophy during this formative period, while wrestling with stressful natural resources problems such as an irruptive deer population that had wiped out its habitat and was subsequently dying *en masse* of starvation.

The only one of Aldo Leopold's children alive today, Estella was not alone in following in her father's footsteps. Siblings Starker (professor of vertebrate zoology, UC Berkeley), Luna (professor of hydrology, UC Berkeley), Nina Bradley (wildlife ecologist and naturalist), and Carl (professor of plant physiology, Purdue University) all distinguished themselves in their fields.