

# CONTEXT-DEPENDENCY RULES THE DAY IN THE GRASS-ENDOPHYTE SYMBIOSIS

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A review of “Ecology and Evolution of the Grass-Endophyte Symbiosis” by Gregory P. Cheplick and Stanley H. Faeth (2009, Oxford University Press, hardback, 256 pages, ISBN13: 978-0-19-530808-2, ISBN10: 0-19-530808-5, \$75.00)

In the Introduction to their book on the grass-endophyte symbiosis, Cheplick and Faeth state that “A general theme will emerge that much of the variation in the nature of the interaction is due to environmental and genetic contingency.” Indeed, one of the striking features of the grass-endophyte symbiosis that emerges in this thorough review of the empirical literature is that contingency and variability run rampant, and generalizations are nonexistent. This theme of contingency is one example of how the book frames the empirical literature on the grass-endophyte symbiosis in an appropriately broad and contemporary framework of basic ecological and evolutionary ideas. In introducing the theme, they highlight parallels with other putative mutualisms, such as mycorrhizal interactions, and draw inspiration from general theory on contingency in putative mutualisms (e.g., Ewald 1987, Bronstein 1994). Overall, the book effectively argues that explorations of the wide variability in ecological outcomes in grass-endophyte symbioses are likely to yield fruits in multiple subfields of ecology and evolution.

The contingency theme, with respect to effects of endophytes on hosts, is continued in Chapter 2, where the continuum of positive to negative effects that fungal endophytes can have on host plants is presented in detail. In this chapter, it becomes apparent that the authors not only highlight most or all of the important work already conducted on the symbiosis, such as key studies doc-

umenting contingency of ecological outcomes on drought stress, but that the review also aims to highlight important gaps in the literature. For example, the authors point out that another continuum present in the symbiosis is the habitation of a range of light conditions from sunny, open fields to dark forest understories, and that this continuum has yet to be thoroughly explored.

In fact, an important argument made in the book is that grass-endophyte symbioses may be particularly useful for answering big questions in ecology and evolution, precisely because they span so many different continua of variables that may influence ecological and evolutionary outcomes. It has recently been argued that comparative studies along environmental gradients provide powerful tests of hypotheses in community ecology (McGill et al. 2006); grass-endophyte symbioses seem to present the opportunity to use gradients of biotic and abiotic factors in a similar manner to test hypotheses about how traits of species interactions influence ecological and evolutionary outcomes. Besides the abiotic gradients discussed above, other gradients in the symbiosis highlighted by the authors include the degree of horizontal versus vertical transmission of the endophyte, sexual versus asexual reproduction of both host and endophyte, and infection frequency, all of which have been observed to vary within and among different species involved in these symbioses. Although such factors are not factorially distributed among different examples of the symbioses, their autocorrelation may provide some interesting clues to the combinations of traits favored by natural selection. One example is the fascinating pattern that asexual endophytes (e.g., *Neotyphodium* spp.) are vertically transmitted by hosts that retain sexual

reproduction ability, whereas sexual endophytes (e.g., *Epichloë* spp.) are horizontally transmitted and also often prevent sexual reproduction in their hosts (effectively killing the Red Queen or at least preventing her from running!). As a consequence, these two symbioses tend to exhibit different patterns of genetic variation.

In Chapter 2, it also becomes clear that the book will serve not only as a highly detailed compendium and review of empirical literature, but also as a best-practices guide for those aspiring to work in these systems. Almost all important studies on grass-endophyte symbiosis to date seem to be mentioned and at least briefly summarized; as such, the book may be overly detailed in places to hold the interest of a general audience. On the other hand, it serves as an essential reading for graduate students and other scientists working on these organisms or considering a foray into them. For example, on pp. 20–21 the reader finds a detailed argument about the best methods to use in eradicating endophytes from seeds with fungicide treatments.

Chapter 3 begins the book's exploration of the consequences of plant–endophyte symbioses for other components of the ecological community, starting with herbivores. Continuing the emphasis on contingency, the chapter argues that effects of endophytes on host resistance to herbivores are erratic, varying from positive to negative, and explores the reasons for this variability. One key explanation offered revolves around the intriguing problem of the alkaloids produced by many fungal endophytes—these chemicals often deter herbivores, but vary greatly in their presence, abundance, and specific chemical composition within and between different grass-endophyte combinations. Indeed, some herbivores have evolved to tolerate, detoxify, or even sequester the alkaloids, becoming even more effective herbivores in the process.

Chapter 4 again balances review of existing literature with highlighting research gaps and needs—in reviewing genetic variation and genotypic specificity in grass-endophyte interactions, the chapter reviews studies showing the potential for ongoing natural selection on traits governing the symbiosis, but also highlights major gaps in the data needed to understand the latter. For example, a reasonable number of studies in wild and agronomic systems provide evidence for significant host genotype by endophyte infection ( $\pm$ ) interactions on components of host fitness, suggesting the potential for ongoing selection on host responses to endophyte infection. However, as the authors acknowledge, our ability to understand the potential for ongoing “coevolutionary” selection in the symbiosis is severely limited by the paucity of studies controlling both host and endophyte genotype. Furthermore, although the relevant coevolutionary theory could have been developed in a bit more depth, the authors show that data do not yet exist to effectively assess whether grass-endophyte symbioses are influenced by coevolutionary selection mosaics, the detection of which requires experiments controlling not only host

and symbiont genotype, but also variability in an additional biotic or abiotic factor.

One compelling aspect of Chapter 5, which builds on Chapter 4 to explore aspects of the evolutionary ecology of grass-endophyte interactions, is the presentation and assessment of hypotheses to explain why infection frequencies observed in nature are often at intermediate levels, rather than reaching equilibria at 100% or 0% within populations. In the wild study system involving *Neotyphodium* infection of Arizona fescue, the endophyte consistently has negative effects on host fitness, raising the question of how endophytes persist at high frequencies. The authors carefully review the evidence relating to multiple hypotheses to explain this observation. One potential explanation developed by the authors is geographic variation in selection, as emphasized by the geographic mosaic theory of coevolution (GMTC; Thompson 1994, Thompson 2005). Here, key aspects of GMTC theory (hot spots and cold spots, and trait remixing processes) are clearly outlined, and observations from grass-endophyte studies are used to suggest how this theory could be tested. On the other hand, the key GMTC concept of selection mosaics, i.e., geographically variable coevolutionary selection, was not explicitly addressed, although the authors do show how the grass-endophyte system could be used to test for its presence. The argument that grass-endophyte symbioses should be useful for testing GMTC is augmented by the continuing argument that many potentially relevant traits of the symbioses fall along continua, potentially allowing comparative analyses to test predictions of theory. For example, some endophyte–host combinations will exhibit strong differentials in gene flow patterns between host and symbiont, and others will not; such differentials should influence coevolutionary outcomes. Ultimately, the authors show that despite the high potential for testing coevolutionary theory using grass–endophyte symbioses, we are a long way from understanding the geographic mosaic of coevolution in these interactions.

Chapter 6, which explores community and ecosystem consequences of grass endophytes, effectively uses a review of this literature to complete the key theme of the book—contingency of ecological outcomes on numerous factors, especially emphasizing that the result of this multifactorial contingency is substantial complexity and variability in the consequences of endophyte infection. As a result, the question emerges of whether endophytes make a net difference for host fitness. As emphasized in earlier chapters, it becomes clear in the empirical review that although we have enough data to feel confident of the strong contingency, complexity, and variability of effects, we still lack the studies necessary to answer this broader question. The authors conclude that empirical studies should begin to emphasize explicitly studying this variability within and among natural systems, rather than continuing to focus on utilizing agronomic systems. In the seventh and final chapter, they extend this argument to develop

specific future directions for research, arguing in particular that the most-studied grass-endophyte symbioses involve a handful of agronomic grasses, and that those agronomic interactions represent only one point along the continuum from antagonism to mutualism that needs to be explored. Although the final chapter develops a number of specific research directions, ranging from particular types of effects of endophytes on host biology that have not explored, to more specific hypotheses on the GMTC in grass-endophyte interactions, a unifying theme is that these studies largely need to be carried out in wild (nonagronomic) systems for progress to be made most rapidly.

Ultimately, for the general reader, the picture that emerges is that although grass-endophyte interactions have the potential to be used to test and contribute to a modification of general theory on the ecology and evolution of species interactions, we are not there yet. The general reader of this relatively short but content-packed book sees a bewildering level of complexity in the set of studies already performed, and the authors are convincing in arguing that the state of the science will only get more complex as natural systems are further used. So, that we are not far along yet in testing and modifying general theory with these systems is not because these interactions have been ignored in general, but rather because many of the difficult but necessary work for such advances still

needs to be done. This synthesis does an excellent job of both pulling together the work already done and highlighting the gaps, to facilitate a next generation of such studies. For readers with a particular interest in grass-endophyte symbioses, or for budding scientists considering delving into these systems, the book will serve as an indispensable resource.

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