
Review: [untitled]

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Reviewed work(s):

Plant Life Histories: Ecology, Phylogeny, and Evolution. by J. Silvertown ; M. Franco ; J. L. Harper

Source: *New Phytologist*, Vol. 142, No. 1 (Apr., 1999), pp. 1-2

Published by: Blackwell Publishing on behalf of the New Phytologist Trust

Stable URL: <http://www.jstor.org/stable/2588635>

Accessed: 29/05/2009 14:07

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Book reviews

Plant life histories: ecology, phylogeny, and evolution.

(Ed. by J. SILVERTOWN, M. FRANCO and J. L. HARPER.) 15 × 23 cm. Pp. 313. Cambridge, UK: Cambridge University Press. Price £19.95. ISBN 0 521 57495 1.

Ecology and the comparative approach

Over the past 30 years, plant evolutionary ecologists have focused on microevolutionary processes through the use of manipulative experiments and by matching optimality models with field data. The product of this focus has been an accumulation of examples of present-day organisms showing traits that can in some sense be considered adaptive. It is easy to conclude that these traits are the result of present-day evolutionary processes; however, recognition is currently emerging that in order to test ecological and evolutionary hypotheses it is necessary to consider historical phylogenies and comparative approaches in order to understand the role of macroevolutionary processes in shaping the observed variation. Silvertown, Franco and Harper suggest that the time is ripe to re-examine the relationship between different plant life-history traits, and between those traits and the selective pressures that shaped them, using the phylogenetic perspective. With the increased application of molecular techniques to a wide variety of taxa, molecular phylogenies are being constructed which can provide hypotheses about the chronicle of evolutionary events. Applying these phylogenies in a comparative analysis of ecological data is an important, indeed perhaps the best, way to establish the generality of experimental results.

Many new comparative methods have been developed in recent years, and the number of discussions and studies on the relative merits of one technique over another has increased. In this book, the relative merits of phylogenetically independent contrasts and tip correlations are actively debated. Whereas all of the authors of this book would agree that comparative approaches can expand our understanding of variation in life-history traits, it is clear from reading this collection of papers that there is no consensus on which particular comparative technique should be used.

The book starts with a chapter by Silvertown and Dodd in which they suggest that because traits are not randomly distributed across taxa, an analysis of trait correlations cannot treat species as independent data points because of problems of pseudo-replication. According to the authors, this problem thus dictates that phylogenetically independent contrasts must be used to reconstruct trait changes along the branches of a tree. This approach is applied in nearly all of the chapters, for example by Crawley in an analysis of traits distinguishing native and alien members of the British flora, by Franco and Silvertown in a comparative analysis of demographic traits in plants, and by Rees in a study of seed dormancy and seed size. As

outlined in a chapter by Westoby *et al.*, phylogenetically independent contrasts are inappropriate for certain models of evolution, for example, for models in which a change in one trait is a prerequisite for a change in another, for models that regard stasis or maintenance of a trait as meaningful events, and for models designed to investigate the present-day ecological function of traits. Westoby *et al.* suggest that these alternative models of evolution are appropriate not only in their own study on the comparative ecology of seed size and dispersal, but also in studies by Barrett *et al.* looking at the comparative biology of pollination and mating in flowering plants, and in a study by van Groenendael *et al.* on the comparative ecology of clonal plants. This disagreement among the authors about the different methods of comparative analysis is the continuation of a controversy which was initiated in the literature several years ago (see *Journal of Ecology* **83**). Clearly, the approach that one uses depends not only on the questions being investigated, but also on the particular model of evolution being applied. In a very balanced chapter on phylogenetic studies and sensitivity analysis, Donoghue and Ackerly suggest that, in addition to phylogenetically independent contrasts, there is much to be learned from the analysis of discrete characters or mixtures of discrete and continuous variables. Their general message is that more than one comparative method should be used because, ideally, comparative biology should integrate both homology and convergence approaches for an understanding of the causes of evolutionary change and ecological patterns.

Whereas the comparative techniques described in this book have been used in a few isolated plant studies in the past, this volume represents the first broad attempt to pull together studies across a range of characters. However, by so doing it also reveals the premature nature of these types of analyses, both with respect to the phylogenies available and the completeness of the ecological data. The primary assumption of phylogenetically based comparative studies is that the study is founded on an accurate phylogeny. The majority of papers in this book use Chase's (1993) phylogeny B of seed plants based on *rbcL* sequences. In other words, they rely on one phylogeny based on a single maternally inherited gene. It is also somewhat disturbing that a more recent re-analysis of the Chase data set has yielded many shorter and more parsimonious trees for the same data (Rice *et al.*, 1997). Clearly, the future of the comparative approach depends on the development of robust phylogenies based on more genes, which will also allow a finer resolution at the species level. Furthermore, as Donoghue and Ackerly suggest, sensitivity analyses need to be applied to the results of comparative studies to assess the robustness of the conclusions.

Comparative studies rely not only on good phylogenies, but also on good data from related species. In several of the

papers it is noted that the data needed for a thorough application of this approach is not currently available. For example, in Franco and Silvertown's analysis of demographic variation, each family was on average represented by two species, most orders by only a single family. A wider data set is needed in order to understand the covariation of traits at lower taxonomic levels. The sparsity of data for closely related species was also a problem for Fitter and Moyersoen's analysis of root-microbe symbioses, for Barrett *et al.*'s analysis of selfing rates, and for Goldberg's analysis of competitive ability.

The majority of papers in this book directly address the issue of applying phylogenetically independent contrasts to evaluate ecological observations. There are a few papers which use other techniques to address issues concerning the evolution and diversity of plant life-history traits. Hamrick and Godt use recent allozyme data to update their previous review on genetic diversity in life-history traits, and Schoen *et al.* use floral ecology and molecular genetics to examine the historical development of selfing in different lineages. Additionally, in a paper by Futuyma and Mitter, the importance of phylogeny in insect-plant associations is evaluated. There are two more theoretical papers, which address issues about effects of selection on plant life-history traits, and while of interest, do not address phylogenetic issues directly. Venable discusses models which consider the simultaneous action of selection on multiple components of the reproductive design, which can help in the interpretation of comparative studies of subsets of traits. Sibly reviews the theories of life-history evolution which are constrained by trade-offs in spatially and temporally heterogeneous environments, and addresses the fact that, given the unique properties of plants, the current theory might not always be appropriate.

The major emphasis of this book is to push studies of plant life-history to the next level of comparative analysis by employing phylogenetic contrasts to reveal general patterns. The common thread among the papers in this book is that, in the next 10–20 years, putting species into a comparative context will be a key to research in ecology for the improved meta-analysis of the large number of studies which have accumulated, and for creating generalizations from the data available. The major value of this book, and more generally of the application of the comparative approach to plant life-history variation, is that it highlights the holes in the available data and therefore serves as a focus for future studies. Whereas there may be problems, with respect to the quality, consistency, and quantity of the current life-history data across a wide range of taxa, and problems with respect to the accuracy of the currently available phylogenies, the impact of this book will be to bring these issues and approaches more to the forefront of the consciousness of plant ecologists.

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Wicken Fen. The making of a wetland nature reserve. (Ed. by L. FRIDAY.) 24.5 × 17 cm. Pp. xvi + 306 with 84 text-figures and 16 colour plates. Colchester, UK: Harley Books. Price £24.50. ISBN 0 946589 58 5.

Rather few British fens have well produced, well illustrated monographs dedicated to them but, as in many matters, Wicken Fen is an exception. Wicken was the pioneer Fenland nature reserve; it is perhaps the most visited fen in Britain; it has (thanks to its proximity to Cambridge) been the focus of much ecological research; and it has, according to the editor of this volume, 'almost iconic status' in the British conservation movement. Certainly, for many people, it is seen as *the* British fen – which in some ways is unfortunate as for the last few decades at least, it has had as much in common with some types of wet grassland as with true fen. One wonders to what extent some of the early ideas about the ecology of British fens might have been different had workers such as H. Godwin and A. G. Tansley been able to spend more time in less idiosyncratic sites (for example, Godwin's conclusion that the limit of scrub invasion at Wicken was fixed by winter water levels lacks general applicability in fens – summer water levels are usually more important).

This book is the second main monograph about Wicken Fen: the first was a series of volumes edited by J. S. Gardiner over the period 1925–1932. Like its predecessor, this publication includes accounts of the ecology, main habitats, biological records, history and management of the site. It is based on the contributions of 24 authors, includes much detailed information and – particularly useful – provides access to many data hitherto unpublished. Much of the material is discussed in a rigorous and informed way. For example, the authors have digested, and report accurately, one of Godwin's more complex papers, in which he observed that daytime water-table reduction in summer could be greater under grassy vegetation than under fen carr – a welcome change from the frequent assertion of some conservationists, that 'trees dry out wetlands'.

There is a wealth of material here for naturalists and ecologists, especially – but by no means exclusively – for those who find wetlands agreeable habitats in which to spend some of their time. The authors were obviously limited by the availability of information and I was interested to observe what was *not* in this book. Given that water is rather important to the character of wetlands, one might have expected some reasonable runs of water-level data from this doyen of wetland reserves, but none is presented here. Presumably they do not exist? The custodians of Wicken undoubtedly feel that their fen has been getting drier, to the extent that low-permeability membranes have been inserted around parts of the site quite recently, but the only evidence I found cited to justify this project was the fact that water levels in 1975 and 1976 were 30 cm lower than those recorded by Godwin 45 years earlier – but then these were drought summers when fen water levels were unusually low throughout East Anglia. Such is the stuff that management decisions are made of and, as is often the case, the chapter on Management (ch. 11) is better at describing what has been done than providing a detailed rationale of why.