

Review: The Highs and Lows of Tropical Forest Canopies

Reviewed Work(s): Tropical Forest Canopies: Ecology and Management by K. E. Linsenmair, A. J. Davis, B. Fiala and M. R. Speight

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historical patterns and involve advanced analyses of multiple taxonomic groups' cladograms (especially from plants) and from these analyses attempt to ascertain the histories of the individual groups. Isn't that the goal?

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- The highs and lows of tropical forest canopies**
- Linsenmair, K.E., Davis, A.J., Fiala, B. & Speight, M.R., (eds) (2001). *Tropical forest canopies: ecology and management*. Kluwer Academic Publishers, Dordrecht, Boston, London. 370 pp., plates, figs, tables, index. Hardback: Price EUR 125.00, 79.00, USA \$115.00. ISBN 079237049X.
- Tropical Forest Canopies* (TFC) should be read almost cover-to-cover by anyone seriously interested in canopy habitats. The book includes well-crafted reviews, and yet, in contrast to its predecessor, *Forest Canopies* (Lowman & Nadkarni, 1995), most chapters also offer new results. Research based in Central America often seems to dominate tropical ecology, but the studies presented in this book bring to mind the comment by Paulo E. Vanzolini that 'the tropics are not a plot of convenient forest in Costa Rica.' I found it refreshing to read about projects from Borneo, French Guiana, Venezuela, and elsewhere. This might reflect the fact that nine out of 10 TFC authors are from outside the USA: TFC is a reprint of volume 153 of the Dutch-based journal *Plant Ecology* (© 2001) and its contents originated as a series of lectures at Oxford in 1998, sponsored by the European Science Foundation.
- Beyond occasional line-editing problems, the content and style of TFC are generally more uniform than in Lowman & Nadkarni (1995) which contains articles that vary from those comprehensible to undergraduate biologists to those impenetrable except to authorities in a narrow subdiscipline. TFC is aimed at ecologists and is especially useful for canopy specialists because it takes over where Lowman & Nadkarni (1995) left off, with chapters surveying the experts or the literature on selected topics to address trends and to discuss problems arising from the climbing methods researchers have used, or the conceptual issues needing further study: I heartily recommend the overview by Martin Barker and Michelle Pinard and the chapter on invertebrates by Yves Basset and on vertebrates by Roland Kays and Allen Allison.
- There is a widespread tendency for forest scientists to treat 'canopy biology' as synonymous with forest research. Happily, all the chapters of TFC spell out their focus on forests, and thereby explicitly exclude other ecosystems, whether natural or agricultural, terrestrial or marine, for which the term canopy can be (and often is) applied. Nonetheless, I was disappointed that none of the chapters in TFC took on the challenge of comparing the canopies of forests with those of other (tropical) systems. Many concepts and models developed for canopies as diverse as mowed lawns, kelp forests, and biofilms might be applied to forests (Moffett, 2001), but a continued myopia has kept these literatures almost entirely separate.
- Frans Bongers' assessment of tropical rain forest canopy structure should have been Chapter 1, especially given his is the only chapter to attempt to clarify the book's topic by asking what a 'forest canopy' is. Bongers shows the word is used in varied ways. He employs the term himself to describe the 'total above ground part of the forest', including thereby the herbs down at our feet, the approach I also prefer (Moffett, 2000). Bongers doesn't give a reason for his choice, but this broad definition avoids arbitrary and imprecise delimitations within above-ground plant parts; reduces semantic entanglements when 'canopy' is used in combination with terms like 'epiphyte' that are applied to organisms regardless of height or location on the host or the host's growth form; includes the more narrow definitions of 'canopy' as special cases; and allows for ready comparison with non-forest canopies.
- Throughout the literature on 'canopy biology', few researchers spell out their views on the word 'canopy' with precision, so that it is often difficult or impossible to tell if two articles are in fact discussing the same thing, and so can be compared.

Elsewhere in TFC, Bongers's definition is used (at least implicitly) only in the chapters on throughfall by Calder and by Chappell *et al.* In all other chapters for which I could glean information, there are phrases to suggest that, for those authors, canopy biology variously encompasses either (1) parts of the forest beyond everyday human reach; (2) all trees (or tree crowns) in combination, regardless of their height (but in contrast to Bongers, Calder and Chappell *et al.* one assumes not herbs and shrubs); or (3) the uppermost tree crowns alone. Other variations, such as using canopy to describe the outermost leaves (i.e. the 'outer canopy'), are absent from TFC but common elsewhere. Some TFC authors try to reduce ambiguity with the phrase 'upper canopy' but never say what a 'lower canopy' might be. Confusion abounds in the literature: it is not unusual to see 'understorey' used to describe a stratum that is *separate* from the canopy stratum (or strata), and then, at another point in the same article, to find the same word used to describe 'part of a canopy' or perhaps equivalently, 'one of the several canopy layers'. In her chapter in TFC, Margaret Lowman questions the overall value of distinguishing the study of the canopies of forests from the general topic of forest ecology; indeed, in reading TFC, it is an interesting exercise to notice where it is possible to remove the word 'canopy' (or to change the word to 'forest') without changing the meaning. In fact, the accuracy of many statements appears to be improved by such an edit. This is notably true for the chapter by Nigel Stork on management implications of canopy research, where arguments regarding the significance of canopies to conservation of biodiversity seem ironic given that—as Yves Basset points out in his earlier chapter—much of Stork's research and writings have focused on countering the view that tropical forests harbour an inordinate diversity of canopy specialists, as compared to, say, the impressive biodiversity of forest soils (e.g. Stork, 1988).

The research findings of Stork and others suggest to me that the best conservation choices should be based on information about forests taken as a whole. This view appears contrary to a proposal by the International Canopy Network, as it is described by Nalini Nadkarni in TFC, to

identify 'canopies of international significance for conservation', or CIS, none of the criteria for which appear to be necessarily canopy-specific. How likely is it that a forest will harbour a 'significant' canopy flora and fauna and at the same time be found 'insignificant' for ground or soil species? It is impossible to conserve the top portion of a system without conserving its bottom. To succeed as conservationists, forest canopy biologists need to work as equals with other forest specialists to develop programmes that make this explicit.

A millennium is a time for reflection in all things, canopy biology among them. K. Eduard Linsenmair notes in his foreword how canopy biology is 'maturing' by 'becoming more experimental and predictive', an idea echoed by Andrew Mitchell. Stephen Sutton describes the history of canopy science as a shift 'away from pure exploration (the 'Wonderland' phase) to tackling the practicalities of rigorous canopy research (the 'Reality' phase), and the underlying emphasis is now shifting from access to the upper canopy *per se* to conducting replicative and manipulative science.' Nadkarni similarly sees a change from early studies that 'identify phenomena and document patterns' to group-based projects that 'address process orientated questions to explain the observed patterns' and on from there to the validation of 'predictive models.' Yet, in examining nearly 2700 forest canopy papers, I have failed to detect any such trends. Numerical and statistical techniques in canopy biology have always been a reflection of their time, and canopy ecology has grown as ecology has grown. It is worth remembering that some of the most creative papers on the subject remain some of the earliest works. To take one example, many classic studies of epiphytes contain numerous experiments and predictive models, superb for their day and still full of useful insights—consider the work of Colin S. Pittendrigh, Mason E. Hale, Jr., Takahide Hosokawa, Dick R. Johansson, and others (e.g. see Barkman, 1958).

Sutton, Nadkarni and others stress the need for standardized research protocols. For conservation endeavours standardization may have its uses, but in developing a robust science I think that, if overemphasized, the idea could be deadening. As

ecology has grown, the available points of view on issues and the options for attacking a problem have expanded, not shrunk; the range of possibilities is what attracts the best minds to a field. Bongers hits the nail on the head in his section 'Canopy structure: what do you want to know?' Similarly, to allow for the growing possibilities, pivotal terms (e.g. canopy and stratification) need to be defined broadly so they can be adapted (explicitly, and with logic and care) to an increasing variety of viewpoints and situations (Moffett, 2000; Parker & Brown, 2000). At the same time, successful implementation of massive common data sets, advocated by several authors in TFC, will require at the minimum a clear expression of the subject of enquiry. As long as scientists are ambiguous even as to what strata they have in mind by the term 'canopy' (and, further, as to what they mean by 'strata'; Parker & Brown, 2000), attempts to manage common data sets or any other form of synthesis will contain serious hidden flaws, and canopy biology, regardless of other successes, will not reach its much-heralded intellectual maturity.

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