Convergence and divergence in fire-prone ecosystems

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Review Title:
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Ecologists aim to develop robust rules to explain how plant and animal communities come to be assembled as they are. These rules should explain, for example, why some plant communities have many more species than others, or why plant communities often differ markedly in structure under seemingly similar conditions. Ecologists should also address ecosystem management, so that research findings can be put to practical use. One approach to addressing these questions has been to examine the structure, composition and management of ecosystems that experience similar conditions in different parts of the world. Comparative studies of Mediterranean-type ecosystems (MTEs) provide an example of such an approach, and have been conducted for almost 40 years.

Mediterranean-type ecosystems share a climate characterised by cool, wet winters and warm, dry summers, and these ecosystems support vegetation that is typical of particular regions – fynbos in the Cape; chaparral and coniferous forests in California; kwongan, heaths and dry sclerophyll forests in southern Australia; maquis and garrigue in the Mediterranean basin; and matorral in Chile. These ecosystems cover just 5% of the earth's land surface, yet they contain 20% of the world's plant species, many of which are not found anywhere else. A pervasive feature of these areas is the frequent occurrence of intense fires in the dry summer season. Historically, biogeographers and ecologists have attempted to explain the structure and composition of vegetation in terms of climate and geology alone. One of the more recent contributions arising from the study of MTEs is an understanding of the critical role that fire plays in shaping vegetation. A central theme of the book is that plant communities cannot be understood without considering the climate–fire–geology filter that controls the assembly of these systems. Another uniting theme within fire-adapted and fire-dependent MTEs is how ecosystem managers can ensure the survival of the remarkable biodiversity that coexists cheek by jowl with dense human settlements.

The tale unfolds in this book in three parts. The first is a broad introduction to MTEs and fire; fuels, fires and fire regimes; fire-related traits in plants; and how plants respond to fire regimes. The second addresses each of the five MTEs separately, covering aspects of the vegetation, fire environment and fire ecology. The third part compares and synthesises the evolution of fire adaptive traits, how fire regimes originated in MTEs and came to shape the modern vegetation, and how these systems are managed.

The vegetation of MTEs is remarkably variable, ranging from sparse shrublands to forests. Fires in these ecosystems include crown fires that kill most of the vegetation, and surface fires that burn in the understory of forests; these fire types differ significantly in frequency and intensity. Understanding these regimes is fundamental to interpreting the many and varied responses of component plant species. The vegetation is often a complex mix of plants that resprout after fire, plants that are killed by fire and have to ensure their seed survival and germination, and plants that are able in other ways to attune their reproduction and dispersal to fire-prone environments.

It is not only the similarities between MTEs that are of interest – the differences are equally fascinating. Fire is a pervasive feature of each of the MTEs, but in each it plays out in very different ways. In Chile, fires have not been a feature of the landscape since the Miocene, when the rising Andes prevented convective thunderstorms from progressing eastwards, robbing the vegetation of a ready source of ignition. As a result, there are fewer fire-adaptive traits in matorral plants, although some plants that retain these traits linger in the landscape as relicts of a past that featured frequent fire. Following European settlement in 1880, fires once again became common in the Chilean matorral, and are a regular feature of the area. In the Mediterranean Basin, an increase in fire has been driven by emigration rather than immigration. Centuries of human settlement created a cultivated landscape in which fires were relatively rare. Socio-economic changes in the 1970s were accompanied by rural depopulation, abandonment of farmlands and a reduction in grazing pressure, leading to a build-up of fuels and an increase in the number, size and severity of fires. California is different in that it has varied fire regimes that include intense

crown fires in shrublands and relatively low-intensity fires in conifer forests, sending the vegetation on very different trajectories of evolution and responses. Relatively low-nutrient environments in the Cape and Australia have driven the evolution of vegetation that is much richer in species than that of the northern hemisphere MTEs.

South African readers will have a particular interest in the account of fynbos fire ecology, and this book provides the first comprehensive synthesis of this topic since the publication of *The ecology of fynbos*[1] 20 years ago. Surprisingly, this earlier volume had no chapter dedicated to fire, although fire was addressed in a chapter on management. The latest synthesis therefore contains a greater depth of coverage than has existed before, and there is also much that is new. Recent research has highlighted the dynamic and competitive interactions between overstory and understory plants that significantly influence the nature of post-fire communities. This research is in contrast to earlier views that explained post-fire assemblages in terms of fire survival attributes only. More recent research has also revealed important differences in plant responses to fires in different seasons between the eastern and western parts of the fynbos. Now, fire regimes, and how they are influenced by management practices, are also far better understood.

The comparative study of MTEs in relation to fire allows for the identification of characteristics of divergence or convergence – 'emergent properties' – that would not have been evident from the study of any one of the regions in isolation. Plants have to cope with an environment in which the vegetation forms a continuous fuel bed that supports spreading fires over large areas. Traits have evolved to include a mixture of re-sprouting and of fire-dependent reproduction, where closed canopies prevent recruitment in mature stands and where seedlings must exploit the resources released by fire to survive and grow. Both traits have persisted because fire regimes are not predictable enough for either to gain dominance. Studies of the origins of Mediterranean-type vegetation have until recently focused largely on the role of climate and soil fertility as determining factors, and fire has received scant attention. However, the Mediterranean climate's seasonally high temperatures and dry conditions have combined to expand fire's footprint on the landscape, which has had profound effects on the vegetation. But the prevailing order is changing rapidly in the face of invasions by alien plants, which often are moved from one MTE to another. These alien plants are frequently spread by fire, and are changing fuel conditions and fire regimes, with devastating consequences for the diversity and functioning of some systems.

Another aspect within the book that will be of interest to South African readers is the almost trivial nature of our 'fire problem'. While wildfires in the Mediterranean Basin, California and southern Australia can – and have – destroyed thousands of dwellings in a bad fire year, the extent of damage in South Africa is typically two to three orders of magnitude smaller. This difference is partly as a result of less severe fire conditions, and partly because of 'hard' edges between urban areas and the veld, a legacy of good planning in the past. Nonetheless, the problem in South Africa is set to grow as populations grow, and the need to reconcile competing demands for safety and ecological health in fire-adapted ecosystems will tax managers of the future, despite the relatively minor magnitude of the current problem.

Overall, this book provides a remarkably comprehensive treatment of an important topic. Syntheses of this nature cannot be found in journal papers or even in special journal issues dedicated to one or another topic. While most ecological books are either written by one or two experts, or are edited volumes with multiple authors, this book is unusual in that it has five authors who have taken joint responsibility for all of the material presented. Each author is a leading world expert in fire ecology, and each calls one or the other of the major MTEs home. Collectively, these authors have more than two centuries of experience, and the depth and scope of their insight is reflected in this book. Almost one fifth of the book (100 pages) contains the references – testimony to the breadth of coverage and a valuable resource in itself. As such, this book should prove indispensible to graduate students, researchers and managers of fire-prone MTEs, and I would recommend it unreservedly.

Reference

1. Cowling RM. The ecology of fynbos: Nutrients, fire and diversity. Cape Town: Oxford University Press; 1992.