

What surprised me most while reading this book is how few generalities we have yet established about speciation in wild populations, other than it tends to be allopatric and that selection plays a major role. Price's knowledge of the literature and scholarship is magnificent, and he makes ground-breaking use of meta-analyses and formal comparative tests where the data are available, yet I was repeatedly struck by the fact that support – or refutation – of key ideas rests on one or two cameo examples rather than on a substantive body of evidence. This even applies to mechanisms as central to the modern speciation debate as reinforcement and divergence via sexual selection. The case examples used to support these mechanisms are often very convincing in their own right but it is difficult to know whether they illustrate general patterns or whether are (albeit alluring) oddities. My instinct is that to substantially advance our understanding of speciation in the wild, we need to make more use of naturally replicated systems that have very recently undergone divergence, because examples based on two- or three-population comparisons, or on anciently diverged species, are simply inadequate to differentiate between the most interesting hypotheses. In addition, if we are to achieve Price's goal of using birds as a model group to synthesise theories of ecology, behaviour and genetics, we also need to make more use of systems for which genetic information can be obtained because, at present, our knowledge of genetics in wild populations is clearly a limiting factor.

In the end, Price's book is both a forceful reminder of why speciation remains one of the big challenges in evolutionary biology and a warning that such important matters should not be left to the fly pushers alone. I would challenge any student of evolutionary biology to read this book and not be struck by how many behavioural and ecological questions remain to be addressed, or be infused with ideas on how to tackle those questions in wild populations. I would, therefore, highly recommend this book, not only to those enlightened souls already fascinated by bird diversity *per se* but also to workers across the broad fields of evolutionary ecology and genetics. Price's message is a very general one: to build a synthetic theory of speciation, we need to think differently about the fundamental processes at the heart of evolutionary divergence.

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doi:10.1016/j.tree.2007.11.013 Available online 4 March 2008

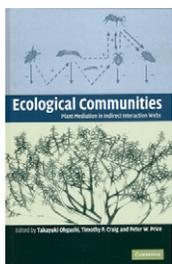
Book Review

Non-trophic interaction webs mediated by plants

Ecological Communities: Plant Mediation in Indirect Interaction Webs by Takayuki Ohgushi, Timothy P. Craig and Peter W. Price, Cambridge University Press, 2007. \$160.00, hbk (458 pages) ISBN 978 0521850391

Sharon Y. Strauss

Dept. of Ecology and Evolution, UC Davis, Davis, CA 95616, USA



Any non-lethal interactor with a plant can induce changes in plant traits, which, in turn, can affect other plant associates. Such trait-mediated indirect interactions (TMIIs [1]) can be generated by a diverse assemblage of species, both above and below ground. While one can immediately think of some obvious TMIIs, such as induced resistance or susceptibility to herbivory caused by prior herbivore attack,

this book also details many less obvious TMIIs (e.g. effects of within-plant endophytes as inhibitors of aphid parasitism, and effects of belowground decomposers and root-feeders on plant–pollinator interactions). The main theme of this book, which is the result of a symposium that the editors organized at the 2004 International Congress of Entomology, is that non-lethal interactions with plants generate rich and complex interaction webs that are likely to promote overall diversity within communities.

The book is divided into sections that document indirect, plant-mediated effects within trophic levels, across trophic levels, and in large multispecies assemblages. It begins with an overview chapter on various mechanisms through which plants mediate indirect interactions among herbivores, pollinators and predators. The book ends with a small section on what we know about the evolutionary impacts of indirect effects on interacting species. Within sections, chapters are generally organized to include a larger review section and a small case study. While the topics of some chapters, such as those describing the effects of induced responses of plants on herbivores (e.g. [2–4]), have already received quite a bit of attention, several chapters contribute new aspects. These include plant-mediated interactions between mammals and insects, hemiparasites and herbivores, arbuscular mycorrhizal fungi (AMF) and herbivores, decomposers and root herbivores and aboveground interactors, and between fungal endophytes and herbivores or parasitoids. There are also several chapters on the effects of herbivores as community and ecosystem engineers through the construction of plant

Corresponding author: Strauss, S.Y. (systraus@ucdavis.edu).

galls, leaf shelters and other herbivore-induced plant constructs.

Two chapters (by Gange and Poveda *et al.*) effectively review the varied and complex interactions among soil biota, plants and aboveground insects. Prior reviews of fungal effects have focused primarily on ectomycorrhizal fungi (e.g. [5]), and Gange focuses mostly on AMF effects, concluding that they depend strongly on the community composition of the fungi rather than on the extent of plant colonization. Poveda *et al.* review the impacts of root feeders and soil decomposers on their aboveground interactions with both herbivores and pollinators. Both chapters note the paradoxical effect that, contrary to the generally well-supported Plant Vigor Hypothesis [6], larger plants associated with soil interactors are neither more heavily attacked by herbivores nor necessarily more nutritious for them. A difficulty highlighted by these chapters is that the patchiness of soil biota over very small scales makes it hard to know how many players a plant interacts with at any one time. In addition, interactions among multiple species cause radically different outcomes than those arising from pairwise interactions, and are difficult to mimic realistically in pot experiments. Such complexity makes these systems challenging to understand and study.

In contrast to TMIIIs, density-mediated indirect effects (DMIIs) occur when one species reduces the resources or density of a second species that is used by a third (or more) species. Sabelis *et al.* emphasize that only with treatments that elicit plant responses without tissue damage can one disentangle DMIIs (through tissue consumption) from TMIIIs caused by changes in plant quality. This chapter on the separation of DMIIs from TMIIIs reviews varied approaches, from applying plant hormone elicitors to genetic manipulations, for inducing changes in plant quality without damaging plants physically; the authors then review the subsequent impacts of these changes on plant quality.

A large focus of the book is on how non-lethal effects of interactions generate rich and complex interaction webs that are likely to promote diversity within communities. Web analysis of non-trophic interactions suggests that there exist underappreciated positive interactions between herbivores (e.g. some early-feeding species stimulate leaf flushes and new tissue production that are subsequently used by later-feeding herbivores). Lill and Marquis link themes of positive interactions among herbivores with those of competition among herbivores. They explore the impacts of insect herbivores as ecosystem engineers producing leaf shelters, stem bores, galls and other physical constructs that promote inquiline communities (groups of organisms that use shelters and galls built by other species). Constructs can often be co-opted by predators as shelters or food sources (e.g. nectar-secreting galls), and they can also influence the distribution and abundance of other herbivores. Other chapters highlight the large impacts of engineer aphid galls (and their ant mutualists) and beavers on the communities of insects on cottonwood trees.

The last section of the book explores whether TMIIIs can have evolutionary effects. Perhaps the most convincing

case of evolutionary responses to indirect plant-mediated effects comes from Benkman and colleagues' work showing that bird beak morphology is under selection from squirrels causing changes in pine cone morphology (e.g. [7,8]). Similarly, selection on parasitoid ovipositor length is determined by host moth gall size, which, in turn, is a function of the abundance of bird predators of galls. Multi-species communities and complex networks of direct and indirect interactions often coalesce to create complex selection surfaces with little directional selection. Thus, an evolutionary response to indirect interaction networks probably happen, but may be hard to detect. Althoff's chapter examines a more-narrow suite of TMIIIs – the degree to which parasitoids use host plant cues to locate hosts – and explores this TMII in a phylogenetic context. Although data are largely incomplete across the phylogenies, this approach should provide fascinating results in the future. Althoff also reviews a few studies that have used artificial selection to increase or decrease the use of plant volatiles for host-finding by parasitoids and that have demonstrated heritable genetic variation for traits that can evolve as a result of TMIIIs.

Overall, this book represents a very useful summary and synthesis of trait-mediated effects caused by plant responses to interacting species. Perhaps the biggest weakness of the book is redundancy. The effect of prior herbivore damage on plant quality has already received extensive attention in the literature; moreover, the literature reviews of several chapters overlap substantially. An area lacking from the book is TMIIIs resulting from pathogen attack. On the whole, however, this compilation of the extensive indirect effects mediated by plants, including the food web and interaction web approaches of the last chapters, strives to move us beyond the details of myriad trait-mediated effects towards a more synthetic and predictive approach for understanding the differences between trophic and non-trophic interaction webs, and the maintenance of diversity in communities.

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