

## **THE GENESIS AND MAINTENANCE OF PHENOTYPIC PLASTICITY**

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## Biodiversity and the Climate Change Coup de Grâce

### Climate Change and Biodiversity.

Thomas E. Lovejoy and Lee Hannah, eds. Yale University Press, New Haven, CT, 2005. 418 pp., illus. \$65.00 (ISBN 0300104251 cloth).

If in the mind's eye one can envision all the animals (including humans), all the plants, and all the microbes in any ecosystem—managed and unmanaged, across any spatial or temporal scale, from soil pores to landscapes, from rural to urban, from the vast stretches of time behind us to those that lie before us—then one has come to grips with the extraordinarily complex concept of biodiversity. It may be surprising that so ungainly a concept has become a cornerstone of environmental ecology, but its success lies in its ability to accommodate the complexity and scope of modern environmental ecology.

Nowhere is its utility more evident than in the conceptual framework of the Millennium Ecosystem Assessment (2003), in which 1400 experts from 95 countries conducted a five-year, multiscale, multisectoral assessment of Earth's environment. The assessment's framework explicitly links changes in biodiversity to changes in ecosystem services, which in turn lead to changes in human well-being. In a nutshell, by understanding biodiversity and the many drivers of its change, humans can better understand, and perhaps better manage, our environmental fate. *Climate Change and Biodiversity*, edited by Thomas E. Lovejoy and Lee Hannah, reviews one such driver—climate change.

Of all the well-known and dramatic drivers of biodiversity change, including habitat change, exotic species invasions, overexploitation, and pollution, why, one might ask, do we need a stand-alone volume on climate change? The answer, at least according to the preface of *Climate Change and Biodiversity*, is simple. Climate change is “threatening to accelerate the loss of biodiversity already under way due to other human stressors,” so much so that “it is now clear that climate change

is the major new threat that will confront biodiversity this century” (p. x). Biodiversity, already being driven to staggeringly low levels by habitat change, invasions, overexploitation, and pollution, will be dealt its deathblow by climate change.

Lovejoy and Hannah organize their volume into six parts: (1) an overview of the issue and general introduction to climate change; (2) current, (3) past, and (4) future trends; and response options for (5) conservation biologists and (6) policymakers. I was immediately struck by a lack of coverage of biodiversity itself, and I also wondered why current trends in biodiversity responses to climate change are discussed before past trends. These oddities aside, the book's impressive lineup of 66 contributors represents a full spectrum of environmental ecologists (e.g., from academic institutions, agencies, and NGOs), a balance seldom achieved by such volumes. Not surprisingly, given the extreme heterogeneity of its authorship, the volume's 24 chapters and its sprinkling of case studies vary in quality, but collectively they provide excellent coverage of a complex topic. More surprising was the fair number of poor-quality figures (with excessive contrast, low resolution, or eclectic font usage, for example). No doubt some readers will be cheered by the now obligatory inclusion of several color plates of tiny Mercator projections of computer-generated visions of Earth.

While there is much to recommend this volume, there is cause for quibbling, which is a good sign, indicating that the book will serve well as material for lively graduate seminars. There are, however, two shortcomings worth mentioning. First, in spite of declarations throughout, the case for the primacy of climate change is never solidly developed. For example, chapters 3 through 6 review the brilliant work of Camille Parmesan, Terry L. Root, Lesley Hughes, Chris D. Thomas, and their many colleagues who have provided, in my opinion, unequivocal proof that the ranges, phenologies,

and population genetic structures of many species of plants and animals have responded to climate change. These changes, however, are subtle in comparison with the horrific impacts other drivers are having on biodiversity. Parmesan acknowledges, for example, that “these trends may appear small compared to massive changes in species distributions caused by habitat loss and land use modification,” but nevertheless concludes that such changes could “alter species interactions, destabilize communities, and drive major biome shifts” (chap. 4, p. 53). Similarly, Thomas reviews convincing evidence that some species already show evolutionary responses to climate change, but concludes from only a small number of examples that, “directly or indirectly, climate change is likely to dominate the evolutionary process over the next century and more” (chap. 6, p. 83). It's not so much that I find these claims implausible, just that a biotic “signature” of climate change does not make it the primary driver of biodiversity loss.

The idea of climate change as a major driver of biodiversity change hardly needs selling. Sala and colleagues' article “Global Biodiversity Scenarios for the Year 2100” (2000) and the Millennium Ecosystem Assessment's *Biodiversity Synthesis Report* (2005), two independently authored (with the exception of the omnipresent Hal Mooney) expert opinion assessments, ranked climate change as second and third, respectively, among the top five anthropogenic drivers of biodiversity change. And the case for effective policy to mitigate the harmful effects of climate change on biodiversity has already been made in the Intergovernmental Panel on Climate Change's technical report of the same title as this volume (Gitay et al. 2002). What is needed now is to go beyond expert opinion and freehanded extrapolation.

The key to cinching climate change as the mother of all drivers, or, more aptly, the driver of drivers, is the enormous number of synergies between climate change and other drivers—the modus

operandi of climate change as coup de grâce. This brings me to the book's second shortcoming. Synergies and feedbacks are both key components of the impacts resulting from climate change, and though they are alluded to in several places, the discussion of their role is never fully developed. I would have thought the dominant portion of such a volume would be devoted to these issues. The chapter by Drake and colleagues (chap. 18), however, is the only chapter devoted to synergistic effects. Although limited in depth and scope, no doubt for reasons of space, its review of many examples of synergistic effects, such as the impacts of climate change on burning, plant community composition, plant-microbe interactions, and vectorborne diseases (with a case study by LaPointe and colleagues on avian malaria in Hawaiian birds), goes a long way toward explaining why climate change is ranked so highly by independent expert assessment as a driver of changes in biodiversity. Allan, Palmer, and Poff's examples of complex feedbacks in freshwater sys-

tems (chap. 17) also provide good examples of synergies and feedbacks. These are what make climate change a real worry and a challenge for developing effective conservation strategies.

Quibbles aside, this volume, like its predecessor, *Global Warming and Biological Diversity* (Peters et al. 1992), will become the standard text on climate change as a driver of biodiversity change. The last chapters (pts. V and VI) make a strong case for two courses of action: bringing climate change more strongly into conservation planning (with some powerful examples using computationally intensive methods presented in chaps. 14 and 15) and getting on board with climate change mitigation. Though one might argue (and certainly I would) about the alleged primacy of climate change among the woes biodiversity faces, the fact remains that climate change is real, it's happening now, it needs to be dealt with, and this volume shows the way. In the penultimate chapter, Bob Watson states the challenge nicely: "Unless we act now to limit human-induced

climate change, history will judge us as having been complacent in the face of compelling scientific evidence.... Leaders from government and industry must stand shoulder to shoulder to ensure that the future of the Earth is not needlessly sacrificed" (chap. 23, p. 385).

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Peters RL, Lovejoy TE, Soulé ME, eds. 1992. *Global Warming and Biological Diversity*. New Haven (CT): Yale University Press.

Sala OE, et al. 2000. Biodiversity: Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

## THE GENESIS AND MAINTENANCE OF PHENOTYPIC PLASTICITY

**Phenotypic Plasticity: Functional and Conceptual Approaches.** Thomas J. DeWitt and Samuel M. Scheiner, eds. Oxford University Press, New York, 2004. 247 pp., illus. \$59.95 (ISBN 0195138961 cloth).

Understanding the evolution of phenotypic plasticity—the environmental induction of phenotypic change owing to altered gene expression—will conceptually unify development, physiology, immunology, and endocrinology. Each of these disciplines uses different terminology to describe phenomena related to plasticity. The editors of *Phenotypic Plasticity: Functional and Conceptual Approaches*—Thomas J. DeWitt, of Texas A&M University, and Samuel M. Scheiner, who works for the National Science Foundation—have brought together a diverse set of approaches to update the state of plasticity research.

The historical chapter by Sarkar (chap. 2) provides a lucid description of key historical issues framing current scientific debates. In particular, debates on plasticity in the 1990s sharpened semantic definitions, allowing a conceptual consensus to emerge. The chapter brings any reader up to speed on key theoretical issues, particularly when followed by the chapters on theory (chap. 6, by Berrigan and Scheiner; chap. 7, by Dewitt and Langerhans; chap. 11, by Wolf and colleagues). Are there “genes for plasticity,” a view championed by Scheiner and colleagues, or does selection arise from a “by-product of selection on trait means,” a view championed by Via? A key issue to emerge from this dialectic is the role of epistatic effects. As noted in the chapters that review theory (chaps. 2, 6, 7,

and 11), models rarely include epistatic interactions, although there are some notable exceptions.

What are the true genetic underpinnings of plasticity? A hierarchical description of genetic effects includes allelic sensitivity, dominance sensitivity, and epistatic sensitivity to the environment. Allelic and dominance sensitivity are easy to visualize, and several of the theoretical chapters provide models incorporating such genetic variation. Epistatic sensitivity is more difficult to grasp. The simplest way, and that adopted in much of the current theory, is to visualize epistasis arising from “regulatory loci that exert environmentally dependent control over structural gene expression” (Schlichting and Pigliucci [1993], cited in chap. 2). A more general perspective is that afforded by the theory of indirect genetic effects (chap. 11), which allows for gene interactions arising both within and between genomes. At a mechanistic level, however, there exists a myriad of interactions among structural, physiological, hormonal, or developmental genes, as well as immunological gene complexes (both within and between individuals), not just interactions from regulatory loci. Whether a simplified approach to regulatory-locus epistasis is justified remains an open question to be resolved by empirical approaches.

Despite the simplifications in the theory regarding epistasis, identifying links to regulatory loci is an important first step in empirical analysis, because it is amenable to the “candidate-gene approach” (chap. 5, by Frankino and Raff). The candidate-gene approach is epitomized by work on plant elongation owing to phytochromes. Plants elongate their stems in response to the red-to-far-red (RFR) ratio of light (cited in chap. 10, by Dudley), and RFR can be manipulated in many environmental treatments. Shading due to plant density causes a shift in RFR ratios and thereby induces the adaptive response of stem elongation. In animals, a similar candidate gene involves regulatory genes of stress, such as corticotropin-releasing hormone, which triggers the release of glucocorticoid steroid hormones (chap. 5). This in

turn induces a variety of plastic responses in vertebrates.

However, as noted above, epistasis could arise from any kind of gene interaction, not just from regulatory loci. To move beyond the candidate gene, plasticity research must adopt genomic approaches, as advocated in two chapters (chap. 5, by Frankino and Raff, and chap. 13, by Scheiner and DeWitt). Genomics, which currently involves linkage mapping or screening with gene chips, remains a daunting task, given that gene interactions must be screened in a variety of biotic and abiotic environments. Perhaps model systems such as *Drosophila* (discussed in chap. 4, by David and colleagues) may be useful in implementing genomic approaches, given the extraordinary detail afforded by current genetic maps and gene sequences. However, many issues involving the adaptive costs of plasticity and natural selection on plastic responses can be resolved only in the wild. Thus, genomic approaches will ultimately need to be implemented in natural systems to fully understand the genomic architecture of plasticity.

In addition to proximate issues, contributors to the volume do discuss adaptive issues, such as costs of plasticity, tradeoffs, and adaptive value (chap. 9, by Doughty and Reznick). To date, no study has measured the fitness consequences of plasticity in nature (i.e., the effects of induced plasticity on the production and survival of offspring); only proxies for lifetime reproductive success have been assessed. Information on actual fitness consequences is essential to comprehensively assess costs and tradeoffs. Other theoretical chapters (chaps. 6 and 7) highlight neglected areas of empirical research, such as the temporal or spatial prevalence of inducing cues. Furthermore, as Sih points out in chapter 8, the social induction of plasticity is rarely treated in a frequency-dependent context. Behavioral ecology and game theory explicitly treat frequency dependence and the cues for inducing adaptive plasticity. Incorporating such frequency dependence will advance the study of plasticity in social systems. The plasticity of mating systems is often linked to traits with direct fitness effects.

Furthermore, game theory provides a number of examples of cyclical dynamics that involve recurring environments. Plasticity should be strongly favored in such varying or cyclical social contexts. Chapter 11 treats the theory of social contexts, but completely ignores frequency-dependent effects. Instead, a quantitative genetic analysis is used to focus, gene by gene, on the important consequences of gene–environment interactions for linkage disequilibrium, pleiotropy, and the formation of genetic correlations. However, frequency dependence and the spatial scale of nearest-neighbor interactions will often strengthen the formation of genetic correlations arising from linkage disequilibrium. Thus, a comprehensive treatment of the evolution of plasticity involving biotic interactions will require an explicit analysis of frequency dependence in conspecifics' interactions and in plant–herbivore, predator–prey, and host–parasite coevolutionary relationships.

There are other neglected adaptive issues. The role of settlement behavior as a correlating force between genes, environment, adaptive response, and ensuing assortative mating is impossible to test in most laboratory settings. An analogous force in plants would be plant-mediated dispersal of seeds by animals or extremely strong microhabitat-dependent selection, which might also strengthen genetic correlations. These forces might be crucial in future models of speciation driven by the evolution of plasticity.

The volume does include a chapter, by Schlichting (chap. 12), on the role of plasticity in diversification and speciation. Ultimately, a theory about this role will require the rigor found in current genetic models of speciation, and this has not yet been achieved. But this chapter does provide a number of potential genetic mechanisms, such as genetic assimilation, that could be modeled in the future. While the chapter is far too short to sketch out the full problem of phenotypic plasticity, it does serve as a useful abstract of ideas on the subject. These ideas are more fully developed in Mary Jane West-Eberhard's (2003) re-

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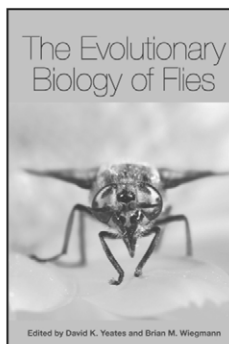
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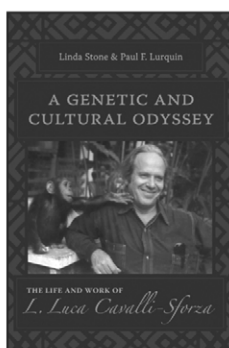
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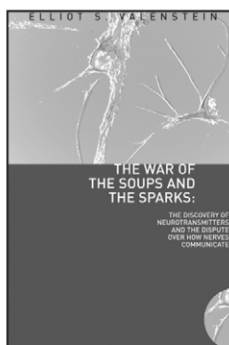
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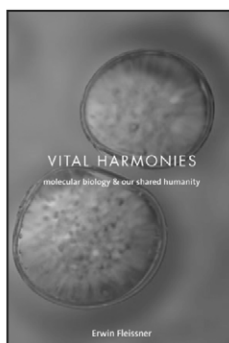
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cent tome, which treats speciation driven by plasticity.

In summary, DeWitt and Scheiner's volume provides a useful summary of current work and future directions for the field. As such, it should be on the shelf of evolutionary ecologists, whatever their specialty (genetics, physiology, endocrinology, or behavior). The editors admit that the field is in a phase of logarithmic increase (chap. 13), with much work yet to be done. I am sure the book will recruit more researchers to plasticity research. Many chapters in the volume are excellent, and must-read material for both established scientists and new students of plasticity.

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## UNINTENDED CONSEQUENCES

**Fishes and Forestry: Worldwide Watershed Interactions and Management.** T G. Northcote and G. F. Hartman, eds. Blackwell, Ames, IA, 2004. 789 pp., illus. \$249.99 (ISBN 0632058099 cloth).

*Fishes and Forestry: Worldwide Watershed Interactions and Management* is an ambitious integration of fish ecology, stream ecology, forest practices and their effects, global understanding of fish–forestry interactions, and future directions in management and education. Thomas Northcote and Gordon Hartman, the editors, are pioneers in the study of fish–forestry relationships in North America, and they have assembled 34

chapters by 55 authors from around the world. This book is the first to present a global perspective on the science and management of fish communities and forest management practices. Fish communities face major threats everywhere—habitat alteration, fish harvest, dams, hatcheries, water pollution, and climate change being prominent examples. *Fishes and Forestry* avoids the regional myopia that commonly limits innovations in management of fishes and forests, and expands the reader's vision of future directions in research and management on the basis of fundamental relationships that occur throughout the world.

The introductory chapter by Northcote and Hartman is an interesting overview of the extent of world forests and the richness of fish assemblages in different regions. The authors make it clear that forestry potentially affects the abundance and distribution of a large portion of the 34 orders and more than 10,000 species of fish found in streams, rivers, lakes, and estuaries around the globe. They explain the extensive overlap in global patterns of precipitation, forest cover, and fish species distributions. The chapter also provides a historical context for fish–forestry interactions by summarizing changes in forest cover over the last millennium and the consequences for fish assemblages.

The second portion of the book provides an ecological overview of forest, stream, lake, and estuarine ecosystems. Scientists trained in ecosystem science will find these four chapters extremely brief and simplified. This approach may be suitable for the book's international audience, however, whose disciplines and applications vary greatly. These chapters briefly summarize major concepts in the ecology of these different ecosystems and provide numerous citations to direct the reader to the major articles in the scientific literature. Though it would have benefited from a chapter on geomorphology and hydrology, this 100-page section of the book is a useful foundation for a broad audience.

The next section includes chapters on the life history and diversity, migration and passage, reproduction, and foraging ecology of fishes. These chapters clearly

are intended to inform the reader about the biological and environmental requirements of different fish species before addressing the consequences of forest practices on fish. The chapter on fish migration and passage is a concise introduction to the subject, and numerous citations are provided to guide the reader who is interested in exploring further. The chapter on reproduction provides data on the major orders of freshwater fish and includes several informative summary figures and tables. The subject of foraging ecology describes fish feeding in temperate and tropical systems, but several topics (such as energy subsidy, or the exchange of energy between adjacent ecosystems) are treated exceedingly briefly, and several major concepts in foraging ecology are completely omitted (for example, trophic cascading, competition, and environmental influences on bioenergetics).

The fourth section describes forest harvest and transportation, silviculture, and manufacturing and effluent discharges. These chapters describe general forest practices, with an emphasis on up-slope forestry. Clearly, forest practices across the landscape shape the interactions between fish and forestry, but the lack of attention to the terrestrial–aquatic interface in this work is surprising. There is no discussion of riparian reserves, streamside buffers, or riparian management zones. Even more important, there is no discussion of the effectiveness of these approaches for fish and aquatic systems. Readers can glean information on the effects of riparian buffers from the four chapters on forestry effects, but the book does not provide an overall synthesis of the approaches and their effectiveness. Silvicultural practices to maintain or restore riparian functions are not addressed in any chapter. Riparian management systems are discussed only in one of the final chapters on guidelines, codes, and legislation. This is unfortunate, because it encourages managers to view riparian practices as a legal requirement rather than a fundamental part of forest management.

The book goes on to review the effects of forestry on basin processes, lakes, estuaries, and water quality. These chap-





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ters at first seem exceedingly brief, but much of the literature on forestry effects is included in subsequent chapters on specific regions. Rather than being repetitive, the editors developed chapters that create a framework for understanding the physical, chemical, and biological effects of forestry on aquatic ecosystems and fish communities. Readers should be aware that greater detail follows in the regional reviews of fish-forestry interactions.

Two subsequent sections are devoted to fish-forestry interactions in North America and in non-North American countries. The section on North America includes the Pacific Northwest, boreal portions of Canada, Atlantic Canada, the Rocky Mountains, and Mexico. These chapters, by authorities from those regions, are informative and well written. Unfortunately, the editors were unable to obtain chapters on the northeastern, southeastern, and southwestern regions of the United States (though forests of Arizona and New Mexico are discussed in the chapter on the Rocky Mountains). The chapter on fish-forestry interactions in Mexico, by Sánchez-Vélez and García-Núñez, is a valuable contribution that outlines the geography of Mexican forests and aquatic systems. Although few studies of the effects of forestry on fishes are available for Mexico and Central America, the chapter clearly describes the resources, population pressures, history of land uses, and emerging issues related to aquaculture.

The section on non-North American countries is particularly informative, especially for North American readers. Chapters by international authors discuss fish-forestry interactions in tropical South America, western Europe, Japan, Southeast Asia, Borneo, Cambodia, Indonesia, New Zealand, and Australia. Again, the editors unfortunately were unable to obtain chapters on some regions, in particular Russia, China, and Africa. The logging and transportation systems used in many of these regions differ markedly from those of North America and western Europe, and subsistence harvest and deforestation have profound impacts on forests in several major regions. This section provides an interest-

ing description of regulatory systems in world forestry and reveals that illegal or unregulated harvest represents the majority of harvest in regions such as the Brazilian Amazon.

The final section of the book addresses different approaches to improving understanding and management of fish-forestry interactions: guidelines, codes, and legislation; restoration practices; education; and a new vision for fish-forestry interactions. The chapter on guidelines, codes, and legislation summarizes and compares current approaches for forest management and riparian regulation. As a vision of the future of fish-forestry interaction, the chapter on restoration briefly describes outcomes of past restoration efforts and lays out a framework for integration of watershed restoration in forest management.

One of the most important contributions of the book is the chapter on better and broader education. The authors use a Food and Agriculture Organization survey to examine the training of resource professionals around the world. Outside of North America, most forest educational centers provide only basic training in fish ecology and aquatic ecology. The chapter notes the dichotomy between training in utilitarian forest management and the broader natural resource management that has emerged in recent decades, and clearly demonstrates the need for improved education for professionals and the public.

The final chapter is the editors' call for a global perspective on fish-forestry interactions. Northcote and Hartman address gaps in their coverage and provide brief overviews of critical regions that were not covered in the book. They identify unique characteristics of major regions of the world and indicate that scientists and resource managers need to carefully apply information on fish-forestry interactions in different biomes and cultures. Their final thoughts on the uncertainties of future change in landscapes and human populations are an eloquent and compelling plea for more deliberate and coordinated actions to conserve and restore the world's forests and aquatic systems.

The editors and authors of *Fishes and Forestry* have provided the first global perspective on fish-forestry interactions. This book is essential reading for any scientist, resource manager, or member of the public interested in forested landscapes. Every university and resource training center should have copies available for the scientists and resource managers of the future.

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## NEW TITLES

**Carpenter Ants of the United States and Canada.** Laurel D. Hansen and John H. Klotz. Cornell University Press, Ithaca, NY, 2005. 224 pp., illus. \$35.00 (ISBN 0801442621 cloth).

**Designs on Nature: Science and Democracy in Europe and the United States.** Sheila Jasanoff. Princeton University Press, Princeton, NJ, 2005. 363 pp., illus. \$35.00 (ISBN 0691118116 cloth).

**Ecology and Evolution in the Tropics: A Herpetological Perspective.** Maureen A. Donnelly, Brian I. Crother, Craig Guyer, Marvalee H. Wake, and Mary E. White, eds. University of Chicago Press, Chicago, 2005. 584 pp., illus. \$45.00 (ISBN 0226156583 paper).

**Environmental Science: A Self-Teaching Guide.** Barbara W. Murck. Wiley, Hoboken, NY, 2005. 360 pp., illus. \$19.95 (ISBN 0471269883 paper).

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