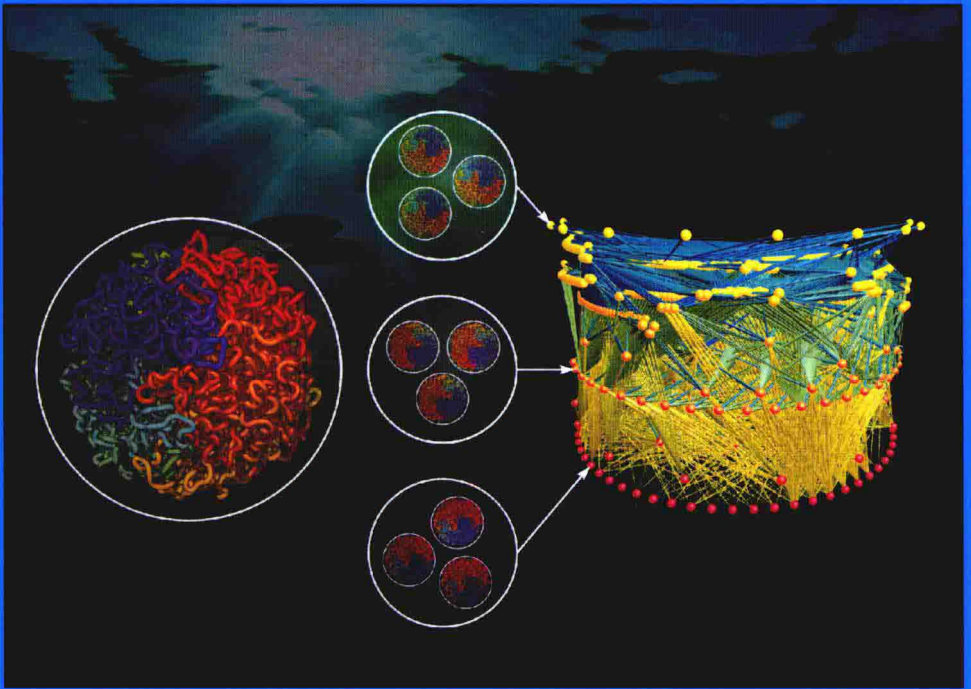


ADVANCES IN ECOLOGICAL RESEARCH

43

INTEGRATIVE ECOLOGY:
FROM MOLECULES TO ECOSYSTEMS



EDITED BY

GUY WOODWARD



Advances in
**ECOLOGICAL
RESEARCH**

VOLUME 43

**INTEGRATIVE ECOLOGY:
FROM MOLECULES TO ECOSYSTEMS**

Edited by

GUY WOODWARD

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Queen Mary University of London,
London E1 4NS, UK



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VOLUME 43

Advances in Ecological Research

Series Editor:

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Preface

This thematic volume of *Advances in Ecological Research* integrates different levels of organisation and biological disciplines, in an attempt to provide a more holistic view of ecological systems. As such, none of these chapters are typical representatives of any single traditional field in ecology, as between them they attempt to forge new links from molecular biology to ecosystems ecology, from microbial to macro-organismal ecology, from individuals to food webs, or from metabolic theory to biodiversity-ecosystem functioning (B-EF) theory. Given that many of the long-established barriers within ecology, and biology as a whole, are rapidly dissolving, this volume reflects as our science as it enters an exciting and evermore interdisciplinary phase. This is being achieved via a combination of new theoretical and empirical perspectives and methodological advances, many of which underpin the chapters presented here.

In recent years, we have witnessed an ever-strengthening link develop between the previously disparate disciplines of community and ecosystems ecology, catalysed in particular by the mushrooming of B-EF and food web research, and the previous companion volume of *Advances in Ecological Research* was devoted to the latter (Volume 42: *Ecological Networks*). These two fields have also started to converge, as vertical and horizontal interactions within communities, and their consequences for ecosystem processes are starting to be considered simultaneously. Further, the fact that interactions occur between individuals operating within metabolic and foraging constraints, is now being recognised and it is becoming increasingly clear that that this level of organisation needs to be considered in B-EF and food web studies, as highlighted in this volume (e.g., Perkins *et al.*, 2010; Reiss *et al.*, 2010a; Woodward *et al.*, 2010). The chapters by Reiss *et al.* (2010a) and Perkins *et al.* (2010), for instance, use the metabolic capacity of individuals to predict ecosystem process rates: the former is one of the first studies to manipulate both microbial and macrofaunal diversity simultaneously in a B-EF experiment and the latter describes a range of potential impacts of climate change on B-EF relationships. In both instances, species richness had no detectable effect on process rates, which were driven primarily by the body size and metabolic demands of the consumers and secondarily by species identity effects *per se*. The chapter by Yvon-Durocher *et al.* (2010) also demonstrates how relatively simple predictions based on individual metabolism can be used to characterise the responses of whole-ecosystem carbon cycling to environmental warming in a long-term field experiment.

The chapter by Woodward *et al.* (2010) includes the first description of a set of food webs constructed from both species- and a size-based perspective simultaneously using individual-level data, and as in the two B-EF papers, this study also revealed size-based redundancy within the system: diet width and the position of feeding links were better explained by body size than by species identity *per se.*, and the allometric diet breadth model predicted up to 84% of the links in a food web correctly, based on body mass data alone.

Within the past two decades, in parallel with the heightened activity in B-EF and food web research, molecular and microbial ecology have also evolved rapidly into mature scientific disciplines in their own right, fuelled by a series of technological breakthroughs, as described in the chapter by Purdy *et al.* (2010). The recent advent of Next Generation Sequencing (NGS) has opened up vast new vistas on a previously hidden world and, perhaps more than any other methodological advance in the last decade, this seems destined to change our view of ecology in radical and unexpected ways for many years to come. Large reservoirs of cryptic biodiversity and even previously unknown ecosystem processes are being unveiled at an astonishing rate, and the first ripples of this are now being felt in general ecology as molecular and microbial ecology become increasingly integrated into the corpus of the wider discipline. This wealth of new information offers novel ways to investigate whether microbial ecology follows general ecological principles, or whether there are inherent differences between the microscopic and macroscopic worlds, both of which are central themes in the chapters of Reiss *et al.* (2010b) and Ptacnik *et al.* (2010). The latter revisits a longstanding question in ecology – Hutchinson’s classic “paradox of the plankton” – from a new perspective and highlights how, even in seemingly homogenous planktonic environments, a large number of species can be supported, and are indeed needed to sustain multiple ecosystem processes.

In summary, the seven chapters in this volume explore themes related to linking structure to functioning and each highlights the role of body size and/or metabolism as playing key roles in achieving this aim. Of course, this does not imply that these are the only variables of importance, rather that they provide a potentially useful means of collapsing a large amount of biologically relevant variation into a small number of dimensions, and this also enables other axes of interest to be explored more easily. In addition, the use of an individual-based perspective can help to bridge different disciplines and levels of organisation, and to provide potentially novel perspectives and insights into both old and new ecological questions.

REFERENCES

- Perkins, D.M., McKie, B.G., Malmqvist, B., Gilmour, S.G., Reiss, J., and Woodward, G. (2010). Environmental warming and biodiversity-ecosystem functioning in freshwater microcosms: Partitioning the effects of species identity, richness and metabolism. *Adv. Ecol. Res.* **43**, 177–208.
- Ptacinik, R., Moorthi, S.D., and Hillebrand, H. (2010). Hutchinson reversed, or why there need to be so many species. *Adv. Ecol. Res.* **43**, 1–43.
- Purdy, K.J., Hurd, P.J., Moya-Laraño, J., Trimmer, M., and Woodward, G. (2010). Systems biology for ecology: From molecules to ecosystems. *Adv. Ecol. Res.* **43**, 87–149.
- Reiss, J., Bailey, R.A., Cássio, F., Woodward, G., and Pascoal, C. (2010a). Assessing the contribution of micro-organisms and macrofauna to biodiversity-ecosystem functioning relationships in freshwater microcosms. *Adv. Ecol. Res.* **43**, 151–176.
- Reiss, J., Cássio, F., Pascoal, C., Forster, J., Stewart, R., and Hirst, A.G. (2010b). When microscopic organisms inform general ecological theory. *Adv. Ecol. Res.* **43**, 45–85.
- Woodward, G., Blanchard, J., Lauridsen, R.B., Edwards, F.K., Jones, J.I., Figueroa, D., Warren, P.H., and Petchey, O.L. (2010). Individual-based food webs: Species identity, body size and sampling effects. *Adv. Ecol. Res.* **43**, 209–265.
- Yvon-Durocher, G., Allen, A.P., Montoya, J.M., Trimmer, M., and Woodward, G. (2010). The temperature dependence of the carbon cycle in aquatic systems. *Adv. Ecol. Res.* **43**, 267–313.

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