Quantitative Analysis of Ecological Networks

Network thinking and network analysis are rapidly expanding features of ecological research. Network analysis of ecological systems includes representations and modelling of the interactions in an ecosystem, in which species or factors are joined by pairwise connections. This book provides an overview of ecological network analysis including generating processes, the relationship between structure and dynamic function, and statistics and models for these networks. Starting with a general introduction to the composition of networks and their characteristics, it includes details on such topics as measures of network complexity, applications of spectral graph theory, how best to include indirect species interactions, and multilayer, multiplex and multilevel networks. Graduate students and researchers who want to develop and understand ecological networks in their research will find this volume inspiring and helpful. Detailed guidance to those already working in network ecology but looking for advice is also included.

Mark R. T. Dale is Professor in Environmental Science at the University of Northern British Columbia. His research interests include the spatial structure of plant communities and the development and evaluation of numerical methods to answer ecological questions, including graph theory and network complexity. His graduate students have worked in a diverse set of systems from prairie to alpine and at a range of spatial scales from plant neighbour competition to landscape disturbance patterns. He wrote *Spatial Pattern Analysis in Plant Ecology* (Cambridge University Press, 1999) and *Applying Graph Theory in Ecological Research* (Cambridge University Press, 2017) and was co-author, with Marie-Josée Fortin, of *Spatial Analysis: A Guide for Ecologists* (Cambridge University Press, 2005, 2nd ed. 2014).

Marie-Josée Fortin is a University Professor in Ecology and Evolutionary Biology at the University of Toronto. She is a Fellow of the Royal Society of Canada and holds a Tier 1 Canada Research Chair in Spatial Ecology. Her research endeavours focus on conservation biology issues. She investigates how ecological processes and environmental factors affect species persistence, species dispersal, and species range dynamics. Her research is at the interface of several disciplines (spatial ecology, conservation, forest ecology, disturbance ecology, community ecology, landscape genetics, spatial epidemiology, spatial statistics, spatially explicit modelling, and network theory) where the most important challenging problems lie.

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CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE
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University Printing House, Cambridge CB2 8BS, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314–321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi – 110025, India

79 Anson Road, #06–04/06, Singapore 079906

Cambridge University Press is part of the University of Cambridge.

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www.cambridge.org
Information on this title: www.cambridge.org/9781108491846
DOI: 10.1017/9781108649018

First published 2021

Printed in the United Kingdom by TJ Books Limited, Padstow Cornwall

A catalogue record for this publication is available from the British Library.

Library of Congress Cataloging-in-Publication Data
Names: Dale, Mark R. T. (Mark Randall Thomas), 1951- author. | Fortin, Marie-Josée, 1958– author.
Title: Quantitative analysis of ecological networks / Mark R.T. Dale, University of Northern British Columbia, Marie-Josée Fortin, University of Toronto.
Description: Cambridge, UK ; New York, NY : Cambridge University Press, 2021. | Includes bibliographical references and index.
Identifiers: LCCN 2020040227 (print) | LCCN 2020040228 (ebook) | ISBN 9781108491846 (hardback) | ISBN 9781108740715 (paperback) | ISBN 9781108649018 (epub)
Subjects: LCSH: Ecology–Statistical methods. | System analysis. | Quantitative research.
Classification: LCC QH541.15.S72 D35 2021 (print) | LCC QH541.15.S72 (ebook) | DDC 577.072/7–dc23
LC record available at https://lccn.loc.gov/2020040227
LC ebook record available at https://lccn.loc.gov/2020040228

ISBN 978-1-108-49184-6 Hardback
ISBN 978-1-108-74071-5 Paperback

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Preface

Ecology is about understanding how organisms interact with other organisms and the environment they inhabit (i.e. fundamental and realised niches). It is easy to imagine an individual organism of any kind as a dot with all sorts of arrows impinging upon it; an arrow can represent abiotic factors (temperature, light, etc.), along with many arrows for all the other organisms (biotic factors, intra- and inter-specific interactions) that affect it. Ecology aims therefore to determine the magnitude and rate associated with some of the arrows and identify which are the most important and why. Each organism also has its own effects on the same list of factors, even if the effects are small, so we can also imagine arrows going out from the same dot, one to each of the same factors (they can be dots too). Again, a challenge is to determine the associated weights and importance of the arrows, some of which are directed towards other organisms. As soon as we consider more than a single organism, even just a few, we immediately have a complex structure of dots and arrows: an ecological network!

It is an obvious step to consider ecological systems as ecological networks, and as such to assess how network theory (concepts and methods) might be applied to them. Network theory and the mathematics of graph theory that underlie network analysis provide simple concepts that can applied to systems that are complex both in structure and dynamics. It is those concepts that allow us to provide a sorted set of methods for the quantitative analysis of ecological networks, together with thoughts and advice on how best to proceed. Through the years, the need to take a network analysis framework to study complex systems has arisen in many fields (physics, computer science, communication science [transportation, electricity, social], and bio- and eco-informatics), and there is a challenging diversity of approaches, methods and measures that should be understood, or at least sorted, before applying them to our own data. The overarching goal of this book is to help ecologists in selecting the appropriate network methods to represent, analyse and model their ecological systems using network theory.

As the title suggests, this book is for ecologists with an interest in ecological networks. Perhaps they have a project in mind or even some potential network data "in hand" but are not sure how to proceed or on which network characteristics to concentrate. This book provides both background and some advice on how to answer interesting ecological questions in the context of network analysis. It does cover some general network material (that is needed as background), but to the breadth of books like Newman (2010) or Estrada (2012). It was partly inspired by Kolaczyk (2009), but

it is less technical in tone and detail and more inclusive of recent developments. All three of the books just cited, together with Kolaczyk and Csárdi (2014) which supplies R code, are excellent resources for more information, as needed. The other inspiration for our current book is Dale (2017), which focused on applying graph theory in ecology, and mentioned, but did not cover, network analysis. The current project moves forward into network analysis from that work but does not assume its material as background.

As is often the case, the book evolved as it was being written. Initially, there was no separate chapter on multilayer and multilevel networks, but it became obvious that it was both necessary and crucial – hence Chapter 4. Similarly, we had not explicitly included causal networks in the original outline, although it now seems central to the presentation. Hence, now a central theme of the book is to stress the interplay between the structure and the dynamics (or between form and function) of these complex networks from ecological systems. Last, the ending of the book started out as only the summary diagram "It all ties together," but when we got to the end, there was more that needed to be said – hence Chapter 5 (we did keep it short). One factor in driving the evolution of this book is the speed at which the field of the study of ecological networks, let us call it "network ecology," is growing, developing and advancing. It is very challenging just to keep pace with developments, but it is also very satisfying to see the subdiscipline getting the attention and application we think it should.

There are many people and organisations to thank for supporting the project, starting with Natural Sciences and Engineering Research Council (NSERC), NSERC Canada Research Chair, the University of British Columbia, and the University of Toronto for financial support. We thank Alex Aravind, Charlotte Brown, Cheryl Smyth, Conan Veitch, and J. C. Cahill for their reading of chapters and their thoughtful advice for improvements. We especially thank J. B. Grace for permission to use material from an unpublished manuscript on statistical models and causal analysis as the basis for Table 3.4.

Writing this book has been an exciting and rewarding journey of discovery through the rapidly changing landscape of network ecology. No book can be completely up to date, but the hope is that the course it has followed is in the right direction for continuation into the future. It is also our hope that the book can serve an as exciting and helpful guide for others on a similar journey of discovery.