

> Even the casual observer of nature soon realizes that there are palpable differences in the breadth and diversity of resources used by species, even quite closely related ones. Species also show disparate propensities to occupy habitat types, some restricted to a very few, while others are to be found in almost any habitat within their geographic ranges. The variation in the breadth of resource use (ecological versatility) and in habitat use (ubiquity) has important implications for understanding ecological diversity. This book is the first to draw back from particular disciplinary foci, such as host-plant use in phytophagous insects, bilateral mutualisms or competitive coevolution, to develop a broader perspective of versatility and ubiquity. This is done by addressing three main questions (1) how do ecologists study versatility and ubiquity, and what do we know from these studies? (2) how well does existing theory account for observations, and what are the common threads between disciplines? and (3) what is the relationship between versatility and ubiquity? The analyses are undertaken from an ecological rather than evolutionary perspective. The outcomes of the review indicate some promise of unification and systematicization. However, there are exceedingly demanding challenges that ecologists must face in their quest for a more thorough understanding of ecological versatility.





Ecological Versatility and Community Ecology

Cambridge Studies in Ecology presents balanced, comprehensive, up-to-date, and critical reviews of selected topics within ecology, both botanical and zoological. The Series is aimed at advanced final-year undergraduates, graduate students, researchers, and university teachers, as well as ecologists in industry and government research.

It encompasses a wide range of approaches and spatial, temporal, and taxonomic scales in ecology, experimental, behavioural and evolutionary studies. The emphasis throughout is on ecology related to the real world of plants and animals in the field rather than on purely theoretical abstractions and mathematical models. Some books in the Series attempt to challenge existing ecological paradigms and present new concepts, empirical or theoretical models, and testable hypotheses. Others attempt to explore new approaches and present syntheses on topics of considerable importance ecologically which cut across the conventional but artificial boundaries within the science of ecology.



### CAMBRIDGE STUDIES IN ECOLOGY

#### Series Editors

H. J. B. Birks Botanical Institute, University of Bergen, Norway, and Environmental Change Research Centre, University College London

J. A. Wiens Department of Biology, Colorado State University, USA

### Advisory Board

P. Adam University of New South Wales, Australia R. T. Paine University of Washington, Seattle, USA F. I. Woodward University of Sheffield, Sheffield, UK

### ALSO IN THE SERIES

H.G. Gauch, Jr

R. H. Peters

C. S. Reynolds

Multivariate Analysis in Community Ecology

The Ecological Implications of Body Size

The Ecology of Freshwater Phytoplankton

K. A. Kershaw Physiological Ecology of Lichens

R. P. McIntosh

The Background of Ecology: Concepts and Theory

A. J. Beattie

The Evolutionary Ecology of Ant–Plant Mutualisms

F. I. Woodward

J. J. Burdon

J. I. Sprent

N. G. Hairston, Sr

Climate and Plant Distribution

Diseases and Plant Population Biology

The Ecology of the Nitrogen Cycle

Community Ecology and Salamander Guilds

H. Stolp
Microbial Ecology: Organisms, Habitats and Activities
R. N. Owen-Smith
Megaherbivores: The Influence of Large Body Size on

Ecology

J. A. Wiens The Ecology of Bird Communities

N. G. Hairston, Sr Ecological Experiments
R. Hengeveld Dynamic Biogeography

C. Little The Terrestrial Invasion: An Ecophysiological Approach to

the Origins of Land Animals

P. Adam Saltmarsh Ecology

M. F. Allen The Ecology of Mycorrhizae

D. J. Von Willert et al. Life Strategies of Succulents in Deserts
J. A. Matthews The Ecology of Recently-deglaciated Terrain

E. A. Johnson Fire and Vegetation Dyanmics
D. H. Wise Spiders in Ecological Webs
J. S. Findley Bats: A Community Pespective

G. P. Malanson Riparian Landscapes

S. R. Carpenter & The Trophic Cascade in Lakes

J. F. Kitchell (Eds.)

R. J. Whelan The Ecology of Fire



# Ecological Versatility and Community Ecology

RALPH C. MAC NALLY

The Department of Ecology and Evolutionary Biology Monash University, Melbourne, Australia





CAMBRIDGE UNIVERSITY PRESS Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo, Delhi, Tokyo, Mexico City

Cambridge University Press The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org Information on this title: www.cambridge.org/9780521405539

© Cambridge University Press 1995

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 1995

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

Library of Congress Cataloguing in Publication data
MacNally, Ralph C.
Ecological versatility and community ecology / Ralph C. MacNally.

p. cm. – (Cambridge studies in ecology)

Includes bibliographical references (p. ) and index.

ISBN 0 521 40553 X (hardback)

1. Ecology 2. Biotic communities. 3. Habitat (Ecology)

I. Title. II. Series. QH541.M225 1995 574.5–dc20 94-41872 CIP

ISBN 978-0-521-40553-9 Hardback ISBN 978-0-521-11926-9 Paperback

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third—party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate. Information regarding prices, travel timetables, and other factual information given in this work is correct at the time of first printing but Cambridge University Press does not guarantee the accuracy of such information thereafter.



For Erica, Aleck and especially Marty





### Contents

Preface	xv
An introduction to ecological versatility What is the significance of ecological versatility?	1 11
Structure of the book	13
A directory	15
Scope	16
Defining and measuring versatility	17
What is ecological versatility?	19
The meaning of fitness	19
What are resources?	20
Resources – the fitness basis and exclusive access	20
Critical and extraneous resources	22
Complementary and substitutable resources	23
Constraints	25
What are the problems in quantifying ecological	
versatility?	25
Spatial scale - ecologists and organisms	26
Resource ordering and aliasing	29
The practicalities of measuring utilization and availability	30
Overview	31
How is versatility measured?	32
Local and global pictures of species' versatilities	35
A case study	37
Summary	38
Studies of versatility in natural populations	40
Survey parameters	41
	What is the significance of ecological versatility? Structure of the book A directory Scope  Defining and measuring versatility What is ecological versatility? The meaning of fitness What are resources? Resources — the fitness basis and exclusive access Critical and extraneous resources Complementary and substitutable resources Constraints What are the problems in quantifying ecological versatility? Spatial scale — ecologists and organisms Resource ordering and aliasing The practicalities of measuring utilization and availability Overview How is versatility measured? Local and global pictures of species' versatilities A case study Summary



<b>x</b> ·	Contents	
3.2	Survey domain	43
	Literature sources and selection criteria	43
	Taxonomy	45
	Habitats	46
	Climatic zones and geography	47
	Numbers of species per study	48
3.3	The survey	49
	Clear specification of resources	49
	Fitness bases	51
	Constraints	54
	Differences between individuals	55
	Population subsets	58
	Availabilities and conformances	59
	Spatial variability	62
	Temporal variability – seasonal trends	65
	Temporal variability – daily trends	68
	Measures of breadth and overlap	69
	Overview	70
3.4	The distribution of versatility in nature	71
3.5	Summary	76
4	The influence of interspecific interactions on	
4	The influence of interspecific interactions on versatility	79
4	The influence of interspecific interactions on versatility  Some caveats	79 80
	versatility Some caveats	80
4.1	versatility Some caveats Herbivory	80 81
	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores	80 81 83
	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects	80 81 83 88
	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores	80 81 83
	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects Herbivory – an overview  Parasitism	80 81 83 88
4.1	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects Herbivory – an overview  Parasitism Parasitoids	80 81 83 88 100 101
4.1	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects Herbivory – an overview  Parasitism Parasitoids Animal parasites	80 81 83 88 100 101 101 102
4.1	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects Herbivory – an overview  Parasitism Parasitoids Animal parasites Animal parasites — an overview	80 81 83 88 100 101 101 102 108
4.1	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects Herbivory – an overview  Parasitism Parasitoids Animal parasites	80 81 83 88 100 101 101 102
4.1	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects Herbivory – an overview  Parasitism Parasitoids Animal parasites Animal parasites Animal parasites Plant parasites  Predation	80 81 83 88 100 101 101 102 108
4.1	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects Herbivory – an overview  Parasitism Parasitoids Animal parasites Animal parasites Animal parasites Plant parasites  Predation Predation Predation and versatility – general ideas	80 81 83 88 100 101 101 102 108 108
4.1	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects Herbivory – an overview  Parasitism Parasitoids Animal parasites Animal parasitism – an overview Plant parasites  Predation Predation Optimal foraging – the contingency model	80 81 83 88 100 101 101 102 108 108
4.1	versatility Some caveats  Herbivory Dietary versatility in 'generalized' herbivores Host-plants of small herbivores, especially phytophagous insects Herbivory – an overview  Parasitism Parasitoids Animal parasites Animal parasites Animal parasites Plant parasites  Predation Predation Predation and versatility – general ideas	80 81 83 88 100 101 101 102 108 108



	Contents	· xi
4.4	Omnivory	122
4.5	Mutualisms Mutualistic associations Mutualisms – an overview	126 128 129 132
4.6	Summary and conclusions	134
5	The influence of population structure on versatility	139
5.1	Facultative exploitation  Ecological polymorphism and behavioural plasticity	142 146
5.2	Adaptive polyphenism and phenotypic plasticity	148
5.3	Polymorphism	152
5.4	Stage-structured populations	156
5.5	An idealized set of exploitation strategies Four idealized exploitation strategies	161 162
5.6	Summary	165
6	Ecological versatility and population dynamics	167
6.1	The principles underlying the models Utilization pressure Functional and numerical responses The marginal utilization rate The flexibility of utilization rates – hard and soft exploitation The model strategies The assumptions of many-resource models The test environments The remainder of Chapter 6	169 170 173 175 175 178 179 180
6.2	The flexibility of utilization rates High density influxes Overview	182 185 186
6.3	<b>Differentiation within populations</b> The stability of ecological polymorphisms Overview	187 190 193
6.4	Specialization Overview	194 200



X11	· Contents	
6.5	Additional remarks Efficiency Metapopulations Ecological modelling	201 202 203 207
6.6	Summary	209
7	Versatility and interspecific competition	213
7.1	Versatility and interspecific competition – a short review Equilibria, invasibility and stability Models of interspecific competition Versatility and interspecific competition Overview	216 216 219 220 224
7.2	Modelling Parameter-space spans and the glyph representation	225 226
7.3	Persistence and invasibility Some factors influencing persistence and coexistence Invasibility Overview	229 229 243 245
7.4	Environmental variability Overview	245 251
7.5	<b>Many populations</b> The impact of background populations – context-specificity The $N$ populations – $N$ resources problem Overview	251 251 253 258
7.6	Additional remarks Absolute rates Strategic and tactical options On coexistence and ecological versatility	259 259 261 261
7.7	Summary	263
8	Ubiquity or habitat versatility Distributions – range and ubiquity	265 267
8.1	Niche pattern Ubiquity and niche position Density and distribution	269 271 275



	Contents	· xiii
8.2	Temporal variation in food availability Seasonal variation Between-year variation	276 276 278
8.3	Habitat selection and competition Compression and release The dominance model Habitat selection in animals Habitat selection in animals – physiognomy and floristics Habitat selection in plants	279 280 281 282 286 289
8.4	Other models of ubiquity  Modelling the ubiquity—position relationship  Contingency models of ubiquity	290 290 293
8.5	Versatility and ubiquity	301
8.6	Summary	305
9	Recapitulation and commentary	308
9.1	Overview of factors influencing ecological versatility General ideas Specific ideas	309 309 323
9.2	Questions and answers	328
9.3	Commentary Improved sampling designs Changing directions in ecological modelling? Idiosyncrasy, contingency and small numbers Prospectus	332 332 335 336 341
	Glossary of terms	343
	Appendix A	351
<b>A.1</b>	List of studies used in the survey	351
<b>A.2</b>	Breadth and overlap meaures	354
	Appendix B	358
<b>B.1</b>	Diagnostic statistics	358
R 2	Variation in resource availability	360



XIV	Contents	
<b>B.3</b>	Resource availability	361
	'Perceived' and actual availabilities	361
<b>B.4</b>	Exploitation algorithms	363
	Hard coherency algorithm	363
	Soft coherency algorithm	364
	Hard resource-like algorithm	365
	Soft resource-like algorithm	367
	Hard specialization algorithm	368
	Soft specialization algorithm	369
<b>B.</b> 5	More on assumptions and limitations	371
<b>B.</b> 6	Implementation, hardware, etc.	375
	References	376
	Index	423



## Preface

When Professor John Birks kindly offered me the opportunity to submit an outline for a book for the Cambridge Studies in Ecology series, I decided that it would be worthwhile to analyze comprehensively ecological specialization and generalization in natural communities (commonly referred to as niche breadth, or niche width). Of course, there has been no shortage of review articles on particular groups of organisms, especially insects, looking at this question (e.g., Fox and Morrow 1981, Schemske 1983, Berenbaum 1990, Jaenike 1990, Andow 1991). Nor has there been any lack of theoretical attention (e.g., MacArthur and Levins 1967, Van Valen and Grant 1970, Roughgarden 1972, Slatkin and Lande 1976, Keast 1977, Siegismund et al. 1990). Futuyma and Moreno (1988) provided an excellent short review of this topic from an evolutionary perspective. However, it seems that a more extensive treatment of reasons for specialized or generalized resource use and its relationship to community dynamics would be an appropriate subject for a book in this series. I did not realize at the time that this seemingly well circumscribed topic would so thoroughly ramify throughout community ecology. However, a retrospective reading of Futuyma and Moreno's (1988) article had (correctly) said as much in the very first paragraph.

An important dichotomy is developed in Chapters 1 and 2 based on specialization—generalization at the local scale, and the capacity of species to occupy few or many different types of habitats. Fox and Morrow (1981) drew attention to the difference between the degree of specialization or generalization at the scale of the local population, and the degree when integrated over the entire range of a species (i.e., all populations of a species). They noted that some species could be 'local' specialists, relying on one species of host plant, for example, in one type of habitat, yet switch hosts in different habitats. Thus, while maintaining a similar degree of specialization of local resource use, the species might still be perceived as a generalized one over the variety of habitats it occupies. Cody (1974) was another who recognized that niche width might be



### xvi · Preface

partitioned into local and global components. He believed that some species of food specialists (e.g., parulid warblers) occupy many types of habitats, while species restricted in habitat use often were food generalists (e.g., emberizid finches). This distinction between local and global specialization and generalization is a crucial one, and dictates the content of this book. Almost all of this volume is concerned with specialization and generalization at the local scale. I ask questions like: how is it framed? how is it studied? what do we know? which ecological processes affect it? and how can we model it? Specialization and generalization in the use of habitats are considered more briefly, being the main focus of Chapter 8. But, generally speaking, the book addresses local specialization and generalization.

Many people have contributed in one way or another to getting this book written, but four were particularly helpful and generous with their time and conceptual and editorial criticisms. My wife, Dr Jane Doolan, deftly wielded her editorial pencil on parts of the manuscript. The project happened to coincide with the arrival of our children, Erica and Aleck, so that Jane also bore the brunt of attending to their (ongoing) constant demands and wishes during this period. For these Herculean tasks, I thank her very fondly.

The main conceptual reviewers of the manuscript (apart from the *Studies* editors) were Dr Peter Fairweather, formerly of Macquarie University but now with the CSIRO, and Dr P. S. 'Sam' Lake, of Monash University. I was indeed fortunate to be able to call upon two such fine and versatile scholars and ecologists for their advice and comments. Their marine littoral and limnological backgrounds helped, no doubt, to broaden the subject-matter from my exclusive experience in temperate, terrestrial systems.

The fourth substantial contributor was Dr Craig Blundell, formerly of BHP Research in Melbourne. Although he is a geophysicist, his broad interests in science and philosophy spurred me on continually. I like to think that I contributed modestly to his doctoral studies spanning the same period in which this book was written. His mathematical acumen and knowledge were a great boon during the development of the modelling algorithms discussed in Chapters 6 and 7 and Appendix B. We shared many tortuous paths before reaching the eventual solutions.

I am also grateful for comments on some chapters by Professor Peter Petraitis of the University of Pennsylvania (Chapters 2 and 3) and Dr Barbara Downes of Melbourne University (Chapters 1 to 4), both of whom prompted important clarifications or additions. I should add the



Preface xvii

usual caveat that all of the opinions in the book ultimately are my responsibility and that none should necessarily reflect on the scientific credibility of any other persons named here.

I also thank Gerry Quinn, Barry Traill, Linc McIntosh, Niall Richardson, Dugal Wallace, Angela Bowles, Tim Monks, Ian Hoyle and 'both' of my families for their assistance or encouragement. The support of Professor J. W. Warren and the Department of Ecology and Evolutionary Biology at Monash University was invaluable. I also thank the Australian Research Council for some support during the latter phases of writing.

And last, but hardly least, I thank the editorial and production staff of Cambridge University Press. Professor Birks provided critical and editorial advice for which I am most grateful; I hope he is pleased with the outcome. I am especially indebted to Professor John Wiens, whose criticisms, suggestions and thoughtful comments on the manuscript were priceless. He kindly devoted time to the task when he was on sabbatical leave at the University of British Columbia, which clearly indicates a high degree of altruism on his part. I also wish to acknowledge Dr Alan Crowden for maintaining a subtle correspondence of coercion across the world.

RCM August 1994, Melbourne

