NULL MODELS IN ECOLOGY

To Dan, Don, Fran, Joe, Larry, and Van

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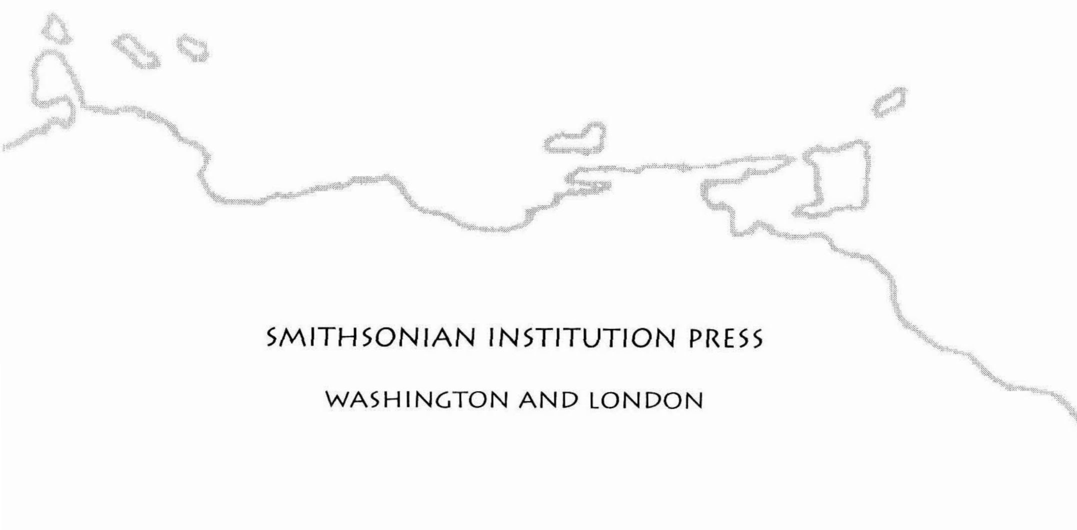

SMITHSONIAN INSTITUTION PRESS

WASHINGTON AND LONDON

Edited and typeset by Princeton Editorial Associates
Designed by Kathleen Sims

Library of Congress Cataloging-in-Publication Data
Gotelli, Nicholas J., 1959–
Null models in ecology / Nicholas J. Gotelli, Gary R. Graves.
p. cm.
Includes bibliographical references and index.
ISBN 1-56098-657-3 (alk. paper).—ISBN 1-56098-645-X (pbk.: alk. paper)
1. Null models (Ecology). 2. Biotic communities—Statistical methods.
3. Monte Carlo method. I. Graves, Gary R. II. Title.
QH541.15.N84G67 1996
574.5′01′5195—dc20 95-26734
CIP

British Library Cataloguing-in-Publication Data is available.

Manufactured in the United States of America
02 01 00 99 98 97 96 5 4 3 2 1

♾ The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48-1984.

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PREFACE

Writing this book was an enormous task. The literature on null models encompasses many subdisciplines in ecology, some of which are characterized by ambiguity and controversy. Some of the controversies are long-standing, and the biological issues have sometimes been lost in the cross fire of statistical criticisms. Perhaps for this reason, some ecologists have rejected the entire null model approach, arguing that it fails to give us useful answers in ecology. We disagree. We see null models as basic tools for community ecologists, especially useful in areas where experiments are impossible and standard analyses fail us. Null models represent statistical tests that are tailored to a particular ecological question. Ideally, they incorporate many important aspects of the biology of the component species.

What should a book on null models cover? A broad coverage might include any statistical test designed to distinguish pattern from randomness, whereas a very narrow definition might cover only randomization tests for competitive patterns in island faunas (usually avifaunas). We aimed for the middle ground. In this book, we review the use of Monte Carlo methods and certain statistical tests that have been important in the intellectual history of community ecology.

In many cases, null models have addressed the most important questions in the discipline. How do species partition resources? What controls species diversity and how do we measure it? How are communities organized at different trophic levels? Historically, questions such as these were often based on fuzzy definitions, clouded by vague terminology, and burdened with excessively complex mathematical models. One of the important contributions of null models has been to force community ecologists to state precisely what they mean and what their models predict.

Because null model tests have frequently contradicted conventional wisdom in ecology, they have often been controversial. During the 1970s and 1980s, the debate over null models and competition theory generated something akin to religious fervor on both sides of the issues (Figure P.1). We have done our best

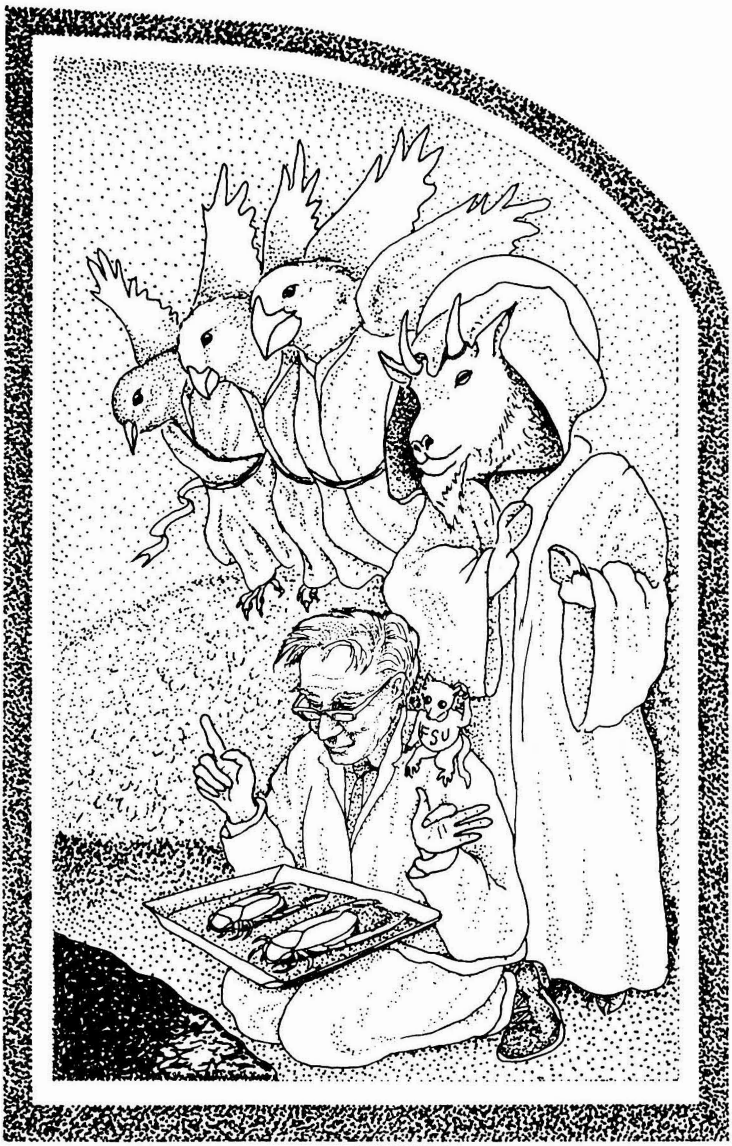

Figure P.1. This drawing reflects the early criticism that competition theory constituted a "religion" for ecology. The ecologist G. Evelyn Hutchinson is depicted noting that two corixids have a size ratio of 1.30, shown by holding up one finger on one hand and one and three fingers on the other hand (much the same way in Christian iconography three up-held fingers symbolize the Trinity). As he was inspired by the corixids found in the pool marked in honor of the patron saint Santa Rosalia, the saint appears behind Hutchinson. However, the bones of Santa Rosalia have been scientifically determined to be the bones of a goat, so Santa Rosalia is portrayed as a goat. The Galápagos finches are depicted in the background because they appear to show Hutchinsonian ratios in bill dimensions. The lemur on Hutchinson's shoulder with "FSU" on its sweatshirt symbolizes Florida State University's challenge to the paradigm that would arise many years later. From a 1991 Christmas card by Shahid Naeem.

to give an even-handed account of these controversies, although our bias in favor of the use of null models cannot be eliminated.

WHAT THIS BOOK IS NOT ABOUT

We chose to limit our discussion of null models to community-level processes. Consequently, we have not discussed null models of population dynamics, animal behavior, landscape ecology, ecosystem modeling, or phylogeny. We have also omitted purely statistical issues such as bootstrapping and jackknifing. Although we occasionally illustrate the probability equations used in these analyses, this is not a cookbook or workbook of null models; we don't present any computer programs for readers to use.

A second null model book needs to be written, one that contains null model software that would allow researchers to analyze data more easily using these tests. For the time being, null model analyses are accessible only to those with some programming expertise, although advances in software design are lowering this threshold. This book describes the application (and misapplication) of available null models and which sorts of tests are appropriate for different problems.

Although we attempted to be comprehensive, the field is active and the literature base is constantly expanding. Our coverage extends approximately through the end of 1993, with some later citations provided by enthusiastic colleagues. Articles that we would like to have discussed but could not include Dayan and Simberloff (1994), Lafferty et al. (1994), Naeem and Hawkins (1994), Pleasants (1994), Silvertown and Wilson (1994), Williams (1995), and Wilson (1995). No doubt this list will have grown further by the time this book is in print.

ORGANIZATION OF THE BOOK

Each chapter in this book discusses an area of research in community ecology that has been the subject of null model analysis. We have tried to review both the specific null model tests and the general questions associated with each research front. Throughout the book, we have used figures taken from original publications whenever possible. Although the book may lack the visual conformity and appeal of redrawn figures, we feel the original illustrations best depict the data as the authors intended. Each chapter concludes with a brief list of recommended tests for a particular question. We included this list of recommendations because many colleagues have requested guidance in choosing among null models. None of the tests is perfect, but we prefer them over the available alternatives. Because this is a dynamic field, some of our recommendations undoubtedly will be supplanted by future developments in null model analysis.

THEMES OF THE BOOK

There is some inevitable redundancy among the chapters, because certain broad themes recur in different contexts. These include the following:

1. What is the distinction between nonrandom patterns and the mechanisms that produce them? Null models can reveal unusual patterns but cannot, by themselves, elucidate a particular mechanism. Additional data are usually necessary to distinguish among competing hypotheses that can explain a pattern detected by a null model analysis. For example, although a null model can be used to establish that the difference in species richness between two assemblages is unlikely to reflect sampling error (Chapter 2), it cannot reveal why they differ.

2. What are the relative merits of conventional statistical tests versus Monte Carlo simulations? Conventional statistical tests may not always be appropriate for questions in community ecology because of nonnormality and nonindependence of data. Monte Carlo simulations are often preferable, although in some cases they generate similar results (e.g., Bowers and Brown 1982). Statistical tests such as rarefaction (Hurlbert 1971) and the variance ratio (Schluter 1984) are useful as null models, but they can be cumbersome to calculate by hand and are unfamiliar to many ecologists.

3. How can problems of redundancy and statistical independence be resolved? In other words, what are the independent units that represent the sampling universe for randomizations? If the same combinations of species recur in different assemblages, it is unclear whether these assemblages represent independent "samples," particularly if they have been collected at a small spatial scale. Similarly, it may not be legitimate to treat individual species as independent replicates if they are closely related and possess many traits that reflect their common ancestry.

4. How much biology should be included in the null model? A null model of "no structure" is easily rejected for most assemblages but does not provide a very powerful test of the predictions of ecological theory. When we incorporate more structure into the model, the simulation becomes more realistic and may provide a better test of model predictions. However, if too much structure is incorporated, the simulations may so closely reflect the observed data that the null hypothesis can never be rejected. This trade-off between generality and realism is common to all model-building strategies (Levins 1966).

5. *What is the relative importance of Type I and Type II errors in null model tests?* Because null model tests are based on techniques of randomization, they control for Type I error (incorrectly rejecting the null hypothesis) by requiring that observed patterns fall in the extreme tail of a distribution of simulated values. However, the possibility of Type II error (incorrectly accepting the null hypothesis) has only recently been explored by evaluating the power of null models to detect pattern when a particular mechanism is in operation. An assessment of Type II error is critical if investigators are going to use the results of a null model to claim that a particular mechanism is not important in producing a pattern (Toft and Shea 1983).

6. *How should appropriate source pools be constructed?* Establishing the source pool of species is a critical step in constructing a null model. Historically, the total species list for an archipelago or set of assemblages has been used, but there are other, more powerful approaches, which we discuss in the Epilogue and elsewhere in the book.

CONTENT OF THE BOOK

Chapter 1 is a review of the history of null models and the philosophical issues surrounding the approach. The literature on hypothesis testing in the philosophy of science is extensive, as is the rhetoric on both sides of the null models issue. We have tried to emphasize the important points of controversy and suggest some possible solutions to the criticisms that have been leveled against null models. We also review the literature on the species/genus (S/G) ratio, one of ecology's earliest null model controversies, and summarize other historical null model studies that have not been so well appreciated.

Chapter 2 discusses species diversity indices and the use of rarefaction as a distribution-free sampling model for comparing species richness of different samples. Because the concept of species diversity is intimately linked to the relative abundance of species in an assemblage, Chapter 3 reviews null models of species abundance distributions, including Caswell's (1976) innovative "neutral models" and MacArthur's (1957) celebrated broken-stick model.

In Chapters 4 and 5, we address null model studies of niche overlap. Chapter 4 describes how complex mathematical models of niche overlap have been translated into simple null models that can be applied to field observations of resource utilization. These null models have been applied to estimates of dietary components or use of small-scale microhabitats. Chapter 5 focuses on time as a niche axis. In animal communities, temporal partitioning may be expressed as differences in the diet of predators that forage synchronously versus asynchronously. In plant communities, temporal partitioning may be expressed as staggered sequences of flowering phenology, which reduce overlap for shared pollinators.

Chapters 6 and 7 are the longest in the book, because they detail the heart of the null model controversies: analyses of size ratios (Chapter 6) and co-occurrence patterns (Chapter 7). Size ratio analyses include tests of character displacement and Hutchinson's 1.3 rule, as well as analyses of more subtle divergence and convergence in ecomorphology.

Chapter 7 addresses community assembly and the lengthy controversy over checkerboard distributions and island co-occurrence patterns. Also included are null model tests for nestedness, incidence functions, minimum patch sizes, guild structure, and functional groups.

Chapter 8 examines the species-area relationship. The passive sampling model is used as a null model for the correlation between area and species richness, and a simple Markov model is used to predict variability in species richness and turnover in species composition. The chapter also suggests ways in which alternative hypotheses, such as habitat diversity, can be critically tested in species-area studies.

We return to co-occurrence patterns in Chapter 9, but in this case, species occurrences are continuous and are not restricted to islands or discrete habitat patches. Examples include small-scale quadrat or line-transect data, and large-scale maps of biogeographic ranges. Such data may be analyzed in one dimension, such as the occurrence of species along environmental gradients, or in two dimensions, such as the overlap of species geographic ranges. This chapter also addresses null model tests of distribution-abundance relationships, bimodality, Pleistocene refugia, taxon cycles, and Rapoport's rule.

Chapter 10 reviews the use of null models in the analysis of food web structure. Beginning with early simulation studies of stability and complexity, null models of food webs have developed somewhat independently of the rest of the community ecology literature, even though similar tests are used in co-occurrence and niche overlap studies. This chapter describes null model tests of food chain length, connectance, guild structure, and the relationship between complexity and stability. The temporal constancy of species rank abundances is also compared to null models as a test of community stability.

Finally, the Epilogue considers more general issues, such as data quality and source pool construction, and gives our perspective on trends in null model studies. Here, as elsewhere in the book, we are unlikely to persuade those readers who have already made up their minds about null models. For example, one anonymous reviewer of the proposal for this book wrote:

> Since I am not a fan of the null model approach, it would not disappoint me if they fail in their enterprise. However, I'd be interested to see how they put it all together and I think many others would also, for I feel we are doomed to have these ideas with us for a long time.

Whatever the reader's persuasion, we hope this book will at least provide grist for discussion and serve as a stimulus for further research with null models.

ACKNOWLEDGMENTS

When we first contemplated this book, we contacted a number of colleagues and asked them to send us reprints and give us their perspective on null models in ecology. Many provided reprints, preprints, unpublished manuscripts, extensive commentary, personal anecdotes, and historical reflections on null models. We thank the following for their thoughtful responses to our initial query: Jim Brown, Ted Case, Hal Caswell, Rob Colwell, Ed Connor, Arthur Ghent, Mike Gilpin, Jim Haefner, Fran James, Craig Loehle, Brian Maurer, Bob May, Earl McCoy, Eric Pianka, Stuart Pimm, Beverly Rathcke, Bob Ricklefs, Peter Sale, Dolph Schluter, Tom Schoener, Jonathan Silvertown, J. Bastow Wilson, and S. Joseph Wright.

Once chapter drafts were ready, the following colleagues provided us with a thorough reading of particular chapters: Scott Armbruster (5), Bill Boecklen (8), Alison Brody (5), Jim Brown (1,6), Ed Connor (1), Mark Lomolino (1,7), Bob May (1), Dolph Schluter (1,6,7), Dan Simberloff (1,2,6,7), and Lewi Stone (7). Jim Brown read the entire manuscript, provided detailed comments throughout, and developed the list of "recurrent themes" that we describe in the preface. Neil Buckley read and edited every single chapter, tracked down literature citations, cleaned up our prose, and suffered through galley proofs as well. We couldn't have completed this book without his help and advice.

Peter Cannell and the staff at Smithsonian Press transformed our manuscript into an actual book. We are grateful to Shahid Naeem for allowing us to publish one of the panels from his ecological triptych. N.J.G. acknowledges the support of the National Science Foundation and the Fulbright Foundation while this book was prepared. He thanks Maryanne for tolerating him while he wrote. G.R.G. thanks the Smithsonian Institution for support, and Sonya and Hillary as reasons to live.