Alain F. Zuur Elena N. Ieno · Graham M. Smith

Analysing Ecological Data



Alain F. Zuur Elena N. Ieno · Graham M. Smith

Analysing Ecological Data



Series Editors M. Gail, K. Krickeberg, J. Samet, A. Tsiatis, W. Wong

Bacchieri/Cioppa: Fundamentals of Clinical Research Borchers/Buckland/Zucchini: Estimating Animal Abundance: Closed Populations Burzykowskil Molenberghs/Buyse: The Evaluation of Surrogate Endpoints Everitt/Rabe-Hesketh: Analyzing Medical Data Using S-PLUS Ewens/Grant: Statistical Methods in Bioinformatics: An Introduction, 2nd ed. Gentleman/Carey/Huber/Irizarry/Dudoit: Bioinformatics and Computational Biology Solutions Using R and Bioconductor Hougaard: Analysis of Multivariate Survival Data Keyfitz/Caswell: Applied Mathematical Demography, 3rd ed. Klein/Moeschberger: Survival Analysis: Techniques for Censored and Truncated Data, 2nd ed. Kleinbaum/Klein: Logistic Regression: A Self-Learning Text, 2nd ed. Kleinbaum/Klein: Survival Analysis: A Self-Learning Text, 2nd ed. Lange: Mathematical and Statistical Methods for Genetic Analysis, 2nd ed. Manton/Singer/Suzman: Forecasting the Health of Elderly Populations Martinussen/Scheike: Dynamic Regression Models for Survival Data Mové: Multiple Analyses in Clinical Trials: Fundamentals for Investigators Nielsen: Statistical Methods in Molecular Evolution Parmigiani/Garrett/Irizarry/Zeger: The Analysis of Gene Expression Data: Methods and Software Proschan/LanWittes: Statistical Monitoring of Clinical Trials: A Unified Approach Siegmund/Yakir: The Statistics of Gene Mapping Simon/Korn/McShane/Radmacher/Wright/Zhao: Design and Analysis of DNA **Microarray Investigations** Sorensen/Gianola: Likelihood, Bayesian, and MCMC Methods in Quantitative Genetics Stallard/Manton/Cohen: Forecasting Product Liability Claims: Epidemiology and Modeling in the Manville Asbestos Case Sun: The Statistical Analysis of Interval-censored Failure Time Data TherneaulGrambsch: Modeling Survival Data: Extending the Cox Model Ting: Dose Finding in Drug Development Vittinghoff/Glidden/Shiboski/McCulloch: Regression Methods in Biostatistics: Linear, Logistic, Survival, and Repeated Measures Models WulMalCasella: Statistical Genetics of Quantitative Traits: Linkage, Map and QTL Zhang/Singer: Recursive Partitioning in the Health Sciences Zuur/Ieno/Smith: Analysing Ecological Data

Alain F. Zuur Elena N. Ieno Graham M. Smith

Analysing Ecological Data



Alain F. Zuur Highland Statistics Ltd. Newburgh AB41 6FN UNITED KINGDOM highstat@highstat.com Elena N. Ieno Highland Statistics Ltd. Newburgh AB41 6FN UNITED KINGDOM bio@highstat.com Graham M. Smith School of Science and the Environment Bath Spa University Bath BA2 9BN UNITED KINGDOM g.m.smith@bathspa.ac.uk

Series Editors M. Gail National Cancer Institute Rockville, MD 20892 USA

K. Krickeberg Le Chatelet F-63270 Manglieu France

J. Sarnet Department of Epidemiology School of Public Health Johns Hopkins University Baltimore, MD 21205-2103 USA

A. Tsiatis Department of Statistics North Carolina State University Raleigh, NC 27695 USA W. Wong Department of Statistics Stanford University Stanford, CA 94305-4065 USA

Library of Congress Control Number: 2006933720

ISBN-10: 0-387-45967-7 ISBN-13: 978-0-387-45967-7 e-ISBN-10: 0-387-45972-3 e-ISBN-13: 978-0-387-45972-1

Printed on acid-free paper.

© 2007 Springer Science + Business Media, LLC

All rights reserved. This work may not be translated or copied in whole or in part without the written permission of the publisher (Springer Science + Business Media, LLC, 233 Spring Street, New York, NY 10013, USA), except for brief excerpts in connection with reviews or scholarly analysis. Use in connection with any form of information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed is forbidden.

The use in this publication of trade names, trademarks, service marks, and similar terms, even if they are not identified as such, is not to be taken as an expression of opinion as to whether or not they are subject to proprietary rights.

Printed in the United States of America

987654321

springer.com

To Asterix, Juultje and Poek, for paying more attention to my laptop

To Norma and Juan Carlos, and to Antonio (d' Aieta) who showed me that it was worthwhile crossing the great waters...

To Moira, for accepting all the hours shared with my computer that I should have been sharing with her

Preface

Which test should I apply? During the many years of working with ecologists, biologists and other environmental scientists, this is probably the question that the authors of this book hear the most often. The answer is always the same and along the lines of 'What are your underlying questions?', 'What do you want to show?'. The answers to these questions provide the starting point for a detailed discussion on the ecological background and purpose of the study. This then gives the basis for deciding on the most appropriate analytical approach. Therefore, a better starting point for an ecologist is to avoid the phrase 'test' and think in terms of 'analysis'. A test refers to something simple and unified that gives a clear answer in the form of a p-value: something rarely appropriate for ecological data. In practice, one has to apply a data exploration, check assumptions, validate the models, perhaps apply a series of methods, and most importantly, interpret the results in terms of the underlying ecology and the ecological questions being investigated.

Ecology is a quantitative science trying to answer difficult questions about the complex world we live in. Most ecologists are aware of these complexities, but few are fully equipped with the statistical sophistication and understanding to deal with them.

Even data gathered from apparently simple ecological research can require a level of statistical awareness rarely taught at the undergraduate or even the postgraduate level. There is little enough time to teach the essentials of ecology, let alone finding the time to teach 'advanced' statistics. Hopefully, for post graduates moving into academia there will be some advanced statistical support available, but many ecologist end up working in government, a voluntary organisation or consultancy where statistical support is minimal.

Although, the authors of this book believe that a quantitative approach is at the core of being a good ecologist, they also appreciate how challenging many ecologists find statistics. This book is therefore aimed at three levels of reader.

At one level it is aimed at making ecologists aware of how important it is to design scientifically robust ecological experiments or monitoring programmes, and the importance of selecting the best analytical technique. For these readers we hope the book, in particular the case studies, will encourage them to develop their personal statistical skills, or convince them they need statistical support.

On the next level it is aimed at the statistically literate ecologist, who may not be fully aware of the techniques we discuss, or when to use them. Hopefully, we have explained things well enough for these readers to feel confident enough to use some of the techniques we describe. Often these techniques are presented in a fairly impenetrable manner, even for the statistically aware ecologist, and we have tried to make our presentation as 'ecologist friendly' as possible.

Finally, we hope the book will be of value to statisticians, whether they have a background in ecology or statistics. Ecological data can be particularly challenging to analyse, and we hope that providing an insight into our approach, together with the detailed case studies, will be of value to statistician readers, regardless of their background and expertise.

Overall, however, we hope this book will contribute in some small way to improving the collection and analysis of ecological data and improve the quality of environmental decision making.

After reading this book, you should be able to apply the following process: 'These are my questions', 'This is my statistical approach', 'Here is proof that I did it all correct (model validation)', 'This is what the data show' and 'Here is the ecological interpretation'.

Acknowledgement

A large part of the material in this book has been used by the first two authors as course material for MSc and PhD students, post-docs, scientists, both as academic and non-academic courses. We are greatly indepted to all 1200–1500 course participants who helped improve the material between 2000 and 2005 by asking questions and commenting on the material.

We would also like to thank a series of persons who commented on parts of this book: Ian Jolliffe, Anatoly Saveliev, Barry O'Neill, Neil Campbell, Graham Pierce, Ian Tuck, Alex Douglas, Pam Sikkink, Toby Marthews, Adrian Bowman, and six anonymous reviewers and the copy-editor. Their criticisms, comments, help and suggestions have greatly improved this book.

The first author would like to thank Rob Fryer and FRS Marine Laboratory for providing the flexibility to start the foundation of this book.

We would also like to thank the people and organizations who donated data for the theory chapters. The acknowledgement for the unpublished squid data (donated by Graham Pierce, University of Aberdeen) used in Chapters 4 and 7 is as follows. Data collection was financed by the European Commission under the following projects: FAR MA 1.146, AIR1-CT92-0573, FAIR CT 1520, Study Project 96/081, Study project 97/107, Study Project 99/063, and Q5CA-2002-00962. We would like to thank Roy Mendelssohn (NOAA/NMFS) for giving us a copy of the data used in Mendelssohn and Schwing (2002). The raw data are summaries calculated from the COADS dataset. The COADS references are Slutz et al. (1985) and Woodruff et al. (1987). We thank Jaap van der Meer (NIOZ) for allowing us to use the Balgzand data, The Bahamas National Trust and Greenforce Andros Island Marine Study for providing the Bahamas fisheries dataset, Chris Elphick (University of Connecticut) for the sparrow data, and Hrafnkell Eiríksson (Marine Research Institute, Revkjavik) for the Icelandic Nephrops time series. The public domain SRTM data used in Chapter 19 were taken from the U.S. Geological Survey, EROS Data Center, Sioux Falls, SD. We thank Steve Hare (University of Washington) for allowing us to use the 100 biological and physical time series

from the North Pacific Ocean in Chapter 17. A small part of Chapter 13 is based on Zuur (1999, unpublished PhD thesis), which was partly financed by the EU project DYNAMO (FAIR-CT95-0710).

A big 'thank you' is also due to the large number of folks who wrote R (www.r-project.org) and its many libraries. We made a lot of use of the lattice, regression, GLM, GAM (mgcv) and mixed modelling libraries (nlme). This thank you is probably also on behalf of the readers of this book as everything we did can be done in R.

Finally, we would like to thank John Kimmel for giving us the opportunity to write this book, and his support during the entire process. On to the next book.

Alain F. Zuur Elena N. Ieno Graham M. Smith

February 2007

Contents

Contributors	xix
1 Introduction	1
1.1 Part 1: Applied statistical theory	1
1.2 Part 2: The case studies	3
1.3 Data, software and flowcharts	6
2 Data management and software	7
2.1 Introduction	7
2.2 Data management	8
2.3 Data preparation	9
2.4 Statistical software	13
3 Advice for teachers	17
3.1 Introduction	17
4 Exploration	23
4.1 The first steps	24
4.2 Outliers, transformations and standardisations	
4.3 A final thought on data exploration	47
5 Linear regression	49
5.1 Bivariate linear regression	49
5.2 Multiple linear regression	67
5.3 Partial linear regression	73
6 Generalised linear modelling	79
6.1 Poisson regression	79
6.2 Logistic regression	
7 Additive and generalised additive modelling	97
7.1 Introduction	97
7.2 The additive model	101
7.3 Example of an additive model	102
7.4 Estimate the smoother and amount of smoothing	104
7.5 Additive models with multiple explanatory variables	108

7.6 Chaosing the amount of amosthing	110
7.0 Choosing the amount of smoothing	
7.9 Convertised addition modelling	
7.8 Generalised additive modelling	
7.9 Where to go from here	
9 Introduction to mixed modelling	175
8 1 Introduction to mixed modelling	
8.1 Introduction	
8.2 The random intercept and slope model	
8.3 Model selection and validation	
8.4 A bit of theory	
8.5 Another mixed modelling example	
8.6 Additive mixed modelling	
	1.42
9 Univariate tree models	
9.1 Introduction	
9.2 Pruning the tree	
9.3 Classification trees	
9.4 A detailed example: Ditch data	
	1.0
10 Measures of association	
10.1 Introduction	
10.2 Association between sites: Q analysis	
10.3 Association among species: R analysis	
10.4 Q and R analysis: Concluding remarks	
10.5 Hypothesis testing with measures of association	
11 Ordination First ancounter	180
11 1 Bray Curtis ordination	180
11.1 blay-cuitis ordination	
12 Principal component analysis and redundancy analysis	
12.1 The underlying principle of PCA	
12.2 PCA: Two easy explanations	
12.3 PCA: Two technical explanations	
12.4 Example of PCA	
12.5 The binlot	200
12.6 General remarks	205
12.0 Constant Fernances	205
12.7 Chord and Henniger transformations	208
12.0 Dedundancy analysis	210
12.10 Destial BDA and variance partitioning	
12.10 Partial RDA and variance partitioning	
12.11 PCA regression to deal with collinearity	221
13 Correspondence analysis and canonical correspondence analy	
13 Correspondence analysis and canonical correspondence analy 13.1 Gaussian regression and extensions	
13 Correspondence analysis and canonical correspondence analy 13.1 Gaussian regression and extensions 13.2 Three rationales for correspondence analysis	
13 Correspondence analysis and canonical correspondence analy 13.1 Gaussian regression and extensions 13.2 Three rationales for correspondence analysis 13.3 From RGR to CCA	

13.4 Understanding the CCA triplat	240
12.5 When to use $PCA = CA$ PDA or PCA	240
12.6 Problems with CA and CCA	242
13.6 Problems with CA and CCA	243
14 Introduction to discriminant analysis	245
14.1 Introduction	245
14.2 Assumptions	
14.3 Example	250
14 4 The mathematics	254
14.5 The numerical output for the sparrow data	255
15 Principal coordinate analysis and non-metric multidimensional scaling	g 259
15.1 Principal coordinate analysis	259
15.2 Non-metric multidimensional scaling	261
16 Time series analysis Introduction	265
16 1 Using what we have already seen before	
10.1 Using what we have alleady seen before	205
16.2 Auto-regressive integrated moving average models with exogenous	201
variables	281
17 Common trends and sudden changes	289
17.1 Repeated LOESS smoothing	289
17.2 Identifying the seasonal component	293
17.3 Common trends: MAFA	299
17.4 Common trends: Dynamic factor analysis	303
17.5 Sudden changes: Chronological clustering	315
19 Analysis and modelling of lattice data	221
10 1 Lettice dete	221
10.1 Lattice data	
18.2 Numerical representation of the fattice structure	323
	327
18.4 Modelling lattice data	
18.5 More exotic models	334
18.6 Summary	338
19 Spatially continuous data analysis and modelling	341
19.1 Spatially continuous data	341
19.2 Geostatistical functions and assumptions	342
19.3 Exploratory variography analysis	346
19.4 Geostatistical modelling. Kriging	358
19.5 A full spatial analysis of the bird radar data	
20 Univariate methods to analyse abundance of decapod larvae	373
20.1 Introduction	373
20.2 The data	374
20.3 Data exploration	277

20.4 Linear regression results	
20.5 Additive modelling results	
20.6 How many samples to take?	
20.7 Discussion	
21 Analysing presence and absence data for flatfish distribution	in the Tagus
estuary, Portugal	
21.1 Introduction	
21.2 Data and materials	
21.3 Data exploration	
21.4 Classification trees	
21.5 Generalised additive modelling	
21.6 Generalised linear modelling	
21.7 Discussion	
22 Crop pollination by honeybees in Argentina using additive m	nixed
modelling	
22.1 Introduction	
22.2 Experimental setup	
22.3 Abstracting the information	
22.4 First steps of the analyses: Data exploration	
22.5 Additive mixed modelling	
22.6 Discussion and conclusions	
23 Investigating the effects of rice farming on aquatic birds with	n mixed
modelling	
23.1 Introduction	
23.2 The data	
23.3 Getting familiar with the data: Exploration	
23.4 Building a mixed model	
23.5 The optimal model in terms of random components	
23.6 Validating the optimal linear mixed model	
23.7 More numerical output for the optimal model	
23.8 Discussion	
24 Classification trees and radar detection of birds for North Se	a wind
farms	
24.1 Introduction	435
24.2 From radars to data	436
24.3 Classification trees	438
24.5 Chassification decision 24.4 A tree for the birds	440
24.5 A tree for birds, clutter and more clutter	445
24.5 A tree for ones, entrer and more entrer manner.	447
	······
25 Fish stock identification through neural network encloses of	narasite
45 FISH SOUR INCHUNCATION ON OUGH NEULAI NEUWOLK ANALYSIS OL	אמו מאונד אאח
144114	

25.1 Introduction	
25.2 Horse mackerel in the northeast Atlantic	
25.3 Neural networks	
25.4 Collection of data	
25.5 Data exploration	
25.6 Neural network results	457
25.5 7 Discussion	460
A Manifesting for the set II is a second land based and an ended	
20 Monitoring for change: Using generalised least squares, non-metri	C
multidimensional scaling, and the Mantel test on western Montana	
grasslands	
26.1 Introduction	
26.2 The data	
26.3 Data exploration	
26.4 Linear regression results	
26.5 Generalised least squares results	
26.6 Multivariate analysis results	
26.7 Discussion	
27 Univariate and multivariate analysis applied on a Dutch sandy bea	nch
community	485
27.1 Introduction	485
27.1 The variables	486
27.2 The variables	/87
27.5 Analysing the data using univariate methods	101
27.4 Analysing the data using multivariate methods	400
27.5 Discussion and conclusions	
28 Multivariate analyses of South-American zoobenthic species — spe	bilt for
choice	
28.1 Introduction and the underlying questions	
28.2 Study site and sample collection	
28.3 Data exploration	506
28.4 The Mantel test approach	509
28.5 The transformation plus RDA approach	
28.6 Discussion and conclusions	
29 Principal component analysis applied to harbour porpoise fatty ac	id
data	
29.1 Introduction	515
29.2 The data	515
29.2 Principal component analysis	517
29.4 Data exploration	
20.5 Principal component analysis results	519
27.5 I interpar component analysis results	574
27.0 Simpler anematives to FUA	
29. (Discussion	