Coral assemblages and neutral theory

Thesis submitted by

Maria Ana Azeredo de Dornelas

in June 2006

For the Degree of Doctor of Philosophy

in Marine Biology

within the School of Marine Biology

James Cook University

STATEMENT OF ACCESS

I, the undersigned, the author of this thesis, understand that James Cook University will make this thesis available for use within the University Library and, via the Australia Digital Theses network (unless granted an exemption), for use elsewhere.

I understand that, as an unpublished work, a thesis has significant protection under the Copyright Act and;

I wish this work to be embargoed until November 2007

Maria Dornelas

27.06.2006

STATEMENT ON SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any other form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given

Maria Dornelas

27.06.2006

ELECTRONIC COPY

I, the undersigned, the author of this work, declare that the electronic copy of this thesis provided to the James Cook University Library is an accurate copy of the print thesis submitted, within the limits of the technology available.

____________________________ ________________

Signature Date

Acknowledgments

A number of people provided priceless support during this project, and I am grateful to them all. Firstly, I want to say a huge thank you to Sean Connolly. Sean was everything I could have wished for in a supervisor, providing invaluable guidance, constant availability, and freedom to disagree. Secondly, I am profoundly grateful to Terry Hughes for his precious advice, for giving me the opportunity to work with his incredible dataset, and for listening to my (sometimes) mad ideas.

I want to thank the staff at the High Performance Computing Section, James Cook University, for all their assistance. Wayne Mallet, in particular, provided great support on using hydra and borg (the two super computers), and even translated some of my MATLAB code into C++, to speed the parametric bootstraps. I am very grateful to Brian McGill and Rampal Etienne for sharing their code and giving helpful advice on fitting neutral models. I also want to thank to Anne Magurran for friendly hospitality in her lab during the final stages of this thesis.

I want to thank everybody that, over the years, participated in the Theoretical Ecology Discussion Group, as well as Laura Castell for listening to and/or reading several versions of this work and providing great feedback. A special thanks to Mia, Ailsa and Matt who also provided feedback, support and company out of the Friday meetings.

I thank H. Cornell, R. Karlson and staff and students of the ARC Centre of Excellence for Coral Reef Studies for collecting, under the leadership of Terry Hughes, the dataset I used in Chapters 3 and 4.

A huge thank you also to Abbi McDonald, Ailsa Kerswell, Alex Kerr, Andrew Baird, Jackie Wolstenholme, Marie Kospartov, Maria Joao Rodrigues, Mia Hoogenboom, Matt Kosnik, Naomi Gardiner and Scott Burgess for helping me collect the dataset I present in Chapter 5. They were not only far more efficient than I could have hoped for, but also lots of fun to work with. A special thanks to Jackie for sharing her precious coral identification skills with me. I'm also very grateful to Anne Hoggett, Lyle Vail, Marianne and Lance Pearce, for providing making the Lizard Island Research Station a great place to do fieldwork.

I have no words to describe how grateful I am to Miguel Barbosa, for all the help he gave me along the way, and for being here for me always. A big, big thank you to Mum and Dad for everything, and to my Grandmother, who made me fall in love with biology.

Finally, I am most grateful to the Fundação para a Ciência e a Tecnologia, Portugal, for supporting me during this PhD.

Abstract

Neutral theory explains patterns of biodiversity based solely on speciation, demographic stochasticity, and dispersal limitation. The validation of this controversial theory depends on empirical support and it has been largely untested in marine communities. Coral assemblages have been repeatedly invoked as the animal communities most likely to conform to the assumptions of neutral theory. This thesis tested the hypothesis that neutral theory explains the macroecological structure of coral assemblages.

Firstly, I assessed whether neutral models can accurately characterise coral species abundance distributions across multiple scales. Simulation-based and analytical neutral models were fitted to a hierarchical dataset of coral species abundance distributions from across the Indo-Pacific gradient of biodiversity. The dataset has three replicate habitats (slope, crest and flat), and three spatial scales (site, island and region). Both models exhibit significant lack of fit to empirical data at the site and island scales, but not at the region scale. The neutral model consistently underestimates the number of rare species, and overestimates the number of common species. Additionally, the neutral model fits coral abundance distributions less accurately than the poisson-lognormal at all scales. Using two formulations of neutral theory, and two goodness-of-fit tests, along with comparisons with the lognormal distribution, ensures that the inferences about coral assemblages and neutral dynamics are robust. Neutral model predictions are consistently and significantly different from observed coral species abundance distributions.

Secondly, I developed a novel test of neutral theory that examines variability between communities of species relative abundances. In neutral communities, species relative abundances are determined by demographic stochasticity or "ecological drift". Thus, communities diverge through time, and are expected to have low community similarity. In contrast, niche apportionment mechanisms have been invoked to argue that higher levels of community similarity should be observed under niche assembly than under neutral dynamics. These contrasting predictions provide an ideal opportunity to test neutral models against empirical data. Relative abundances of species across local communities differ markedly from neutral theory predictions: coral communities exhibit community similarity values that are far more variable, and lower on average, than neutral theory can predict. Surprisingly, empirical community similarities deviate from the neutral model in a direction opposite to that suggested in previous critiques of neutral theory. Instead, the results support spatio-temporal environmental stochasticity as a major driver of community structure at the macroecological scale.

Thirdly, I unveiled a coral local community species abundance distribution. Community structure patterns are notoriously sensitive to sampling issues, and a comprehensive characterization of such patterns requires extremely large sample sizes. Consequently, the fit of biodiversity models to species abundance distributions, and parameter estimates in particular may be sensitive to sample size. To address these questions, over 44,000 corals were counted and identified to species at an exposed crest in Lizard Island, Great Barrier Reef. A neutral model was fitted to the species abundance distribution of the total dataset, and to sub-samples of various sizes. Parameter estimates and fit of the neutral model at different sample sizes were compared. The unveiled species abundance distribution appears to be multimodal. Parameter estimates are not affected by sample size.

These results strongly indicate that the limited suite of ecological and evolutionary processes included in neutral theory do not suffice to explain diversity patterns in coral assemblages. In combination, the three approaches included in this thesis suggest that neutral theory is most useful as a null model for community structure. Furthermore, the thesis highlights differences in species' responses to environmental fluctuations as a potential major driver of species abundance patterns.

Table of Contents

List of Figures