

ECOLOGICAL RESISTANCE AND BUFFERS OF ENVIRONMENTAL CHANGE



GIULIA GHEDINI

Presented for the degree of Doctor of Philosophy

School of Biological Sciences

The University of Adelaide

August 2016



THE UNIVERSITY
of ADELAIDE

Cover Image: Leafy seadragons live within southern kelp forests of Australia.
Photo credit: Jeffery Jeffords (Copyright purchased by The University of
Adelaide, signed by Sean Connell.)

DECLARATION

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968.

The author acknowledges that copyright of published works contained within this thesis resides with the copyright holder(s) of those works.

I also give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

Giulia Ghedini

August, 2016

CONTENTS

ECOLOGICAL RESISTANCE AND BUFFERS OF ENVIRONMENTAL CHANGE.....	I
DECLARATION	III
CONTENTS.....	IV
ABSTRACT.....	VII
ACKNOWLEDGMENTS	IX
CHAPTER ACKNOWLEDGMENTS	X
CHAPTER 1 – GENERAL INTRODUCTION	1
1.1 Stability <i>via</i> resistance and resilience to disturbance	3
1.2 Compensatory dynamics buffer change	5
1.3 Organismal responses might stabilise community dynamics.....	8
1.4 Environmental variability and extreme events.....	11
1.5 Biotic mediation of environmental change	13
1.6 Kelp forest resistance to global and local change	15
1.7 Thesis scope and outline	17
1.7.1 Thesis summary	18
1.8 References	23
CHAPTER 2 – TROPHIC COMPENSATION REINFORCES RESISTANCE: HERBIVORY ABSORBS THE INCREASING EFFECTS OF MULTIPLE DISTURBANCES	39
Statement of authorship.....	40
2.1 Published manuscript	41
2.2 Supplementary material	48
CHAPTER 3 – ORGANISMAL HOMEOSTASIS BUFFERS THE EFFECTS OF ABIOTIC CHANGE ON COMMUNITY DYNAMICS	51
Statement of authorship.....	52
3.1 Abstract	53
3.2 Introduction	54
3.3 Material and methods.....	58
3.3.1 Experimental setup	58
3.3.2 Herbivores and algae	60

3.3.3 <i>Response variables</i>	61
3.3.4 <i>Statistical analyses</i>	62
3.4 Results	63
3.5 Discussion	70
3.6 References	74
3.7 Supplementary material	83
CHAPTER 4 – RAPID LOSS OF RESISTANCE AS A FUNCTION OF COLLAPSE OF COMPENSATORY DYNAMICS	97
Statement of authorship.....	98
4.1 Abstract	99
4.2 Introduction	100
4.3 Methods.....	105
4.3.1 <i>Experimental design and set-up</i>	105
4.3.2 <i>Experimental treatments</i>	105
4.3.2 <i>Consumers and producers</i>	107
4.3.3 <i>Response variables and analyses</i>	108
4.4 Results	109
4.5 Discussion	116
4.6 References	119
4.7 Supplementary material	127
CHAPTER 5 – BEYOND SPATIAL AND TEMPORAL AVERAGES: ECOLOGICAL RESPONSES TO EXTREME EVENTS MAY BE EXACERBATED BY LOCAL DISTURBANCES	129
Statement of authorship.....	130
5.1 Published manuscript	131
5.2 Supplementary material	139
CHAPTER 6 – WARMING INCREASES VARIANCE OF CONSUMPTION VIA DENSITY-DEPENDENT EFFECTS	141
Statement of authorship.....	142
6.1 Abstract	143
6.2 Introduction	144
6.3 Materials and methods	145
6.3.1 <i>Experimental system and set-up</i>	145
6.3.2 <i>Experimental treatments of temperature and density</i>	146
6.3.3 <i>Response variables and analyses</i>	147

6.4 Results	148
6.5 Discussion	151
6.6 References	153
CHAPTER 7 – GENERAL DISCUSSION	159
7.1 Exploring resistance to change.....	162
7.2 The influence of fine-scale responses on broad-scale patterns	167
7.3 Building a resistance-resilience framework	171
7.4 Accounting for context-dependencies.....	173
7.5 Complementarity between compensatory dynamics might contribute to community stability.....	177
7.6 Conclusions	180
7.7 References	181
APPENDIX A – RESISTING REGIME-SHIFTS: THE STABILISING EFFECT OF COMPENSATORY PROCESSES.....	195
Statement of authorship.....	196
Published manuscript	197
APPENDIX B – MANAGING LOCAL COASTAL STRESSORS TO REDUCE THE ECOLOGICAL EFFECTS OF OCEAN ACIDIFICATION AND WARMING	201
Statement of authorship.....	202
Published manuscript	203
APPENDIX C	213
Permission to reproduce published material	214

ABSTRACT

The development of frameworks that account for community stability and its loss to environmental disturbance (e.g. regime shifts) is central to ecology, particularly for reducing uncertainty of ecological change in increasingly variable environments. Notably, community responses to disturbance often appear abrupt and surprising, raising concerns for our ability to anticipate and manage such regime shifts. In this thesis, I explore the conceptual model that compensatory dynamics may negate the effects of disturbance prior to community restructure (i.e. changes in species composition) and that their recognition may advance our ability to anticipate loss of stability. I examine the idea that the failure to recognise the weakening of mechanisms of resistance to intensifying disturbance underpins the surprise of regime shifts. My assessment centred on a plant-herbivore interaction (herbivorous gastropods-turf algae) that counters the loss of kelp forests to competitors (turf expansion) as driven by abiotic disturbances that coalesce across multiple scales of space (global to local) and time (gradual to abrupt).

My tests of the hypothesis that herbivores negate the positive effects of abiotic change on turf production suggested that ecological systems might compensate for disturbance *via* mechanisms that prevent structural changes. Whilst global (carbon enrichment) and local abiotic change (nutrient enrichment) may drive shifts in ecological systems by altering dominance relationships between competing species (e.g. shifts from kelp- to turf-dominated reefs), adjustments in strength of herbivory appeared to negate such change. My tests suggested that resistance to change may result from the aggregate effects of individual responses (*per capita*

consumption) where these generate dynamics that prevent change in community processes (productivity). Such dynamics may be underpinned by the necessity of individuals to maintain homeostasis in varying environments. Critically, combinations of gradual (warming) and abrupt abiotic change (heat waves) appeared to disrupt these buffering mechanisms and resulted in rapid loss of resistance. Further tests indicated that, if we are to anticipate the extent of ecological change, we may not only have to consider spatial and temporal variability in abiotic conditions, but also biotic processes that might increase the range of variation in ecological responses.

Overall, these results suggest that, if we understand compensatory dynamics as mechanisms of resistance to the effects of disturbance (i.e. that prevent community restructure), we may not only improve predictions of community change, but also be able to prevent undesirable change in the first place. Critically, our ability to manage for ecological change cannot only rely on building resilience, but needs to move towards a more explicit consideration of resistance mechanisms; such shift in thinking is necessary to fully understand how ecological communities respond to disturbance. Assessments of how fine-scale responses (individual and species responses) stabilise broad-scale patterns (community processes and ecosystem functioning) may offer critical insights not only to advance theories of community stability, but also to improve our capacity to anticipate and manage regime shifts.

ACKNOWLEDGMENTS

Firstly, I would like to express my gratitude to my supervisors Sean Connell and Bayden Russell for their continuous support and guidance. Sean, I am really grateful for the long hours spent discussing about ecological theory, elaborating ideas and helping me writing these ideas on paper. Bayden, thank you for your insights and continuous encouragement, for being always available despite the distance. Thank you both for helping me building the foundations of my scientific career and for believing in me more than I did.

An immense thank you goes to my parents, Franca and Maurizio. You have always been wonderfully supporting and provided me with strength and enthusiasm to go after my dreams. I would certainly not be here without you and this thesis is also yours.

Thanks to Jennie Pistevos and Tullio Rossi, my great office mates and incredible friends. Thank you for the countless coffees, the cries, the laughs and for sharing with me this wonderful adventure. You made every day of these three years enjoyable even during the tough times. Mehdi, thank you for your love. Thank you for always asking about my work and for providing your unique support. You made my life easier.

A big thank you to all the members of the Southern Seas Ecology Laboratories and School of Biological Sciences for creating a wonderful and friendly work environment. In particular, thanks to Katherine Heldt, Silvan Goldenberg, Nicole Mertens, Laura Falkenberg, Chloe McSkimming, Claudia Junge, Camilo Ferreira and Marc Jones for their endless smiles, energy and advice.

Finally, I would like to thank all my friends outside the lab and, in particular, Chiara Ravaglioli, Simona Drago, Ana Bugnot, Fabio Arsego and Nicole Dib. You are a bit spread all over the world, but you have always helped me during the hard times, putting my work into perspective and, more importantly, enjoying life.

CHAPTER ACKNOWLEDGMENTS

Chapter 2

Research funding was provided by ARC grants to SDC and BDR. Support was provided by an IPRS Scholarship (University of Adelaide) to GG and an ARC Future Fellowship to SDC. Funds were also provided by a Nature Foundation SA grant and Dr. Paris Goodsell Marine Ecology Research Grant to GG.

Chapter 3

This study was supported by an Australian Research Council Future Fellowship FT0991953 and Discovery Project grant DP150104263 to SDC. Funds were also provided by the Conchological Society of Great Britain and Ireland to GG.

Chapter 4

We thank Nicole Mertens for providing the picture used in Figure 1. This study was supported by an Australian Research Council Future Fellowship FT0991953 and Discovery Project grant DP150104263 to SDC and BDR. Funds were also provided by the Conchological Society of Great Britain and Ireland.

Chapter 5

Research funding was provided by an Australian Research Council grant to BDR and SDC. Support was provided by an IPRS Scholarship (University of Adelaide) to GG and an ARC Future Fellowship to SDC. Funds were also provided by a Nature Foundation SA grant and Dr. Paris Goodsell Marine Ecology Research Grant. The authors declare no conflict of interest.

Chapter 6

Research funding was provided by an Australian Research Council Future Fellowship FT0991953 to SDC and Discovery Project grant DP150104263 to BDR and SDC.