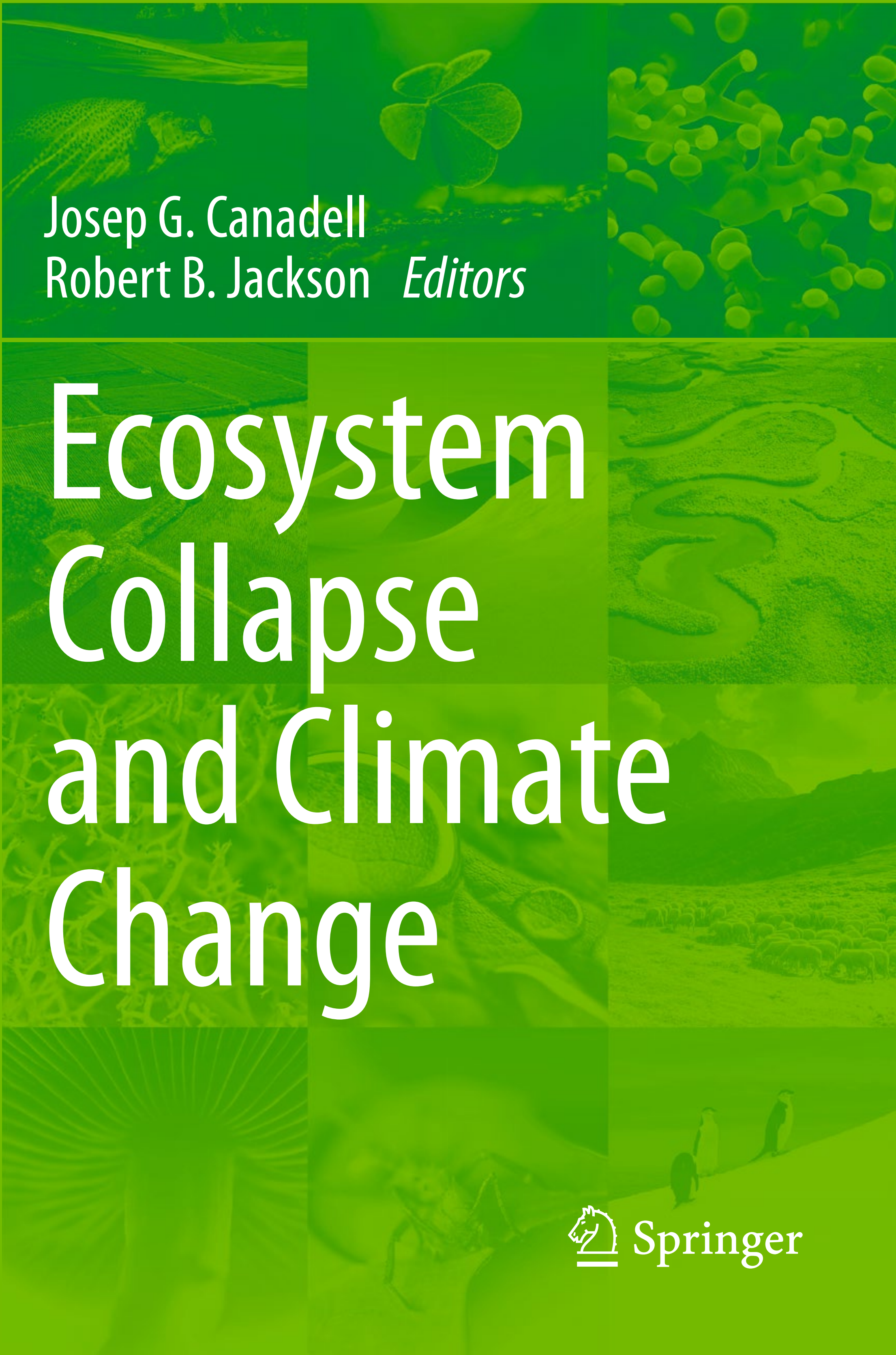
Ecological Studies 241



Josep G. Canadell
Robert B. Jackson *Editors*

Ecosystem Collapse and Climate Change

Springer

Ecological Studies

Analysis and Synthesis

Volume 241

Series Editors

Josep G. Canadell
CSIRO Oceans and Atmosphere, Canberra, ACT, Australia

Sandra Díaz
National University of Córdoba, Córdoba, Argentina

Gerhard Heldmaier
University of Marburg, Marburg, Germany

Robert B. Jackson
Stanford University, Stanford, CA, USA

Delphis F. Levia
University of Delaware, Newark, DE, USA

Ernst-Detlef Schulze
Max Planck Institute for Biogeochemistry, Jena, Germany

Ulrich Sommer
GEOMAR | Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

David A. Wardle
Nanyang Technological University, Singapore, Singapore

Ecological Studies is Springer's premier book series treating all aspects of ecology. These volumes, either authored or edited collections, appear several times each year. They are intended to analyze and synthesize our understanding of natural and managed ecosystems and their constituent organisms and resources at different scales from the biosphere to communities, populations, individual organisms and molecular interactions. Many volumes constitute case studies illustrating and synthesizing ecological principles for an intended audience of scientists, students, environmental managers and policy experts. Recent volumes address biodiversity, global change, landscape ecology, air pollution, ecosystem analysis, microbial ecology, ecophysiology and molecular ecology.

More information about this series at http://www.springer.com/series/86

Josep G. Canadell • Robert B. Jackson
Editors

Ecosystem Collapse and Climate Change

Springer

Editors
Josep G. Canadell
CSIRO Oceans and Atmosphere
Canberra, Australia

Robert B. Jackson
Stanford University
Stanford, CA, USA

ISSN 0070-8356 ISSN 2196-971X (electronic)
Ecological Studies
ISBN 978-3-030-71329-4 ISBN 978-3-030-71330-0 (eBook)
https://doi.org/10.1007/978-3-030-71330-0

© Springer Nature Switzerland AG 2021, corrected publication 2021
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG.
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Preface

Concerns about climate-related “collapse” of ecosystems are increasing, including the potential irreversible loss of habitats and species. California’s record fire year of 2020 and high-intensity fires caused unusual mortality among giant sequoias (*Sequoiadendron giganteum*), raising questions about the preservation of these ancient organisms. Likewise, diverse and unconnected terrestrial and marine ecosystems in Australia experienced simultaneous and abrupt collapse in response to the strong El Niño in 2015–2016, on top of long-term warming trends. Those changes triggered the question as to whether we were seeing predicted future climate impacts now with the rapid transformation and loss of ecosystems as we know them.

In this volume, we, and the contributing authors, document cases of ecosystem collapse around the world. In each case, the authors believe that climate change is playing a dominant or, at least, contributing role in the ecosystem’s apparent demise, sometimes interacting with other pressures. The word “collapse” is challenging to apply because in many cases we do not know (i.e., it is too early to tell) whether a given ecosystem may recover through time. In other cases, however, the ecosystem’s prognosis is poor and the chance of recovery to its initial state appears unlikely, particularly so in the face of the continuing intensification of climate change.

Our book covers three broad latitudinal regions encompassing many biome types, including (1) polar and boreal ecosystems, (2) temperate and semiarid ecosystems, and (3) tropical and temperate coastal ecosystems. Examples of ecosystem collapse in polar and boreal systems include an alpine ecosystem on sub-Antarctic Macquarie Island, approximately 650 km southwest of New Zealand, where water stress from a changing climate is interacting with a novel pathogen. The volume also examines forest collapse in southern Siberia, where warming and a lengthening fire season are leading to post-fire recruitment failure and the large-scale replacement of boreal forests with grasslands.

Studies in temperate and semiarid ecosystems include the rapid transition of a relict alpine ecosystem in Tasmania. There, fire killed a paleo-endemic ecosystem characterized by the slow-growing conifer, *Athrotaxis cupressoides*. Other chapters examine forest dieback and forest transitions to grassland and shrublands, with interactions among droughts, heatwaves, and insect outbreaks contributing to the observed transitions in places like western USA, Northen Africa and the Mediterranean region.

Examples of coastal ecosystem collapses include synchronous mangrove dieback along a 1500-km coastal mangrove ecosystem in northeastern Australia; mass bleaching and mortality in coral reefs of the Great Barrier Reef and Mediterranean Sea; the local extinction of 100 km of kelp forest in western Australia and its replacement by turf algae, attributable to marine heat waves and elevated background ocean temperatures; and the collapse of ~1300 km^2 of seagrass ecosystems attributable to a marine heat wave in 2010–2011.

The changes observed by the authors often go far beyond the biotic shifts described here. Seagrass and mangrove ecosystem experienced sediment erosion and depleted carbon stocks, and permafrost-driven changes in high latitude ecosystems are rapidly changing emissions of greenhouse gases and carbon stores in soils and vegetation.

One goal of this book is to raise awareness of the transitions that are already occurring through climate change today, and particularly those transitions associated with abrupt dynamics in response to one of the most important manifestations of climate change: the increasing intensity and sometimes frequency of climate variability and extremes. Some of the transitions might be critical, in so far that they may be irreversible or signal the beginning of a new level of abrupt changes that will ultimately lead to an irreversible outcome. Finally, we hope that by documenting such changes, increased awareness will help scientists and managers restore lost or degraded ecosystems, and where possible, their species and ecosystem functioning. In other instances, there may be opportunities to assist in a guided transition toward more resilient ecosystems in the face of rapid changes.

Canberra, Australia Josep G. Canadell
Stanford, CA Robert B. Jackson

Contents

Part I Polar and Boreal Ecosystems

Part II Temperate and Semi-arid Ecosystems

Part III Tropical and Temperate Coastal Ecosystems

Ecosystem Collapse and Climate Change: An Introduction

1

Josep G. Canadell and Robert B. Jackson

Abstract

Concerns about climate-related "collapse" of ecosystems are growing, including the irreversible loss of habitats, species, and critical ecosystem functions. Diverse terrestrial and marine ecosystems have experienced collapse-like dynamics throughout the world, particularly over the past decade. This book addresses the over-arching question: "Are we seeing predicted "future" climate impacts now, with the rapid transformation and loss of ecosystems as we know them?"

In each case of ecosystem collapse documented here, the authors believe that climate change is playing a dominant or contributing role to the ecosystem's apparent demise, often interacting with other pressures. The book covers three latitudinal regions: (1) polar and boreal ecosystems, such as the impacts of water stress with a novel pathogen on alpine vegetation mosaics in Antarctic Macquarie Island, forest transitions to shrublands and grasslands due to interactions between temperature and fire in Southern Siberia and North America, and rapid changes in vegetation and ecosystem functions in the permafrost region as thawing is rapidly taking place; (2) temperate and semi-arid ecosystems, including the impacts of fire on a paleo-endemic alpine ecosystem in Tasmania, and the interactions between drought and heatwaves in forests in the Mediterranean, Western USA, and elsewhere; (3) tropical and temperate coastal ecosystems, including the

---

J. G. Canadell (✉)
Global Carbon Project, Climate Science Centre, CSIRO Oceans and Atmosphere, Canberra, ACT, Australia
e-mail: pep.canadell@csiro.au

R. B. Jackson (✉)
Department of Earth System Science, Woods Institute for the Environment, and Precourt Institute for Energy, Stanford University, Stanford, CA, USA
e-mail: rob.jackson@stanford.edu

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_1

impacts of marine heatwaves on coral reefs of the Great Barrier Reef and Mediterranean Sea, and kelp forests and seagrass meadows in Western Australia.

One goal of this book is to raise awareness of the abrupt transitions already occurring today. We hope that the changes documented here will increase awareness and help scientists and managers restore lost or degraded ecosystems, and where possible, their species and ecosystem functioning or guide transitions towards more resilient ecosystems in the face of rapid changes.

1.1 Introduction

Ecosystem collapse in response to rapid changes in environmental conditions has been an integral part of the evolution and dynamics of the biosphere and marine ecosystems through geologic time. Paleo records reveal rapid ecosystem collapse, recovery, and shifts in response to gradual and abrupt climate changes over decades to centuries. Documented changes include rapid transitions between forest, shrublands, and grasslands in the northern and southern borders of the boreal biome since the end of present interglacial (Jasinski and Payette 2005; de Lafontaine and Payette 2011), and continental mass mortality and ecosystem collapse due to drought in Australia in the early twentieth century (Godfree et al. 2019). Deep-sea benthic community collapses have occurred in response to millennia-long climate events over the past 20,000 years (Yasuhara et al. 2008)

Current trends in climate change are now dominated by increasing emissions of greenhouse gases from human activities arising from the combustion of fossil fuels, land clearing, and food production (Friedlingstein et al. 2019; Saunois et al. 2020; Tian et al. 2020; Hong et al. 2021). The resulting human-driven climate change, particularly in recent decades, has increased the velocity of change in the climate mean state and the frequency and/or intensity of many climate extremes well above historical levels (Loarie et al. 2009; Reboita et al. 2015; Fischer and Knutti 2016; Frölicher and Laufkötter 2018; Smale et al. 2019; Aghakouchak et al. 2020). These changes are setting the conditions for more rapid and abrupt ecosystem dynamics, some of which are already being observed in many ecosystems across the world, and that are expected to intensify as the climate continues to warm.

Ecosystem collapse is associated with the crossing of critical thresholds not only as a result of gradual climate changes, but more often due to abrupt climate extremes or compounded effects of multiple disturbances occurring at greater than historical frequencies. Although single well characterized thresholds are associated with some abrupt changes, for instance, thermal thresholds for many marine coastal ecosystems (e.g. seagrass meadows, kelp forests, coral reefs), it is the combination of multiple climate, weather, and human disturbances (compound events) that more commonly lead to abrupt ecosystem responses. Compound events might include one or more extreme climate events occurring simultaneously or successively, or the combination of climate extremes with underlaying ecosystem conditions that amplify the impact of disturbances (e.g., vulnerability from pollution), or the combination of multiple progressive disturbances (Seneviratne et al. 2012).

1.2 Defining Ecosystems Collapse

We adopt a broad definition of ecosystem collapse building on previous efforts (Keith et al. 2013; Lindenmayer et al. 2016; Cumming and Peterson 2017; Bland et al. 2018) as when the transformation of ecosystem identity occurs through altered structure, function, or biodiversity, is irreversible or persists for much longer than past dynamics, and happens abruptly or at rates well above historical trends.

Note the difficulty in requiring changes to be "irreversible" or permanent over long timeframes, which requires both the time for that permanency to be established and a clearly defined end point sufficiently discrete to characterize the change of identity (Keith et al. 2013). A "collapsed" ecosystem could have the capacity to recover, and in some instances, active restoration can play a role (Fig. 1.1). However, for those collapse in which anthropogenic climate change is a dominant driver, the long-term prognosis is more likely of a permanent transition. The reason is because global warming is likely to intensify for decades, then stabilize at best in the strongest mitigation scenarios, but not revert to prior levels during this century (Collins et al. 2013).

In characterizing ecosystem collapse, it is important and helpful to mention the framing and features of previously published definitions. (Keith et al. 2013) define ecosystem collapse as a transition beyond a bounded threshold in one or more variables that define the identity of the ecosystem; collapse as a transformation of identity, loss of defining features, and replacement by a novel ecosystem. (Lindenmayer et al. 2016) call for three key conditions to be met, with changes being: (1) irreversible or time- and energy-consuming to reverse, (2) widespread, and (3) undesirable in terms of impairing ecosystem services or major losses of biodiversity. (Cumming and Peterson 2017) take the broadest view of collapse from a biophysical, social-ecological, and complex systems perspective, and suggest that collapse can also be viewed as the opposite of ecosystem resilience with collapse

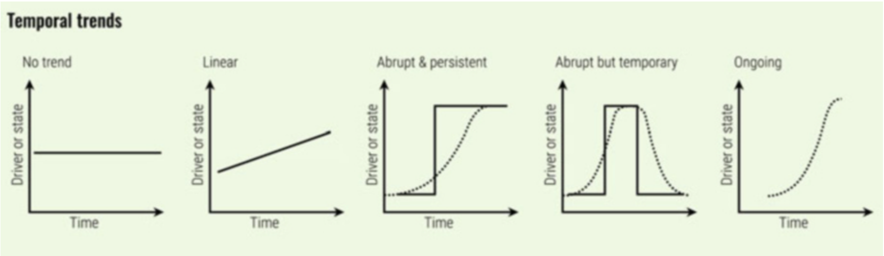


Fig. 1.1 Several classes of temporal trends of drivers or states. The focus of this book is on abrupt (persistent or temporary) and ongoing changes, with underlying long-term and often linear climate trends. Redrawn and modified from Ratajczak et al. (2018)

occurring when resilience has been lost. They define collapse through four criteria adapted here for ecological systems: (1) The identity of the ecological system must be lost by the disappearance of key system components and interactions; (2) Loss of identify should happen quickly relative to regeneration times and turnover rates of identify-defining components of the system; (3) Substantial losses of ecological capital occur; and (4) Consequences must be lasting, persisting longer than a single generation or much longer than dynamics typical for the system.

Transitions to ecosystem collapse or components of it that are described in the literature include regime shifts, critical transitions, thresholds, tipping points, hysteresis, alternative states, rapid loss of ecological integrity and state change, among others (Scheffer et al. 2001; Folke et al. 2004; Rocha et al. 2015, 2018; Vasilakopoulos et al. 2017; Munson et al. 2018; Ratajczak et al. 2018; Duke et al. 2019). Although some of these transitions and components of collapse can be clearly ascribed to the ecosystem responses presented in this book, others cannot because the dynamics are too recent and therefore lack the necessary long-term observations; this is particularly true for relatively long-lived ecosystems such as forests.

1.3 Observed Dynamics as They Occur

This book (Canadell and Jackson 2021) presents a collection of case studies across the world with ecosystem collapse-like dynamics over the past few decades and particularly over the most recent decade (Fig. 1.2). We have chosen ecosystem dynamics for which human-driven climate change and variability appear to have been the dominant or at least an important cause of the observed abrupt change, often in combination with other natural and human perturbations. Although it is not always possible to attribute the specific dynamics or collapse events to human-induced climate change, the description of drivers, their trends, and the broader context in which those dynamics occur help to establish causal links to the influence of climate change.

Each chapter describes and characterizes individual events or regional ecosystem dynamics, the drivers of change, and the unprecedented nature of the change, when possible. Given what is known about the evolution of climate change and other disturbances in each region/ecosystem, authors explore the likely evolution of those ecosystems and the challenge to manage those ecosystems in the face of abrupt dynamics. A key component to understand possible future trajectories is to explore ways to build resilience in those ecosystems or facilitate desirable transitions between states.

For most case studies in this book, however, the collapse dynamics are too recent or still emerging to have observations available long enough to determine whether the changes are irreversible and, therefore, the likelihood of transitioning into an alternate or permanent state, degraded or novel.

The book covers three broad latitudinal regions encompassing most biome types including polar and boreal ecosystems, temperate and semi-arid ecosystems, and tropical/temperate coastal ecosystems.

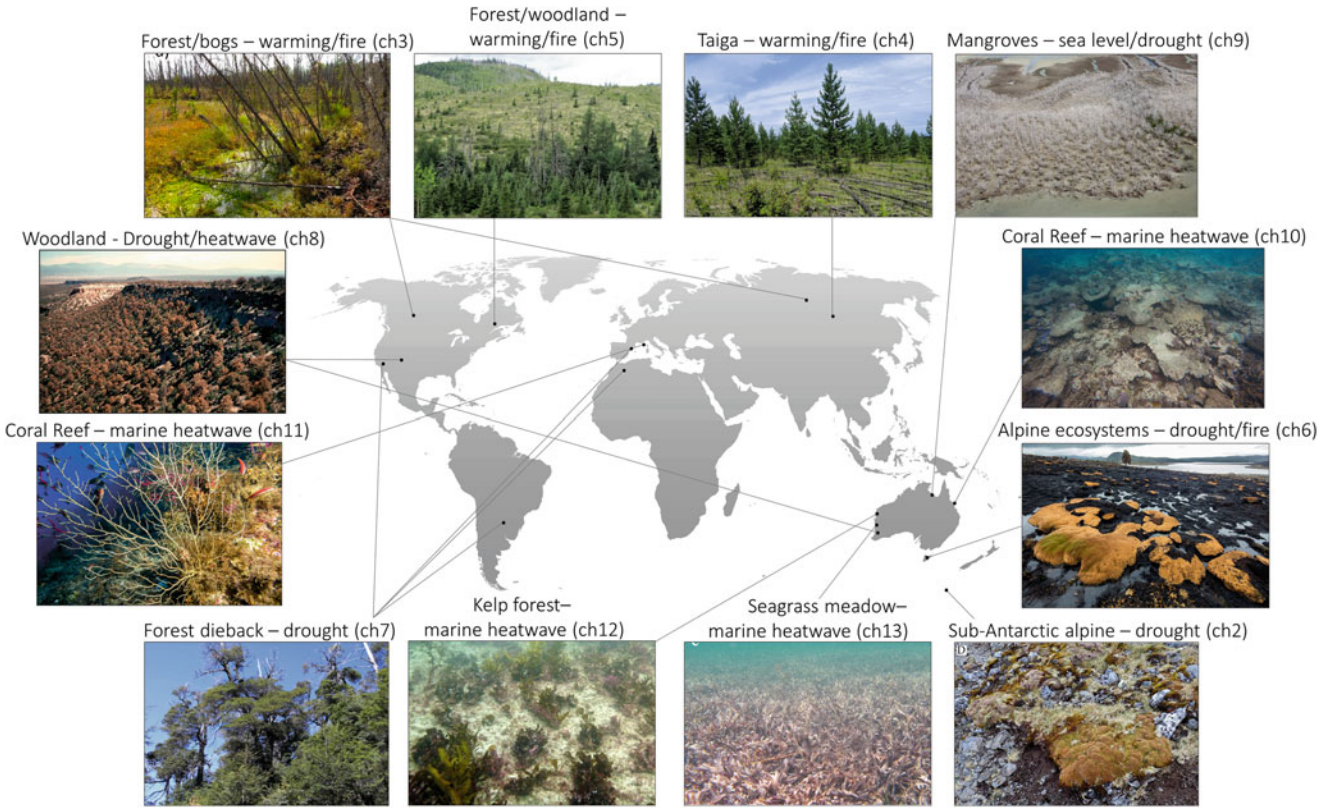


Fig. 1.2 A selection of the ecosystems showing collapse-like dynamics found around the world and described in the chapters of the book (Canadell and Jackson 2021). Photo credits provided in each chapter

1.3.1 Polar and Boreal Ecosystems

Chapter 2 (Bergstrom et al. 2021). The section on boreal and polar systems begins with a description of the collapse of an alpine ecosystem on sub-Antarctic Macquarie Island, about 650 km southwest from New Zealand. Initially driven by water stress linked to multi-decadal changes in climate, and followed by a novel pathogen, ecosystem decline has continued for more than a decade (Chap. 2).

Chapter 3 (Olefeldt et al. 2021). Rapid physical and biological changes are occurring in the vast permafrost region in response to the fastest rates of air and soil warming in the world. The thawing of permafrost observed in the region is leading to rapid landscape changes, with surface collapses of several meters affecting the physical substrate, hydrology, and aerobic conditions, to which plant community and ecosystems are rapidly responding.

Chapter 4 (Burrell et al. 2021) addresses a key process causing forest collapse in southern Siberia. The rapid warming of the region and lengthening of the fire season are leading to documented post-fire recruitment failure and replacement of large areas of forest ecosystems with grasslands.

Chapter 5 (Payette 2021) provides important paleo context for ecosystem collapse as a feature of the evolution of boreal ecosystems in North America over millennia, before humans began to alter the long-term climate trends. The interaction of climate, fire, and insects have been important in boreal regions in the past, continue to be today and likely to intensify in the future.

1.3.2 Temperate and Semi-arid Ecosystems

Chapter 6 (Bowman et al. 2021) provides a clear example of rapid transition of a relict alpine ecosystem in Tasmania threated by both climate change and increased fire activity. The chapter focuses on a specific event in which fire destroyed a palaeoendemic ecosystem dominated by the slow growing conifer *Athrotaxis cupressoides* with individuals hundreds of years old. This fire-sensitive ecosystem, including peat soils, has little or no capacity to survive fire or rapidly re-establish after it.

Chapter 7 (Lloret and Batllori 2021) explores the role of changing heatwaves and drought on forest dieback, particularly for semi-arid and temperate forests, and state shifts to shrubland and grassland ecosystems. The chapter frames ecosystem collapse within the broader context of successional, and novel ecosystems forming due to climate change, interacting with other natural and human impacts.

Chapter 8 (Ruthrof et al. 2021) further explores forest dieback and coastal marine ecosystem collapse in two regions with some climatic similarities, the southwestern United States and western Australia. The selected ecosystems include diverse forest ecosystems with dieback driven by complex interactions among drought, heat, and other disturbances, including fire and insect damage. For the marine ecosystems, coastal and algae blooms are largely driven by abrupt temperature changes brought about by increasingly stronger large-scale climate modes such as the El Niño/La Niña Southern Oscillation.

1.3.3 Tropical and Temperate Coastal Ecosystems

Chapter 9 (Duke et al. 2021) provides an overview of mangrove dynamics and their drivers, and examines the extraordinary mangrove dieback event in 2015 and early 2016 in which a 1500 km shoreline of mangroves in the Gulf of Carpentaria in northeast of Australia synchronously died. It was a complex phenomenon with multiple drivers including sea level drop, and changes in climate and weather.

Chapter 10 (Pratchett et al. 2021) covers mass bleaching events of the Great Barrier Reef in Australia that occurred in 2016, 2017, and 2020. The recurrent mass bleaching events took place with compounding impacts from previous bleaching events and other disturbances showing many characteristics of an ecosystem collapse profile.

Chapter 11 (Garrabou et al. 2021) presents a new analysis of recurrent and large-scale mass mortality events in Coralligenous communities of the Mediterranean Sea driven by marine heatwaves. The analysis covers the recovery of communities over years and explores plausible futures based on climate projections for the Mediterranean.

Chapter 12 (Wernberg 2021) presents the impacts of an exceptional marine heatwave in 2011 in Western Australia over 2000 km of seashore that resulted in the local extinction of 100 km of kelp forest. Turf algae took the place of the kelp forest aided by the elevated background ocean temperatures due to climate change that made recovery difficult. To date, the ecosystem has not recovered.

Chapter 13 (Serrano et al. 2021) presents an unprecedented event in which about 1300 km^2 of seagrass ecosystems collapsed as a result of a marine heatwave in 2010/11 in Shark Bay, western Australia. The loss of the seagrass canopy resulted in the erosion of sediments and loss of large carbon stocks over the following 6 years.

References

Aghakouchak A et al (2020) Climate extremes and compound hazards in a warming world. Annu Rev Earth Planet Sci 48:519–548. https://doi.org/10.1146/annurev-earth-071719-055228

Bergstrom DM et al (2021) Ecosystem collapse on a Sub-Antarctic island. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Bland LM et al (2018) Developing a standardized definition of ecosystem collapse for risk assessment. Front Ecol Environ 16(1):29–36. https://doi.org/10.1002/fee.1747

Bowman DM, Rodriguez-Cubillo D, Prior LD (2021) The 2016 Tasmanian wilderness fires: fire regime shifts and climate change in a Gondwanan biogeographic refugium. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Burrell A et al (2021) Post-fire recruitment failure as a driver of forest to non-forest ecosystem shifts in boreal regions. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Canadell JG, Jackson RB (2021) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Collins M et al (2013) Long-term climate change: projections, commitments and irreversibility. In: Stocker TF et al (eds) Climate change 2013: the physical science basis. Contribution of Working Group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, pp 1029–1136. https://doi.org/10.1017/CBO9781107415324.024

Cumming GS, Peterson GD (2017) Unifying research on social–ecological resilience and collapse. Trends Ecol Evol 32(9):695–713. https://doi.org/10.1016/j.tree.2017.06.014. Elsevier Ltd

de Lafontaine G, Payette S (2011) Shifting zonal patterns of the southern boreal forest in eastern Canada associated with changing fire regime during the Holocene. Quat Sci Rev 30 (7–8):867–875. Elsevier Ltd. https://doi.org/10.1016/j.quascirev.2011.01.002

Duke NC et al (2019) Rainfall and its possible hysteresis effect on the proportional cover of tropical tidal-wetland mangroves and saltmarsh-saltpans. Mar Freshw Res 70(8):1047–1055. https://doi.org/10.1071/MF18321

Duke NC et al (2021) Processes and factors driving change in mangrove forests—an evaluation based on the mass dieback event in Australia's Gulf of Carpentaria. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Fischer EM, Knutti R (2016) Observed heavy precipitation increase confirms theory and early models. Nat Clim Change 6(11):986–991. https://doi.org/10.1038/nclimate3110. Nature Publishing Group

Folke C et al (2004) REGIME shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711

Friedlingstein P et al (2019) Global carbon budget 2019. Earth Syst Sci Data 11(4):1783–1838. https://doi.org/10.5194/essd-11-1783-2019

Frölicher TL, Laufkötter C (2018) Emerging risks from marine heat waves. Nat Commun 9(1):650. https://doi.org/10.1038/s41467-018-03163-6

Garrabou J et al (2021) Sliding towards the collapse of Mediterranean coastal marine rocky ecosystems. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Godfree RC et al (2019) Historical reconstruction unveils the risk of mass mortality and ecosystem collapse during pancontinental megadrought. Proc Natl Acad Sci U S A 116(31):15580–15589. https://doi.org/10.1073/pnas.1902046116

Hong C et al (2021) Global and regional drivers of land-use emissions 1961-2017. Nature 589:554–561

Jasinski JPP, Payette S (2005) The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecol Monogr 75(4):561–583. https://doi.org/10.1890/04-1621

Keith DA et al (2013) Scientific foundations for an IUCN red list of ecosystems. PLoS One 8(5). https://doi.org/10.1371/journal.pone.0062111

Lindenmayer D, Messier C, Sato C (2016) Avoiding ecosystem collapse in managed forest ecosystems. Front Ecol Environ 14(10):561–568. https://doi.org/10.1002/fee.1434

Lloret F, Batllori E (2021) Climate-induced global forest shifts due to heatwave-drought. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Loarie SR et al (2009) The velocity of climate change. Nature 462(7276):1052–1055. https://doi.org/10.1038/nature08649. Nature Publishing Group

Munson SM et al (2018) Ecosystem thresholds, tipping points, and critical transitions. New Phytol 218(4):1315–1317. https://doi.org/10.1111/nph.15145

Olefeldt D et al (2021) Permafrost thaw in northern peatlands: rapid changes in ecosystem and landscape functions. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Payette S (2021) A paleo-perspective on ecosystem collapse in boreal North America. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Pratchett MS et al (2021) Recurrent mass-bleaching and the potential for ecosystem collapse on Australia's Great Barrier Reef. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Ratajczak Z et al (2018) Abrupt change in ecological systems: inference and diagnosis. Trends Ecol Evol 33(7):513–526. https://doi.org/10.1016/j.tree.2018.04.013. Elsevier Ltd

Reboita MS et al (2015) Trend and teleconnection patterns in the climatology of extratropical cyclones over the Southern Hemisphere. Clim Dyn. Springer, Berlin 45(7–8):1929–1944. https://doi.org/10.1007/s00382-014-2447-3

Rocha J et al (2015) Marine regime shifts: drivers and impacts on ecosystems services. Philos Trans R Soc B Biol Sci 370(1659):1–12. https://doi.org/10.1098/rstb.2013.0273

Rocha JC et al (2018) Cascading regime shifts within and across scales. bioRxiv 1383:1379–1383. https://doi.org/10.1101/364620

Ruthrof KX et al (2021) Extreme events trigger terrestrial and marine ecosystem collapses in the southwestern United States and southwestern Australia. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Saunois M et al (2020) The global methane budget 2000–2017. Earth Syst Sci Data 12 (3):1561–1623. https://doi.org/10.5194/essd-12-1561-2020

Scheffer M et al (2001) Catastrophic shifts in ecosystems. Nature 413(6856):591–596. https://doi.org/10.1038/35098000

Seneviratne SI et al (2012) Changes in climate extremes and their impacts on the natural physical environment. In: Managing the risks of extreme events and disasters to advance climate change adaptation: special report of the intergovernmental panel on climate change, pp 109–230. https://doi.org/10.1017/CBO9781139177245.006

Serrano O et al (2021) Impact of marine heatwaves on seagrass ecosystems. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Smale DA et al (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Change 9(4):306–312. https://doi.org/10.1038/s41558-019-0412-1

Tian H et al (2020) A comprehensive quantification of global nitrous oxide sources and sinks. Nature 586(7828):248–256. https://doi.org/10.1038/s41586-020-2780-0

Vasilakopoulos P et al (2017) Resilience and regime shifts in a marine biodiversity hotspot. Sci Rep 7(1):1–11. https://doi.org/10.1038/s41598-017-13852-9. Springer

Wernberg T (2021) Marine heatwave drives collapse of kelp forests in Western Australia. In: Canadell JG, Jackson RB (eds) Ecosystem collapse and climate change. Ecological Studies 241. Springer, Cham

Yasuhara M et al (2008) Abrupt climate change and collapse of deep-sea ecosystems. Proc Natl Acad Sci U S A 105(5):1556–1560. https://doi.org/10.1073/pnas.0705486105

Part I

Polar and Boreal Ecosystems

Ecosystem Collapse on a Sub-Antarctic Island

2

Dana M. Bergstrom, Catherine R. Dickson, David J. Baker,
Jennie Whinam, Patricia M. Selkirk, and Melodie A. McGeoch

Abstract

Sub-Antarctic Macquarie Island has been the location of a rapid ecosystem collapse in its most dominant vegetation assemblage, the Macquarie Island alpine mosaic, beginning around 2008 and continuing today. An ecosystem engineer and endemic, keystone species, the cushion plant, *Azorella macquariensis* (Apiaceae), and associated bryophyte species have undergone sudden and widespread dieback. Additional species, particularly the megaherb daisy, *Pleurophyllum hookeri* (Asteraceae), are currently also showing widespread

---

The original version of this chapter was revised. A correction to this chapter can be found at https://doi.org/10.1007/978-3-030-71330-0_14

D. M. Bergstrom (✉)
Australian Antarctic Division, Department of Agriculture, Water and the Environment, Kingston, TAS, Australia

Global Challenges Program, University of Wollongong, Wollongong, NSW, Australia
e-mail: Dana.Bergstrom@awe.gov.au

C. R. Dickson · M. A. McGeoch
School of Biological Sciences, Monash University, Clayton, VIC, Australia
e-mail: cath.dickson@monash.edu; M.McGeoch@latrobe.edu.au

D. J. Baker
Environment & Sustainability Institute, University of Exeter, Penryn, Cornwall, UK
e-mail: D.Baker2@exeter.ac.uk

J. Whinam
Geography and Spatial Studies, University of Tasmania, Hobart, TAS, Australia
e-mail: j.whinam@utas.edu.au

P. M. Selkirk
Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia
e-mail: pselkirk@pip.com.au

© Springer Nature Switzerland AG 2021, corrected publication 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_2

mortality. Initially, water stress linked to long-term changes in climate appeared to be the primary pressure causing dieback, with a secondary putative pathogen emerging. However, over the last 10 years there has been a shift in fundamental ecosystem processes with the pathogenic system appearing to be the current predominant cause of dieback. This change suggests that a threshold has been crossed into a new operating state. Furthermore, an ecosystem regime shift with two clear new states (grassland and bare ground) appears to be emerging with the loss of the ecosystem engineering species from many areas of fellfield. Modelling suggests that cold refugia may allow current elements to survive into the future, but as interstitial species, rather than as dominants present at the start of the twenty-first century. This ecosystem presents a potential exemplar for climate change response in patchy, resource-concentrated ecosystems elsewhere. In particular, showing how interactions change in response to climate change and how longer-term consequences may emerge following short-term effects.

2.1 Background

Sub-Antarctic islands are globally rare ecosystems found dotted around the Southern Ocean between 48° and 53°S (Bergstrom and Chown 1999). These islands have been recognised very early on as sentinels to study the impacts of climate change. Almost 30 years ago, Selkirk (1992) stated that climate change would alter their physical and biological characteristics because of their location at the margin of the Southern high latitude region. This prediction has proven true (Chown et al. 2013; Frenot et al. 1998; le Roux and McGeoch 2008; Lee and Chown 2016; Smith 1994) and for one such island, this change has occurred surprisingly rapidly.

Macquarie Island (158°55′E; 54°30′S) is a small elongate island, only 32 km in length and a maximum 5 km wide. The closest land mass is the New Zealand Auckland Islands, approximately 650 km to the northeast. Part of the Australian state of Tasmania, the island is managed as a nature reserve and World Heritage site by Tasmania Parks and Wildlife Service. Macquarie Island is low in profile (max. altitude 433 m), consisting mainly of a N-S ridged plateau with steep slopes to the coast, often intersected with bays. The island is covered in various forms of treeless vegetation, including feldmark, grasslands and herbfields (Selkirk et al. 1990). The oceanic climate on the island is cool and windy, with limited temperature variability (mean air temperature range, 3.8–6.6 °C—Pendlebury and Barnes-Keoghan 2007). The island is a World Heritage site with one of the two outstanding Universal Value criteria that supports the listing being “Macquarie Island provides an outstanding spectacle of wild, natural beauty”, which includes “vegetation cover which can vary from lush grassland to sparse feldmark within the space of a few metres” (UNESCO 1997).

The Macquarie alpine vegetation is a mosaic of feldmark (or fellfield), open grassland, open rocky slopes and terraces with alternating stripes of vegetation and gravel (Kitchener and Harris 2013); it is the most extensive vegetation community on the island. The sub-Antarctic feldmark systems, similarly to other water-limited systems, display properties thought to be associated with systems prone to catastrophic regime shifts, where a system rapidly transitions from one state to another with only a small perturbation (Andersen et al. 2009; Lenton 2013). These properties include self-organised patchiness, concentration of resources (specifically moisture) associated with these patches, and the presence of ecosystem engineers that play a significant role in resource concentration (Rietkerk et al. 2004). Systems with such properties are particularly prone to a shift from patterned vegetation dominated landscapes to homogenous systems dominated by bare ground.

An important reason to examine the current and ongoing change on Macquarie Island, a dedicated nature reserve, is that the island provides a simplified system with a reduced number of pressures compared with other locations worldwide. Local human impacts have been restricted to primarily buildings situated on the coast (huts and a scientific station) and associated local contamination such as rare contemporary fuel spills; past marine mammal harvesting from the early last century sealing industry's activities are also contained to the shoreline; and limited localised foot tracks across the island. The most significant widespread human impacts were from the introduction of non-native vertebrates including cats, rabbits and rodents associated with early sealing activities. These vertebrate pests have all been eradicated with a concomitant recovery of ecosystems on lower valleys and coastal slopes and plains (Bergstrom and Selkirk 2007; Copson and Whinam 2001; Shaw et al. 2011; Springer 2016). In contrast to many places elsewhere, there has been no extensive land clearing or wide-scale polluting industries on the island. There is a very controlled, educational tourist visitation program, with limits on the number of tourists per year (>300) and visitation allowed on only two coastal beaches and the research station. Tourists are not allowed into the interior or plateau of the island.

2.2 The Collapse

2.2.1 Former State

The Macquarie Island alpine mosaic (~200–400 m asl) is a patchy environment, where the very slow growing cushion plant *Azorella macquariensis* Orchard (Apiaceae) is both an ecosystem engineer and a keystone species. It characteristically dominates plant biomass on the plateau, and generates vegetation patterning with spots, stripes and terraces (Fig. 2.1, and see Selkirk-Bell and Selkirk 2013). Its growth form and vitality are significantly associated with water availability, including wind-borne moisture. Growing with and around *A. macquariensis* cushions are turves of mosses and liverworts. Vascular plant epiphytes, including the grass *Agrostis magellanica* also grow amongst these vegetation patches, often in sheltered microhabitats on the leeward sides. Interspersed between the terraces and vegetation patches are cushions of mosses, and bare, often patterned ground from cryoturbation (Fig. 2.1a, b). The patterned vegetation is influenced by wind exposure, aspect, slope, frost and surface water transport (Selkirk-Bell and Selkirk 2013) and is a defining component of the intrinsic wild value of the island.

As an ecosystem engineer, *A. macquariensis* directly collects carbon within the cushion through the accumulation of dead leaves, diverse epiphytes (e.g. mosses,

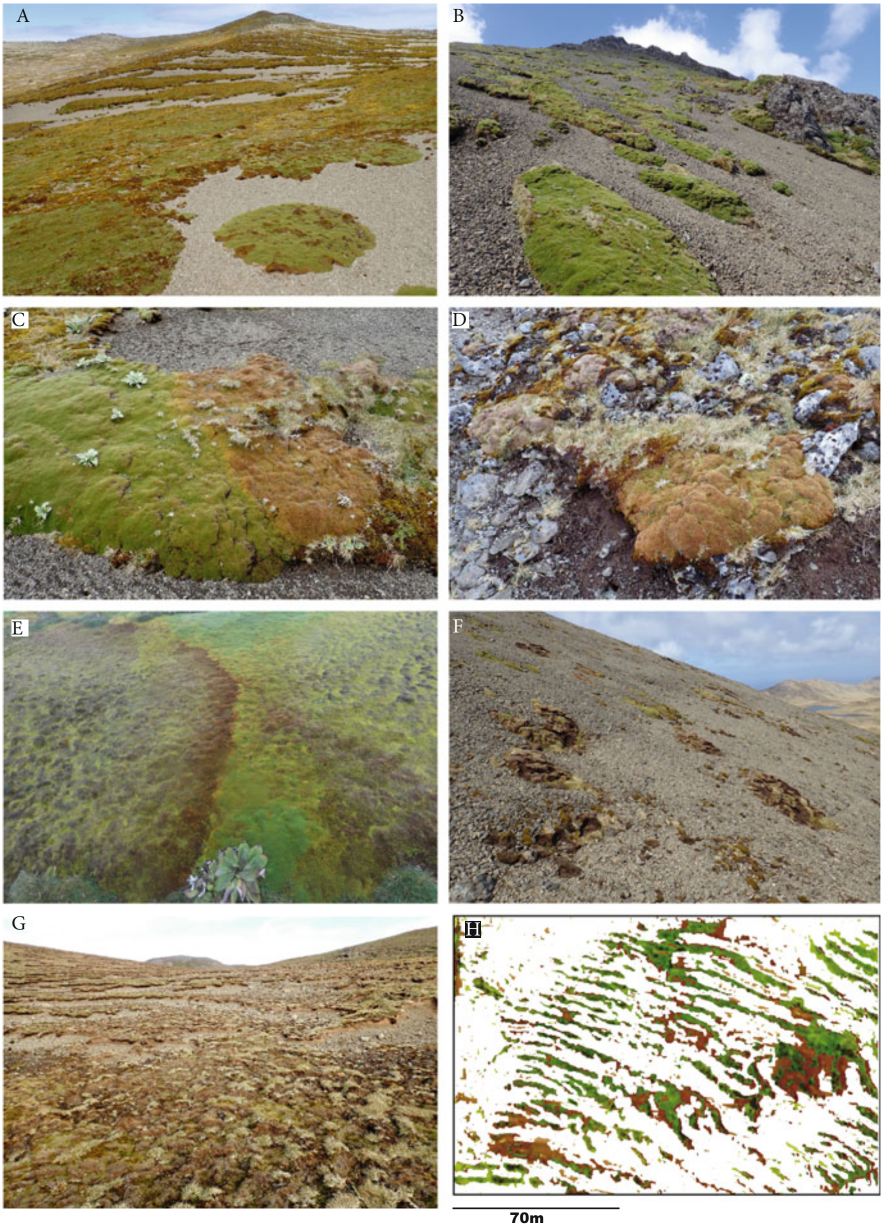


Fig. 2.1 (**a**) Remaining healthy fellfield with *Azorella macquariensis* cushions and bryophyte turves in the southmost (and highest altitude) areas on Macquarie Island. Patterned ground obvious in background; (**b**) close-up of heathy cushions and patterned ground with epiphytes of *Agrostis magellanica:* (**c**) Dieback and chlorosis line moving across cushion right to left; (**d**) Substantial dieback in cushion with some foreground erosion: (**e**) Multiple waves of pathogen chlorosis across cushion. Light green on left hand side of cushion, liverworts colonising hollows of dead cushion; (**f**) death and erosion of cushions in sparse feldmark; (**g**) Extensive death in (brown patches) an area with high cover leaving *A. magellanica* to dominate site. Evidence of erosion of dead cushion

liverworts, lichens, graminoids, herbs) that grow and die within the cushion, and the collection of aeolian particles (Bergstrom et al. 2015). Within cushions a distinct microarthropod community occurs, which is generally more abundant and diverse in comparison to the adjacent bare ground (Bergstrom et al. 2015).

2.2.2 Progression to the New State

In the Austral summer of 2008, we noted that numerous *A. macquariensis* cushions were not emerging from their winter semi-deciduous brown state (where leaves die but remain to rot on the stem). Thus, the cushions remained brown and did not produce spring leaves (as in Fig. 2.1c, d). On further observation, some plants were grey and dead—indicating that some plants had died in previous years. A survey at the time found 88% of 115 stratified random sites across the range of the species contained affected cushions and 84% contained dead bryophytes. Within-site dieback increased over time. By 2009 cushion death was observed across the entire range of the species, severely impacting up to 90% of cushions in some areas, and thus the species was declared critically endangered in 2010 (Threatened Species Section 2009; Whinam et al. 2014; Bergstrom et al. 2015—see Bergstrom et al. 2015, for management action associated with the discovery and initial response to dieback).

On some plants, a yellow band, suggestive of a plant pathogen infection, was observed to sweep across cushions with time, damaging and killing tissue in its wake (Fig. 2.1c, d). We have now observed evidence of multiple waves of infection across sites and individual cushions (Fig. 2.1e). Using both standard direct and indirect isolation techniques and next generation DNA sequence analysis of both plant tissue and rhizosphere soil, a suite of possible pathogens (bacterial, fungal and oomycete taxa) were identified including *Rhizoctonia* sp., although no consistent pattern between healthy and unhealthy plants was found. A strong association between unidentified fungus, *Rosellinia* sp., and large roots of unhealthy and dead *A. macquariensis* however was noted (Bergstrom et al. 2015).

One of the critical observations made between 2008 and 2012 was that many plants exhibited a relaxation of form (i.e. the cushion surface was undulating, rather than a smooth plane and was soft to touch) indicating water stress, which created a negative feedback loop of increasing plant surface area, opening up the canopy to more water loss (Bergstrom et al. 2015). While these individuals did not display the yellow chlorosis line, the canopy showed signs of stress with dead stems and browning of stems on the more exposed rises.

Nearly a decade after the initiation of the island-wide dieback event, an *A. macquariensis* survey during the 2017 Austral summer (90 sites, randomly

Fig. 2.1 (continued) material mid-ground (images CR Dickson). (**h**) Visual analysis of loss of cushion and bryophytes cover in terraces on the north side of North Mountain (near Gadget and overland track junction) between 2007 (brown plus green) and 2018 (green) only. Base satellite imagery from Google Earth using historical imagery feature stratified across range) found that dieback continues to be a conspicuous feature of *A. macquariensis* populations (98.7%), with an average of 26.9% (± s.d. 21.5%) cushion cover affected (Dickson et al. 2019). Similar to *A. macquariensis,* which grows in a range of densities and forms, dieback was highly variable across the island ranging from 0.0 to 86.8% affected cushion cover (Dickson et al. 2019). Some sites showed near-complete death of *A. macquariensis* cushions and bryophytes (Fig. 2.1f, g). Dieback was most extensive and advanced in the northern region of the island, while it was most active in the central region of the island, reflecting a shift southwards from the recent historical records (Dickson 2019). There was a significant latitudinal gradient in the proportion of dieback that increased towards the north of the island (Dickson et al. 2019). This suggested, as was later shown, that latitude provides a partial proxy for macroclimate on the island—the southern half is higher in elevation and more often shrouded in cloud than the north. Additionally, there is a significant elevation-independent temperature gradient down the island, with the south significantly colder with more freezing days (Dickson 2019). The extent of *A. macquariensis* dieback has also been found to be related to a low number of freezing days and very high humidity (Dickson 2019), microclimate conditions that are regularly associated with disease in other plant populations (Chakraborty 2013; Garrett et al. 2016). This provides a plausible explanation for the natural *A. macquariensis* refugia observed in the south of the island, where colder conditions are less conducive for pathogen activity and plants are less likely to be stressed (Dickson 2019).

Over the last decade the consequence of sustained island-wide dieback has been a loss of cushion cover, particularly in the northern and central regions (Dickson et al. 2019), however what is not known is exactly how much of the population has been lost. When assessing the changing conservation status of the species, conceptual models have shown the importance of taking the previous loss into account (Dickson et al. 2019).

In recent, wetter years, limited recovery has been recorded in cushions that lost only a proportion, not all, of their branches to dieback. Individual branches have survived and grown, creating "mini-cushions"—small spheres (~<5 cm in diameter) atop remaining dead cushion surface. In addition, many cushions have regained their full turgor and now maintain firm canopies, albeit some with the bumpy surface features (observed earlier) now fixed as part of the cushion structure (Fig. 2.1b–e). Furthermore, despite the proportion of dieback at a site, *A. macquariensis* seedlings have also been observed and spot recovery of new plants within dead cushions, showing the potential for recruitment into areas of former dieback (Dickson 2019; Dickson et al. 2019). However, these positive recent observations should be treated with caution, as the ecology of this slow growing, non-competitive species indicates that recovery is likely to be slow and variable (Dickson et al. 2019) if recovery occurs at all.

Dieback has also been observed in other feldmark species of mosses, liverwort and the megaherb *Pleurophyllum hookeri* Buchanan (Asteraceae) generally growing in association with *A. macquariensis*, (see foreground Fig. 2.1e) but not always. Pathogen driven dieback of *P. hookeri* was recorded across the island at a third of the

2017 *A. macquariensis* survey sites, where the species was present ($n = 10$ of 30 occupied sites) (Dickson 2019). At these sites *P. hookeri* dieback occurred in conjunction with the surrounding *A. macquariensis* dieback. In April 2019, death of *P. hookeri* occurred over wider areas than had been previously observed during earlier vegetation surveys. (M. Visoiu pers. comm.).

2.2.3 Functional Changes

Primary functional ecosystem impacts of such rapid collapse within the Macquarie Island alpine mosaic have been twofold. Firstly, in areas prone to wind exposure or water erosion from flooding, dead cushions and moss turves have been blown or washed away leaving bare gravel surfaces (Fig. 2.1d, f). This represents loss of habitat and a substantial loss of ecosystem carbon (which had accumulated slowly with slow cushion growth), particularly as this dry habitat is known to have very low soil organic carbon accumulation (Wilson et al. 2019). Secondly, in less wind exposed areas where cushions and moss are dead but have not been lost to the system, new colonists, such as lichens and other vascular species, are taking advantage of the new habitat enriched with carbon and nutrients. In particular, the native grass *Agrostis magellanica* at low to moderate elevations is increasingly prevalent on and around cushions, with an increase in mean and extreme maximum temperatures, irrespective of dieback (Dickson 2019). The expansion of *Agrostis magellanica* appears to be reducing some terraces of the fellfield, by covering and subsequently smoothing of areas into contiguous grassland. Qualitative modelling shows that the expansion of *Agrostis magellanica,* corresponding to the increasingly warm maximum temperatures and the removal grazing pressure, represents a similar level of threat to the Macquarie Island alpine mosaic as *A. macquariensis* dieback (Dickson 2019).

Figure 2.1h shows the reduction in *A. macquariensis* cushion and bryophyte cover at a terraced northern site between 2007 and 2018. We have observed *Agrostis magellanica* becoming more abundant at this locality. In 2004, Rietkerk et al. made the general prediction that ecosystems with resource-concentrating ecosystem engineers are more prone to a shift from patterned, vegetation dominated landscapes to homogenous systems. This prediction seems to describe the emerging position on Macquarie Island, with the progression towards two system states: bare ground and grassland (Hoffmann et al. 2019).

2.2.4 Context of the Change

Azorella macquariensis and the closely related *A. selago* are recognised as colonisers (Bergstrom et al. 1997). They are the dominant and often the only vascular plant species at high altitudes or on recently exposed ground at glacial margins on sub-Antarctic islands (see Bergstrom and Selkirk 2000; Frenot et al. 1998).

Bergstrom et al. (2015) noted that the presence and persistence of *A. macquariensis* extending back into the Holocene (Bergstrom et al. 2002) and suggested that, until very recently, there was long-term, positive gross primary productivity in the species. Indeed, analysis of the spatial genetic patterns across populations of *A. macquariensis* across the island reveals a lack of spatial genetic structure and high genetic diversity compared to *A. selago* on Marion Island. This is consistent with persistence of a large population across the island throughout the Late Quaternary (Chau et al. 2019).

Appearance and loss of an *A. macquariensis* signal in Holocene paleo-vegetation records (see those in Bergstrom et al. 2002; Selkirk et al. 1988) are interpreted as successional or local changes within communities. However, from this gross palynological record we do not have a firm picture of fluctuations of *A. macquariensis* with time at an island scale, nor the pressures driving change. Furthermore, the records are not detailed or extensive enough to recognise dieback events similar to the present one, followed by recovery/re-establishment. Local dieback (at the site scale) had been occasionally noted before 2008 (Bergstrom et al. 2015), in the 1980s (Patricia Selkirk, personal observations) and 1999 at a site west of Mt Eitel (located centrally on the island). At Mt Eitel, chlorosis bands were observed in doughnut and crescent shaped cushions (Dana Bergstrom, personal observations) at a site approximately 100 m × 200 m in area. These doughnut and crescent shaped cushions were not found on a return inspection of the location in December 2016.

2.3 Major Causes

Complex elements in both climate and biotic response to climate change appear to be driving the change in state on Macquarie Island alpine mosaic. Firstly, both *A. macquariensis* and associated bryophytes including mosses *Racomitrium crispulum*, *Ditrichum strichtum* and the liverwort, *Syzygiella colorata* are primarily ombrotrophic (with the roots of the cushion plant primarily for anchoring only). Thus, the major elements of the initial state of the ecosystem are extremely sensitive to water fluctuations. Indeed, functional traits of *A. macquariensis* are symptomatic of a species selected for a cold, wet and misty environment, and vulnerable to drought stress (Bergstrom et al. 2015; Rolland et al. 2015).

The island's climate has undergone significant complex changes in the recent past. Weather systems in the region have had marked southward, latitudinal shift since the 1970s, resulting in changes to principal wind directions and increased wind speeds (Adams 2009). The island has become stormier and the number of larger precipitation events increased with extreme events, including floods. Eight of the eleven highest daily rainfall events (38.4–59.2 mm) have occurred since 2015 (Bureau of Meteorology 2020, weather station #300004). Annual rainfall has increased, with this change occurring primarily in the winter (Bergstrom et al. 2015). Yet despite the increase in precipitation, these storms have occurred against a background of a windier, drier atmosphere (Adams, 2009). Sunshine hours, wind speed and evapotranspiration rates also increased, resulting in accumulated deficits of plant available water spanning 17 years (1992–2008) leading up to the initiation of landscape scale dieback in the plateau ecosystem (Bergstrom et al. 2015). Regional warming is also occurring in the sub-Antarctic (Pendlebury and Barnes-Keoghan 2007). While not as pronounced as some sub-Antarctic islands, on Macquarie Island the mean and extreme maximum temperatures across most months have significantly increased since 1948, particularly during the summer months (Dickson 2019).

Thus, the environment has shifted from being consistently wet and misty to a stormier climate interspersed with drying sunny periods in summer and wetter winters when *A. macquariensis* is in a state of winter dormancy. This represents a shift of climate away from the fundamental niche of the cushion plant and the bryophytes of the fellfield.

Post-initial climate-driven dieback, the associated yellow banding that occurs on the cushions plants indicates the emergence of a pathogen (see Whinam et al. 2014). Although conclusive evidence has yet to be collected of what the specific disease is in *A. macquariensis*, the presence of bacterial, fungal and oomycete taxa associated with dieback, some potentially pathogenic, indicated that stressed cushions are susceptible to infection (Bergstrom et al. 2015). Bands of moving chlorosis across cushions, followed by death, are being repeatedly observed on the island (Dickson et al. 2019, Fig. 2.1). Pathogens are now the most conspicuous driver of dieback (Bergstrom et al. 2021). Dieback extent from recent years was related to *in-situ* microclimate conditions that promote pathogen ecology (less freezing events/ warmer and very high humidity/saturation), while those variables indicative of water-stress were unimportant in the modelling conducted (Dickson 2019). However, it is likely that the change in climate on the island (higher sunshine hours, maximum temperatures and increasingly stormy conditions during the summer growing season) continues to generate a level of background stress and weakens plants susceptible to water-loss, such as *A. macquariensis*. This is suggestive of crossing of the threshold into a new operating state, where drought is no longer the primary driver of dieback. Furthermore, all indications are that there is a clear new state with loss of the ecosystem engineer species from so many areas of fellfield.

The initial climate triggers are linked to number of global changes in climate in the region. Stratospheric ozone depletion and resultant cooling in the upper atmosphere over Antarctica have resulted in the Hadley Cell and the polar jet stream moving southward as well as increasing in speed. This change coupled with an increase in greenhouse gases, atmospheric and oceanic circulation has moved towards a more positive phase of the Southern Annular Mode. This has resulted in Southern Ocean winds shifting further south, along with increases in temperature and changes in rainfall, dependent on the location within the Southern Ocean (Wang and Cai 2013; Robinson and Erickson 2015; Turney et al. 2017; Barnes et al. 2019). These changes are more pronounced in the summer associated with the formation of the polar vortex (Thompson and Solomon 2002; Eyring et al. 2013) and are predicted to continue with repair of the ozone hole under a RCP4.5 scenario. The summer poleward shifts in atmospheric circulation will however accelerate under a RCP8.5 scenario in the post-recovery period, presenting more southerly ocean circulation especially in winter (Wang and Cai 2013). Thus, we can anticipate the current climate conditions to continue or amplify in future. If the pathogen has emerged from a decomposer microbe, then warmer and wetter winters may amplify the effects of the pathogen as decomposition opportunities within the Macquarie Island alpine mosaic ecosystem increases.

2.4 Prognosis and Management Strategies

The “no action” prognosis for the future of the Macquarie Island alpine mosaic ecosystem appears to be one of habitat simplification, moving to a predominantly short-grassland system interspersed with bare ground (Hoffmann et al. 2019). This is tending toward a regime shift with a new stable alternate state. Figure 2.2 presents a simple model of the trajectory that *A. macquariensis* populations appear to have traversed since we first observed small amounts of dieback in the 1980s and 1990s. These first events appeared not to have an obvious impact on the populations, hence the recovery trajectory. While Bergstrom et al. (2015) calculated that summer water stress began in the 1990s, the first major crash in population size and condition was not observed until 2008. Subsequently, over time and with repeat pathogen waves, the populations have continued to decline across the species’ distribution, particularly in the north (Dickson et al. 2019), despite the small amount of recovery observed in some plants and some recruitment.

The feldmark system has been simplified with the loss of *A. macquariensis* and its related keystone interactions (Dickson 2019). This loss of facilitative interactions on the feldmark is a key step in the process of ecosystem collapse from plant dieback to loss of functions, such as ecosystem engineer and carbon sink in the system (Dickson 2019).

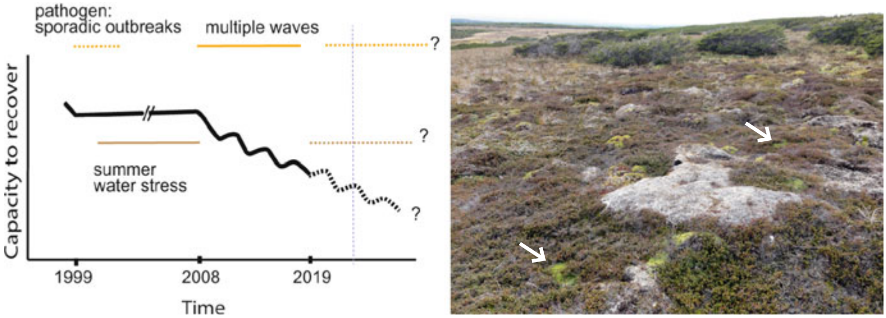


Fig. 2.2 Left—Model of *Azorella macquariensis* population trajectory (species cover and capacity to recovery) from the 1990s to the potential future showing multiple stepwise decrease followed by some recovery. Overall population direction is downwards. Right—*Azorella selago* (arrows) as interstitial elements in alpine cushion and shrub vegetation on Mt Fenton, Punta Arenas in 2014. Note grey patches of undocumented dieback in major elements of the ecosystem (image DM Bergstrom)

Modelling of potential cold refugia, however, has shown that the variation of plateau terrain provides a buffer against thermal and hydrological extremes during the summer growing season (David Baker unpublished data). Thus, while the Macquarie Island alpine mosaic will change with time, the likelihood of the endemic cold-specialist *A. macquariensis* going extinct could be reduced if such areas act as refugia under future climate change conditions. One model that may assist with the imagining of the future for Macquarie Island is the presence of the closely related species *A. selago* in warmer southern South America. In Patagonia, *A. selago* is not a keystone species but an interstitial element of the ecosystem, found in shaded, moister and cooler hollows (Fig. 2.2).

While potential refugia provide some optimism for the long-term persistence of an *A. macquariensis* dominated Macquarie Island alpine mosaic habitat on the island, these models do not consider the role of yet to be identified pathogen in driving population decline. However, as hypothesised above, warmer wetter conditions under a RCP8.5 scenario may be more positive for the pathogen than *A. macquariensis.* Already the winters on Macquarie Island have become 55% wetter (Bergstrom et al. 2015) and extreme and mean maximum temperatures are higher across most months (Dickson 2019). A "no regrets" strategy would be to continue current management activities to secure the endemic species, which include an on-island seed orchard and off-island seed storage, and research into breaking the germination dormancy of *A. macquariensis*. Identification of the putative pathogen is urgently needed to provide greater understanding of the ecosystem processes. Expansion of *A. macquariensis* long-term monitoring of study areas coupled with establishment of long-term *in situ* microclimate data would also allow the collection of the best available information on the stability and persistence of microrefugia most likely to be suitable for *A. macquariensis* survival (David Baker unpublished data). Additional microclimate modelling to capture higher resolution, measurement of wind strength and direction and island soil/ substrate modelling may also aid the development of future management strategies.

2.5 Wider Context

The emergence of island-wide dieback of the dominant vascular plant on Macquarie Island illustrates the increasing vulnerability of high altitude and latitudes to novel pathogen under changing climates. Cold regions have been previously protected by extreme cold events, however, under warming climates it is predicted that they will be increasingly susceptible to novel pathogens (Pauchard et al. 2016). Furthermore, this rapid loss of cover also provides a clear example of how islands with a very low functional redundancy and low topographic complexity are particularly susceptible to novel pathogens under climate change (see Harter et al. 2015). Macquarie Island remains a sentinel for climate change in the sub-Antarctic (Bergstrom and Chown 1999) and more widely high altitude regions, reinforcing the need to prevent movement of novel pathogens through stringent biosecurity as well as minimise other pressures, as climates warm.

References

Adams N (2009) Climate trends at Macquarie Island and expectations of future climate change in the sub-Antarctic. Pap Proc R Soc Tasmania 143:1–8

Andersen T, Carstensen J, Hernández-García E et al (2009) Ecological thresholds and regime shifts: approaches to identification. Trends Ecol Evol 24:49–57. https://doi.org/10.1016/jtree200807014

Barnes PW, Williamson CE, Lucas RM et al (2019) Ozone depletion ultraviolet radiation climate change and prospects for a sustainable future. Nat Sustain. https://doi.org/10.1038/s41893-019-0314-2

Bergstrom DM, Chown SL (1999) Life at the front: history ecology and change on southern ocean islands. Trends Ecol Evol 14:472–477

Bergstrom DM, Selkirk PM (2000) Terrestrial vegetation and environments on Heard Island. Pap Proc R Soc Tasmania 133:33–46

Bergstrom DM, Selkirk PM (2007) Human impacts on sub-Antarctic terrestrial environments. Pap Proc R Soc Tasmania 141:33–46

Bergstrom DM, Selkirk PM, Keenan HM et al (1997) Reproductive behaviour of ten flowering plant species on subantarctic Macquarie Island. Opera Bot 132:109–120

Bergstrom DM, Stewart GR, Selkirk PM et al (2002) 15 N natural abundance of fossil peat reflects the influence of animal-derived nitrogen on vegetation. Oecologia 130:309–314

Bergstrom DM, Bricher PK, Raymond B et al (2015) Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. J Appl Ecol 52:774–783

Bergstrom DM, Wienecke BC, van den Hoff J et al (2021) Combating ecosystem collapse from the tropics to the Antarctic. Glob Change Biol. https://doi.org/10.1111/gcb.15539

Bureau of Meteorology (2020) Daily rainfall Macquarie Island Weather Station #300004. http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=136&p_display_type=dailyDataFile&p_startYear=2019&p_c=-18000476595&p_stn_num=300004. Accessed 13 Jan 2020

Chakraborty S (2013) Migrate or evolve: options for plant pathogens under climate change. Glob Change Biol 19:1985–2000

Chau J, Born C, McGeoch MA et al (2019) The influence of landscape climate and history on the spatial genetic structure of keystone plants (*Azorella*) on sub-Antarctic islands. Mol Ecol 28:3291–3305. https://doi.org/10.1111/mec15147

Chown SL, le Roux PC, Ramaswiela T et al (2013) Climate change and elevational diversity capacity: do weedy species take up the slack? Biol Lett 9:20120806

Copson G, Whinam J (2001) Review of ecological restoration programme on sub-Antarctic Macquarie Island: pest management progress and future directions. Ecol Manag Restor 2:129–138

Dickson CR (2019) Impact of climate change on a sub-Antarctic keystone cushion plant *Azorella macquariensis* (Apiaceae). Dissertation, Monash University Melbourne

Dickson CR, Baker DJ, Bergstrom DM et al (2019) Spatial variation in the ongoing and widespread decline of keystone plant species. Austral Ecol 44:891–905. https://doi.org/10.1111/aec12758

Eyring V, Arblaster JM, Cionni I, Sedláček J et al (2013) Long-term ozone changes and associated climate impacts in CMIP5 simulations. J Geophys Res-Atmos 118:5029–5060. https://doi.org/10.1002/jgrd50316

Frenot Y, Gloaguen J, Cannavacciuolo M, Bellido A (1998) Primary succession on glacier forelands in the sub-Antarctic Kerguelen Islands. J. Veg Sci 9:75–84

Garrett KA, Nita M, De Wolf ED, Esker PD, Gomez-Montano L, Sparks AH (2016) Plant pathogens as indicators of climate change. In: Letcher TM (ed) Climate change, 2nd edn. Elsevier, Boston

Harter DEV, Irl SDH, Seo B et al (2015) Impacts of global climate change on the floras of oceanic islands – Projections, implications and current knowledge. Perspect Plant Ecol Evol Syst 17:160–183

Hoffmann AA, Rymer PD, Byrne M et al (2019) Impacts of recent climate change on terrestrial flora and fauna: some emerging Australian examples. Austral Ecol 44:3–27

Kitchener A, Harris S (2013) From forest to Fjaeldmark: descriptions of Tasmania's vegetation, 2nd edn. Department of Primary Industries Parks Water and Environment Tasmania. http://www.dpipwe.tas.gov.au/Documents/f2f_macquarie_islandpdf. Accessed 15 Jan 2020

Lee JE, Chown SL (2016) Range expansion and increasing impact of the introduced wasp *Aphidius matricariae* Haliday on sub-Antarctic Marion Island. Biol Invasions 18:1235–1246

Lenton TM (2013) Environmental Tipping Points. Annu Rev Env Resour 38:1–29. https://doi.org/10.1146/annurev-environ-102511-084654

le Roux PC, McGeoch MA (2008) Rapid range expansion and community reorganization in response to warming. Glob Change Biol 14:2950–2962

Pauchard A, Milbau A, Albihn A et al (2016) Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. Biol Invasions 18:345–353

Pendlebury SF, Barnes-Keoghan IP (2007) Climate and climate change in the sub-Antarctic. Pap Proc R Soc Tasmania 141:67–82

Rietkerk M, Dekker SC, de Ruiter PC et al (2004) Self-organized patchiness and catastrophic shifts in ecosystems. Science 305:1926–1929

Robinson SA, Erickson DJ III (2015) Not just about sunburn—the ozone hole's profound effect on climate has significant implications for Southern Hemisphere ecosystems. Glob Change Biol 21:515–527

Rolland V, Bergstrom DM, Lenne T et al (2015) Easy come easy go: capillary forces enable rapid refilling of embolized primary xylem vessels. Plant Physiol 168:1636–1647

Selkirk PM (1992) Climate change and the subAntarctic. In: Quilty PG (ed) Impact of climate change, Australia-Antarctica. Australian Government Printing Service, Canberra

Selkirk DR, Selkirk PM, Bergstrom DM et al (1988) Ridge top peats and paleolake deposits on Macquarie Island. Pap Proc R Soc Tasmania 122:83–90

Selkirk PM, Seppelt RD, Selkirk DR (1990) Subantarctic Macquarie Island: environment and biology. Cambridge University Press, Cambridge

Selkirk-Bell JM, Selkirk PM (2013) Vegetation-banked terraces on Sub-Antarctic Macquarie Island: a reappraisal. Arct Antarc Alp Res 45:261–274

Shaw JD, Terauds A, Bergstrom DM (2011) Rapid commencement of ecosystem recovery following aerial baiting on sub-Antarctic Macquarie Island. Ecol Manag Restor 12:241–244. https://doi.org/10.1111/j1442-8903201100611x

Smith RIL (1994) Vascular plants as bioindicators of regional warming in Antarctica. Oecologia 99:322–328

Springer K (2016) Methodology and challenges of a complex multi-species eradication in the sub-Antarctic and immediate effects of invasive species removal. N Z J Ecol 40:273–278

Thompson DWJ, Solomon S (2002) Interpretation of recent Southern Hemisphere climate change. Science 296:895–899. https://doi.org/10.1126/science1069270

Threatened Species Section (2009) Notesheet for *Azorella macquariensis* (Macquarie cushions). Department of Primary Industries and Water, Hobart

Turney CSM, Fogwill CJ, Palmer JG et al (2017) Tropical forcing of increased Southern Ocean climate variability revealed by a 140-year sub-Antarctic temperature reconstruction. Clim Past 13:231–248. https://doi.org/10.5194/cp-13-231-2017

UNESCO (1997) Macquarie Island World Heritage List. https://whc.unesco.org/en/list/629. Accessed 13 Mar 2019

Wang G, Cai W (2013) Climate-change impact on the 20th-century relationship between the Southern Annular Mode and global mean temperature. Sci Rep 3:2039

Whinam J, Abdul-Rahman JA, Visoiu M et al (2014) Spatial and temporal variation in damage and dieback in a threatened sub-Antarctic cushion species. Aust J Bot 62:10–21

Wilson BR, Wilson SC, Sindel B et al (2019) Soil properties on sub-Antarctic Macquarie Island: fundamental indicators of ecosystem function and potential change. Catena 177:167–179

Permafrost Thaw in Northern Peatlands: Rapid Changes in Ecosystem and Landscape Functions

3

David Olefeldt, Liam Heffernan, Miriam C. Jones, A. Britta K. Sannel, Claire C. Treat, and Merritt R. Turetsky

Abstract

Peatlands within the northern permafrost region cover approximately 2 million km^2 and are characterized by organic soils that can be several meters thick, and a fine-scale mosaic of permafrost and non-permafrost landforms interspersed by shallow ponds and lakes. Ongoing permafrost thaw is transforming these peatlands, causing abrupt changes to their morphology, hydrology, ecology, and biogeochemistry. In this review we show how changes to individual peatlands depend on both their Holocene developmental history and their location within current permafrost zones. Permafrost thaw in peatlands often leads to land surface collapse between 0.5 and 5 m, the so-called thermokarst. Thermokarst in peatlands can lead to the development of ice-wedge troughs, waterlogged

---

D. Olefeldt (✉)
University of Alberta, Edmonton, AB, Canada
e-mail: olefeldt@ualberta.ca

L. Heffernan
Uppsala University, Uppsala, Sweden
e-mail: liam.heffernan@ebc.uu.se

M. C. Jones
US Geological Service, Reston, VA, USA
e-mail: miriamjones@usgs.gov

A. B. K. Sannel
Stockholm University, Stockholm, Sweden
e-mail: britta.sannel@natgeo.su.se

C. C. Treat
Alfred Wegener Institute, Bremerhaven, Germany

M. R. Turetsky
University of Colorado, Denver, CO, USA
e-mail: merritt.turetsky@colorado.edu

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_3

thermokarst bogs and fens, and the initiation, expansion, and drainage of thermokarst lakes. Permafrost thaw in peatlands can thus completely alter vegetation composition and shift patterns of landscape inundation and hydrological connectivity. These changes in turn have implications for magnitude and timing of runoff, downstream water quality, habitat suitability for birds and larger mammals, traditional land-use, and the exchange of greenhouse gases with the atmosphere. Ongoing permafrost thaw is largely irreversible at relevant human time-scales, and peatland thermokarst has been accelerating over the last few decades. Complete permafrost loss is expected this century for peatlands in relatively warmer permafrost zones, and all peatlands in the northern permafrost region will be profoundly transformed by permafrost thaw.

3.1 Introduction

Peatlands are widespread in many boreal and tundra regions, with more than half of all northern peatlands found within the current permafrost zones (continuous, discontinuous, and sporadic/isolated) (Fig. 3.1). Peatlands are defined by their thick (>40 cm) organic soils, which have accumulated slowly over millennia. The build-up of organic soils has been facilitated by cool and wet soil conditions that slow the decomposition of plant material (Yu et al. 2010; Charman et al. 2013). Due to the cold climate of northern regions and the insulating qualities of peat itself, much of these peat soils have become incorporated into perennially frozen ground, i.e. permafrost (Hugelius et al. 2014). Peatlands in the northern permafrost region range in size from small landscape depressions to vast flat landscapes that extend hundreds of kilometers. Regardless of size, these peatlands are often best characterized as complexes composed of a fine-scale, discrete mosaic of permafrost and non-permafrost peatland landforms interspersed by shallow aquatic ecosystems (Figs. 3.2, 3.3, and 3.4). Many permafrost peatland landforms have very ice-rich ground, and thaw consequently often leads to land surface collapse, the so-called thermokarst. Thermokarst can lead to local collapse and formation of non-permafrost peatland landforms or aquatic ecosystems, but can also facilitate improved drainage at the peatland scale as new flow-paths are opened. Permafrost thaw thus often completely re-organizes peatland hydrology, including surface wetness and inundation patterns, which in turn affects vegetation composition and biogeochemical cycling. As such, climate change is not causing the gradual transition of permafrost peatlands towards the structure and function of peatlands currently south of the permafrost boundary, but rather causing dramatic changes and the development of novel ecosystems. Permafrost thaw and associated thermokarst has accelerated in the last few decades and is expected to further accelerate this century as high-latitude climate continues to warm at twice the rate of global warming, and as disturbances like wildfire become more frequent.

While morphology, hydrology, and vegetation composition of peatlands vary across permafrost zones, they have many similarities with regard to the ecosystem

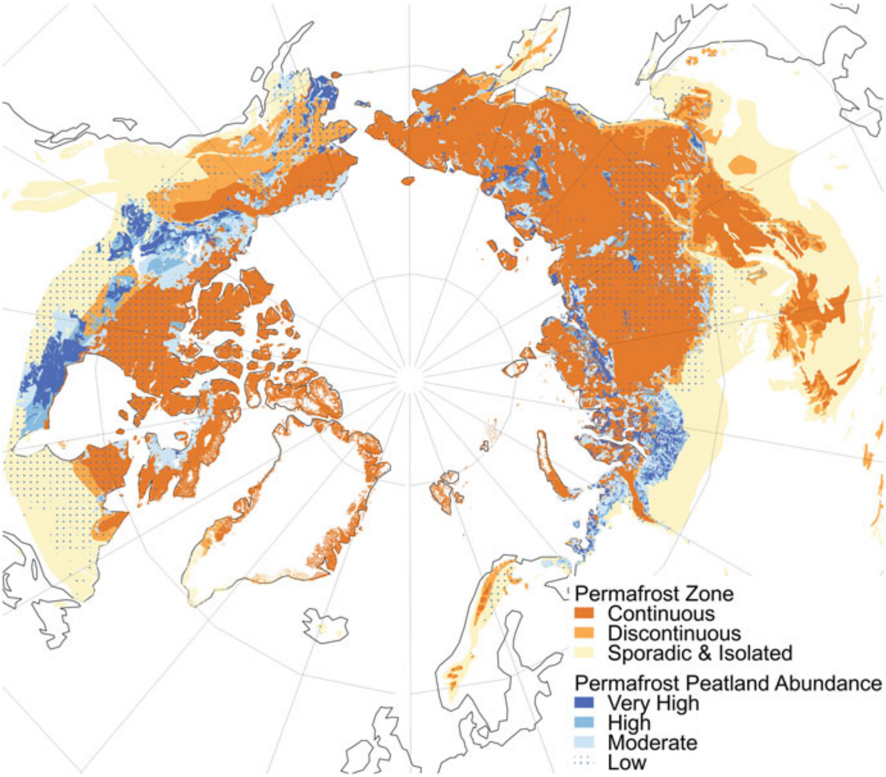


Fig. 3.1 Distribution of peatlands affected by permafrost across the northern permafrost region. Peatlands in this region contain both permafrost and non-permafrost landforms, as well as abundant ponds and lakes. Fractional coverage of peatlands defined as >60% for very high, 30–60% for high, 10–30% for moderate, 1–10% for low, and <1% outside these areas (Olefeldt et al. 2016). Permafrost zonation from Brown et al. (2002)

services they presently provide. Peatlands in the permafrost region are key habitats for many species of migratory waterfowl (Järvinen and Sammalisto 1976), as well as for larger mammals such as reindeer/caribou (*Rangifer tarandus*) (Dunford et al. 2006), and exhibit a higher biodiversity of bryophytes than peatlands south of the permafrost region (Beilman 2001). As such, permafrost peatlands provide ecosystem services for indigenous and local communities with regard to animal herding (Istomin and Habeck 2016), game hunting and food gathering and storage (Calmels et al. 2015), and water quantity and quality from a downstream drinking-water perspective (Gordon et al. 2016). Peatlands in the northern permafrost region have furthermore accumulated globally significant stores of soil organic carbon, which overall has cooled the climate during the Holocene by removing carbon dioxide (CO_2) from the atmosphere to a greater extent than these peatlands have been releasing methane (CH_4) (Frolking and Roulet 2007). Future changes to the balance of greenhouse gases from peatlands could therefore either help mitigate

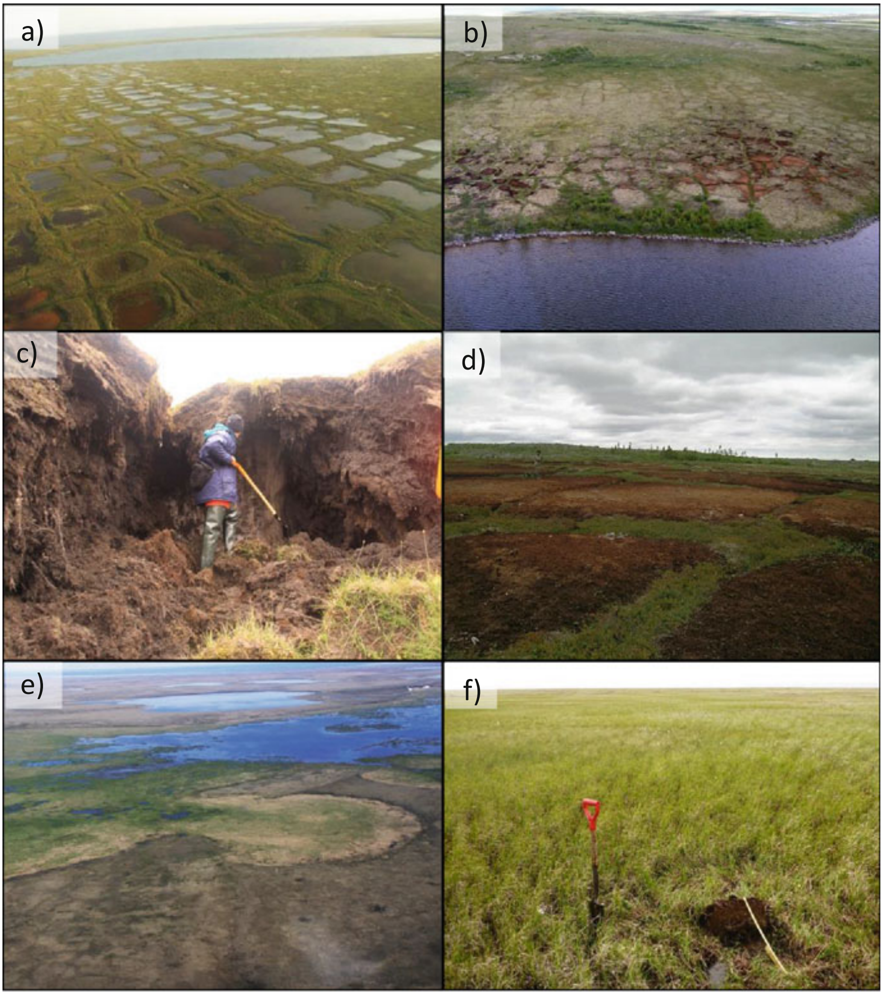


Fig. 3.2 Examples of peatlands and ecosystem transitions associated with permafrost dynamics in the continuous permafrost zone: (**a**) Low-center polygonal peatland (North Slope, Alaska), (**b**) High-center polygonal peatland (Southern Nunavut, Canada), (**c**) Thermal erosion in an ice wedge trough. Note the ~1.5 m wide ice wedge behind the researcher (Lena delta, Russia), (**d**) Wind-erosion of high-center polygonal peatland (Southern Nunavut, Canada), (**e**) Drained thermokarst lake basin with new peatland development, permafrost aggradation, and ice-wedge formation (Seward Peninsula, Alaska), (**f**) Peatland initiation and sedge peat accumulation within a thermokarst basin after thermokarst lake drainage (North Slope, Alaska). Photo credits: **a,c,e,f**—Guido Grosse; **b,d**—Britta Sannel

anthropogenic emissions or conversely push the climate towards further warming. With rapid warming and permafrost thaw, many ecosystem services from peatlands are anticipated to be impacted over the coming decades and beyond.

Fig. 3.3 Examples of peatlands and ecosystem transitions associated with permafrost dynamics in the discontinuous permafrost zone: (**a**) Peatland with forested peat plateaus, circular non-forested thermokarst bogs, and elongated thermokarst fens (Northwest Territories, Canada), (**b**) Peat plateaus surrounding thermokarst ponds which are draining due to permafrost thaw that has opened up new surface flow connections (Northwest Territories, Canada), (**c**) Thermokarst fen expansion due to thaw (Saskatchewan, Canada), (**d**) Rapid thermokarst bog expansion 3 years following a wildfire (Alberta, Canada), (**e**) Thermokarst pond expansion (Northwest Territories, Canada), (**f**) Stable thermokarst pond with infilling of vegetation (Alberta, Canada). Photo credits: **a**—Mason Stothart; **b, d, e, f**—David Olefeldt; **c**—Britta Sannel

The objective of this review is to describe observed and anticipated impacts of permafrost thaw and thermokarst in peatlands, including impacts on hydrology, ecology, and biogeochemistry. For this purpose, we will describe peatlands found across permafrost zones, highlighting some of their differences in Holocene

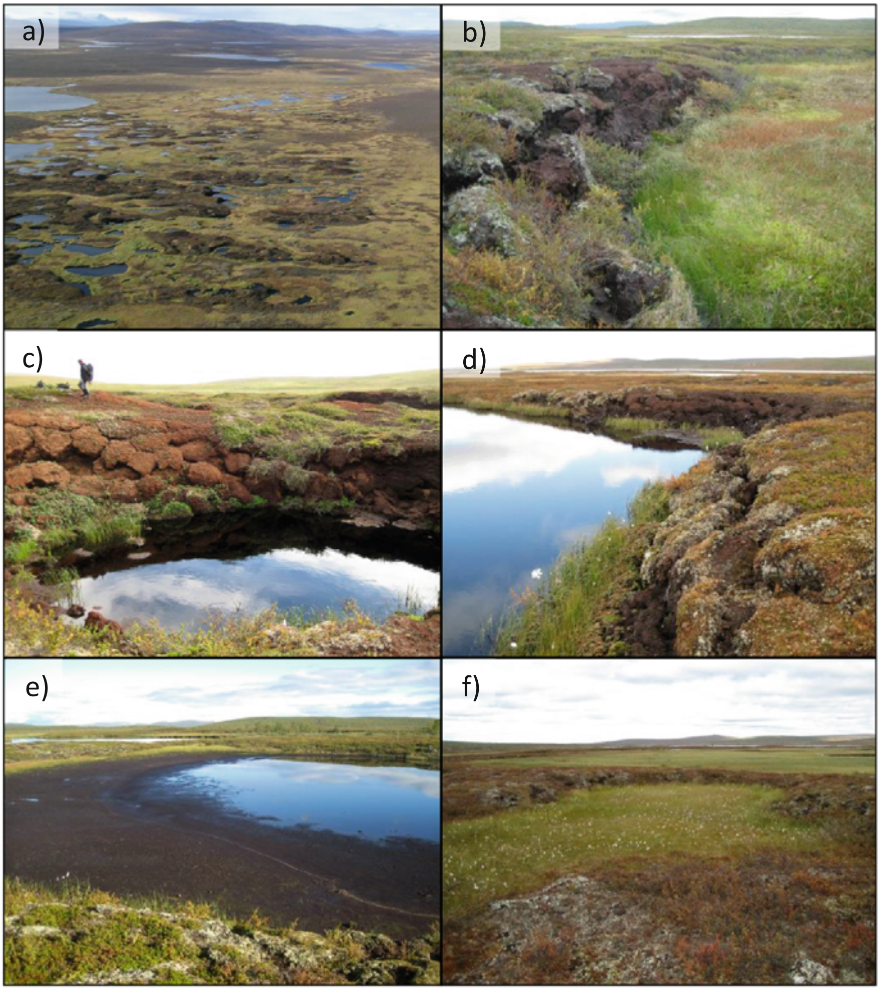


Fig. 3.4 Examples of peatlands and ecosystem transitions associated with permafrost dynamics in the sporadic/isolated permafrost zone: (**a**) Peatland with raised palsas, thermokarst ponds, and fens, (**b**) Palsa collapse into thermokarst fen, (**c**) Palsa collapse into new pond formation, (**d**) Continued thermokarst pond expansion, (**e**) Thermokarst pond drainage, (**f**) Peatland succession in large thermokarst fens. All photos from Northern Sweden, Photo credits: Britta Sannel

development and their current conditions, and how these variations influence predominant modes and impacts of permafrost thaw. We will focus on rapid ecosystem transformations associated with permafrost thaw, such as collapse of permafrost peatlands into thermokarst peatlands, expansion of thermokarst ponds and lakes, and the drainage of lakes and polygonal peatlands. We will describe the knowledge of current and projected rates of these peatland transformations and highlight impacts that are of relevance at both local and global scales.

3.2 Current Distribution and Characteristics of Peatlands in the Northern Permafrost Region

3.2.1 Current Peatland Distribution and Major Regions

Peatlands affected by permafrost cover between 1.6 and 2.3 million km^2, i.e. between 9 and 13% of the northern permafrost region (Hugelius et al. 2014; Olefeldt et al. 2016) (Fig. 3.1). These peatlands generally include both permafrost and non-permafrost peatland landforms, along with abundant ponds and lakes (Figs. 3.2, 3.3, and 3.4). Overall, permafrost and non-permafrost landforms are roughly equally abundant. However, the relative abundance of permafrost over non-permafrost peatland landforms shifts from low percentages in the warmer sporadic permafrost zone where mean annual average temperatures (MAAT) are between +1 and –3 °C, increasing through the discontinuous zone (MAAT –3 to –7 °C) to near complete dominance in the continuous zone (MAAT below –7 °C) (Smith and Riseborough 2002; Hugelius et al. 2014). Pools, ponds, and lakes within these peatlands occupy at least 0.2 million km^2, i.e. at least 10% of the peatland area. This includes an estimated 35,000 lakes between 0.1 and 50 km^2 in size (Smith et al. 2007) and at least an additional 0.05–0.15 million km^2 of ponds less than 0.1 km^2 in size (Verpoorter et al. 2014; Muster et al. 2017).

Three regions contain a majority of northern peatlands; the West Siberian Lowlands east of the Ural Mountains in Russia, The Hudson Bay Lowlands in central Canada, and the Mackenzie River Basin in continental western Canada. These three peatland regions span all permafrost zones and also extend beyond the current southern limit of permafrost (Fig. 3.1). Other permafrost regions with significant peatland cover include lowlands along the coast of the Arctic Ocean in eastern Russia, northernmost Europe (Scandinavia and western Russia), and Alaska. Peatlands in the northern permafrost region can thus be found in climates with MAAT ranging between +1 and –15 °C (Olefeldt et al. 2016), i.e. from the very southern border of permafrost to well into the continuous permafrost zone.

3.2.2 Peatland Characteristics Across Permafrost Zones

Dominant landforms within peatlands vary across permafrost zones. Polygonal peatlands, peat plateaus, and palsas are considered the typical permafrost peatland landforms in the continuous, discontinuous, and sporadic permafrost zone, respectively (Figs. 3.2, 3.3, and 3.4). These peatland landforms differ in terms of their morphology, developmental histories, hydrology, and ecology, and each is described in detail below. Their shift in dominance across permafrost zones is however gradual, and there are both spatial overlaps of these landforms, particularly for peat plateaus and palsas, as well as transitional peatland landforms such as polygonal peat plateaus (Zoltai and Tarnocai 1975; Kremenetski et al. 2003; Dyke and Sladen 2010).

3.2.2.1 Peatlands in the Continuous Permafrost Zone

Polygonal peatlands in the continuous permafrost zone are distinguished by the presence of ice wedges, which outline polygons with a diameter of between 5 and 30 m (Fig. 3.2) (Minke et al. 2007; Liljedahl et al. 2016). Polygonal peatlands are abundant on the arctic coastal plains in Siberia, Alaska, and within the Mackenzie River delta in Canada (Fig. 3.1) (Kremenetski et al. 2003; Minke et al. 2007). The distribution of polygonal peatlands in these lowland landscapes is often irregular and surrounded by tundra vegetation on mineral soils, with peatland locations confined to river terraces, flood plains, and drained thermokarst lake basins. The ice wedges that outline the polygons in these peatlands form over centuries to millennia due to thermal contraction and soil cracking during winters followed by infiltration and refreezing of snowmelt (Lachenbruch 1962). The width and depth of ice wedges depend on landscape position, climate, and the time to develop, but are commonly ~1 m wide and 2–4 m deep and often covered by a thin (20–40 cm) layer of peat (Fig. 3.2c) (Zoltai and Tarnocai 1975). The overall peat depth within polygons is also generally shallow, 20–150 cm, although occasionally deeper (Zoltai and Tarnocai 1975; Kremenetski et al. 2003; Fritz et al. 2016).

Polygonal peatlands can be further classified into low-center or high-center polygons (c.f. Fig. 3.2a, d). While both types can be found in close proximity, high center polygons are considered to develop over time from low center polygons either due to peat accumulation within the polygon center that is faster than the vertical growth of the ice wedge or as a result of ice wedge thaw and degradation (Zoltai and Tarnocai 1975). As a result, high center polygons are more common in relatively warmer regions within the continuous permafrost zone. Low-center polygons have centers that are dominated by wet sedge species, brown mosses, and wet adapted *Sphagnum* communities, or remain as open water, while their elevated rims have dry adapted dwarf shrubs, forbs, lichens, and mosses (Kutzbach et al., 2007; Fritz et al. 2016). Conversely, centers of high-center polygons are dominated by dry-adapted *Sphagnum* moss, shrubs, and lichens, while the ice-wedge troughs are dominated by sedges and mosses. In low-center polygons, the elevated polygonal rims act as hydrological barriers and the hydrologically disconnected polygon centers thus often act as evaporation pans (Helbig et al. 2013). Conversely, ice wedge troughs in high center polygonal peatlands often act as the main hydrological drainage network within the peatland.

3.2.2.2 Peatlands in the Discontinuous Permafrost Zone

Peat plateaus, referred to as flat mound-bogs in Siberia, are found both in the discontinuous and sporadic permafrost zones and are elevated 1–3 m above surrounding non-permafrost fens and bogs while extending 10s–100s of meters horizontally (Fig. 3.3) (Zoltai and Tarnocai 1975; Kremenetski et al. 2003; Dyke and Sladen 2010). The rise in elevation is largely due to ice expansion and development of segregated ice lenses within the mineral soil that underlies the peat profile (Kremenetski et al. 2003; Pelletier et al. 2017). As a result of permafrost aggradation and frost heave, peat plateaus are relatively dry and nutrient poor. The vegetation is often dominated by dry-adapted *Sphagnum* and feather mosses, lichens, and ericaceous shrubs. Development of peat plateaus over time is associated with further gradual drying of the surface and a relative shift from *Sphagnum* and feather mosses to lichens or even to bare surfaces with apparent wind erosion (Peteet et al. 1998; Oksanen et al. 2001; Sannel and Kuhry 2008). Peat plateaus in Canada and Alaska have an open canopy of black spruce (*Picea mariana*) (Fig. 3.3), which become successively sparser and more stunted towards the transition to the continuous permafrost zone where non-forested polygonal peat plateaus become more common (Dyke and Sladen 2010).

It is common for peat plateaus to cover between 30 and 70% of peatlands within the discontinuous permafrost zone, with the remainder made up of ponds and non-permafrost fens and bogs (Kremenetski et al. 2003; Baltzer et al. 2014; Gibson et al. 2018). Interactions between permafrost and hydrology are responsible for the organization of these peatland landforms within individual peatlands. Raised peat plateaus efficiently generate runoff to their adjacent surroundings, but can also prevent drainage of thermokarst bogs that are completely surrounded by peat plateaus (Quinton et al. 2009). Narrow, wet, and nutrient rich fens that are spatially constricted and flanked by peat plateaus act as the main drainage network within peatland of the discontinuous zone (Fig. 3.3a). Vegetation of these channel fens is often dominated by tall sedges (e.g. *Carex rostrata*), cotton grass (e.g. *Eriophorum angustifolium*), cattail (*Typha latifolia*), or willows, interspersed with diverse brown moss species. Development of large peat plateaus can trigger permafrost thaw by creating localized areas of subsurface water pooling centrally within a peat plateau. Subsurface water pooling increases thermal conductivity and causes thaw and surface collapse. This collapse is the initial development of either thermokarst bogs or thermokarst ponds (Fig. 3.2c–e), which then continue to expand due to the wet conditions along their edges. These thermokarst bogs and ponds can be hydrologically isolated or connected to channel fens.

Thermokarst bog development and succession can be cyclical, eventually leading to permafrost re-aggradation and returning to a peat plateau stage after several centuries. Early thermokarst bog development is characterized by inundation of the peat surface and a drastic shift in vegetation communities as the dry, slow-growing vegetation of the peat plateau is replaced by rapidly growing, hydrophilic *Sphagnum* mosses and sedges. Thermokarst bogs then go through autogenic succession with peat accumulation, with earlier wetter phases transitioning to relatively drier mature stages where after about 100 years the peat surface is raised (~25–30 cm) above the water table and dominated by dry-adapted *Sphagnum* and shrubs (Camill 1999; Gibson et al. 2018). In boreal Canada, and some locations of boreal Eastern European Russia, permafrost re-aggradation occurs in this later, mature stage and peatlands can undergo several cycles of permafrost aggradation and degradation, driven by interactions between hydrology and autogenic succession and often triggered by wildfire (c.f. Fig. 3.3b) (Zoltai 1993; Oksanen et al. 2001; Kuhry 2008; Treat and Jones 2018). The lack of documented cyclicity in many other permafrost peatlands could in part be because permafrost aggradation in many discontinuous permafrost peatlands is relatively recent (Treat and Jones 2018).

3.2.2.3 Peatlands in the Sporadic Permafrost Zone

Palsas, also known as frost mounds or large hill-bogs, common in the sporadic permafrost zone, are small circular to elongated mounds with a width of a few meters to tens of meters, but with heights up to 6 m above the surrounding non-permafrost fens (Fig. 3.4) (Seppälä 1986). As such they have many similarities with peat plateaus, but are smaller in lateral extents and often occupy a smaller fraction of peatlands. In larger peatlands, palsas are most likely to develop away from main flowpaths due to convection of heat from moving water. As palsas often occupy only a small fraction of larger peatlands (Beilman et al. 2001) they are less likely than peat plateaus to have a large influence on overall peatland surface hydrology and runoff patterns.

Development of palsas involves the gradual growth of mounds due to frost heave and development of ice lenses, with associated shifts towards drier conditions that are reflected in the vegetation composition shifting from sedge/moss of early stages to lichen/shrub communities as the mound grows (Zuidhoff and Kolstrup 2005; Seppälä 2011). The top of mature palsas is often unvegetated due to frost action and subsequent wind erosion (Seppälä 2003). The growth of mature palsas can also lead to cracks in the peat surface, which reduce the insulating properties of the peat layer and in turn trigger thaw and palsa collapse into fen or open water ecosystems (Fig. 3.4b–e) (Seppälä 1986). This cyclical development of palsas has led to peatlands with very fine spatial heterogeneity of palsas, fens, and ponds (Fig. 3.4a) (Luoto et al. 2004).

3.3 Holocene Development of Peatlands in the Northern Permafrost Region

Developmental histories of permafrost peatlands strongly influence both impacts and patterns of permafrost thaw, since developmental histories determine both the spatial configuration of peatland landform types within peatlands and peat profile characteristics. Important characteristics of permafrost peat profiles from this perspective include peat thickness, peat botanical origin, degree of humification, quantity of excess ground ice (i.e. volume of ground ice which exceeds total pore volume under unfrozen conditions), and distribution of ground ice (e.g. as pore ice, ice lenses, or ice wedges). These characteristics are in turn influenced interactions between local climate, hydrological setting, timing and mode of peatland initiation (e.g. developing from a terrestrial or aquatic ecosystem), timing of permafrost aggradation, disturbances (e.g. fire), and vegetation composition. The influence of local climate suggests that peatlands within each permafrost zone have broad commonalities in their development, yet the other factors suggest that regional and local conditions can cause important variations.

3.3.1 Timing and Mode of Peatland Initiation

The timing of peatland initiation has varied both within and between permafrost peatland regions. The earliest peatland initiation occurred in non-glaciated regions of Russia and Alaska, up to 16,000 calendar years before present (cal yr BP) (Kremenetski et al., 2003; Jones and Yu 2010; Schulze et al. 2015); however, widespread peatland initiation in these regions mainly occurred 11,000–8000 cal yr BP (Ruppel et al. 2013; Kremenetski et al. 2003; Smith et al. 2004). Peatland initiation in glaciated regions of Canada and Scandinavia transgressed with ice sheet retreat across the continent (Ruppel et al. 2013; Dyke 2004), and with the emergence of land following glacioisostatic rebound (Packalen et al. 2014). As such, widespread peatland initiation in the Mackenzie River Basin occurred 9000–7000 cal yr BP (Halsey et al. 1998; Gorham et al. 2007; Pelletier et al. 2017), while it occurred between 7000 and 4000 cal yr BP in the Hudson Bay Lowlands (Packalen et al. 2014). In all regions, there has been a continued peatland initiation and expansion until present day (Halsey et al. 1998; Kremenetski et al. 2003; Packalen et al. 2014), although at reduced rates as most of the suitable landscape positions have already been developed into peatlands.

Three modes of northern peatland initiation have been identified: primary mire formation, terrestrialization, and paludification (Ruppel et al. 2013). Primary mire formation involves peat accumulation on newly exposed wet mineral soils, e.g. following glacial retreat, pro-glacial lake drainage, or marine isostatic uplifting. Terrestrialization is the succession of lake to peatland, caused by infilling of vegetation and organic sediments, whereas paludification is the colonization by peatland vegetation on long exposed land, triggered by increased local wetness due to climate shifts or disturbances (e.g. fire or beaver activity). All three processes have been documented both among all major northern peatland regions and across all permafrost zones (Peteet et al. 1998; Oksanen 2006; Kuhry 2008; Ruppel et al. 2013; Packalen et al. 2014; Pelletier et al. 2017). In general, the earliest peat initiation in each region is associated with primary mire formation, followed by terrestrialization and paludification last (Ruppel et al. 2013). An exception may be unglaciated tundra regions within the continuous permafrost zone, where primary mire formation has occurred throughout the Holocene in drained thermokarst lake basins (Fig. 3.2e) (Minke et al. 2007; de Klerk et al. 2011; Jones et al. 2012; Fritz et al. 2016). Both current day depth of peat and quantity of excess ground ice of a permafrost peatland may be influenced by mode of initiation, with generally shallower peat and less excess ground ice in peatlands that formed through paludification (Turunen et al. 2002; Fritz et al. 2016).

3.3.2 Timing and Processes of Permafrost Aggradation

The timing of permafrost aggradation has varied strongly among permafrost zones, with earlier aggradation in the continuous permafrost zone and generally the most recent aggradation in the sporadic permafrost zone (Fig. 3.5; Treat and Jones 2018).

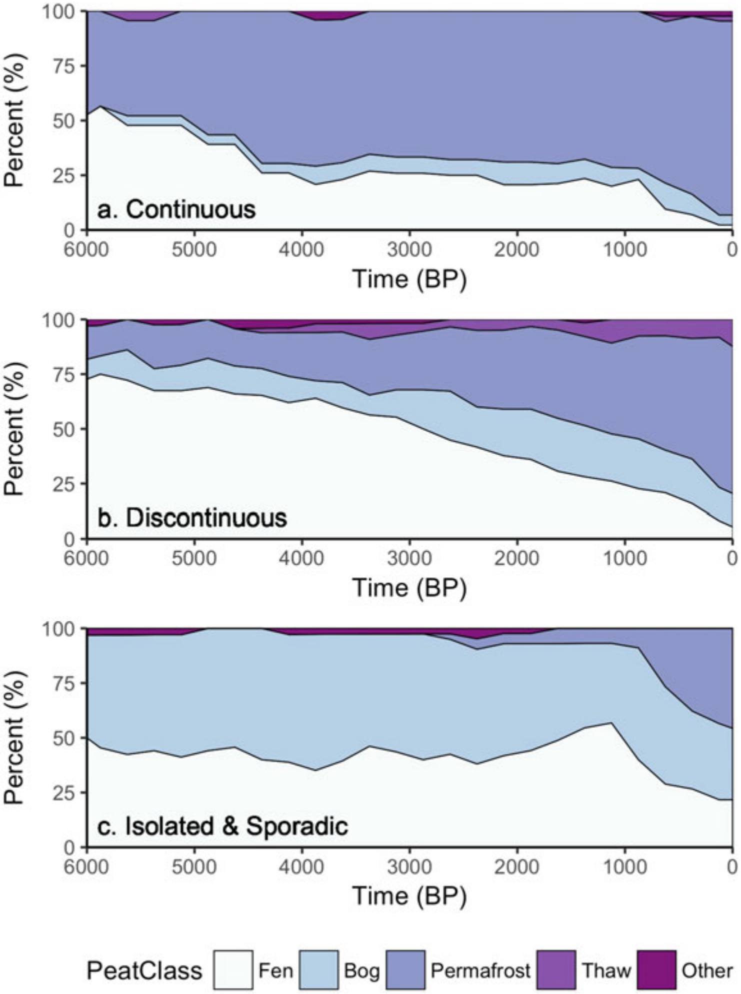


Fig. 3.5 The timing of permafrost aggradation within peatlands found in different permafrost zones including (**a**) continuous permafrost; (**b**) discontinuous permafrost; and (**c**) isolated and sporadic permafrost. Analysis is based on 45, 75, and 40 peat cores from the continuous, discontinuous, and sporadic/isolated permafrost zones, respectively (Treat and Jones 2018). Not all cores have basal dates >6000 cal yr BP, but at least 20 cores from each permafrost zone have ages >6000 cal yr BP. The classification of peatland types is based on a synthesis of detailed plant macrofossil analysis from peat cores. The percent of peat cores does not necessarily translate into areal extent due to bias in sampling locations, which favored data from present-day permafrost landforms, while present-day permafrost-free peatlands landforms and open water ecosystems are under-sampled

In the cold climates of the continuous permafrost zone, stratigraphic evidence indicate that permafrost often aggraded almost simultaneously with peatland initiation, e.g. following brief non-permafrost wet sedge fen phase or following thermokarst lake drainage (de Klerk et al. 2011; Fritz et al. 2016). As such, a majority of peat in polygonal peatlands is likely to have undergone syngenetic permafrost aggradation, i.e. where the base of the active layer rises alongside with peat accumulation and thus potentially incorporates less humified peat into permafrost (Treat et al. 2014). In contrast, permafrost aggradation in peatlands of the discontinuous and sporadic permafrost zone often occurred several thousand years after peatland initiation, the so-called epigenetic permafrost aggradation (Fig. 3.5; Treat and Jones 2018). Much of the peat in these regions thus spent several millennia in non-permafrost peatlands prior to permafrost aggradation.

The timing of permafrost aggradation in peat plateaus and palsas has been linked to both climate cooling and autogenic succession. Widespread permafrost aggradation in the discontinuous permafrost zone coincides with climate cooling following the Holocene thermal maximum. The Holocene thermal maximum began as early as 11,000 cal yr BP in Siberia and western North America and lasted until 5000 cal yr BP in eastern North America and Europe, and during this period mean annual temperatures at high latitudes were up to 5 °C above preindustrial levels (Renssen et al. 2012) and permafrost zones were shifted northwards by 300–500 km (Zoltai 1995). Permafrost aggradation in the sporadic permafrost zone in turn often, but not always, coincide with the further cooling of the Little Ice Age which started ~700 cal yr BP and lasted until the late nineteenth century (Fig. 3.5c) (Sannel et al. 2018; Treat and Jones 2018; Kjellman et al. 2018).

For individual peat plateau and palsa sites however, the timing of permafrost aggradation often appears to coincide with shifts in vegetation to *Sphagnum* mosses of poor fens or bogs (Beilman 2001). These shifts in vegetation could be associated with hydrological changes tied to autogenic peatland development, i.e. the slow accumulation of peat from plant material generated within the peatland itself. This ecological succession could potentially trigger permafrost aggradation due to the associated reduced surface wetness and increased thermal insulation of *Sphagnum* peat (Zoltai and Tarnocai 1975; Oksanen et al. 2001; Bhiry and Robert 2006; Kuhry 2008; Treat et al. 2016; Pelletier et al. 2017). Increased stature and abundance of coniferous trees has in western Canada also been linked to permafrost aggradation, likely associated with reduced insulation from a thinner snowpack on the ground. At the same time, it is also possible that the observed shift in vegetation to dry-adapted *Sphagnum* mosses and spruce tree in itself is a response to the initial frost heave during early stages of permafrost aggradation. It has also been shown that vegetation shifts to *Sphagnum* dominance are not required for permafrost aggradation, as many palsas in Scandinavia develop directly from wet sedge fens (Sannel et al. 2018; Kjellman et al. 2018).

3.3.3 Holocene Carbon Accumulation in Permafrost Peatlands

Peatlands within the northern permafrost region store 350 ± 50 Pg C (1 Pg = 10^{15} g) in the top 3 m, with approximately half of this in permafrost landforms (Hugelius et al. 2014; Olefeldt et al. 2016). This is a globally significant reservoir of soil carbon, equivalent to roughly a third of the carbon stored as CO_2 in the atmosphere, and about a quarter of all soil carbon in the top 3 m of soils in the northern permafrost region. While soil carbon has gradually accumulated throughout Holocene, there are distinct differences in the rate of carbon accumulation among permafrost zones and also between different stages of peatland succession.

Long-term carbon accumulation in peatlands has largely been assessed from analysis of peat cores, where the mass of soil C found between two or more peat layers is divided by the difference in radiocarbon age of those layers, yielding the apparent carbon accumulation rate (ACAR) which is expressed as g C m^{-2} $year^{-1}$ (Tolonen and Turunen 1996). ACAR can be estimated for the full core, which yields the average rate of carbon accumulation since peatland initiation, or it can also be estimated for sections of the peat core which correspond to distinct ecosystem stages. Because ACAR reflects the carbon that remains in the soil at the time of core extraction, it should be interpreted with caution, as subsequent changes in hydrology or climate can increase decomposition down core, altering the earlier ACAR (Frolking et al. 2014). Therefore, ACAR does not necessarily indicate the annual net ecosystem carbon balance (NECB), i.e. the actual annual carbon balance as determined by direct measurements of all individual carbon fluxes (Packalen and Finkelstein 2014). Nonetheless, measures of ACAR from different permafrost zones and from earlier developmental phases still provide some of the best information for anticipating patterns of future peatland C accumulation.

Early non-permafrost peatland stages, such as open water wetlands, marshes, and rich fens, have generally high ACAR, at ~25 g C m^{-2} $year^{-1}$ (Vardy et al. 2000; Loisel et al. 2014; Packalen and Finkelstein 2014; Treat et al. 2016). This is likely due, in part, to the warmer climate during early Holocene (Charman et al. 2013), but high ACAR rates during early peatland development have also been found for peatlands that were more recently initiated in drained lake basins (Hunt et al. 2013). This suggests that the high ACAR during early peatland development is strongly related to relatively wet and nutrient rich conditions. Continued autogenic succession into non-permafrost fen and bog stages often shows slightly reduced ACAR compared to earlier stages, at ~15–20 g C m^{-2} $year^{-1}$ (Treat et al. 2016; Pelletier et al. 2017).

Permafrost aggradation generally leads to reduced ACAR compared to earlier peatland stages (Treat et al. 2016). However, reduced ACAR can lag permafrost aggradation by centuries and often depend on the persistence of *Sphagnum* mosses (Oksanen 2006; Sannel and Kuhry 2009; Hunt et al. 2013). The increasingly drier conditions of developing high-center polygonal peatlands, peat plateaus, and palsas compared to earlier developmental stages gradually lead to a shift in ground cover from *Sphagnum* mosses to feather mosses, lichens, and shrubs and concurrently reduced ACAR. Thus early permafrost stages with *Sphagnum* dominance can have similar or higher ACAR compared to previous non-permafrost stages (Oksanen 2006; Sannel and Kuhry 2009; Bauer and Vitt 2011; Pelletier et al. 2017), while ACAR of high-center polygonal peatlands, peat plateaus and palsas that are dominated by lichens and shrubs is <15 g C m^{-2} $year^{-1}$, and often <5 g C m^{-2} $year^{-1}$ or even indeterminate (Botch et al. 1995; Vardy et al. 2000; Sannel and

Kuhry 2009). The sylvic peat type accumulated under these dry permafrost conditions consists primarily of rootlets and lichen remains and is distinct from *Sphagnum* peat, not only with regard to ACAR but also peat quality, including higher C/N ratio (Treat et al. 2016; Pelletier et al. 2017). Low ACAR of non-*Sphagnum* permafrost peatlands is likely due to a combination of factors: low productivity associated with the dry and nutrient poor conditions, increased respiration of the oxic active layer (Turetsky et al. 2007), greater probability of wildfires (Robinson and Moore 2000; Sannel and Kuhry 2009), and surface erosion from wind scouring (Peteet et al. 1998; Seppälä 2003).

3.4 Observed Peatland Change Associated with Permafrost Thaw

Permafrost peatlands are dynamic ecosystems, and individual peatlands are likely to have had simultaneous occurrence of both permafrost aggradation and degradation throughout much of their development due to interactions between ecological succession, soil development, disturbances, and hydrology. However, recent warming has accelerated rates of permafrost degradation and of complete thaw. Near-surface permafrost degradation is more common than complete thaw in the continuous permafrost zone and is causing shifting patterns of inundation as ice-wedge troughs and lakes expand, erode, or drain (Liljedahl et al. 2016). Changes in the discontinuous and sporadic permafrost zones are primarily associated with complete permafrost thaw and collapse of peat plateaus and palsas into thermokarst bogs, fens, and ponds (Jones et al. 2016; Borge et al. 2017). Permafrost peatlands in the sporadic permafrost zone are likely to completely thaw in the next few decades (Payette et al. 2004; Bauer and Vitt 2011), yet the greatest areal loss of permafrost over the next few decades is expected in the discontinuous permafrost zone (Chasmer and Hopkinson 2017).

3.4.1 Peatland Change in the Continuous Permafrost Zone

Several recent landscape changes associated with permafrost dynamics have been observed within polygonal peatlands of the continuous permafrost zone, despite the prevailing cold climates and colder permafrost temperatures (Figs. 3.6, 3.7, and 3.8). In the zone of continuous permafrost, peat soils are thinner, providing less of an insulative buffer against heat waves that can lead to permafrost thaw in even cold high arctic permafrost (Farquharson et al., 2019). Landscape positions that are vulnerable to permafrost degradation in these peatlands include ice-wedges and perimeters of ponds and lakes (Figs. 3.6, 3.7, and 3.8). Few studies in the continuous permafrost zone have been able to directly detect an increased rate of permafrost degradation in response to recent warming, yet broad changes to landscape inundation patterns described below suggest a recent acceleration of permafrost

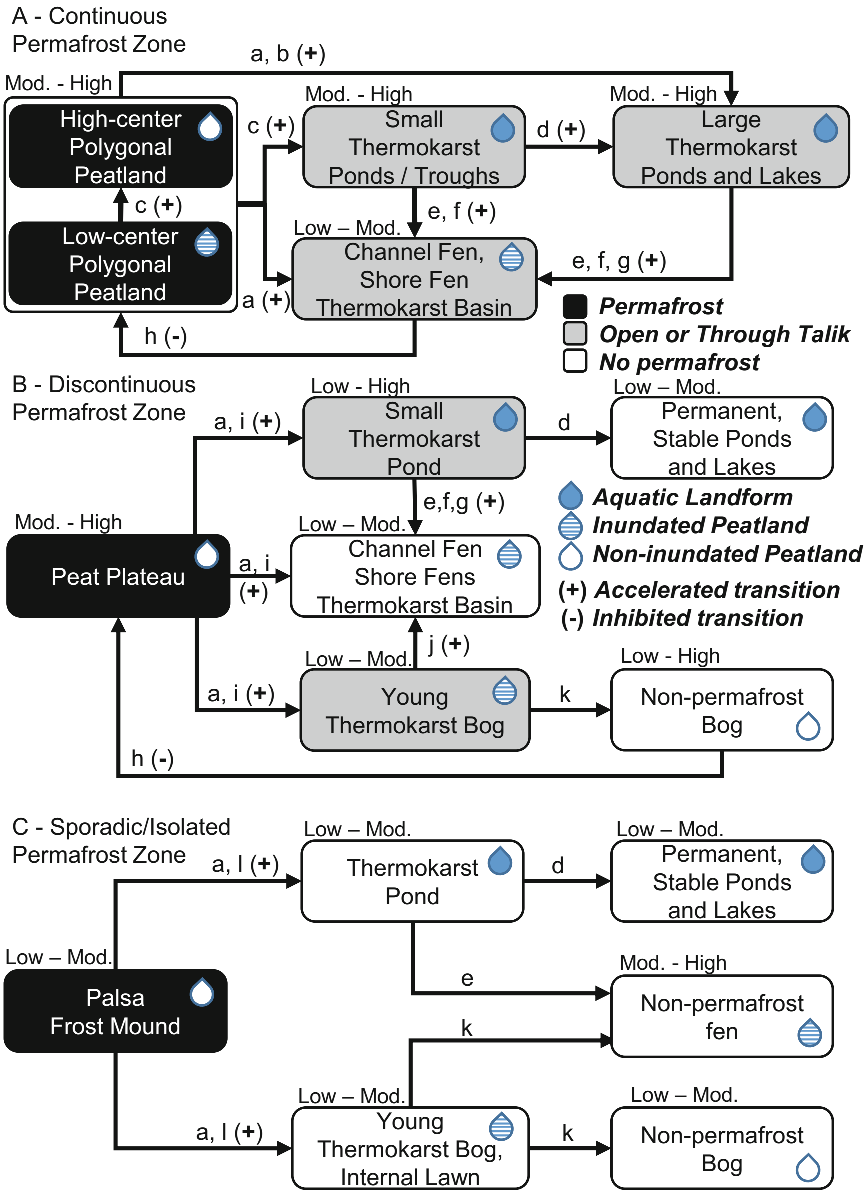


Fig. 3.6 Generalized scheme of dominant landforms and transitions within peatlands of the (**A**) continuous permafrost zone, (**B**) discontinuous permafrost zone, and (**C**) sporadic/isolated permafrost zone. Shading of boxes indicates likely landform permafrost conditions, with black indicating the presence of near-surface permafrost, gray indicating the presence of taliks—i.e. where there is an unfrozen peat or sediment layer between the seasonally frozen active layer and the permafrost ground below, and white indicating complete absence of permafrost. Drop symbols indicate inundation, where filled symbols indicate aquatic landforms, hashed symbols indicate seasonally or continuously inundated peatland landforms, and white symbols indicate non-inundated peatland landforms. Arrows indicate ecosystem transitions that have been observed under the current

degradation which is likely to continue under further warming (Sannel and Kuhry 2011; Liljedahl et al. 2016).

Ice-wedge degradation in polygonal peatlands has likely accelerated in the last few decades. Ice-wedge ridges in low-center polygonal peatlands are particularly vulnerable to thaw, since ice-wedges often are covered only by a thin (<20 cm) layer of insulating peat. Degradation of ice-wedge ridges lead to a shift in vegetation on both the ridges, which collapse into troughs and become wetter with increased sedge vegetation, and in the polygon centers which then often drain into the troughs and become drier with increased abundance of moss and shrubs (Liljedahl et al. 2016). Continued ice-wedge degradation and collapse can lead to formation of troughs with open water which may continue to expand into ponds. Troughs can however also increase hydrological connectivity at the landscape scale and improve peatland drainage, leading to overall reduced peatland inundation. Ice-wedge degradation can at any stage be reversed and lead to ice-wedge re-formation, as early stages of degradation often increase the thermal insulation with a thicker active layer and drier polygonal centers (Kanevskiy et al. 2017). Hence the degradation and re-formation of ice-wedges, and the associated polygon ridges and troughs, is highly dynamic and dependent on the interactions between climate, ice, water, soils, and vegetation (Minke et al. 2007). While ice-wedge degradation has been linked to individually wetter summers when there is greater heat conductance from the adjacent inundated polygon centers (de Klerk et al. 2011; Gao and Couwenberg 2015), recent inter-decadal warming has also been linked to widespread ice-wedge degradation (Liljedahl et al. 2016; Farquharson et al., 2019). Ten of eleven recently studied polygonal peatlands in coastal tundra regions around the Arctic Ocean showed clear evidence of widespread ice-wedge degradation over the last few decades, with a general transition from low-center to high center polygons (Liljedahl et al. 2016).

Lake initiation and expansion in polygonal peatlands is likely to accelerate in a warming climate, but this increase in peatland inundation may be more than offset by catastrophic lake drainage and lake infilling by vegetation (Figs. 3.6, 3.7, and 3.8). Lake initiation can occur when massive ice-wedges thaw, and the resulting depression is confined by surrounding permafrost. While new lake formation due to ice wedge degradation in polygonal peatlands may be uncommon (Kanevskiy et al.

◀

Fig. 3.6 (continued) climate, with letters indicating the processes responsible for each ecosystem transition; a—thermokarst along permafrost peatland edges due to heat conduction from adjacent non-permafrost ecosystems, b—thermokarst and erosion due to wave action, c—ice wedge degradation, d—coalescing of lakes due to thermokarst lake lateral expansion, e—terrestrialization, f—lake drainage due to lateral expansion across hydrological divide, g—lake drainage through ground water recharge as a result of through talik development, h—permafrost aggradation, i—thermokarst resulting from effects of wildfire, j—conversion of isolated thermokarst bogs into fen through lateral expansion across permafrost barrier, k—autogenic succession through *Sphagnum* peat accumulation, l—complete permafrost thaw of palsas or frost mounds. The plus and minus signs indicate whether these transitions have been observed or are expected to become more or less common this century. Relative abundance of landforms within peatlands is indicated, where low is <5%, moderate is 5–25%, and high is >25% peatland cover

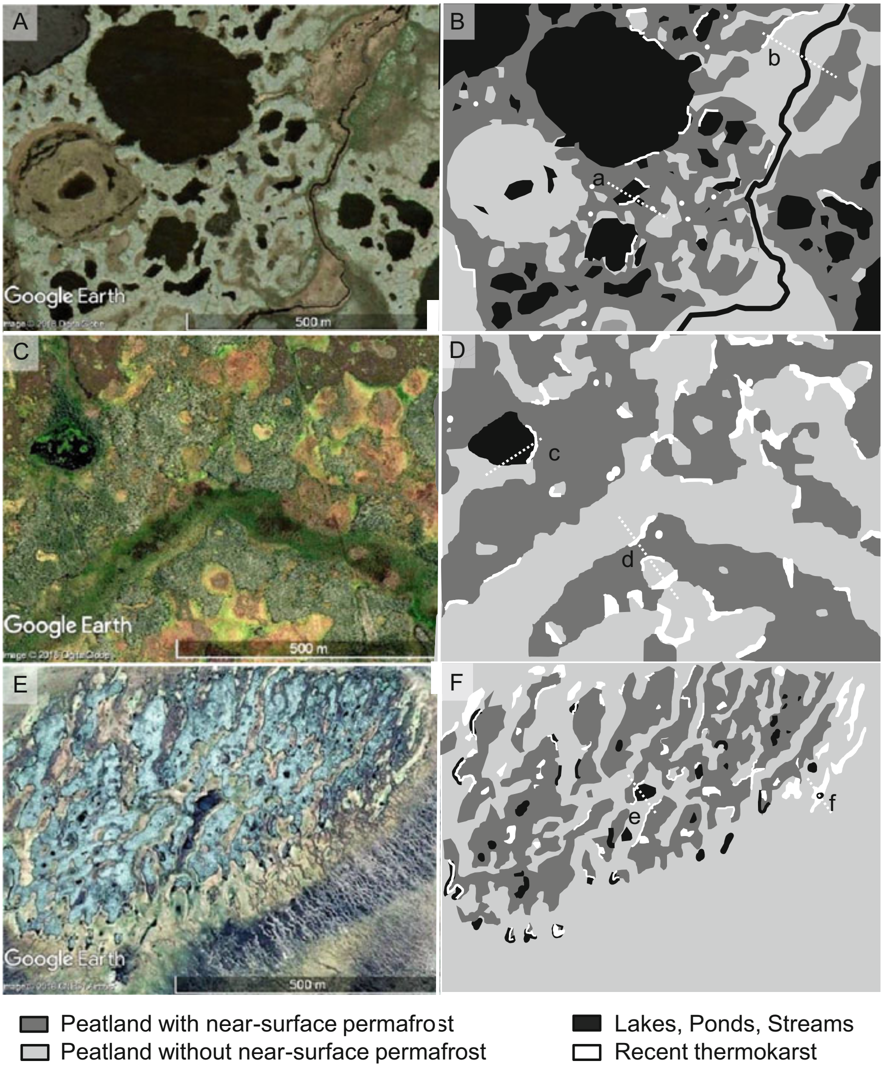


Fig. 3.7 Examples of peatlands within (**A**) the continuous permafrost zone, Hudson Bay Lowlands (polygonal peat plateau peatland) (58.1°N, 94.1W), (**C**) the discontinuous permafrost zone (peat plateau peatland), Mackenzie River Basin (59.9°N 120.5°W), and (**E**) the sporadic/isolated permafrost zone, eastern European Russia (palsa peatland) (65.9°N 59.9°W). Copyright **A**: CNES/Airbus, **C/E**: Digital Globe. Plates **B**, **D**, and **F** show image interpretations of permafrost conditions and dynamics, where dark grey areas indicate peatland types with near-surface permafrost (polygonal peatlands, peat plateaus, palsas), light grey areas indicate peatland types without near-surface permafrost, and white areas indicate areas of likely recent (last few decades) permafrost thaw / thermokarst. Lower-case letters a-–f associated with white dotted lines indicate transects shown in detail in Fig. 3.8

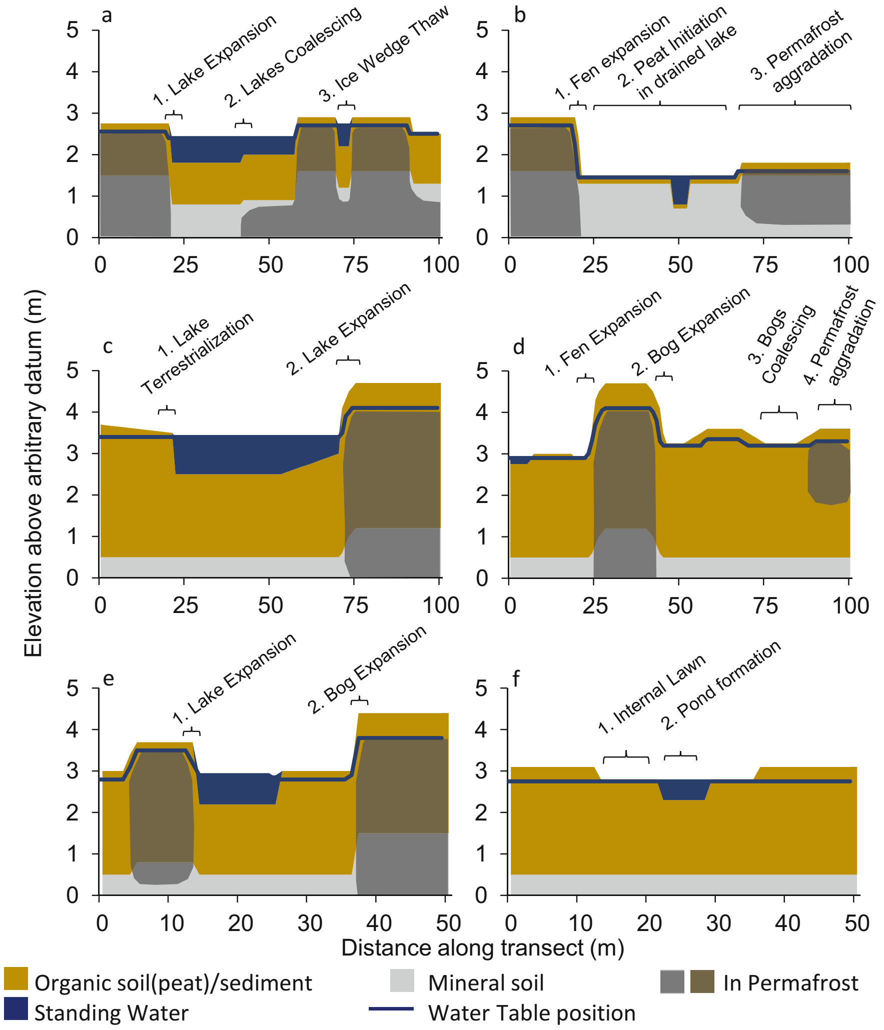


Fig. 3.8 Examples of ecosystem transitions in peatlands due to permafrost dynamics, along transects **a–f**, shown in Fig. 3.7. These ecosystem shifts may be due to permafrost thaw, permafrost aggradation, or autogenic succession. Transects **a** and **b** are examples from continuous permafrost, **c** and **d** from discontinuous permafrost, and **e** and **f** from sporadic permafrost zones. In Transect **a**, a polygonal peatland with shallow peat may be experiencing permafrost thaw, thermokarst expansion, and coalescing of ponds, as well as initiation of new ponds due to ice wedge degradation. Transect **b** crosses a drained thermokarst lake (thermokarst basin) which is also having continued expansion due to thermokarst along its edges, but also permafrost aggradation. Transect **c** shows a thermokarst pond that is expanding on one side due to thermokarst of a peat plateau, but also terrestrialization on the opposite lake edge due to vegetation infilling. Transect **d** shows a peat plateau which is experiencing thermokarst on both sides, but on one side it collapses into a fen, while on the other side it collapses into a thermokarst bog. This thermokarst bog has also recently coalesced with another thermokarst bog, which at the same time has started to experience permafrost aggradation in its central parts. Transect **e** shows Palsa thermokarst into ponds or bogs. Transect **f** shows the complete loss of permafrost which leaves a depression which can be vegetated (internal lawn) or open water

2017), it has been observed, e.g. in the Hudson Bay Lowlands (Dredge and Nixon 1979). Expansion of small, young thermokarst lakes is generally slow and dependent on thermal expansion only, while larger lakes become susceptible to wave erosion as well (Dyke and Sladen 2010). As thermokarst lakes expand they may coalesce with other lakes. The recent rate of expansion for larger lakes in the Hudson Bay Lowlands is up to 0.7 m year^{-1} (Sannel and Kuhry 2011). Over the last two decades, lake expansion in peatland-rich tundra regions within the continuous permafrost zone has increased lake area by ~1.5%; however, at the same time there has been a lake loss of ~2.2% due to catastrophic lake drainage and lake vegetation infilling—resulting in a minor overall reduction in lake area (Nitze et al. 2017). Catastrophic lake drainage occurs when lakes expand across a hydrologic divide, allowing the lakes to drain laterally as they connect with the stream network (Jones et al. 2011; Nitze et al. 2017) (Figs. 3.2e and 3.7a). Lake vegetation infilling can occur simultaneously as lake expansion, along different parts of a lake perimeter. Given the slow rates of lake expansion, and the stochastic nature of lake drainage, no studies have to date been able to ascertain an accelerated rate of either lake expansion or drainage in response to climate warming. However, polygonal peatlands in relatively warmer regions have been found to have higher rates of both lake expansion and drainage than relatively colder regions, suggesting that both processes are responsive to climatic warming (Sannel and Kuhry 2011; Nitze et al. 2017).

Lake drainage has throughout the Holocene been an important process facilitating new peatland development, particularly within unglaciated tundra lowland regions with ice-rich mineral Pleistocene deposits (Jones et al. 2011; Walter Anthony et al. 2014; Nitze et al. 2017). In such regions, lake drainage results in flat-bottomed basins where both peatland initiation and permafrost re-aggradation often occur (Jones et al. 2012) (Figs. 3.2e–f and 3.6a). Drained lake basins with subsequent peatland development currently cover >50% of some lowland regions in the continuous permafrost zone (Jones et al. 2012). Hence, accelerated lake drainage may allow for peatland expansion in the continuous permafrost region. An estimated 0.25% of the total area of lowland regions of Alaskan North Slope, Western Alaska, and the Kolyma lowlands have experienced catastrophic drainage over the last few decades (Nitze et al. 2017). Permafrost aggradation in drainage basins occurs rapidly (years to decades) following lake drainage, but it can take more than 500 years before ice wedges establish (de Klerk et al. 2011) and 1000–2000 years before a 30 cm peat profile develops (Hinkel et al. 2003; Jones et al. 2012). With continued warming, it is however likely that new peatlands that develop have more in common with peatlands of the current discontinuous permafrost zone than the current continuous permafrost zone.

3.4.2 Peatland Change in the Discontinuous and Sporadic Permafrost Zones

Peatlands in the discontinuous and sporadic permafrost zones have many similarities with regard to ecosystem transitions caused by permafrost thaw (Figs. 3.6, 3.7, and

3.8). Described in further detail below, main impacts of permafrost thaw include the gradual deepening of the active layer (Åkerman and Johansson 2008; Quinton and Baltzer 2013) and the complete permafrost loss and thermokarst collapse along peat plateau edges (Chasmer and Hopkinson 2017) or of whole palsas (Payette et al. 2004; Borge et al. 2017) (Figs. 3.3 and 3.4). Thermokarst collapse can develop into thermokarst bogs, fens, or ponds (Figs. 3.6, 3.7, and 3.8), depending on peatland region, ground-ice content, and landscape position (Sannel and Kuhry 2011; Kirpotin et al. 2011; Chasmer and Hopkinson 2017). With recent warming in the discontinuous and sporadic permafrost zones, succession leading to permafrost re-aggradation in thermokarst bogs is unlikely to occur (Camill 1999). In several peatland regions within the discontinuous permafrost zone, a net loss of open water has resulted from pond drainage and vegetation infilling outpacing pond expansion (Smith et al. 2005; Sannel and Kuhry 2011; Karlsson et al. 2014). These ecosystem transitions are currently rapid and accelerating and causing widespread peatland transformations with regard to both vegetation composition and peatland hydrology.

Active layer depths of many peat plateaus in the discontinuous and sporadic permafrost zones have been thickening in the last two decades, with reported shifts in active layer depths from 30–50 cm to 50–80 cm (Åkerman and Johansson 2008; Quinton and Baltzer 2013). Active layer depths of individual years increase with warmer summers (Åkerman and Johansson 2008; Jean and Payette 2014; Sannel et al. 2016), but wetter summers in particular increase the active layer thickness by increasing the thermal conductivity (Quinton and Baltzer 2013). In many locations, active layer thickening has become too deep to completely freeze up during the winter, leaving a continuously thawed peat layer between the seasonal frost and the top of the permafrost—the so called taliks (Sjöberg et al. 2015; Connon et al. 2018; Gibson et al. 2018). With continuing thickening of the active layer for a region in discontinuous permafrost zone of European Russia, it is projected that the proportion of the peat profile held in permafrost will decrease from 70 to 30% during the twenty-first century (Hugelius et al. 2011). Active layer deepening may lead to slightly drier conditions at the peat surface, but no vegetation shifts have been associated with this deepening. Yet, active layer deepening likely influences both peatland runoff patterns and soil carbon cycling and often precedes complete permafrost thaw and thermokarst collapse (Åkerman and Johansson 2008).

The predominant form of thermokarst associated with peat plateaus and palsas varies between regions. For example, collapse of peat plateaus and palsas in the sporadic and southern discontinuous permafrost zones of the Mackenzie River Basin and Alaska leads predominately to the development of thermokarst bogs and fens (Vitt et al. 1994; Jones et al. 2016; Chasmer and Hopkinson 2017), while thermokarst pond initiation and expansion dominates in the West Siberian Lowlands (Kirpotin et al. 2011) and is common in Scandinavia (Borge et al. 2017) and eastern Canada (Payette et al. 2004) (Figs. 3.3, 3.4, and 3.7). It has not been established which factors determine the predominate mode of thermokarst, but both climate and the history of peatland and permafrost development may contribute. For example, thermokarst pond formation may be predominant over bog/fen formation in regions with wetter climates, in regions with thicker and more extensive permafrost which may prevent drainage through groundwater recharge, or where greater potential for vertical collapse is likely due to greater accumulation of excess ground ice.

Rates of peat plateau and palsa thaw have increased significantly in the last few decades in response to recent warming. Peatlands in the sporadic permafrost zone of Scandinavia, Alaska, and Canada have recorded >50% permafrost loss in the last 60 years and include rates of loss which have doubled since the 1990s (Payette et al. 2004; Åkerman and Johansson 2008; Jones et al. 2016; Mamet et al. 2017; Borge et al. 2017). Similarly, the expansion rate of thermokarst bogs along edges of peat plateaus of the discontinuous permafrost zone in Manitoba, Canada, has increased from 10 cm/year for the period 1941–1988 to 25 cm/year for the period 1995–2002 in response to a warming of 1.3 °C (Camill 2005). Thus, the rate of peat plateaus collapse into thermokarst bogs and fens has increased from 0.4% of the area of peatlands per year for the period 1970–2000 to 1.2% for the period 2000–2015 (Chasmer and Hopkinson 2017). An estimated 9500 km^2 of peat plateaus, i.e. >15% of total peat plateau area, have thawed and collapsed into bogs in the last 30 years in the sporadic and discontinuous permafrost zone of the Mackenzie River Basin (Baltzer et al. 2014; Gibson et al. 2018), and accelerated rates of thaw suggests that complete loss of peat plateaus is expected by 2050 (Chasmer and Hopkinson 2017).

Despite rapid permafrost thaw and collapse of peat plateaus and palsas into thermokarst ponds, overall inundation in many peatlands of the discontinuous and sporadic permafrost zone has decreased. Net change in the area of lakes and ponds in peatland complexes is determined not only by the rate of thermokarst lake expansion, but also by frequency of lake drainage and vegetative lake infilling (Sannel and Kuhry 2011; Karlsson et al. 2014). Lake drainage in the discontinuous permafrost zone is likely most often associated with loss of permafrost under the lake, which allows for drainage through groundwater recharge (Yoshikawa and Hinzman 2003; Kirpotin et al. 2008). Some regions within the discontinuous permafrost region have had no net change in thermokarst lake area over the last few decades, but this includes complete or partial drainage of 8–15% of lakes compensated for by expansion of other lakes (Karlsson et al. 2014). Many regions within the discontinuous permafrost zone have however had a net loss of thermokarst lakes, including the West Siberian Lowland where there was a 9% reduction in lake area between 1973 and 1997 (Smith et al. 2005) and a 12% loss of closed basin lakes in subarctic Alaska between 1950 and 2002 (Riordan et al. 2006). Following lake drainage, these ecosystems have previously had the potential for rapid invasion of peatland vegetation and permafrost re-aggradation (Kirpotin et al. 2011) but warming will make permafrost aggradation less commonplace and instead the developing ecosystems may remain as non-permafrost fens or bogs (Fig. 3.2e–f).

3.5 Implications of Permafrost Thaw

3.5.1 Hydrology and Water Quality

Permafrost thaw has major impacts on peatland hydrology, as thaw alters patterns of inundation and wetness at both local and regional scales and further influences the magnitude and dominant pathways for peatland runoff. These shifts can have significant impacts on overall landscape water storage, especially considering that northern peatlands store as much or more water than northern lakes (Smith et al. 2012). Shifts in runoff magnitude and dominant runoff pathways can also affect downstream water quality, both due to increased groundwater connectivity and greater interactions between surface water and recently thawed peat soils.

Impacts of permafrost thaw on inundation patterns and runoff from peatlands are likely to vary across permafrost zones. In low-center polygonal peatlands, raised ice-wedges of low-center polygonal peatlands cause the inundation and water storage within polygons, which in turn is associated with relatively high evapotranspiration and low lateral runoff generation (Helbig et al. 2013; Liljedahl et al. 2016). With ice-wedge degradation, inundation patterns shift with often initial increases in inundation as open water troughs develop, while advanced ice wedge degradation increases connectivity between polygons troughs and thus cause drainage and increased runoff generation (Liljedahl et al. 2016). In the discontinuous permafrost zone, collapse of peat plateaus and palsas due to thermokarst is associated with increased local wetness, with transitions into thermokarst pond, bog, or fen. However, expansion of thermokarst ponds, bogs, and fens can at the same time increase the hydrological connectivity at the peatland scale, as the capacity of peat plateaus and palsas to act as hydrological barriers to lateral near-surface runoff is reduced (Quinton et al. 2009; Karlsson et al. 2012; Kurylyk et al. 2016). As such, advancing permafrost thaw within the discontinuous permafrost zone can lead to both increased runoff generation and a relative drying of non-permafrost bogs and fens within the complex (Chasmer and Hopkinson 2017; Gibson et al. 2019a). It is less likely that collapse of palsas and peat plateaus in the sporadic permafrost zones will have equally strong influences on peatland runoff, due to their already limited extent and thus limited ability to influence either surface or groundwater flow.

Across permafrost zones, advancing permafrost thaw is also likely to increase groundwater connectivity (Woo and Winter 1993), which may influence both water movement and water quality. Development of thawed taliks under ponds and lakes in peatland complexes can thus enable groundwater recharge and lake drainage (Yoshikawa and Hinzman 2003; Kirpotin et al. 2008). However, increased groundwater connectivity will also allow for increased groundwater discharge in lower landscape positions, and in the West Siberian Lowlands a large increase in stream alkalinity and concentrations of total dissolved inorganic solutes across the permafrost boundary is associated with increased groundwater contributions (Frey et al. 2007b). Increased groundwater contribution has also been indicated to increase stream flow during base flow periods (St Jacques and Sauchyn 2009; Kurylyk et al. 2016).

Permafrost thaw is further likely to increase the hydrological interaction with recently thawed peat deposits, which may increase concentrations and downstream export of dissolved organic matter, which contains both carbon and nutrients. Streams draining permafrost peatlands have been found to have significantly lower concentrations of dissolved organic carbon (DOC), total dissolved nitrogen (DON), and total dissolved phosphorous (TDP) than streams south of the permafrost boundary in both the Mackenzie River Basin and the West Siberian Lowlands (Frey and Smith 2005; Frey et al. 2007a; Olefeldt et al. 2014). To be noted, other large-scale surveys have not observed the same trends across the permafrost boundary in the West Siberian Lowlands, suggesting that other catchment factors could have equal or greater influence on stream chemistry (Vorobyev et al. 2017). Yet, detailed catchment studies and investigations of lake sediments have indicated that it is likely that peatland DOC export will increase following palsa and peat plateau collapse as fens and bogs become increasingly connected to surface water flow-paths (Olefeldt and Roulet 2014; Coleman et al. 2015). Radiocarbon measurements suggest, however, that increases in DOC export following permafrost thaw may be less derived from deep, old peat than arising from an increase in hydrological connectivity of surface peat in thermokarst fens and bogs (Guo et al. 2007; Olefeldt and Roulet 2012; Burd et al. 2018). Increased downstream export of DOC and nutrients from thawing peatlands may have implications for both primary production and microbial metabolism in lakes (Breton et al. 2009).

Peatlands are known both as large stores of atmospherically deposited mercury (Grigal 2003; Schuster et al. 2018), and as downstream sources of methyl mercury which is highly toxic, and prone to accumulate in fish. Peatlands, and fens in particular, have the right environmental conditions to promote methylation of mercury—including anaerobic conditions with an available pool of mercury, organic carbon, and sulfate (Coleman Wasik et al. 2012). Due to the role of peatlands as sources of methylated mercury, there are a large number of advisories for fish consumption from lakes in peatland-rich permafrost regions of Canada (www.hss.gov.nt.ca—accessed April 6th, 2019). However, collapse of peat plateaus and palsas is tied to further increase the downstream export of both mercury and methylated mercury (Rydberg et al. 2010; Korosi et al. 2015; Gordon et al. 2016; Fahnestock et al. 2019), potentially due to more favorable conditions for methylation as dry, ombrotrophic conditions shift to anoxic conditions with higher likelihood for groundwater connectivity (Gordon et al. 2016).

3.5.2 Ecology and Human Use

Peatlands in the northern permafrost region have unique vegetation biodiversity and habitat quality for waterfowl and large mammals. The higher biodiversity of both bryophytes and birds compared to peatlands south of the permafrost boundary has been attributed to the fine-scale mosaic of permafrost peatlands, bogs, fens, and open water (Beilman 2001; Luoto et al. 2004; Minke et al. 2009). Peat plateaus are furthermore important winter foraging habitat for the vulnerable woodland caribou

(Bradshaw et al. 1995) and can act as denning habitat for polar bears (Dyke and Sladen 2010). While human settlements are absent in peatlands, there are several traditional land uses such as herding, hunting, and harvesting which likely will be impacted by advancing permafrost thaw (Calmels et al. 2015; Istomin and Habeck 2016). These impacts on traditional land use are due to habitat alterations and loss, but also due to more difficult travel across the landscape as thermokarst leads to expansion of ponds, bogs, and fens which are waterlogged and soft and do not even always allow for safe winter travels (Calmels et al. 2015)

State shifts in vegetation composition following collapse of peat plateaus and palsas are largely due to inundation and changes in nutrient availability that accompany new hydrological connections (Camill 1999). Prior to thaw, the presence of permafrost provides a stable but shallow rooting zone for terrestrial vegetation, including trees and shrubs. The groundcover of permafrost peatlands can be dominated by *Sphagnum* mosses, feather mosses, or lichens, which is partly dependent on whether the permafrost plateaus is in an early or late developmental stage (Zoltai and Tarnocai 1975; Kremenetski et al. 2003). Inundation following permafrost thaw in these systems triggers a state shift to either aquatic or wetland vegetation, including *Sphagnum* mosses adapted to wet conditions or sedges (Figs. 3.3c, d and 3.4b, f). Trees that survived in a permafrost state become unstable and form the drunken forests that are important diagnostics for recognizing permafrost thaw in these ecosystems (Fig. 3.3c, d). As the ground subsides with thaw, tree roots become inundated and the trees die, giving way to the *Sphagnum* and sedge vegetation characteristic of thermokarst bogs and fens. As described in earlier sections, thermokarst ponds, bogs, and fens undergo autogenetic succession over time. Peat accumulation above the water table leads to ecosystem drying and this is reflected in vegetation community structure with increasing time following thaw (Camill 1999). The dependence of the vegetation community on permafrost conditions and stage of autogenic succession thus increases overall biodiversity of these peatlands compared to non-permafrost peatlands south of the permafrost boundary (Beilman 2001; Minke et al. 2009).

Habitat loss due to permafrost thaw in peatlands has not been thoroughly assessed. At large scales, peatland permafrost thaw and thermokarst development can have detrimental impacts on large boreal animals such as the woodland caribou (*Rangifer tarandus caribou*) which is threatened in Canada (Festa-Bianchet et al. 2011). Woodland caribou forage on lichens found on peat plateaus and palsas in winter (Bradshaw et al. 1995; Joly et al. 2010) and thus permafrost thaw and thermokarst development constitute loss of critical habitat and food source. Lichens also recover slowly after fire, with full recovery only after 60 years, which suggests that recent increases in fire frequency is reducing habitat (Joly et al. 2010; Gibson et al. 2018). Another example of habitat loss includes palsa complexes in northern Scandinavia which are known for their rich bird life (Järvinen and Sammalisto 1976). The spatial mosaic of both drier and wetter peatland landforms and many small open water ecosystems increase diversity and abundance of waders in particular. However, palsa peatland complexes are listed as a threatened habitat within the

EU and are expected to have near-complete loss in the coming decades (Luoto et al. 2004).

3.5.3 Carbon Cycling and Greenhouse Gas Exchange

Permafrost thaw has the potential to significantly affect soil carbon storage and the greenhouse gas exchange between peatlands and the atmosphere. Impacts of peatland permafrost thaw and thermokarst on the exchange of greenhouse gases were identified already 30 years ago as a potentially globally important biogeochemical feedback to climate change (Gorham 1991). Several approaches have since been employed to help improve estimates of the strength of this feedback, including both direct measurements of emissions of greenhouse gases and investigations of carbon stocks and carbon accumulation rates based on analysis of peat cores (Fig. 3.9). Many of the key factors that influence production and release of CO_2, CH_4, and

Fig. 3.9 Examples of techniques used to monitor the greenhouse gas exchange of peatlands in the northern permafrost region. From top left: (**a**) Using soil chambers to measure CO_2 and CH_4 exchange at a rapidly expanding thermokarst bog (Northern Alberta, Canada), (**b**) Collecting a peat core in a thermokarst bog with 4.5 m deep peat profile (Northwest Territories, Canada), (**c**) A 50 cm collected core, including the transition from underlying mineral soil to basal peat, later dated to 8900 cal yr BP (Northwest Territories, Canada), (**d**) Eddy covariance monitoring of CO_2 exchange at a palsa peatland (Northern Sweden), (**e**) Floating chambers and inverted funnels to monitor diffusive and ebullition emissions of CH_4 from a thermokarst pond (Northern Alberta, Canada)

nitrous oxide (N_2O) are impacted by permafrost thaw, including soil temperatures, soil moisture content, and vegetation composition and productivity, as described below. Many, but not all of these factors, have recently been incorporated into global land surface models and have thus been shown to be crucial for improving overall projections of future high-latitude land-atmosphere exchange of greenhouse gases (Wania et al. 2009; Koven et al. 2015; Wu et al. 2016; Chaudhary et al. 2017).

Emissions of CH_4 from northern permafrost peatlands are likely to increase with projected warming and permafrost thaw. While peat plateaus and palsas have low CH_4 emissions, or even uptake, due to their dry, cold, and predominately aerobic active layers, emissions are higher from thermokarst bogs, fens, and ponds with predominately anaerobic soils and sediments (Bubier et al. 1995; Liblik et al. 1997; Turetsky et al. 2002; Christensen et al. 2004; Glagolev et al. 2011; Olefeldt et al. 2013; Matveev et al. 2016). Particularly high emissions have been measured in thermokarst ponds (Shirokova et al. 2013; Matveev et al. 2016; Kuhn et al. 2018; Serikova et al. 2019), and from channel fens and shore fens with high productivity where sedges and other tall emergent plants can enhance emissions both by providing labile root exudates and by providing a pathway of emissions through plant aerenchyma (Ström et al. 2005; Olefeldt et al. 2013; Hodgkins et al. 2014). Palsa collapse and transition into thermokarst bogs and fens alone has been estimated to have increased methane emissions from an individual peatland in northern Sweden by ~50% between 1970 and 2000 (Christensen et al. 2004). A majority of these increasing CH_4 emissions are derived from recent plant photosynthesis rather than from the degradation of deep, old, and recently thawed peat (Prater et al. 2007; Klapstein et al. 2014; Cooper et al. 2017). Methane production and net emissions from wetlands furthermore have a high temperature sensitivity (Christensen et al. 2003; Lupascu et al. 2012) and an increase in air temperature by 5 °C, all else equal, is likely to increase CH_4 emissions by an additional 50–100%. Conversely, peatland CH_4 emissions may reduce if peatlands become drier as a result of thaw, e.g. due to pond drainage, improved lateral runoff, or increased evapotranspiration (Merbold et al., 2009). On longer century timescales, thermokarst bogs become drier through autogenic succession and peat accumulation. These moderating effects on future CH_4 emissions have not yet been properly assessed. Current CH_4 emissions from wetlands and lakes in the northern permafrost region are in the range 20–50 Tg CH_4 per year, compared to total global wetland and lake methane emissions of ~225 Tg CH4 per year (Saunois et al. 2016). Atmospheric monitoring of CH_4 has not been able to detect increased CH_4 emissions from high latitude wetlands over the last two decades, although increases would need to be very substantial in order to be detectable (Saunois et al. 2016). Overall, while potential increases in CH_4 emissions from northern peatlands due to climate change may be sufficiently large to consider at the global scale, they are highly likely to continue to represent only a minor component of total global wetland and lake CH_4 emissions (Saunois et al. 2016; Christensen et al. 2019).

Limited research has been made on monitoring and assessing impacts of permafrost thaw on N_2O emissions. Microbial production of N_2O is enhanced under conditions of near-saturation, and in the absence of plants that compete with microbes for uptake of inorganic nitrogen. Accordingly, the highest N_2O emissions from permafrost peatlands have been found from eroding non-vegetated palsas, emissions which are ~90% lower when plants are present, and negligible from inundated thermokarst fens and ponds (Marushchak et al. 2011; Voigt et al. 2017). Permafrost thaw through active layer deepening and soil warming of palsas has the potential to increase N_2O emissions significantly, but expanding thermokarst bogs and fens will likely reduce emissions (Voigt et al. 2017), with unknown net impact.

Permafrost thaw and thermokarst will influence peatland net CO_2 balance both by altering plant CO_2 uptake and soil CO_2 respiration losses. Permafrost thaw and degradation can exclude vegetation through thermokarst collapse into lakes and ponds or through active layer deepening in palsas which leads to wind scouring. Thermokarst collapse into lakes and ponds will thus in most settings lead to net CO_2 losses to the atmosphere (Kirpotin et al. 2011; Abnizova et al. 2012; Sturtevant and Oechel 2013; Serikova et al. 2019). Conversely, thermokarst can also increase plant productivity by changing nutrient availability and vegetation composition, e.g. by collapsing palsa and peat plateaus from a nutrient-poor ombrotrophic settings into relatively nutrient-rich minerotrophic thermokarst fen settings associated with a shift to productive, tall emergent vegetation (Bäckstrand et al. 2010). Drained lake basins with fen vegetation dominated by sedges and mosses are similarly landscape locations with high plant productivity, where more recently drained lake basins have the highest productivity (Sturtevant and Oechel 2013). Thermokarst bogs remain nutrient poor, but increased moisture conditions allow for the colonization by *Sphagnum* mosses. While *Sphagnum* mosses in thermokarst bogs are not highly productive, analysis of peat cores shows that surface C accumulation often is several times greater in thermokarst bogs compared to peat plateaus or palsas (Camill et al. 2001; Beilman et al. 2009; Lamarre et al. 2012; Jones et al., 2013; Pelletier et al. 2017).

Increased plant productivity and surface peat accumulation in thermokarst bogs and fens do however not guarantee net CO_2 uptake, as the net CO_2 balance also depends on the stability of recently thawed deep, old peat stores. As large stores of soil carbon thaw in peatlands, understanding the rate at which old soil carbon will be respired is a key question. Both environmental conditions (e.g. availability of terminal electron acceptors, soil temperature, and pH) and the quality of the peat itself (e.g. botanical origin, degree of humification, and nutrient content) are likely to influence the rate of which thawed peat is microbially decomposed (Treat et al., 2014). A deepened, dry, oxic active layer of peat plateaus and palsas thus leads to increase respiration of deep, old peat (Dorrepaal et al. 2009; Gibson et al. 2019a, b). Under inundated, anoxic, conditions in thermokarst bogs, stability of old soil carbon may depend on peat quality, which in turn is influenced by site history. Diverging findings have either suggested rapid loss of deep, old C during the first few decades following thaw in Alaskan thermokarst bogs using space-for-time sampling and analysis of peat profile C storage (O'Donnell et al. 2012; Jones et al. 2017), or relative stability of aged soil C in the discontinuous permafrost zone within the Mackenzie River Basin as indicated by radiocarbon monitoring of surface CO_2 fluxes (Cooper et al. 2017; Estop-Aragonés et al. 2018). A main difference between these studies, other than their method of analysis, are characteristics of the peat profiles, where rapid losses were predicted for peat profiles dominated by less decomposed sylvic peat at sites where permafrost had aggraded syngenetically over many millennia, while stability of old soil carbon was found for peat profiles dominated by *Sphagnum* moss at sites where permafrost was epigenetic and permafrost had only aggraded in an existing peatland within the last millenia. Peat quality, which is influenced both by plant botanical origin and degree of humification, has accordingly been shown through incubations to influence rate of CO_2 production following thaw (Sjögersten et al. 2016). Peatland developmental history may thus influence the net CO_2 balance following permafrost thaw; however, more research is needed to better understand these links.

Spatial and temporal variability in CO_2 fluxes makes it hard to assess the current net CO_2 balance of many northern peatlands. Spatially, each of the landforms that make up a larger peatland has their unique CO_2 balance, and each may respond differently to interannual climate variability. Temporal variability at the peatland scale is measured using eddy co-variance techniques which integrate fluxes over large areas, and these often show large inter-annual variability in the net annual CO_2 balance due to variability in moisture conditions, soil temperatures, and available light (Kutzbach et al. 2007; Christensen et al. 2012; Euskirchen et al. 2014; Helbig et al. 2017). Relatively short data records, often less than a decade, make it hard to determine using eddy co-variance techniques whether climate change and permafrost thaw are altering the net CO_2 balance of northern peatlands. Eddy co-variance studies have however shown that wetness, winter temperatures, and growing season length are likely to have a large influence on future net peatland CO_2 balance. Drier years can lead to moisture stress and reduce plant CO_2 uptake by $>50\%$, particularly for mosses which can only wick water ~10–40 cm depending on species (Olefeldt et al. 2017). Whether the northern permafrost region will have more available water is currently uncertain, as both precipitation and evapotranspiration are expected to increase—yet evidence from the last century indicate that many peatlands in both colder and warmer parts of the northern permafrost region have become drier (Magnan et al. 2018; Zhang et al. 2018). Increasing winter temperatures are likely to increase winter CO_2 respiration (Natali et al. 2019), which may be particularly important for peatlands where development of taliks allows for thick peat layers to decompose throughout the winter (Connon et al. 2018; Gibson et al. 2018). Longer growing seasons will however have the chance to more than offset increased soil CO_2 respiration in a warming climate. Both direct observations of CO_2 fluxes and analysis of peat cores from across the northern permafrost region suggest that the length of the growing season and available growing season light are main variables influencing peatland net CO_2 balance (Christensen et al. 2012; Charman et al. 2013; Nijp et al. 2015). Maintaining long-term records of atmospheric CO_2 and CH_4 exchange from various peatland sites is a key priority to further our understanding of future greenhouse gas emissions.

3.5.4 Interactions Between Wildfire, Permafrost Thaw, and Peatland Carbon Balance

Wildfire will influence the future carbon balance of northern peatlands, both directly through peat combustion and loss as CO_2 but also indirectly by accelerating permafrost thaw and associated ecosystem transitions. Wildfire activity in the boreal biome has increased in the last few decades (Flannigan et al. 2009; Kelly et al. 2013), and warmer summers have even been linked to increased occurrence of rare wildfires in tundra regions (Masrur et al. 2018). Peat plateaus with black spruce trees burn with the same frequency as other boreal ecosystems in Canada, and ~25% of peat plateaus in the discontinuous permafrost zone of boreal western Canada has burned in the last 30 years (Gibson et al. 2018). Wildfire in both boreal and tundra peatlands can combust 2.0–3.5 kg C m^{-2} (Mack et al. 2011; Turetsky et al. 2011; Walker et al. 2018), which means that individual wildfires combust more soil carbon than a peatland has accumulated over the last 100–200 years. However, wildfire also causes permafrost thaw and thermokarst which in turn can further affect emissions of greenhouse gases. Although peatland soil thermal regimes are considered to be less sensitive to wildfire than ecosystems with thinner organic soils (Yoshikawa et al. 2002; Jafarov et al. 2013), wildfire effects in peatlands can last for up to 30 years and lead to irreversible thermokarst (Bauer and Vitt 2011; Jones et al. 2015; Gibson et al. 2018). The dark charred surface and loss of trees and shrubs cause decreased albedo and alters snow-pack insulating capacity, which leads to soil temperatures in peat plateaus that can be up to 5 °C warmer at 40 cm depth and active layers that are 40 cm deeper even 15 years after a wildfire (Gibson et al. 2018). Warmer soil temperatures and thicker active layers have been found to increase respiration of deep, old peat (Estop-Aragonés et al. 2018; Gibson et al. 2019a, b). Soil warming following wildfire has also been associated with a tripled rate of thermokarst bog expansion, lasting for up to 30 years (Fig. 3.3d) (Gibson et al. 2018). Similarly, wildfire has been found to cause substantial ice wedge degradation and thermokarst trough development 7 years after a tundra fire in the continuous permafrost zone (Jones et al. 2015). Thermokarst development following wildfire is often associated with collapse and inundation, and as such with increased CH_4 emissions. Overall, wildfire is thus likely to play a central role in the overall response of the carbon balance of northern peatlands in the next century.

3.6 Conclusions

There is widespread evidence that rates of permafrost thaw and associated thermokarst collapse have accelerated in northern peatlands over the last few decades due to climate change. Peatland transitions due to permafrost thaw vary in dominance across permafrost zones and between regions, but include the degradation of ice-wedges causing transitions of low-center polygonal peatlands to high-center polygons, the expansion of thermokarst lakes which is more than counterbalanced by lake drainage and vegetative infilling, the collapse of peat plateaus and palsas into thermokarst ponds, bogs, and fens, and the general deepening of the active layer. While thermokarst is slow at individual locations, e.g. with thermokarst ponds, bogs, and fens often expanding at rates much less than 1 m/year, the widespread abundance of thermokarst within peatlands has ensured rapid, abrupt changes to peatland ecosystem functions over the last few decades.

Permafrost thaw in peatlands has major implications for peatland vegetation composition, runoff and inundation patterns, downstream water quality, peatland habitat for waterfowl and large mammals, traditional land-use, and the exchange of greenhouse gases between peatlands and the atmosphere. We are starting to understand ways in which peatland developmental histories have ensured specific peatland landform configurations and peat profile characteristics which in turn influence the specific implications of permafrost thaw for an individual peatland. These regional differences will be important to better understand in order to improve our ability to project future greenhouse gas emissions from northern peatlands.

High latitudes regions where peatlands are widespread are warming at twice the rate of the global average. Thus, despite the protective insulating properties of thick organic soils, permafrost is thawing quickly. Between 15 and 50% of peat plateaus in the sporadic and discontinuous permafrost zone of boreal western Canada has thawed and collapsed into ponds, bogs, and fens over the last 30–45 years (Chasmer and Hopkinson 2017; Gibson et al. 2018), and complete permafrost loss is expected this century. Rates of permafrost thaw have been slower in the continuous permafrost zone, but local ice-wedge degradation is leading to rapidly altered patterns of inundation within polygonal peatlands (Liljedahl et al. 2016). Many of the changes observed in northern peatlands are largely irreversible at human time-scales as warming temperatures are making permafrost aggradation highly unlikely in the current sporadic and discontinuous permafrost zones, while permafrost aggradation in the continuous permafrost zone is unlikely to lead to the development of landforms similar to those which have been lost. As such, it is really a new landscape that is being formed as permafrost thaw reshapes one of the largest terrestrial ecosystems of the world.

References

Abnizova A, Siemens J, Langer M, Boike J (2012) Small ponds with major impact: the relevance of ponds and lakes in permafrost landscapes to carbon dioxide emissions: small ponds with major impact. Global Biogeochem Cycles 26:GB2041. https://doi.org/10.1029/2011GB004237

Åkerman HJ, Johansson M (2008) Thawing permafrost and thicker active layers in sub-arctic Sweden. Permafrost Periglacial Process 19:279–292. https://doi.org/10.1002/ppp.626

Bäckstrand K, Crill PM, Jackowicz-Korczyñski M et al (2010) Annual carbon gas budget for a subarctic peatland, Northern Sweden. Biogeosciences 7:95–108. https://doi.org/10.5194/bg-7-95-2010

Baltzer JL, Veness T, Chasmer LE et al (2014) Forests on thawing permafrost: fragmentation, edge effects, and net forest loss. Glob Chang Biol 20:824–834. https://doi.org/10.1111/gcb.12349

Bauer IE, Vitt DH (2011) Peatland dynamics in a complex landscape: development of a fen-bog complex in the sporadic discontinuous permafrost zone of northern Alberta, Canada. Boreas 40:714–726. https://doi.org/10.1111/j.1502-3885.2011.00210.x

Beilman DW (2001) Plant community and diversity change due to localized permafrost dynamics in bogs of western Canada. Can J Bot 79:983–993. https://doi.org/10.1139/b01-070

Beilman DW, Vitt DH, Halsey LA (2001) Localized permafrost peatlands in Western Canada: definition, distributions, and degradation. Arctic Antarct Alpine Res 33:70–77. https://doi.org/10.1080/15230430.2001.12003406

Beilman DW, MacDonald GM, Smith LC, Reimer PJ (2009) Carbon accumulation in peatlands of West Siberia over the last 2000 years. Global Biogeochem Cycles 23:GB1012. https://doi.org/10.1029/2007GB003112

Bhiry N, Robert E (2006) Reconstruction of changes in vegetation and trophic conditions of a palsa in a permafrost peatland, subarctic Québec, Canada. Écoscience 13:56–65. https://doi.org/10.2980/1195-6860(2006)13[56:ROCIVA]2.0.CO;2

Borge AF, Westermann S, Solheim I, Etzelmüller B (2017) Strong degradation of palsas and peat plateaus in northern Norway during the last 60 years. Cryosphere 11:1–16. https://doi.org/10.5194/tc-11-1-2017

Botch MS, Kobak KI, Vinson TS, Kolchugina TP (1995) Carbon pools and accumulation in peatlands of the former Soviet Union. Global Biogeochem Cycles 9:37–46. https://doi.org/10.1029/94GB03156

Bradshaw CJA, Boutin S, Hebert DM, Rippin AB (1995) Winter peatland habitat selection by woodland caribou in northeastern Alberta. Can J Zool 73:1567–1574. https://doi.org/10.1139/z95-185

Breton J, Vallières C, Laurion I (2009) Limnological properties of permafrost thaw ponds in northeastern Canada. Can J Fish Aquat Sci 66:1635–1648. https://doi.org/10.1139/F09-108

Brown J, Ferrians O, Heginbottom JA, Melnikov E (2002) Circum-Arctic map of permafrost and ground-ice conditions. NSIDC: National Snow and Ice Data Center National Snow and Ice Data Center, Boulder, CO

Bubier JL, Moore TR, Bellisario L et al (1995) Ecological controls on methane emissions from a Northern Peatland Complex in the zone of discontinuous permafrost, Manitoba, Canada. Global Biogeochem Cycles 9:455–470. https://doi.org/10.1029/95GB02379

Burd K, Tank SE, Dion N et al (2018) Seasonal shifts in export of DOC and nutrients from burned and unburned peatland-rich catchments, Northwest Territories, Canada. Hydrol Earth Syst Sci 22:4455–4472. https://doi.org/10.5194/hess-22-4455-2018

Calmels F, Laurent C, Brown R et al (2015) How permafrost thaw may impact food security of Jean Marie River First Nation, NWT. In: GeoQuebec Conference proceedings

Camill P (1999) Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. Can J Bot 77:721–733. https://doi.org/10.1139/b99-008

Camill P (2005) Permafrost thaw accelerates in boreal peatlands during late-20th century climate warming. Clim Change 68:135–152. https://doi.org/10.1007/s10584-005-4785-y

Camill P, Lynch JA, Clark JS et al (2001) Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. Ecosystems 4:461–478. https://doi.org/10.1007/s10021-001-0022-3

Charman DJ, Beilman DW, Blaauw M et al (2013) Climate-related changes in peatland carbon accumulation during the last millennium. Biogeosciences 10:929–944. https://doi.org/10.5194/bg-10-929-2013

Chasmer L, Hopkinson C (2017) Threshold loss of discontinuous permafrost and landscape evolution. Glob Chang Biol 23:2672–2686. https://doi.org/10.1111/gcb.13537

Chaudhary N, Miller PA, Smith B (2017) Modelling past, present and future peatland carbon accumulation across the pan-Arctic region. Biogeosciences 14:4023–4044. https://doi.org/10.5194/bg-14-4023-2017

Christensen TR, Ekberg A, Ström L et al (2003) Factors controlling large scale variations in methane emissions from wetlands. Geophys Res Lett 30:1414. https://doi.org/10.1029/2002GL016848

Christensen TR, Johansson T, Åkerman HJ et al (2004) Thawing sub-arctic permafrost: effects on vegetation and methane emissions. Geophys Res Lett 31:L04501. https://doi.org/10.1029/2003GL018680

Christensen TR, Jackowicz-Korczyński M, Aurela M et al (2012) Monitoring the multi-year carbon balance of a Subarctic Palsa Mire with micrometeorological techniques. Ambio 41:207–217. https://doi.org/10.1007/s13280-012-0302-5

Christensen TR, Arora VK, Gauss M et al (2019) Tracing the climate signal: mitigation of anthropogenic methane emissions can outweigh a large Arctic natural emission increase. Sci Rep 9:1146. https://doi.org/10.1038/s41598-018-37719-9

Coleman Wasik JK, Mitchell CPJ, Engstrom DR et al (2012) Methylmercury declines in a boreal peatland when experimental sulfate deposition decreases. Environ Sci Technol 46:6663–6671. https://doi.org/10.1021/es300865f

Coleman KA, Palmer MJ, Korosi JB et al (2015) Tracking the impacts of recent warming and thaw of permafrost peatlands on aquatic ecosystems: a multi-proxy approach using remote sensing and lake sediments. Boreal Environ Res 20:363–377

Connon R, Devoie É, Hayashi M et al (2018) The influence of shallow taliks on permafrost thaw and active layer dynamics in Subarctic Canada. J Geophys Res Earth 123:281–297. https://doi.org/10.1002/2017JF004469

Cooper MDA, Estop-Aragonés C, Fisher JP et al (2017) Limited contribution of permafrost carbon to methane release from thawing peatlands. Nat Clim Change 7:507–511. https://doi.org/10.1038/nclimate3328

de Klerk P, Donner N, Karpov NS et al (2011) Short-term dynamics of a low-centred ice-wedge polygon near Chokurdakh (NE Yakutia, NE Siberia) and climate change during the last ca 1250 years. Quat Sci Rev 30:3013–3031. https://doi.org/10.1016/j.quascirev.2011.06.016

Dorrepaal E, Toet S, van Logtestijn RSP et al (2009) Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature 460:616–619. https://doi.org/10.1038/nature08216

Dredge LA, Nixon FM (1979) Thermal sensitivity and the development of tundra ponds and thermokarst lakes in the Manitoba portion of the Hudson Bay Lowlands. Curr Res Part C Geol Surv Can:23–26

Dunford JS, Mcloughlin PD, Dalerum F, Boutin S (2006) Lichen abundance in the peatlands of northern Alberta: implications for boreal caribou. Écoscience 13:469–474. https://doi.org/10.2980/1195-6860(2006)13

Dyke AS (2004) An outline of North American deglaciation with emphasis on central and northern Canada. In: Developments in quaternary sciences. Elsevier, pp 373–424

Dyke LD, Sladen WE (2010) Permafrost and peatland evolution in the Northern Hudson Bay Lowland, Manitoba. Arctic 63:429–441

Estop-Aragonés C, Czimczik CI, Heffernan L et al (2018) Respiration of aged soil carbon during fall in permafrost peatlands enhanced by active layer deepening following wildfire but limited following thermokarst. Environ Res Lett 13:085002. https://doi.org/10.1088/1748-9326/aad5f0

Euskirchen ES, Edgar CW, Turetsky MR et al (2014) Differential response of carbon fluxes to climate in three peatland ecosystems that vary in the presence and stability of permafrost. J Geophys Res Biogeosci 119:1576–1595. https://doi.org/10.1002/2014JG002683

Fahnestock MF, Bryce JG, McCalley CK et al (2019) Mercury reallocation in thawing subarctic peatlands. Geochem Perspect Lett 11:33–38. https://doi.org/10.7185/geochemlet.1922

Farquharson LM, Romanovsky VE, Cable WL et al (2019) Climate change drives widespread and rapid thermokarst development in very cold permafrost in the Canadian High Arctic. Geophys Res Lett 46:6681–6689. https://doi.org/10.1029/2019GL082187

Festa-Bianchet M, Ray JC, Boutin S et al (2011) Conservation of caribou (Rangifer tarandus) in Canada: an uncertain. Can J Zool 89:419–434. https://doi.org/10.1139/z11-025

Flannigan M, Stocks B, Turetsky M, Wotton M (2009) Impacts of climate change on fire activity and fire management in the circumboreal forest. Glob Chang Biol 15:549–560. https://doi.org/10.1111/j.1365-2486.2008.01660.x

Frey KE, Smith LC (2005) Amplified carbon release from vast West Siberian peatlands by 2100. Geophys Res Lett 32:L09401. https://doi.org/10.1029/2004GL022025

Frey KE, McClelland JW, Holmes RM, Smith LC (2007a) Impacts of climate warming and permafrost thaw on the riverine transport of nitrogen and phosphorus to the Kara Sea. J Geophys Res Biogeosci 112:G04S58. https://doi.org/10.1029/2006JG000369

Frey KE, Siegel DI, Smith LC (2007b) Geochemistry of west Siberian streams and their potential response to permafrost degradation. Water Resour Res 43. https://doi.org/10.1029/2006WR004902

Fritz M, Wolter J, Rudaya N et al (2016) Holocene ice-wedge polygon development in northern Yukon permafrost peatlands (Canada). Quat Sci Rev 147:279–297. https://doi.org/10.1016/j.quascirev.2016.02.008

Frolking S, Roulet NT (2007) Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. Glob Chang Biol 13:1079–1088. https://doi.org/10.1111/j.1365-2486.2007.01339.x

Frolking S, Talbot J, Subin ZM (2014) Exploring the relationship between peatland net carbon balance and apparent carbon accumulation rate at century to millennial time scales. Holocene 24:1167–1173. https://doi.org/10.1177/0959683614538078

Gao Y, Couwenberg J (2015) Carbon accumulation in a permafrost polygon peatland: steady long-term rates in spite of shifts between dry and wet conditions. Glob Chang Biol 21:803–815. https://doi.org/10.1111/gcb.12742

Gibson CM, Chasmer LE, Thompson DK et al (2018) Wildfire as a major driver of recent permafrost thaw in boreal peatlands. Nat Commun 9:3041. https://doi.org/10.1038/s41467-018-05457-1

Gibson CM, Estop-Aragonés C, Flannigan M et al (2019a) Increased deep soil respiration detected despite reduced overall respiration in permafrost peat plateaus following wildfire. Environ Res Lett 14:125001. https://doi.org/10.1088/1748-9326/ab4f8d

Gibson JJ, Yi Y, Birks SJ (2019b) Isotopic tracing of hydrologic drivers including permafrost thaw status for lakes across Northeastern Alberta, Canada: a 16-year, 50-lake assessment. J Hydrol Reg Stud 26:100643. https://doi.org/10.1016/j.ejrh.2019.100643

Glagolev M, Kleptsova I, Filippov I et al (2011) Regional methane emission from West Siberia mire landscapes. Environ Res Lett 6:045214. https://doi.org/10.1088/1748-9326/6/4/045214

Gordon J, Quinton W, Branfireun BA, Olefeldt D (2016) Mercury and methylmercury biogeochemistry in a thawing permafrost wetland complex, Northwest Territories, Canada. Hydrol Process 30:3627–3638. https://doi.org/10.1002/hyp.10911

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195. https://doi.org/10.2307/1941811

Gorham E, Lehman C, Dyke A et al (2007) Temporal and spatial aspects of peatland initiation following deglaciation in North America. Quat Sci Rev 26:300–311. https://doi.org/10.1016/j.quascirev.2006.08.008

Grigal DF (2003) Mercury sequestration in forests and peatlands. J Environ Qual 32:393–405. https://doi.org/10.2134/jeq2003.3930

Guo L, Ping C-L, Macdonald RW (2007) Mobilization pathways of organic carbon from permafrost to arctic rivers in a changing climate. Geophys Res Lett 34. https://doi.org/10.1029/2007GL030689

Halsey LA, Vitt DH, Bauer IE (1998) Peatland initiation during the holocene in continental Western Canada. Clim Change 40:315–342. https://doi.org/10.1023/A:1005425124749

Helbig M, Boike J, Langer M et al (2013) Spatial and seasonal variability of polygonal tundra water balance: Lena River Delta, northern Siberia (Russia). Hydrgeol J 21:133–147. https://doi.org/10.1007/s10040-012-0933-4

Helbig M, Chasmer LE, Desai AR et al (2017) Direct and indirect climate change effects on carbon dioxide fluxes in a thawing boreal forest–wetland landscape. Glob Chang Biol 23:3231–3248. https://doi.org/10.1111/gcb.13638

Hinkel KM, Eisner WR, Bockheim JG et al (2003) Spatial extent, age, and carbon stocks in drained thaw lake basins on the Barrow Peninsula, Alaska. Arctic Antarct Alpine Res 35:291–300. https://doi.org/10.1657/1523-0430(2003)035

Hodgkins SB, Tfaily MM, McCalley CK et al (2014) Changes in peat chemistry associated with permafrost thaw increase greenhouse gas production. PNAS 111:5819–5824. https://doi.org/10.1073/pnas.1314641111

Hugelius G, Virtanen T, Kaverin D et al (2011) High-resolution mapping of ecosystem carbon storage and potential effects of permafrost thaw in periglacial terrain, European Russian Arctic. J Geophys Res Biogeosci 116:G03024. https://doi.org/10.1029/2010JG001606

Hugelius G, Strauss J, Zubrzycki S et al (2014) Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. Biogeosciences 11:6573–6593. https://doi.org/10.5194/bg-11-6573-2014

Hunt S, Yu Z, Jones M (2013) Late glacial and Holocene climate, disturbance and permafrost peatland dynamics on the Seward Peninsula, western Alaska. Quat Sci Rev 63:42–58. https://doi.org/10.1016/j.quascirev.2012.11.019

Istomin KV, Habeck JO (2016) Permafrost and indigenous land use in the northern Urals: Komi and Nenets reindeer husbandry. Pol Sci 10:278–287. https://doi.org/10.1016/j.polar.2016.07.002

Jafarov EE, Romanovsky VE, Genet H, McGuire AD, Marchenko S (2013) The effects of fire on the thermal stability of permafrost in lowland and upland black spruce forests of interior Alaska in a changing climate. Environ Res Lett 8:035030. https://doi.org/10.1088/1748-9326/8/3/035030

Järvinen O, Sammalisto L (1976) Regional trends in the avifauna of Finnish peatland bogs. Annales Zoologici Fennici 13:31–43

Jean M, Payette S (2014) Dynamics of active layer in wooded palsas of northern Quebec. Geomorphology 206:87–96. https://doi.org/10.1016/j.geomorph.2013.10.001

Joly K, Chapin FS III, Klein DR (2010) Winter habitat selection by caribou in relation to lichen abundance, wildfires, grazing, and landscape characteristics in northwest Alaska. Écoscience 17:321–333. https://doi.org/10.2980/17-3-3337

Jones MC, Yu Z (2010) Rapid deglacial and early Holocene expansion of peatlands in Alaska. PNAS 107:7347–7352. https://doi.org/10.1073/pnas.0911387107

Jones BM, Grosse G, Arp CD et al (2011) Modern thermokarst lake dynamics in the continuous permafrost zone, northern Seward Peninsula, Alaska. J Geophys Res Biogeosci 116:G00M03. https://doi.org/10.1029/2011JG001666

Jones MC, Grosse G, Jones BM, Walter Anthony K (2012) Peat accumulation in drained thermokarst lake basins in continuous, ice-rich permafrost, northern Seward Peninsula, Alaska. J Geophys Res Biogeosci 117:G00M07. https://doi.org/10.1029/2011JG001766

Jones MC, Booth RK, Yu Z, Ferry P (2013) A 2200-year record of permafrost dynamics and carbon cycling in a collapse-scar bog, interior Alaska. Ecosystems 16:1–19. https://doi.org/10.1007/s10021-012-9592-5

Jones BM, Grosse G, Arp CD et al (2015) Recent Arctic tundra fire initiates widespread thermokarst development. Sci Rep 5:15865. https://doi.org/10.1038/srep15865

Jones BM, Baughman CA, Romanovsky VE et al (2016) Presence of rapidly degrading permafrost plateaus in south-central Alaska. Cryosphere 10:2673–2692. https://doi.org/10.5194/tc-10-2673-2016

Jones MC, Harden J, O'Donnell J et al (2017) Rapid carbon loss and slow recovery following permafrost thaw in boreal peatlands. Glob Chang Biol 23:1109–1127. https://doi.org/10.1111/gcb.13403

Kanevskiy M, Shur Y, Jorgenson T et al (2017) Degradation and stabilization of ice wedges: implications for assessing risk of thermokarst in northern Alaska. Geomorphology 297:20–42. https://doi.org/10.1016/j.geomorph.2017.09.001

Karlsson JM, Lyon SW, Destouni G (2012) Thermokarst lake, hydrological flow and water balance indicators of permafrost change in Western Siberia. J Hydrol 464–465:459–466. https://doi.org/10.1016/j.jhydrol.2012.07.037

Karlsson JM, Lyon SW, Destouni G (2014) Temporal behavior of lake size-distribution in a thawing permafrost landscape in Northwestern Siberia. Remote Sens (Basel) 6:621–636. https://doi.org/10.3390/rs6010621

Kelly R, Chipman ML, Higuera PE et al (2013) Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. Proc Natl Acad Sci U S A 32:13055–13060. https://doi.org/10.1073/pnas.1305069110

Kirpotin S, Polishchuk Y, Zakharova E et al (2008) One of the possible mechanisms of thermokarst lakes drainage in West-Siberian North. Int J Environ Stud 65:631–635. https://doi.org/10.1080/00207230802525208

Kirpotin S, Polishchuk Y, Bryksina N et al (2011) West Siberian palsa peatlands: distribution, typology, cyclic development, present day climate-driven changes, seasonal hydrology and impact on CO2 cycle. Int J Environ Stud 68:603–623. https://doi.org/10.1080/00207233.2011.593901

Kjellman SE, Axelsson PE, Etzelmüller B et al (2018) Holocene development of subarctic permafrost peatlands in Finnmark, northern Norway. Holocene 28:1855–1869. https://doi.org/10.1177/0959683618798126

Klapstein SJ, Turetsky MR, McGuire AD et al (2014) Controls on methane released through ebullition in peatlands affected by permafrost degradation. J Geophys Res Biogeosci 119:418–431. https://doi.org/10.1002/2013JG002441

Korosi JB, McDonald J, Coleman KA et al (2015) Long-term changes in organic matter and mercury transport to lakes in the sporadic discontinuous permafrost zone related to peat subsidence. Limnol Oceanogr 60:1550–1561. https://doi.org/10.1002/lno.10116

Koven CD, Schuur EAG, Schaedel C et al (2015) A simplified, data-constrained approach to estimate the permafrost carbon–climate feedback. Philos Trans Roy Soc A 373:20140423. https://doi.org/10.1098/rsta.2014.0423

Kremenetski KV, Velichko AA, Borisova OK et al (2003) Peatlands of the Western Siberian lowlands: current knowledge on zonation, carbon content and Late Quaternary history. Quat Sci Rev 22:703–723. https://doi.org/10.1016/S0277-3791(02)00196-8

Kuhn M, Lundin EJ, Giesler R et al (2018) Emissions from thaw ponds largely offset the carbon sink of northern permafrost wetlands. Sci Rep 8:9535. https://doi.org/10.1038/s41598-018-27770-x

Kuhry P (2008) Palsa and peat plateau development in the Hudson Bay Lowlands, Canada: timing, pathways and causes. Boreas 37:316–327. https://doi.org/10.1111/j.1502-3885.2007.00022.x

Kurylyk BL, Hayashi M, Quinton WL et al (2016) Influence of vertical and lateral heat transfer on permafrost thaw, peatland landscape transition, and groundwater flow. Water Resour Res 52:1286–1305. https://doi.org/10.1002/2015WR018057

Kutzbach L, Wille C, Pfeiffer E-M (2007) The exchange of carbon dioxide between wet arctic tundra and the atmosphere at the Lena River Delta, Northern Siberia. Biogeosciences 4:869–890. https://doi.org/10.5194/bg-4-869-2007

Lachenbruch AH (1962) Mechanics of thermal contraction cracks and ice-wedge polygons in permafrost. Geological Society of America

Lamarre A, Garneau M, Asnong H (2012) Holocene paleohydrological reconstruction and carbon accumulation of a permafrost peatland using testate amoeba and macrofossil analyses, Kuujjuarapik, subarctic Québec, Canada. Rev Palaeobot Palynol 186:131–141. https://doi.org/10.1016/j.revpalbo.2012.04.009

Liblik LK, Moore TR, Bubier JL, Robinson SD (1997) Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, Northwest Territories, Canada. Global Biogeochem Cycles 11:485–494. https://doi.org/10.1029/97GB01935

Liljedahl AK, Boike J, Daanen RP et al (2016) Pan-Arctic ice-wedge degradation in warming permafrost and its influence on tundra hydrology. Nat Geosci 9:312–318. https://doi.org/10.1038/ngeo2674

Loisel J, Yu Z, Beilman DW et al (2014) A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. Holocene 24:1028–1042. https://doi.org/10.1177/0959683614538073

Luoto M, Heikkinen RK, Carter TR (2004) Loss of palsa mires in Europe and biological consequences. Environ Conserv 31:30–37. https://doi.org/10.1017/S0376892904001018

Lupascu M, Wadham JL, Hornibrook ERC, Pancost RD (2012) Temperature sensitivity of methane production in the permafrost active layer at Stordalen, Sweden: a comparison with non-permafrost Northern Wetlands. ArcticAntarct Alpine Res 44:469–482. https://doi.org/10.1657/1938-4246-44.4.469

Mack MC, Bret-Harte MS, Hollingsworth TN et al (2011) Carbon loss from an unprecedented Arctic tundra wildfire. Nature 475:489–492. https://doi.org/10.1038/nature10283

Magnan G, van Bellen S, Davies L et al (2018) Impact of the Little Ice Age cooling and 20th century climate change on peatland vegetation dynamics in central and northern Alberta using a multi-proxy approach and high-resolution peat chronologies. Quat Sci Rev 185:230–245. https://doi.org/10.1016/j.quascirev.2018.01.015

Mamet SD, Chun KP, Kershaw GGL et al (2017) Recent increases in permafrost thaw rates and areal loss of palsas in the Western Northwest Territories, Canada. Permafrost Periglacial Process 28:619–633. https://doi.org/10.1002/ppp.1951

Marushchak ME, Pitkämäki A, Koponen H et al (2011) Hot spots for nitrous oxide emissions found in different types of permafrost peatlands. Glob Chang Biol 17:2601–2614. https://doi.org/10.1111/j.1365-2486.2011.02442.x

Masrur A, Petrov AN, DeGroote J (2018) Circumpolar spatio-temporal patterns and contributing climatic factors of wildfire activity in the Arctic tundra from 2001–2015. Environ Res Lett 13:014019. https://doi.org/10.1088/1748-9326/aa9a76

Matveev A, Laurion I, Deshpande BN et al (2016) High methane emissions from thermokarst lakes in subarctic peatlands. Limnol Oceanogr 61:S150–S164. https://doi.org/10.1002/lno.10311

Merbold L, Kutsch WL, Corradi C et al (2009) Artificial drainage and associated carbon fluxes (CO_2/CH_4) in a tundra ecosystem. Glob Chang Biol 15:2599–2614. https://doi.org/10.1111/j.1365-2486.2009.01962.x

Minke M, Donner N, Karpov N et al (2007) Distribution, diversity, development and dynamics of polygon mires: examples from Northeast Yakutia (Siberia). Peatlands Int 1:36–40

Minke M, Donner N, Karpov N et al (2009) Patterns in vegetation composition, surface height and thaw depth in polygon mires in the Yakutian Arctic (NE Siberia): a microtopographical characterisation of the active layer. Permafrost Periglacial Process 20:357–368. https://doi.org/10.1002/ppp.663

Muster S, Roth K, Langer M, et al (2017) PeRL: a circum-Arctic permafrost region pond and lake database. Earth System Sci Data 9:317–348. https://doi.org/10.5194/essd-9-317-2017

Natali SM, Watts JD, Rogers BM et al (2019) Large loss of CO2 in winter observed across the northern permafrost region. Nat Clim Change 9:852–857. https://doi.org/10.1038/s41558-019-0592-8

Nijp JJ, Limpens J, Metselaar K et al (2015) Rain events decrease boreal peatland net CO2 uptake through reduced light availability. Glob Chang Biol 21:2309–2320. https://doi.org/10.1111/gcb.12864

Nitze I, Grosse G, Jones BM et al (2017) Landsat-based trend analysis of lake dynamics across Northern Permafrost Regions. Remote Sens (Basel) 9:640. https://doi.org/10.3390/rs9070640

O'Donnell JA, Jorgenson MT, Harden JW et al (2012) The effects of permafrost thaw on soil hydrologic, thermal, and carbon dynamics in an Alaskan Peatland. Ecosystems 15:213–229. https://doi.org/10.1007/s10021-011-9504-0

Oksanen PO (2006) Holocene development of the Vaisjeäggi palsa mire, Finnish Lapland. Boreas 35:81–95. https://doi.org/10.1111/j.1502-3885.2006.tb01114.x

Oksanen PO, Kuhry P, Alekseeva RN (2001) Holocene development of the Rogovaya River peat plateau, European Russian Arctic. Holocene 11:25–40. https://doi.org/10.1191/095968301675477157

Olefeldt D, Roulet NT (2012) Effects of permafrost and hydrology on the composition and transport of dissolved organic carbon in a subarctic peatland complex. J Geophys Res Biogeosci 117. https://doi.org/10.1029/2011JG001819

Olefeldt D, Roulet NT (2014) Permafrost conditions in peatlands regulate magnitude, timing, and chemical composition of catchment dissolved organic carbon export. Glob Chang Biol 20:3122–3136. https://doi.org/10.1111/gcb.12607

Olefeldt D, Turetsky MR, Crill PM, McGuire AD (2013) Environmental and physical controls on northern terrestrial methane emissions across permafrost zones. Glob Chang Biol 19:589–603. https://doi.org/10.1111/gcb.12071

Olefeldt D, Persson A, Turetsky MR (2014) Influence of the permafrost boundary on dissolved organic matter characteristics in rivers within the Boreal and Taiga plains of western Canada. Environ Res Lett 9:035005. https://doi.org/10.1088/1748-9326/9/3/035005

Olefeldt D, Goswami S, Grosse G et al (2016) Circumpolar distribution and carbon storage of thermokarst landscapes. Nat Commun 7:13043. https://doi.org/10.1038/ncomms13043

Olefeldt D, Euskirchen ES, Harden J et al (2017) A decade of boreal rich fen greenhouse gas fluxes in response to natural and experimental water table variability. Glob Chang Biol 23:2428–2440. https://doi.org/10.1111/gcb.13612

Packalen MS, Finkelstein SA (2014) Quantifying Holocene variability in carbon uptake and release since peat initiation in the Hudson Bay Lowlands, Canada. Holocene 24:1063–1074. https://doi.org/10.1177/0959683614540728

Packalen MS, Finkelstein SA, McLaughlin JW (2014) Carbon storage and potential methane production in the Hudson Bay Lowlands since mid-Holocene peat initiation. Nat Commun 5:4078. https://doi.org/10.1038/ncomms5078

Payette S, Delwaide A, Caccianiga M, Beauchemin M (2004) Accelerated thawing of subarctic peatland permafrost over the last 50 years. Geophys Res Lett 31. https://doi.org/10.1029/2004GL020358

Pelletier N, Talbot J, Olefeldt D et al (2017) Influence of Holocene permafrost aggradation and thaw on the paleoecology and carbon storage of a peatland complex in northwestern Canada. Holocene 27:1391–1405. https://doi.org/10.1177/0959683617693899

Peteet D, Andreev A, Bardeen W, Mistretta F (1998) Long-term Arctic peatland dynamics, vegetation and climate history of the Pur-Taz region, Western Siberia. Boreas 27:115–126. https://doi.org/10.1111/j.1502-3885.1998.tb00872.x

Prater JL, Chanton JP, Whiting GJ (2007) Variation in methane production pathways associated with permafrost decomposition in collapse scar bogs of Alberta, Canada. Global Biogeochem Cycles 21. https://doi.org/10.1029/2006GB002866

Quinton WL, Baltzer JL (2013) The active-layer hydrology of a peat plateau with thawing permafrost (Scotty Creek, Canada). Hydrgeol J 21:201–220. https://doi.org/10.1007/s10040-012-0935-2

Quinton WL, Hayashi M, Chasmer LE (2009) Peatland hydrology of discontinuous permafrost in the Northwest territories: overview and synthesis. Can Water Resour J / Revue canadienne des ressources hydriques 34:311–328. https://doi.org/10.4296/cwrj3404311

Renssen H, Seppä H, Crosta X et al (2012) Global characterization of the holocene thermal maximum. Quat Sci Rev 48:7–19. https://doi.org/10.1016/j.quascirev.2012.05.022

Riordan B, Verbyla D, McGuire AD (2006) Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images. J Geophys Res Biogeosci 111. https://doi.org/10.1029/2005JG000150

Robinson SD, Moore TR (2000) The influence of permafrost and fire upon carbon accumulation in high boreal peatlands, Northwest Territories, Canada. Arctic Antarct Alpine Res 32:155–166. https://doi.org/10.1080/15230430.2000.12003351

Ruppel M, Väliranta M, Virtanen T, Korhola A (2013) Postglacial spatiotemporal peatland initiation and lateral expansion dynamics in North America and northern Europe. Holocene 23:1596–1606. https://doi.org/10.1177/0959683613499053

Rydberg J, Klaminder J, Rosén P, Bindler R (2010) Climate driven release of carbon and mercury from permafrost mires increases mercury loading to sub-arctic lakes. Sci Total Environ 408:4778–4783. https://doi.org/10.1016/j.scitotenv.2010.06.056

Sannel ABK, Kuhry P (2008) Long-term stability of permafrost in subarctic peat plateaus, west-central Canada. Holocene 18:589–601. https://doi.org/10.1177/0959683608089658

Sannel ABK, Kuhry P (2009) Holocene peat growth and decay dynamics in sub-arctic peat plateaus, west-central Canada. Boreas 38:13–24. https://doi.org/10.1111/j.1502-3885.2008.00048.x

Sannel ABK, Kuhry P (2011) Warming-induced destabilization of peat plateau/thermokarst lake complexes. J Geophys Res 116. https://doi.org/10.1029/2010JG001635

Sannel ABK, Hugelius G, Jansson P, Kuhry P (2016) Permafrost warming in a Subarctic Peatland—which meteorological controls are most important? Permafrost Periglacial Process 27:177–188. https://doi.org/10.1002/ppp.1862

Sannel ABK, Hempel L, Kessler A, Prskienis V (2018) Holocene development and permafrost history in sub-arctic peatlands in Tavvavuoma, northern Sweden. Boreas 47:454–468. https://doi.org/10.1111/bor.12276

Saunois M, Bousquet P, Poulter B, et al (2016) The global methane budget 2000–2012. Earth Syst Sci Data 8:697–751. https://doi.org/10.5194/essd-8-697-2016

Schulze ED, Lapshina E, Filippov I et al (2015) Carbon dynamics in boreal peatlands of the Yenisey region, western Siberia. Biogeosciences 12:7057–7070. https://doi.org/10.5194/bg-12-7057-2015

Schuster PF, Schaefer KM, Aiken GR et al (2018) Permafrost stores a globally significant amount of mercury. Geophys Res Lett 45:1463–1471. https://doi.org/10.1002/2017GL075571

Seppälä M (1986) The origin of palsas. Geogr Ann Ser B 68:141–147. https://doi.org/10.1080/04353676.1986.11880167

Seppälä M (2003) Surface abrasion of palsas by wind action in Finnish Lapland. Geomorphology 52:141–148. https://doi.org/10.1016/S0169-555X(02)00254-4

Seppälä M (2011) Synthesis of studies of palsa formation underlining the importance of local environmental and physical characteristics. Quatern Res 75:366–370. https://doi.org/10.1016/j.yqres.2010.09.007

Serikova S, Pokrovsky OS, Laudon H et al (2019) High carbon emissions from thermokarst lakes of Western Siberia. Nat Commun 10:1552. https://doi.org/10.1038/s41467-019-09592-1

Shirokova LS, Pokrovsky OS, Kirpotin SN et al (2013) Biogeochemistry of organic carbon, CO2, CH4, and trace elements in thermokarst water bodies in discontinuous permafrost zones of Western Siberia. Biogeochemistry 113:573–593. https://doi.org/10.1007/s10533-012-9790-4

Sjöberg Y, Marklund P, Pettersson R, Lyon SW (2015) Geophysical mapping of palsa peatland permafrost. Cryosphere 9:465–478. https://doi.org/10.5194/tc-9-465-2015

Sjögersten S, Caul S, Daniell TJ et al (2016) Organic matter chemistry controls greenhouse gas emissions from permafrost peatlands. Soil Biol Biochem 98:42–53. https://doi.org/10.1016/j.soilbio.2016.03.016

Smith MW, Riseborough DW (2002) Climate and the limits of permafrost: a zonal analysis. Permafrost Periglacial Process 13:1–15. https://doi.org/10.1002/ppp.410

Smith LC, MacDonald GM, Velichko AA et al (2004) Siberian peatlands a net carbon sink and global methane source since the early holocene. Science 303:353–356. https://doi.org/10.1126/science.1090553

Smith LC, Sheng Y, MacDonald GM, Hinzman LD (2005) Disappearing Arctic lakes. Science 308:1429–1429. https://doi.org/10.1126/science.1108142

Smith LC, Sheng Y, MacDonald GM (2007) A first pan-Arctic assessment of the influence of glaciation, permafrost, topography and peatlands on northern hemisphere lake distribution. Permafrost Periglacial Process 18:201–208. https://doi.org/10.1002/ppp.581

Smith LC, Beilman DW, Kremenetski KV et al (2012) Influence of permafrost on water storage in West Siberian peatlands revealed from a new database of soil properties. Permafrost Periglacial Process 23:69–79. https://doi.org/10.1002/ppp.735

St Jacques J-M, Sauchyn DJ (2009) Increasing winter baseflow and mean annual streamflow from possible permafrost thawing in the Northwest Territories, Canada. Geophys Res Lett 36: L01401. https://doi.org/10.1029/2008GL035822

Ström L, Mastepanov M, Christensen TR (2005) Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. Biogeochemistry 75:65–82. https://doi.org/10.1007/s10533-004-6124-1

Sturtevant CS, Oechel WC (2013) Spatial variation in landscape-level CO2 and CH4 fluxes from arctic coastal tundra: influence from vegetation, wetness, and the thaw lake cycle. Glob Chang Biol 19:2853–2866. https://doi.org/10.1111/gcb.12247

Tolonen K, Turunen J (1996) Accumulation rates of carbon in mires in Finland and implications for climate change. Holocene 6:171–178. https://doi.org/10.1177/095968369600600204

Treat CC, Jones MC (2018) Near-surface permafrost aggradation in Northern Hemisphere peatlands shows regional and global trends during the past 6000 years. Holocene 28:998–1010. https://doi.org/10.1177/0959683617752858

Treat CC, Wollheim WM, Varner RK et al (2014) Temperature and peat type control CO_2 and CH_4 production in Alaskan permafrost peats. Glob Chang Biol 20:2674–2686. https://doi.org/10.1111/gcb.12572

Treat CC, Jones MC, Camill P et al (2016) Effects of permafrost aggradation on peat properties as determined from a pan-Arctic synthesis of plant macrofossils. J Geophys Res Biogeo 121:78–94. https://doi.org/10.1002/2015JG003061

Turetsky MR, Wieder RK, Vitt DH (2002) Boreal peatland C fluxes under varying permafrost regimes. Soil Biol Biochem 34:907–912. https://doi.org/10.1016/S0038-0717(02)00022-6

Turetsky MR, Wieder RK, Vitt DH et al (2007) The disappearance of relict permafrost in boreal north America: effects on peatland carbon storage and fluxes. Glob Chang Biol 13:1922–1934. https://doi.org/10.1111/j.1365-2486.2007.01381.x

Turetsky MR, Kane ES, Harden JW et al (2011) Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. Nat Geosci 4:27–31. https://doi.org/10.1038/ngeo1027

Turunen J, Tomppo E, Tolonen K, Reinikainen A (2002) Estimating carbon accumulation rates of undrained mires in Finland—application to boreal and subarctic regions. Holocene 12:69–80. https://doi.org/10.1191/0959683602hl522rp

Vardy SR, Warner BG, Turunen J, Aravena R (2000) Carbon accumulation in permafrost peatlands in the Northwest Territories and Nunavut, Canada. Holocene 10:273–280. https://doi.org/10.1191/095968300671749538

Verpoorter C, Kutser T, Seekell DA, Tranvik LJ (2014) A global inventory of lakes based on high-resolution satellite imagery. Geophys Res Lett 41:6396–6402. https://doi.org/10.1002/2014GL060641

Vitt DH, Halsey LA, Zoltai SC (1994) The bog landforms of Continental Western Canada in relation to climate and permafrost patterns. Arctic Alpine Res 26:1–13. https://doi.org/10.1080/00040851.1994.12003032

Voigt C, Marushchak ME, Lamprecht RE et al (2017) Increased nitrous oxide emissions from Arctic peatlands after permafrost thaw. PNAS 114:6238–6243. https://doi.org/10.1073/pnas.1702902114

Vorobyev SN, Pokrovsky OS, Serikova S et al (2017) Permafrost boundary shift in Western Siberia may not modify dissolved nutrient concentrations in rivers. Water 9:985. https://doi.org/10.3390/w9120985

Walker XJ, Rogers BM, Baltzer JL et al (2018) Cross-scale controls on carbon emissions from boreal forest megafires. Glob Chang Biol 24:4251–4265. https://doi.org/10.1111/gcb.14287

Walter Anthony KM, Zimov SA, Grosse G et al (2014) A shift of thermokarst lakes from carbon sources to sinks during the Holocene epoch. Nature 511:452–456. https://doi.org/10.1038/nature13560

Wania R, Ross I, Prentice IC (2009) Integrating peatlands and permafrost into a dynamic global vegetation model: 2. Evaluation and sensitivity of vegetation and carbon cycle processes. Global Biogeochem Cycles 23:GB003413. https://doi.org/10.1029/2008GB003413

Woo M-K, Winter TC (1993) The role of permafrost and seasonal frost in the hydrology of northern wetlands in North America. J Hydrol 141:5–31. https://doi.org/10.1016/0022-1694(93)90043-9

Wu Y, Verseghy DL, Melton JR (2016) Integrating peatlands into the coupled Canadian Land Surface Scheme (CLASS) v3.6 and the Canadian Terrestrial Ecosystem Model (CTEM) v2.0. Geosci Model Dev 9:2639–2663. https://doi.org/10.5194/gmd-9-2639-2016

Yoshikawa K, Bolton WR, Romanovsky VE, Fukuda M, Hinzman LD (2002) Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska. J Geophys Res 107:FFR 4-1-FFR 4-14. https://doi.org/10.1029/2001JD000438

Yoshikawa K, Hinzman LD (2003) Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near council, Alaska. Permafrost Periglacial Process 14:151–160. https://doi.org/10.1002/ppp.451

Yu Z, Loisel J, Brosseau DP et al (2010) Global peatland dynamics since the Last Glacial Maximum. Geophys Res Lett 37:L13402. https://doi.org/10.1029/2010GL043584

Zhang H, Piilo SR, Amesbury MJ et al (2018) The role of climate change in regulating Arctic permafrost peatland hydrological and vegetation change over the last millennium. Quat Sci Rev 182:121–130. https://doi.org/10.1016/j.quascirev.2018.01.003

Zoltai SC (1993) Cyclic development of permafrost in the Peatlands of Northwestern Alberta, Canada. Arctic Alpine Res 25:240–246. https://doi.org/10.1080/00040851.1993.12003011

Zoltai S (1995) Permafrost distribution in peatlands of West-Central Canada during the holocene warm period 6000 Years BP. Géographie physique et Quaternaire 49:45–54. https://doi.org/10.7202/033029ar

Zoltai SC, Tarnocai C (1975) Perennially frozen peatlands in the Western Arctic and Subarctic of Canada. Can J Earth Sci 12:28–43. https://doi.org/10.1139/e75-004

Zuidhoff FS, Kolstrup E (2005) Palsa development and associated vegetation in Northern Sweden. Arctic Antarct Alpine Res 37:49–60. https://doi.org/10.1657/1523-0430(2005)037

Post-fire Recruitment Failure as a Driver of Forest to Non-forest Ecosystem Shifts in Boreal Regions

4

Arden Burrell, Elena Kukavskaya, Robert Baxter, Qiaoqi Sun, and Kirsten Barrett

Abstract

Climate change and land-use are driving large changes in forest ecosystems around the globe. In the boreal biome it is likely that increases in temperature and the associated lengthening of the growing season will cause the forest to expand into the northern tundra and upwards in elevation, whilst potentially contracting at its southern limits. This increase in temperature is also driving an increase in the frequency and severity of boreal forest fires. A growing number of studies have observed the failure of forest species to re-establish after a stand-replacing fire event, which results in the shift to a non-forested ecosystem. In this chapter, this process is referred to as post-fire recruitment failure. We provide multiple lines of evidence for boreal forests, and more specifically for southern

---

A. Burrell (✉)
Centre for Landscape and Climate Research, School of Geography, Geology and Environment, University of Leicester, Leicester, UK

Woodwell Climate Research Center, Falmouth, MA, USA
e-mail: aburrell@woodwellclimate.org

E. Kukavskaya
V.N. Sukachev Institute of Forest of the Siberian Branch of the Russian Academy of Sciences, Separate Subdivision of the FRC KSC SB RAS 660036 Russia, Akademgorodok, Russia
e-mail: kukavskaya@ksc.krasn.ru

R. Baxter · Q. Sun
Department of Biosciences, University of Durham, Durham, UK
e-mail: robert.baxter@durham.ac.uk; qiaoqi.sun@nefu.edu.cn

K. Barrett
Centre for Landscape and Climate Research, School of Geography, Geology and Environment, University of Leicester, Leicester, UK

Leicester Institute for Space and Earth Observation, University of Leicester, Leicester, UK
e-mail: kirsten.barrett@leicester.ac.uk

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_4

Siberia forests, that a possible regional tipping point is unfolding, which could lead to the rapid replacement of large areas of forest ecosystems with low-stature non-forest ecosystems. This change would come with significant consequences for the carbon balance, surface albedo and the resulting altered energy balance.

4.1 Introduction

The boreal forest biome, also known in some regions as taiga, covers the high-latitude regions of Canada, Russia, China, Fennoscandia, as well as the United States, accounting for ~30% of all of the world's forested area (Gauthier et al. 2015) and ~20% of the world's terrestrial carbon sink (Bradshaw and Warkentin 2015; Pan et al. 2011). These regions also have some of the largest areas of intact and unmanaged forest in the world (Potapov et al. 2017) and changes in this ecosystem can result in large-scale climate feedbacks (Chen and Loboda 2018; Helbig et al. 2016; Liu et al. 2019). Boreal forests are dominated by a small number of slow growing tree species from four main genera, pine (*Pinus)*, aspen (*Populus*), larch (*Larix*) and spruce (*Picea.*) (de Groot et al. 2013; Rogers et al. 2015). Tree growth in boreal forests is strongly limited by air temperature with most growth occurring in the spring and summer months (Huang et al. 2010; Kauppi et al. 2014; Xu et al. 2013).

Over the last 100 years anthropogenic climate change has caused the boreal forest zone to warm at a much faster rate than most other terrestrial biomes (D'Orangeville et al. 2018) with this pattern expected to continue over the next century (IPCC 2013). The warmer temperatures resulting from climate change have already resulted in increased vegetation productivity (Chen et al. 2016; Goetz et al. 2005; Kauppi et al. 2014; Keenan and Riley 2018; Liu et al. 2015) and have driven the expansion of woody vegetation north into the tundra (Brodie et al. 2019; Forbes et al. 2010; Mekonnen et al. 2019; Myers-Smith et al. 2011; Suarez et al. 1999).

While climate change is causing boreal forests to expand northward and upward, there is growing evidence that it is driving a contraction along the southern edge (Guay et al. 2014; Huang et al. 2010; Koven 2013; Lapointe-Garant et al. 2010; Payette and Delwaide 2003). It remains an open question as to whether the extent of the boreal forest zone will increase or decrease due to future climate change (Brown and Johnstone 2012; Camill and Clark 2000; Guay et al. 2014; Lapointe-Garant et al. 2010; Walker et al. 2019). Growth in southern boreal regions is often strongly limited by water availability, with parts of Siberia receiving less than 200 mm of rainfall per year (Fig. 4.1). Droughts (Allen et al. 2010; Hogg et al. 2008; McDowell and Allen 2015; Michaelian et al. 2011; Worrall et al. 2013), changes in fire regimes (Curtis et al. 2018) and direct human impacts (Svensson et al. 2019) have all been implicated in catastrophic forest loss (Achard et al. 2006) and the expansion of steppe vegetation especially in the southern boreal regions (Kukavskaya et al. 2016). Of particular concern is the change in fire regime, with some studies suggesting that increases in the frequency and severity of fires resulting in the permanent shift from forests to non-forested ecosystems which could in turn lead to a reversal of the boreal

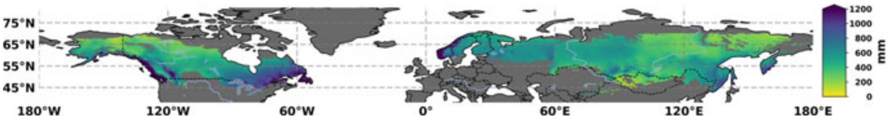


Fig. 4.1 Mean annual precipitation (mm) for the period 1958–2017 over the boreal forest. Non-boreal forest ecosystems are masked in grey. Data: TerraClimate (Abatzoglou et al. 2018a), the boreal forest mask (Potapov et al. 2008)

carbon sink (Bradshaw and Warkentin 2015; Flanagan et al. 2016; Koven 2013; Scheffer et al. 2012).

There is strong evidence that the boreal zone is experiencing large gains and losses in forested area (Hansen et al. 2013; Keenan et al. 2015). There is an urgent need to understand whether post-fire recruitment failure will cause ecosystem collapse in large parts of the boreal forest and its permanent replacement with grassland ecosystems. This chapter is broken down into three sections. The first discusses the important role that fire plays in boreal forests and the growing evidence for post-fire recruitment failure. The second section describes how climate change and forest management are driving changes in the boreal zone. The third discusses the difficult of quantifying the scale of post-fire recruitment failure and why this may be impairing our ability to predict future climate change. The final section outlines the management options.

4.2 Role of Fire in Boreal Forests

Forest disturbance can be defined as any period where the total amount of carbon in an ecosystem decreases beyond the normal interannual variability (Brazhnik et al. 2017). Wildfires are the dominant cause of disturbance in boreal forests (Bond-Lamberty et al. 2007; Curtis et al. 2018; de Groot et al. 2013; Goldammer and Furyaev 2013; Hansen et al. 2013) with stand-replacing fire in particular shaping forest extent, composition, structure and floristic diversity (Bonan and Shugart 1989; Hart et al. 2019; Rowe and Scotter 1973). Fire is a natural part of the boreal ecosystem (Johnstone et al. 2010) with palaeoecological reconstruction indicating that variations in fire frequency have been shaping species composition over the Holocene (El-Guellab et al. 2015; MacDonald et al. 1991; Novenko et al. 2016; Rolstad et al. 2017). Boreal forest fires are characterized by large areas of forest burnt in a single year followed by a gradual recovery (Curtis et al. 2018).

Globally, an average of between 10 and 20 million hectares of boreal forest burn annually, though there is considerable uncertainty around this estimate especially within Siberia (Brazhnik et al. 2017; Conard et al. 2002; de Groot et al. 2013; Flannigan et al. 2009; Kukavskaya et al. 2012; Rogers et al. 2020). There is also considerable interannual variability in the extent and severity of wildfires (Abatzoglou et al. 2018b; de Beurs et al. 2018; de Groot et al. 2013; Kasischke and Turetsky 2006), with the largest and most severe fire years associated with large-scale climate modes including the El Niño Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO) and the Artic Oscillation (AO) (Balzter et al. 2007; Macias Fauria and Johnson 2008; Monks et al. 2012; Ward et al. 2016). While decadal climate variability does lead to larger fire years, it should be noted that the source of ignition of almost 90% of fires is anthropogenic (Mollicone et al. 2006).

Fire intensity, size and mean fire return interval (FRI) vary considerably among different parts of the boreal zone (Archibald et al. 2018; Kharuk et al. 2011; Parisien et al. 2011; Sannikov and Goldammer 1996). For example, in Siberia FRI decreases along a north-south gradient and more gradually from west to east (Abatzoglou et al. 2018b; Soja et al. 2006) whilst within North America, the FRI is shortest in central Canada and longer near coastlines and on the northern boundary of the boreal zone (Potter et al. 2020; Rogers et al. 2013). In the colder and wetter boreal regions, the FRI ranges between 100 and >1000 years (Balshi et al. 2007; Kharuk et al. 2016; Kim et al. 2020; Mollicone et al. 2002; Schulze et al. 2005; Shuman et al. 2017). This follows a gradient through the warmer and drier parts of the southern boreal forest where the FRI is between 25 and 75 years (Chu et al. 2016; Rolstad et al. 2017) to the grassland and steppe vegetation that border the boreal forest, which have FRI of less than 17 years (Frelich et al. 2017). Similar patterns are apparent in the fraction of forest burnt each year (Abatzoglou et al. 2018b).

4.2.1 Post-fire Recruitment Dynamics

Given a stable climate and a time scale of centuries to millennia, boreal forests reach an equilibrium state where the amount of biomass lost to wildfire disturbances is balanced by the rate of recovery (Brazhnik et al. 2017) and where the species composition is adapted to the fire regime (Johnstone et al. 2010). In the colder and wetter parts of the boreal zone, the long FRI allows sufficient time for relay succession (Kurkowski et al. 2008; Ott et al. 2006). In these regions, the initial post-fire recruitment is dominated by broadleaf deciduous trees and then the ecosystem is overtaken by conifers over the course of centuries (Bergeron and Fenton 2012; Kurkowski et al. 2008). In the warmer and drier parts of the boreal zone the seedlings that establish in the 1–5 year recruitment window after a stand-replacing fire event determine future canopy composition because the FRI's are too short to allow for relay succession (Johnstone et al. 2010; Moser et al. 2010).

Increases in the frequency and/or severity of the disturbance regime, or a decrease in an ecosystem's resilience to that disturbance, can trigger a tipping point that leads to complete state change in that ecological system (Brazhnik et al. 2017; Hart et al. 2019; Héon et al. 2014; Johnstone et al. 2010; Walker et al. 2019). There is growing evidence that the frequency, extent and severity of fires are increasing (Brazhnik et al. 2017; de Groot et al. 2013; Malevsky-Malevich et al. 2008; Rogers et al. 2020; Turetsky et al. 2011; Young et al. 2017) and that tree regeneration is decreasing (Stevens-Rumann et al. 2018) within the boreal zone. In some regions, this is resulting in a species composition shift from conifers to deciduous trees, as a result of intense fires destroying the aerial seed banks that conifers rely upon for rapid post-fire establishment as well as the shorter FRI which favours faster-maturing species (Hart et al. 2019; Héon et al. 2014; Johnstone et al. 2010; Johnstone and Chapin 2006). These fire-induced species balance shifts have been observed in sites across the boreal zone (Héon et al. 2014; Johnstone et al. 2010; Johnstone and Chapin 2006; Lara et al. 2016).

4.2.2 Post-fire Recruitment Failure

In the warmer and drier parts of the boreal zone, there is growing evidence of post-fire recruitment failure, with tree species failing to re-establish entirely (Stevens-Rumann et al. 2018). Whilst the window of opportunity for seedling establishment varies between regions, it is generally short (1–5 years) and the canopy composition is determined by the seedlings established during this period (Moser et al. 2010). Given the importance of this 5 year window (Johnstone et al. 2010), it is generally assumed that if tree species fail to establish in this time it will result in permanent forest loss and the expansion of non-forested ecosystems (Enright et al. 2015; Scheffer et al. 2012; Seidl et al. 2017). Whilst a documented lack of large-scale, very long-term (>20 years), post-fire vegetation studies (Gitas et al. 2012) makes the assumption difficult to confirm, it is consistent with some regional data.

A study of vegetation 30 years post-fire along the Canadian Alaskan border region found that the vast majority of recruitment occurred "*in the first 5 years after fire, and additional net establishment was not observed after 10 years*" (Johnstone et al. 2004). Similarly, an unpublished 2019 field survey of tree demographics at 16 long-term (greater than 20 years) burn sites in Siberia found that >90% of Scots pine trees present at the sites established within 5 years of the burn (authors, unpublished). There is also evidence that analysis of existing canopy gaps in jack pine forests is driven by early poor regeneration density (Pacé et al. 2019), which supports the conclusion that recruitment failure in the first 5 years will result in permanent forest loss. Assuming that the 5 year establishment window is consistent in all regions, then post-fire recruitment failure and its associated permanent forest cover loss have been observed in Siberia (Barrett et al. 2020; Kukavskaya et al. 2016; Shvetsov et al. 2019), Europe (Moser et al. 2010), Canada (Payette and Delwaide 2003; Splawinski et al. 2019; Whitman et al. 2018) and the United States (Frelich et al. 2017; Hansen et al. 2018; Stevens-Rumann et al. 2018). Whilst recruitment failure has been observed in multiple studies throughout the boreal zone, almost all of the existing literature (including the studies cited above) is focused upon understanding and quantifying species balance shifts between forest types rather than on a shift to non-forested ecosystem types. This means that empirical quantification of post-fire recruitment failure is "*scarce, and their underlying processes are not well understood*" (Boucher et al. 2019).

Despite the above, it is known that there are some factors that cause recruitment failure that have hard thresholds beyond which recruitment failure is almost certain (Hansen et al. 2018; Kukavskaya et al. 2016). These factors include post-fire water availability, the FRI, the disturbance history and the distance to seed source. The most common of these is FRI, with multiple studies from throughout the boreal zone finding that a short interval between stand-replacing fires (≤20 years) will almost guarantee recruitment failure (Brown and Johnstone 2012; Kukavskaya et al. 2016; Whitman et al. 2018). However, in other regions the cause of post-fire recruitment is multifaceted and related to a "*resilience debt*" (Johnstone et al. 2016) which makes it difficult to ascribe attribution in the absence of extensive site histories. An excellent example of this issue comes from a study of managed forests in Canada (Perrault-Hébert et al. 2017). The latter authors found that a site had a ~50% chance of experiencing post-fire recruitment failure if it had had undergone logging at any point in the previous 50 years, which is almost double the rate of non-logged sites. The lack of data means that many of the recent attribution studies have used modelling to determine the causes of post-fire recruitment failure (Boucher et al. 2019; Splawinski et al. 2019; Stevens-Rumann et al. 2018).

Post-fire recruitment failure is also under-studied, poorly quantified (Boucher et al. 2019) and extremely difficult to quantify at a large scale given existing data (Sect. 4.4). In possibly the most extensive study of post-fire recruitment failure in a pine and aspen dominated ecosystem in the US alpine region, Stevens-Rumann et al. (2018) found that shifts in climate had resulted in a significant increase in the rate of recruitment failure since 2000. If similar increases in recruitment failure are occurring throughout the boreal zone, these particular findings may indicate an imminent risk of a widespread state change from boreal forest to a non-forested ecosystem. This increase in the rate of post-fire recruitment failure, combined with both the growing number of studies that have observed it (Barrett et al. 2020), as well as the observed and projected increases in fires frequency and severity (see Sect. 4.3.1.1) raises the alarming possibility of the ecological collapse of large parts of the boreal ecosystem, leading to the reversal of the boreal carbon sink (Bradshaw and Warkentin 2015).

4.2.3 A Case Study of Post-fire Recruitment Failure in Southern Siberia

Southern Siberia is one of the driest and hottest parts of the boreal forest with an average annual precipitation of ~200–300 mm (Fig. 4.1) and is among the fastest warming parts of the boreal zone (Sect. 4.3.1). As such, it is expected to be the most vulnerable to climate change and the changes currently observed in this region may be indicative of the future of the boreal zone as the climate warms. This region has already experienced an increase in the length of the fire season and a shortening of the FRI that is expected to continue with climate change (Malevsky-Malevich et al. 2008; Shvetsov et al. 2016) as is considered a hotspot of global forest loss (Achard et al. 2006). A number of recently published studies have looked at long-term post-fire recruitment failure in the southern Eurasian boreal forest range, in the Zabaykalsky Krai and the Republic of Buryatia, immediately southeast of Lake Baikal (Barrett et al. 2020; Kukavskaya et al. 2016; Shvetsov et al. 2016, 2019). In the early 2000s, this region experienced a number of severe fire seasons and in the almost two decades since these fires, it has become apparent that widespread recruitment failure has caused large areas to transition abruptly to grassland ecosystem types (Barrett et al. 2020; Kukavskaya et al. 2016; Shvetsov et al. 2019).

There is currently no automated method that can be applied to remotely sensed data to identify the different recruitment trajectories in the first 5–10 years after fire, and even 20 years after fire, discriminating recruitment trajectories reliably is difficult (see Sect. 4.4). Whilst some indicators do show promise, with initial differences in greenness and moisture among sites characterized by abundant recruitment, intermediate recruitment and recruitment failure becoming larger over the 10 years post-fire (Barrett et al. 2020), further work is needed to be able to use them to quantify recruitment trajectories. This means it is currently impossible to do a systematic large-scale assessment of post-fire recruitment failure.

All these recent studies use a combination of field observations to determine the recruitment trajectory and remotely sensed data to determine the impact of factors such as burn severity (Barrett et al. 2020; Kukavskaya et al. 2016; Shvetsov et al. 2019). Barrett et al. (2020) observed complete recruitment failure in 13 of 64 sites, with a further 37 sites showing less than optimal recruitment (Fig. 4.2). This is nearly double the ~11% recruitment failure observed in the sites examined by Shvetsov et al. (2016). It should be noted that these sites used in all three studies were chosen for accessibility and the ability to clearly see fire impacts in remotely sensed data. As such, they may not be a representative sample of the post-fire recruitment trajectories across the entire region.

The regional trend in NDVI, as well as the loss of forest cover since 2000, is shown in Fig. 4.3. Between 1982 and 2017 the region had an average change in $\text{NDVI}_{\max}$ of -0.0002 ± 0.0015 with 9.2% showing a significant ($\alpha_{\text{FDR}} = 0.10$) positive trend and 13.1% a significant negative trend ($\alpha_{\text{FDR}} = 0.10$). Large hotspots of negative trend can also been seen in the shorter MODIS Terra and MODIS aqua trend (Fig. 4.3b, c). This region has also seen a loss of ~15.9% of the forest cover over the same period (Fig. 4.3d). Whilst these negative trends in NDVI and the widespread forest loss cannot be used to directly quantify the extent of recruitment failure (see Sect. 4.4), the fact that they are occurring in the same regions where recruitment failure is being observed in field observations does provide some degree of corroboration.

Even in areas where post-fire recruitment failure has been identified, determining the exact cause is difficult because vegetation recovery is controlled by complex interactions of multiple factors, including pre- and post-fire climate condition, the FRI, the distance to a seed source, as well as successive disturbances (Liu 2016; Payette and Delwaide 2003). All of these factors have been found to play a role in recruitment failure in this region, with multiple fire events being especially predictive of total recruitment failure (Barrett et al. 2020; Kukavskaya et al. 2016; Shvetsov et al. 2019). The importance of these factors has also been observed across the border in northern Mongolia (Otoda et al. 2013).

Barrett et al. (2020) also found evidence of a possible snow feedback mechanism that would act to reinforce initial differences in recruitment over the intermediate and long term. In the first year after fire, the winter snow coverage as measured by the

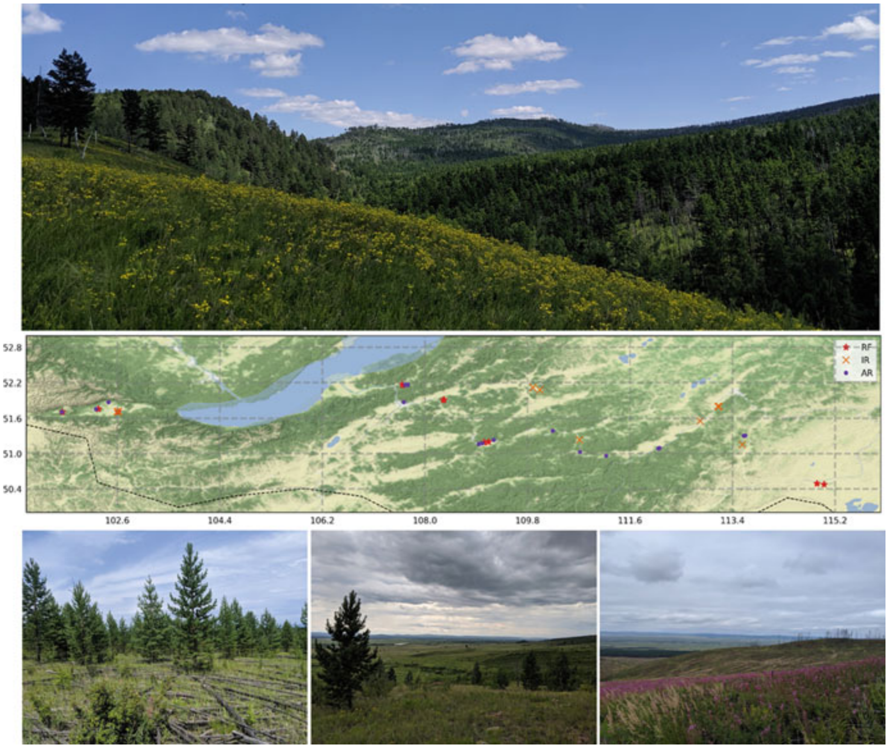


Fig. 4.2 Photos and map of Siberian field sites. Top: landscape photo showing both the grassland and forest ecosystems present in the study region. Middle: Map of the field sites with recruitment failure (RF), intermediate recruitment (IR) and abundant recruitment (AR) marked. The black dotted line is the Russian-Mongolian border Bottom: Examples of sites with AR (left, IR (middle) and RF (right)

Normalized Difference Snow Index (NDSI) showed no difference between abundantly recruiting sites and those experiencing recruitment failure (Fig. 4.4). However, 3–4 years after the fire, NDSI values at abundantly recruiting sites were substantially higher than at the recruitment failure sites. Snow cover in winter provides seedlings insulation from cold temperatures (Myers-Smith et al. 2011) plus protection from wind shear and herbivory (Barrett et al. 2020; Myers-Smith et al. 2011; Tape et al. 2010). Snowmelt also acts as an important source of water in spring (Buermann et al. 2018). These results suggest the possibility of a snow-seedling feedback mechanism whereby a greater density of seedlings traps more snow, which in turn protects seedlings from cold temperatures and wind.

Whilst the findings of these studies are interesting, they are not definitive and require significant further research for two main reasons. The first is that the field observations took place almost two decades after the stand-replacing fires (Barrett et al. 2020). As such, information about factors known to cause recruitment failure such as the fire history and the land management post fire (e.g. salvage logging) is

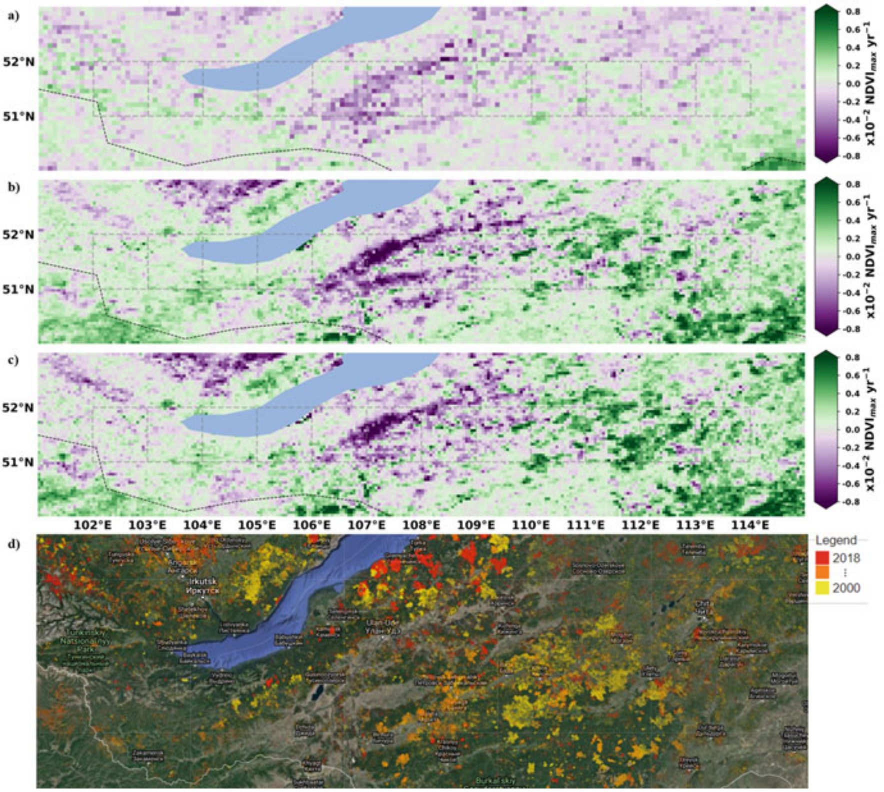


Fig. 4.3 Maps of the Theil-sen slope in annual NDVI$_{max}$ for (**a**) GIMMS (1982–2017), (**b**) MODIS Terra (2000–2018), (**c**) MODIS Aqua (2002–2018) and (**d**) Hansen forest loss (2000–2018). The yellow-orange patches are areas of forest loss

dependent upon the somewhat incomplete satellite record and the memories of individual foresters, if it exists at all. This is especially problematic in the case of salvage logging as successive disturbances are strongly linked to recruitment failure (Kukavskaya et al. 2016). The practice is widespread in this region (Kukavskaya et al. 2013) and it varies greatly in impact depending upon the exact method used. Post-fire logging is also linked with increased soil erosion, a reduction in the seed bank and a shortening of the FRI (Kukavskaya et al. 2013), which can all cause recruitment failure in their own right.

The second reason further study is needed is that evidence from other regions suggest that multiple drivers are often required for regeneration to fail, which is complicated further by the fact that interactions between drivers are often non-linear and non-independent (Hansen et al. 2018; Payette and Delwaide 2003). For example, it has been shown that sites adjacent to the edge of a mature forest do better because of much greater seed availability (Kukavskaya et al. 2016). Forests can also act as wind-breaks which can result it in the deposition of more snow from lowered

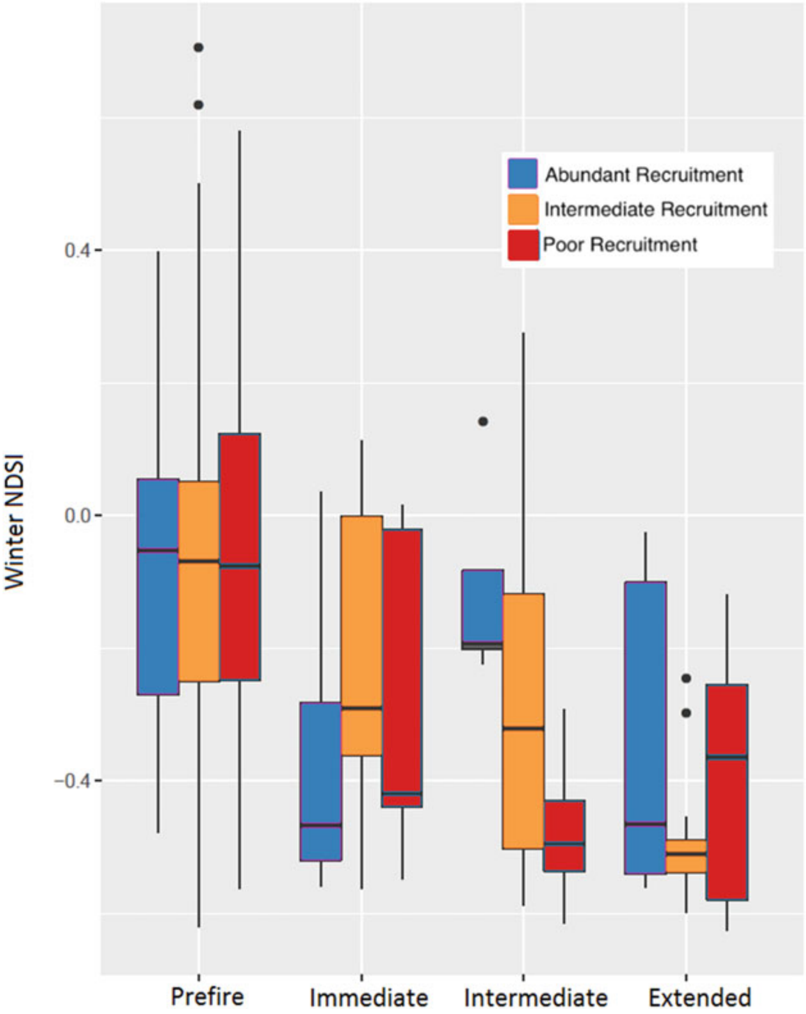


Fig. 4.4 Winter NDSI values for all assessment periods. Values for AR and RF are significantly different in the intermediate period. Figure adapted from Barrett et al. (2020)

wind speeds. As such, it is possible, though unlikely, that some, or all, the effect shown in Fig. 4.4 is a secondary impact of distance to forest.

Despite the uncertainty regarding the exact extent and precise combination of the drivers leading to recruitment failure in this region, current evidence from both field studies (Barrett et al. 2020; Kukavskaya et al. 2016; Shvetsov et al. 2019), and remotely sensed data (Fig. 4.4), suggest that it is widespread. Given that southern Siberia is currently experiencing rapid warming, which will increase in the future, and the growing number of observations of recruitment failure in Europe (Moser et al. 2010), Canada (Payette and Delwaide 2003) and the United States (Frelich et al. 2017; Hansen et al. 2018; Stevens-Rumann et al. 2018), there is a real possibility that we are seeing the rolling of a regional tipping point leading to the rapid replacement of forest with grasslands with significant consequences for the carbon balance, surface albedo and the resulting altered energy balance.

4.3 Drivers of Change in the Boreal Forest Zone

The drivers of change in boreal forests can be divided into two broad categories: climate change and land-use; both of which have a range of direct and indirect effects. Though discussed separately, the processes described below are strongly interlinked with a range of positive and negative feedbacks that act to amplify or mitigate the problem.

4.3.1 Climate Change

Over the last 100 years the boreal forest zone has been one of the fastest warming regions in the world (D'Orangeville et al. 2018). The change in temperature and precipitation resulting from climate change over the boreal region is shown in Fig. 4.5a and b, respectively. Over the period 1982–2017, all the boreal forests experienced significant increases in mean annual temperature, with an average increase of 0.04 °C year^{-1}. Some regions, including northern Canada and southern Siberia, experienced rates as high as 0.06 °C year^{-1}. For comparison, the global mean warming observed over land was 0.03°C year^{-1}.

The global trends in precipitation are more complex than temperature, with 15.9% of boreal forests experiencing significant decreases in rainfall, compared to 64.9% increasing and 19.2% with no significant trend (Fig. 4.5b). Whilst not the largest negative trends, the decreases in rainfall over southern Siberia are of

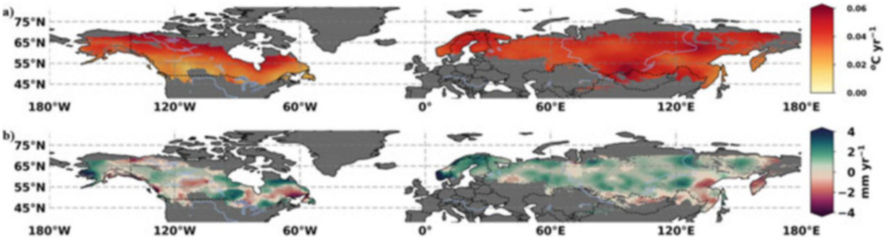


Fig. 4.5 Trend in (**a**) mean annual temperature for the period 1982–2017 and (**b**) annual precipitation (mm). To control for the impacts of large-scale climate oscillations, a 20 year moving window smoothing was applied and then the trend was estimated using the Theil-sen (Theil 1950). *P*-values were calculated using a non-parametric Spearman Rho test and then adjusted for multiple comparisons using the Benjamini–Hochberg procedure with a False Discovery Rate of 0.10. Stippling indicates statistical significance and non-boreal forest ecosystems are masked in grey. Data: TerraClimate (Abatzoglou et al. 2018a)

particular importance because they are occurring in an area that already experiences the lowest annual precipitation of the boreal zone (see Fig. 4.1).

4.3.1.1 Climate Change and Increases in the Fire Regime

In the boreal forest zone, there are strong empirical and conceptual links between burnt area and climate variables such as precipitation and temperature; hotter and drier years generally having larger and more severe fires, with an increase in the frequency of hot dry years linked to shorter FRI's (de Groot et al. 2013; Hanes et al. 2018; Héon et al. 2014; Rogers et al. 2020; Young et al. 2017). Climate change is also linked to increases in the number of lightning strikes, which are the primary source of ignition for many boreal forests (Krawchuk et al. 2009; Veraverbeke et al. 2017). Increases in both the frequency and severity of the fire regime associated with the observed boreal warming have been seen in continental North America (Abatzoglou and Williams 2016; Turetsky et al. 2015), Canada (Coops et al. 2018; Gillett et al. 2004), Alaska (Beck et al. 2011; Hoecker and Higuera 2019), China (Liu et al. 2012), Fennoscandia (Aakala et al. 2018) and Siberia (Ponomarev et al. 2016; Stephens et al. 2014). Climate change may also be leading to an increase in the frequency and/or severity of droughts (Pachauri et al. 2014) which are also strongly linked with fires (Aakala et al. 2018; Héon et al. 2014) and with higher fire-induced tree mortality (Ferster et al. 2016).

Increases in fire size and severity, as well as shortening of the FRI, are linked with recruitment failure and forest loss (Hansen et al. 2018; Moser et al. 2010). In the steppe and grassland ecosystems that border boreal forests the FRI is less than 17 years (Frelich et al. 2017), which is less than the ~20 years it takes for the dominant tree species in the drier parts of the boreal forest to reach sexual maturity. In a study of recruitment failure in the alpine region of the continental USA, the regeneration of serotinous lodgepole pine only failed when fire return intervals were <20 yr and stands were far (1 km) from a seed source (Hansen et al. 2018).

4.3.1.2 Climate Change and Decreased Ecosystem Resilience

In addition to increasing the frequency and/or severity of the fire disturbance regime, climate change is also reducing ecosystem resilience (Reich et al. 2018; Stevens-Rumann et al. 2018). Studies have observed an increase in the mortality of mature boreal forest trees, which are the source of seed for post-fire recruitment (Hansen et al. 2018). This increased mortality has been linked to direct climate effects such as drought and extreme temperature, as well as indirect effects including increased insect predation (Kharuk et al. 2013) (see (Allen et al. 2010) for a summary of literature by region). Climate can also directly impact post-fire recruitment, with drought in the 1–2 years after a fire decreasing tree recruitment and greatly increasing the likelihood of recruitment failure (Moser et al. 2010; Whitman et al. 2019).

It should be noted that, whilst this section is focused on the challenges climate change presents to boreal forests, there is strong evidence of a greening of large parts of the boreal forest, resulting from the increased temperature in conjunction with CO_2 fertilization and nitrogen deposition (Chae et al. 2015; Forbes et al. 2010; Keenan and Riley 2018; Zhu et al. 2016). In the CMIP-5 ensemble results, global greening is projected across the boreal zone for the next century (Piao et al. 2020). However these models have serious limitations in the way they represent vegetation because they cannot capture ecosystem change driven by a range of processes including land-use or changes in the fire regime (Arneth et al. 2017; Bayer et al. 2017; Piao et al. 2020; Zhu et al. 2016). The results of a recent modelling study which used more advanced ecosystem dynamics suggest that large parts of the boreal zone, mostly southern Siberia and central Canada, will see reductions in tree cover by 2050 under all of the IPCC emissions scenarios (Bastin et al. 2019). Ecosystem models have also found similar reductions in regional studies (Mokhov and Chernokulsky 2010; Stralberg et al. 2018).

4.3.2 Management and Human Influence

Nearly two thirds of boreal forests are managed with even unmanaged forest being by tourists, fishermen, hunters and beekeepers. (Gauthier et al. 2015). After fire, the largest cause of boreal forest disturbance comes from timber harvesting (Brandt et al. 2013; Potapov et al. 2017). In contrast to the deforestation observed in tropical forests, the aim of forest management is a sustainable long-term harvest of timber (Burton et al. 2003). However, forest management reduces the extent of older forests, which can result in lower biological, genetic and structural diversity (Cyr et al. 2009; Gauthier et al. 2015; Melvin et al. 2018). This has the potential to reduce forest resilience to disturbance, especially considering that the ecological impacts of many management strategies remain poorly understood (Melvin et al. 2018; Perrault-Hébert et al. 2017).

4.3.2.1 Forest Management and the Fire Regime

Whilst there is a widely held belief that logging reduces fuel loads thereby resulting in less severe and less frequent fires (Bradley et al. 2016), studies in boreal regions have found that managed forests experience more fires (Achard et al. 2008; Kukavskaya et al. 2013). This increase has been attributed to two main causes: firstly that logging debris can lead to much higher surface and ground fuel loads (Kukavskaya et al. 2013). Secondly, that humans are the main source of ignition (Achard et al. 2008; Campos-Ruiz et al. 2018; Liu et al. 2012) with more than 80% of fires in some regions being anthropogenic in origin (Brazhnik et al. 2017; Mollicone et al. 2006).

Forest management may also be a factor in post-fire recruitment failure. A common practice in managed forests is to log dead trees after a fire event (Taboada et al. 2018; Thorn et al. 2018). Whilst fires can occur in a forest of any age, structure and composition data (Brazhnik et al. 2017) suggest that the probability of fire is lower in the initial decade after fire (Hart et al. 2019). Post-fire logging offsets this reduced risk and has been linked to increased fire frequency (Donato et al. 2006; Taboada et al. 2018) which has been linked to post-fire recruitment failure (Hansen et al. 2018; Moser et al. 2010). Post-fire logging has been found to hinder the regeneration of forests (Donato et al. 2006), increase soil compaction and erosion

(Malvar et al. 2017) and to increase the number of open habitat plant species (Thorn et al. 2018). The negative impact of salvage logging may be especially high in Scots pine ecosystems, such as those found in southern Siberia, as dead standing trees provide a source of seeds in the 1–5 year recruitment window and continue to play a vital role in the ecosystem for up to 200 years after the stand-replacing fire occurs (Kuuluvainen et al. 2017). Most studies that assess post-fire logging only look at the first 5 years after the fire event (Boucher et al. 2014; Taboada et al. 2018; Thorn et al. 2018) and further research is needed to examine the link between post-fire recruitment failure and logging after fires.

4.4 Measuring the Scale of the Problem

Due to the size of the boreal forest zone, the only way to directly measure large-scale changes is to use remote sensing (Marchand et al. 2018). Remote sensing is being used in two ways: direct disturbance detection (Hansen et al. 2013) and long-term vegetation trend analysis (Marchand et al. 2018). The results have been inconsistent between these various approaches, with significant divergence in the estimates of boreal forest gain and loss (Myers-Smith et al. 2020; Piao et al. 2020; Polar Research Board et al. 2019). For example, a recent review of the published studies of trends in productivity of the Canadian boreal forest found that about half the studies identified increasing trends while the other half showed negative trends (Marchand et al. 2018). The authors of that review attributed this discrepancy in the estimates as resulting primarily from differences in the methodology used and the spatial scale of the study.

4.4.1 Disturbance Detection

There have been two approaches to disturbance detection in boreal forests. The first assesses forest loss regardless of the type of disturbance and the second measures parameters specific to fire disturbances. Forest loss detection generally uses Landsat or other medium to high spatial resolution remotely sensed data along with some form of classification algorithms to measure the extent of forest at specific times, with the differences between observed dates indicating areas of forest loss and gain (Hansen et al. 2013; Potapov et al. 2008, 2011; Schroeder et al. 2011). In ecosystems where there is also large interannual variability in the natural disturbance regime, as is the case with fire in the boreal zone (de Beurs et al. 2018), this is especially problematic because different study periods can result in opposing apparent trends.

Even when the data are produced annually, such as the widely used Global Forest Change (GFC) product (Hansen et al. 2013), there are limitations that prevent assessment of the long-term trends in disturbance. The GFC data currently covers the period 2000–2018 but, at the time of writing, an improvement to the algorithm implemented in v1.6 to improve the detection of boreal forest loss due to fire means that the period 2000–2010 is not directly comparable to the results from 2011 to

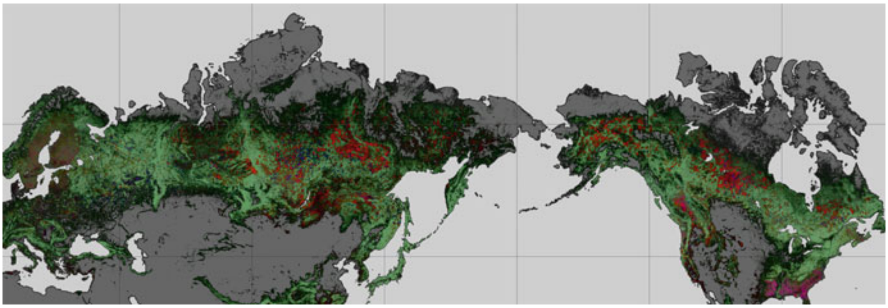


Fig. 4.6 Global Forest extent (dark green for low tree cover, light green for high tree cover), gain (Blue) (2000–2012), loss (red) (2000–2018) and both loss and gain (purple) determined using the Google Earth Engine and v1.6 of the Hansen et al. (2013) Global forest change dataset

2018. In addition to the issues with temporal resolution, there are considerable inconsistencies in the results of different datasets (Li et al. 2017). Despite these limitations, these forest loss datasets offer the best insight into the recent changes in forest extent over the boreal region. In a 2013 study of global forest loss, Hansen et al. (2013) found that boreal forests had both the largest gains of any forest zone and the second largest area of forest lost in both absolute and proportional terms (Fig. 4.6). This finding is consistent with the results of the 2015 Global Forest Resources Assessment performed by the Food and Agriculture Organization of the United Nations (Keenan et al. 2015).

The second disturbance detection remote sensing approach focuses on the detection of forest fires. A diverse range of methods have been developed to measure the extent and characteristics of active fires, the area burnt (Humber et al. 2019), the burn severity and the recovery of vegetation after the fire event (Chu and Guo 2014). The strengths and weakness of these approaches have been addressed in review articles (Chu and Guo 2014; Mouillot et al. 2014) and dataset comparison studies (Giglio et al. 2010; Humber et al. 2019; Moreno-Ruiz et al. 2019). These articles found that global annual estimates are consistent but there are considerable differences between datasets at regional or biome scales (Humber et al. 2019; Padilla et al. 2014).

Despite the limitations and uncertainties, fire disturbance detection products are more reliable in the boreal zone than in other biomes (Humber et al. 2019; Zhu et al. 2017) with one study finding that MODIS burned area product only under-estimated the extent of the burnt area by 27% compared to a global average of 48% (Padilla et al. 2014). By combining forest loss and fire detection data, recent studies have been able to detect and attribute forest loss (Liu et al. 2019).

4.4.2 Large-Scale Trends in Vegetation

The other way to examine long-term changes in boreal forest is to look at trends in vegetation indexes (VI), with the VI is the Normalized Difference Vegetation Index

(NDVI) being the most widely used. NDVI is a proxy for Net Primary Production (NPP) (Burrell et al. 2020; Polar Research Board et al. 2019; Prince and Tucker 1986; Tucker et al. 1985; Wessels et al. 2006; Yang et al. 2017). In the boreal zone, positive changes in NDVI have been linked to field observations of temperature driven increases in NPP whilst browning trends have been linked with fire and climate disturbance (Beck et al. 2011; Myers-Smith et al. 2020; Polar Research Board et al. 2019; Yang et al. 2017).

The main advantage of a trend detection approach is that it is easy to replicate and there are range of datasets available with larger temporal ranges and different resolutions. For example, there are currently four datasets providing global sub-monthly NDVI with more than 17 years of continuous records (GIMMS3.1g, MODIS terra, MODIS aqua and Copernicus). These data sets use the same NDVI formula, enabling researchers to identify and quantify the uncertainties that comes from sensor and scale differences (Burrell et al. 2018), which is difficult with the more direct disturbance quantification approaches. An intercomparison of commonly used NDVI datasets is shown in Fig. 4.7.

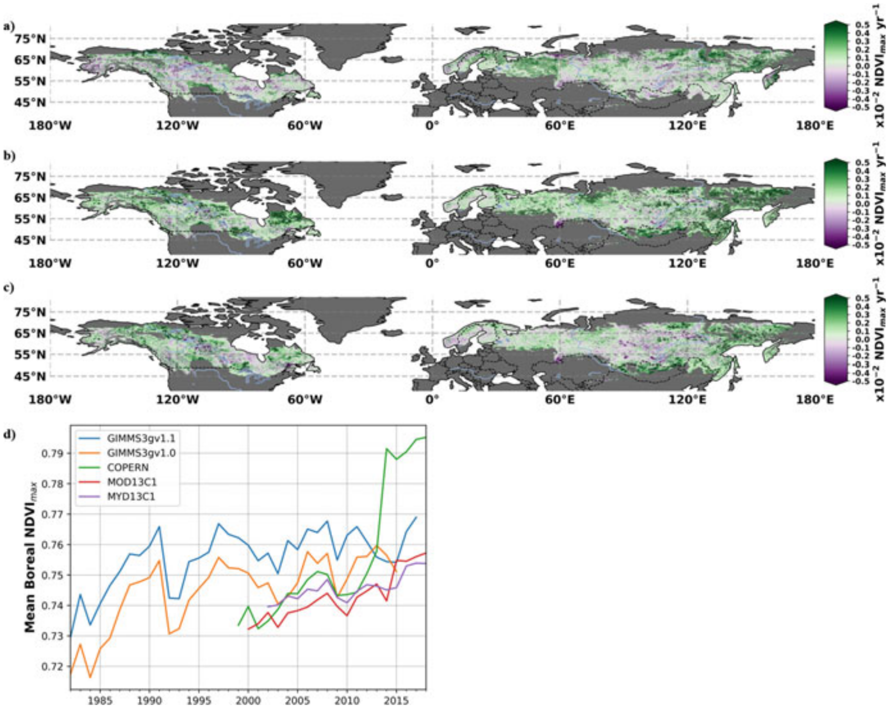


Fig. 4.7 Slope in Annual Maximum NDVI (1982–2017) determined using the Theil-sen Slope estimator with (**a**) GIMMS3gv1.1 (1982–2017), (**b**) MODIS TERRA (MOD13C1) (2000-2018), (**c**) MODIS AQUA (MYDD13C1) (2002–2018) data, (**d**) Mean Boreal NDVI. *p*-values were calculated using a non-parametric Spearman Rho test and then adjusted for multiple comparisons using the Benjamini–Hochberg procedure with a False Discovery Rate of 0.10. Stippling indicates statistical significance

In general, the NDVI datasets shown in Fig. 4.7 have similar large-scale trends, with the boreal zone having greened by an average of 0.00056 ± 0.000003 in the GIMMS dataset (1982–2017), 0.001288 ± 0.000004 in the MODIS TERRA data (2000–2018) and 0.000758 ± 0.000006 in the MODIS Aqua (2002–2018). These findings are consistent with the observed trends in existing studies (Guo et al. 2018; Marchand et al. 2018; Myers-Smith et al. 2020; Sulla-Menashe et al. 2018). In a study of vegetation trends in the Canadian boreal forest, it was found that greening and browning not caused by the disturbance/recovery regime was primarily located near boundaries of the boreal forest zone, with browning in the dry regions and greening in the wet regions (Sulla-Menashe et al. 2018). Whilst overall vegetation trends are consistent between datasets, regional patterns vary considerably (Fig. 4.7a–c) and this difference can be attributed to differences in the start and end dates, it may also result from errors and uncertainties in the data itself (Burrell et al. 2018). An example of this problem is shown in Fig. 4.7d. The Copernicus NDVI produce is a 1 km global NDVI product that covers 1999 to present. In 2013 this dataset changes from SPOT data to the newer high resolution PROBA-V. It is apparent that, for the boreal forest region, the cross-sensor calibration has not worked. All datasets have uncertainties and errors and even small errors can produce contradictory trends in some cases (Burrell et al. 2018). These difference may account for some of the ongoing debate about the arctic and boreal green trends (Duncan et al. 2020; Polar Research Board et al. 2019).

4.4.3 Detecting Post-fire Recruitment Failure

The threat facing boreal forests is that post-fire recruitment failure will cause large parts of the boreal forest ecosystem to collapse with climate change-driven increases in the fire regime (Walker et al. 2019). Trend analysis alone cannot be used to separate out normal fire loss and recovery from recruitment failure. This is especially problematic because a recent study found that disturbance recovery dynamics account for the majority of NDVI trends in boreal forest (Sulla-Menashe et al. 2018).

This limitation is compounded by the fact that trend detection approaches can be unreliable in any ecosystem where productivity is impacted by natural interannual variability in climate, especially when that variability is linked with decadal time-scale climate oscillation (Burrell et al. 2017). This is the case in the parts of the boreal forest most at risk of collapse due to post-fire recruitment failure (Bradshaw and Warkentin 2015). Similarly, direct disturbance detection methods measure forest loss but not recruitment failure (Hansen et al. 2013) and consequently cannot distinguish natural disturbance recovery cycles from a state change.

In reviewing remote sensing of fire impacts, Chu and Guo (2014) argued that methods for evaluating post-fire vegetation recovery has received “little effort” and that considerable further research is required (Chu and Guo 2014). The authors of this chapter are aware of no study published to date that has estimated the extent of recruitment failure at a large spatial scale. However, a number of studies have shown promising results by combining disturbance detection and NDVI or other vegetation index trends to monitor post-fire vegetation recovery dynamics (Cai et al. 2018; Chu et al. 2016; Liu 2016; Yang et al. 2017). In addition, it may be possible to use methods developed in other ecosystems that improve trend detection by accounting for climate variability and ecosystem disturbance (Abel et al. 2019; Burrell et al. 2019) though validating and improving on these methods remains difficult without large-scale grid-based inventories currently lacking in Siberia.

4.4.4 Post-fire Recruitment Failure and the Prediction of Future Climate

The boreal forest has a large impact upon regional and global climate (Chen and Loboda 2018; Helbig et al. 2016; Liu et al. 2019). If post-fire recruitment failure results in the collapse of large parts of the boreal forest, it may potentially have a large impact upon global climate that is not currently integrated into many of the models used to predict climate change.

Over the next 100 years, global circulation models (GCM) predict that the boreal region will experience the largest increase in temperatures of any forest biomes (Gauthier et al. 2015). This, along with the associated lengthening of the growing season, is predicted to result in the continued expansion of boreal forests into the tundra region (Forbes et al. 2010; Rocha et al. 2018). GCM's incorporate vegetation in necessarily simplistic ways and there is growing evidence for rapid and non-linear response to changes in climate that are poorly understood, not incorporated into current models and may be leading to significant overestimations of the long-term benefits of warming in the boreal zone (Chen et al. 2016; D'Orangeville et al. 2018; Reich et al. 2018; Soja et al. 2007; Thurner et al. 2017).

One current limit of GCM's and their associated global vegetation models (GVM's) is that, while these models include fire in the carbon cycle, they only consider fire frequency and do not incorporate feedbacks between fire, vegetation and climate (Harris et al. 2016; Syphard et al. 2018). Consequently, forest loss caused by processes such as post-fire recruitment cannot be captured. This is problematic because studies predict large increases in fire frequency over the next century (Lehtonen et al. 2016; Wotton et al. 2010, 2017). Given the complex feedbacks that exist between the boreal forest zone and the global climate (Chen and Loboda 2018; Helbig et al. 2016; Johnstone et al. 2011; Liu et al. 2019; Zhang et al. 2011) widespread collapse of the boreal forest ecosystem due to post-fire recruitment failure may change the regional albedo as well as releasing significant amounts of CO_2 and aerosols into the atmosphere. While some of these issues may be addressed with the development of dynamic global vegetation models (DGVMs) that more accurately represent vegetation processes and fire dynamics (Harris et al. 2016; Syphard et al. 2018), significant further research into forest loss due to post-fire recruitment failure is needed.

4.5 Future Management

Given that negative impacts of climate change will continue to increase for at least the next century, even under the lowest emissions scenarios, it is necessary to implement management strategies to prevent widespread forest loss or facilitate more desirable transitions. Without knowing the scale of the problem, it is difficult to formulate effective management practices. With increasing fire activity, forests become more vulnerable to changes in species composition and structure (Shvetsov et al. 2019) and monitoring of post-fire recovery is necessary to determine appropriate management approaches. Several forest management and adaptation strategies have been proposed to mitigate the negative impacts of climate change which can be grouped into three broad categories: (1) societal adaptation (e.g. forest policy to encourage adaptation, revision of conservation objectives, changes in expectations), (2) adaptation of the forest (e.g. species selection, tree breeding, stand management) and (3) adaptation to the forest (e.g. changes in forestry rotation age, use more salvage wood, modify wood processing technology)(Spittlehouse 2005).

There is a documented lack of published forest management and restoration research from the Siberian region, with almost all the published literature coming from North America, Finland and Sweden (Bernes et al. 2015). In southern Siberia, a range of different management strategies are being tested by the regional forestry organizations but they remain mostly unstudied and so their effectiveness is unknown. Most of the strategies employed in this region are focused heavily upon salvage logging immediately after the fire (Kukavskaya et al. 2013) followed by replanting in areas where recruitment failure has been observed. A recent study on global forest regeneration potential found that Russia has about 150 million ha of land suitable for forest restoration, the largest amount of any country (Bastin et al. 2019). By comparison, the annual rate of reforestation in Russia over the last 15 years has been 800,000–950,000 ha with forest plantations averaged 22% (http://rosleshoz.gov.ru/). Furthermore, the effectiveness of these measures in reducing the risk of permanent forest loss is dubious due to the usage of low-quality seeds and seedlings, the lack or absence of subsequent measures for protection of seedlings from diseases, insects and fires as well as a lack of erosion mitigation. Most problematic of all is that ~50% of the areas replanted in the most fire prone parts of Siberia burn again within 15 years (Kukavskaya et al. 2016).

In order to stimulate natural reforestation and to decrease recruitment failure following management intervention, a recent Decree published by the Ministry on Natural Resources and Ecology of the Russian Federation suggested the following measures: preservation of seedlings during harvesting, maintenance of seed sources, enclosing regenerating areas (e.g. cattle fencing), sanitation thinning, seedlings care (e.g. tree setting, fertilizer application, herbicide treatment), mechanical or fire soil mineralization (Decree 188 2019, p. 139). These measures can be carried out both separately and in combination with each other. For example, to enhance the reforestation effect, thinning of stands and undergrowth, along with increased light input to the crowns (increased seed production) and under the canopy (improved light conditions for regeneration) could be supplemented by soil mineralization. This Decree also provides guidance for forest management on the number of seedlings required for successful regeneration, depending upon the forest zone, dominant tree species, soil type and moisture.

It should be noted that many of the strategies outlined above are already implemented over the extensive areas of Russian boreal forest, despite which, the rate of re-burning and then subsequent recruitment failure remains high (Kukavskaya et al. 2016). As such, the improvement of reforestation management should include strengthening of fire prevention measures, including education of local communities to decrease number of ignitions, as well as construction and maintenance of a fuel break system (prioritizing nearby settlements and tree plantations) to inhibit development of large fires and to decrease the negative impact of fires on forests. Active replanting of forests in western North America following salvage logging of burnt forest may make them more susceptible to re-burning due to high density of saplings. Lindenmayer et al. (2017), therefore, suggested reducing the numbers of planted seedlings and increasing the spacing between trees to reduce the risk of recurrent high-severity fire. Other appropriate actions to improve seedling survival after replanting are to modify seed transfer zones and to introduce more fire-resistant and drought-tolerant species, to change replanting methodology and techniques (e.g. shading of planted seedlings on the overheated sites), to conduct sanitation thinning.

Even if all of these strategies are implemented, they may prove ineffective because they are predicated on the assumption that direct management of an ecosystem post-fire is an effective strategy for ecosystem recovery. A recent global multi ecosystem assessment of management interventions in the wake of natural disturbance events like fires found that active management actually worsened long-term outcomes (Lindenmayer et al. 2017). There is a good reason to think this may be the case in Siberia, with salvage logging linked to shorter FRI and recruitment failure (Kukavskaya et al. 2013; Shvetsov et al. 2019) and recent field observations finding extensive soil erosion at some recent replanting sites.

In summary, the current lack of knowledge about the exact scale and mechanisms of boreal forest recruitment failure as well as the effectiveness of measures being implemented to address it means that developing an effective long-term strategy to prevent widespread boreal forest collapse is extremely difficult. There is a need to reconsider our human response to natural disturbances and to reduce the risks of forest degradation by implementing appropriate forest management strategies based upon the local climate and ecological conditions as well as disturbance levels. Without these improvements, there is a risk that the increasing number of disturbed ecosystems and recruitment failure worldwide will lead to irreversible negative consequences affecting both the environment and human wellbeing.

References

Aakala T, Pasanen L, Helama S, Vakkari V, Drobyshev I, Seppä H, Kuuluvainen T, Stivrins N, Wallenius T, Vasander H, Holmström L (2018) Multiscale variation in drought controlled historical forest fire activity in the boreal forests of eastern Fennoscandia. Ecol Monogr 88:74–91. https://doi.org/10.1002/ecm.1276

Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. Proc Natl Acad Sci USA 113:11770–11775. https://doi.org/10.1073/pnas.1607171113

Abatzoglou JT, Dobrowski SZ, Parks SA, Hegewisch KC (2018a) TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. Sci Data 5:170191. https://doi.org/10.1038/sdata.2017.191

Abatzoglou JT, Williams AP, Boschetti L, Zubkova M, Kolden CA (2018b) Global patterns of interannual climate–fire relationships. Glob Chang Biol 24:5164–5175. https://doi.org/10.1111/gcb.14405

Abel C, Horion S, Tagesson T, Brandt M, Fensholt R (2019) Towards improved remote sensing based monitoring of dryland ecosystem functioning using sequential linear regression slopes (SeRGS). Remote Sens Environ 224:317–332. https://doi.org/10.1016/j.rse.2019.02.010

Achard F, Mollicone D, Stibig H-J, Aksenov D, Laestadius L, Li Z, Popatov P, Yaroshenko A (2006) Areas of rapid forest-cover change in boreal Eurasia. For Ecol Manage 237:322–334. https://doi.org/10.1016/j.foreco.2006.09.080

Achard F, Eva HD, Mollicone D, Beuchle R (2008) The effect of climate anomalies and human ignition factor on wildfires in Russian boreal forests. Philos Trans R Soc B Biol Sci 363:2331–2339. https://doi.org/10.1098/rstb.2007.2203

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg (Ted) EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259:660–684. Adaptation of forests and forest management to changing climate. https://doi.org/10.1016/j.foreco.2009.09.001

Archibald S, Lehmann CER, Belcher CM, Bond WJ, Bradstock RA, Daniau A-L, Dexter KG, Forrestel EJ, Greve M, He T, Higgins SI, Hoffmann WA, Lamont BB, McGlinn DJ, Moncrieff GR, Osborne CP, Pausas JG, Price O, Ripley BS, Rogers BM, Schwilk DW, Simon MF, Turetsky MR, der Werf GRV, Zanne AE (2018) Biological and geophysical feedbacks with fire in the Earth system. Environ Res Lett 13:033003. https://doi.org/10.1088/1748-9326/aa9ead

Arneth A, Sitch S, Pongratz J, Stocker BD, Ciais P, Poulter B, Bayer AD, Bondeau A, Calle L, Chini LP, Gasser T, Fader M, Friedlingstein P, Kato E, Li W, Lindeskog M, Nabel JEMS, Pugh T a M, Robertson E, Viovy N, Yue C, Zaehle S (2017) Historical carbon dioxide emissions caused by land-use changes are possibly larger than assumed. Nat Geosci 10:79–84. https://doi.org/10.1038/ngeo2882

Balshi MS, McGuire AD, Zhuang Q, Melillo J, Kicklighter DW, Kasischke E, Wirth C, Flannigan M, Harden J, Clein JS, Burnside TJ, McAllister J, Kurz WA, Apps M, Shvidenko A (2007) The role of historical fire disturbance in the carbon dynamics of the pan-boreal region: a process-based analysis. J Geophys Res Biogeosci 112. https://doi.org/10.1029/2006JG000380

Balzter H, Gerard F, George C, Weedon G, Grey W, Combal B, Bartholomé E, Bartalev S, Los S (2007) Coupling of vegetation growing season anomalies and fire activity with hemispheric and regional-scale climate patterns in Central and East Siberia. J Climate 20:3713–3729. https://doi.org/10.1175/JCLI4226

Barrett K, Baxter R, Kukavskaya E, Balzter H, Shvetsov E, Buryak L (2020) Postfire recruitment failure in Scots pine forests of southern Siberia. Remote Sens Environ 237:111539. https://doi.org/10.1016/j.rse.2019.111539

Bastin J-F, Finegold Y, Garcia C, Mollicone D, Rezende M, Routh D, Zohner CM, Crowther TW (2019) The global tree restoration potential. Science 365:76–79. https://doi.org/10.1126/science.aax0848

Bayer AD, Lindeskog M, Pugh TAM, Anthoni PM, Fuchs R, Arneth A (2017) Uncertainties in the land-use flux resulting from land-use change reconstructions and gross land transitions. Earth Syst Dynam 8:91–111. https://doi.org/10.5194/esd-8-91-2017

Beck PSA, Goetz SJ, Mack MC, Alexander HD, Jin Y, Randerson JT, Loranty MM (2011) The impacts and implications of an intensifying fire regime on Alaskan boreal forest composition and albedo. Glob Chang Biol 17:2853–2866. https://doi.org/10.1111/j.1365-2486.2011.02412.x

Bergeron Y, Fenton NJ (2012) Boreal forests of eastern Canada revisited: old growth, nonfire disturbances, forest succession, and biodiversity. Botany 90:509–523. https://doi.org/10.1139/b2012-034

Bernes C, Jonsson BG, Junninen K, Lõhmus A, Macdonald E, Müller J, Sandström J (2015) What is the impact of active management on biodiversity in boreal and temperate forests set aside for conservation or restoration? A systematic map. Environ Evid 4:25. https://doi.org/10.1186/s13750-015-0050-7

Bonan GB, Shugart HH (1989) Environmental factors and ecological processes in boreal forests. Annu Rev Ecol Syst 20:1–28. https://doi.org/10.1146/annurev.es.20.110189.000245

Bond-Lamberty B, Peckham SD, Ahl DE, Gower ST (2007) Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature 450:89–92. https://doi.org/10.1038/nature06272

Boucher D, Gauthier S, Noël J, Greene DF, Bergeron Y (2014) Salvage logging affects early post-fire tree composition in Canadian boreal forest. For Ecol Manage 325:118–127. https://doi.org/10.1016/j.foreco.2014.04.002

Boucher D, Gauthier S, Thiffault N, Marchand W, Girardin M, Urli M (2019) How climate change might affect tree regeneration following fire at northern latitudes: a review. New For. https://doi.org/10.1007/s11056-019-09745-6

Bradley CM, Hanson CT, DellaSala DA (2016) Does increased forest protection correspond to higher fire severity in frequent-fire forests of the western United States? Ecosphere 7:e01492. https://doi.org/10.1002/ecs2.1492

Bradshaw CJA, Warkentin IG (2015) Global estimates of boreal forest carbon stocks and flux. Global Planet Change 128:24–30. https://doi.org/10.1016/j.gloplacha.2015.02.004

Brandt JP, Flannigan MD, Maynard DG, Thompson ID, Volney WJA (2013) An introduction to Canada’s boreal zone: ecosystem processes, health, sustainability, and environmental issues. Environ Rev 21:207–226. https://doi.org/10.1139/er-2013-0040

Brazhnik K, Hanley C, Shugart HH (2017) Simulating changes in fires and ecology of the 21st century Eurasian Boreal Forests of Siberia. Forests 8:49. https://doi.org/10.3390/f8020049

Brodie JF, Roland CA, Stehn SE, Smirnova E (2019) Variability in the expansion of trees and shrubs in boreal Alaska. Ecology e02660. https://doi.org/10.1002/ecy.2660

Brown CD, Johnstone JF (2012) Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on Picea mariana regeneration. For Ecol Manage 266:34–41. https://doi.org/10.1016/j.foreco.2011.11.006

Buermann W, Forkel M, O’Sullivan M, Sitch S, Friedlingstein P, Haverd V, Jain AK, Kato E, Kautz M, Lienert S, Lombardozzi D, Nabel JEMS, Tian H, Wiltshire AJ, Zhu D, Smith WK, Richardson AD (2018) Widespread seasonal compensation effects of spring warming on northern plant productivity. Nature 562:110–114. https://doi.org/10.1038/s41586-018-0555-7

Burrell AL, Evans JP, Liu Y (2017) Detecting dryland degradation using Time Series Segmentation and Residual Trend analysis (TSS-RESTREND). Remote Sens Environ 197:43–57. https://doi.org/10.1016/j.rse.2017.05.018

Burrell AL, Evans JP, Liu Y (2018) The impact of dataset selection on land degradation assessment. ISPRS J Photogramm Remote Sens 146:22–37. https://doi.org/10.1016/j.isprsjprs.2018.08.017

Burrell AL, Evans JP, Liu Y (2019) The addition of temperature to the TSS-RESTREND methodology significantly improves the detection of dryland degradation. IEEE J Sel Top Appl Earth Obs Remote Sens 1–7. https://doi.org/10.1109/JSTARS.2019.2906466

Burrell AL, Evans JP, De Kauwe MG (2020) Anthropogenic climate change has driven over 5 million km 2 of drylands towards desertification. Nat Commun 11:3853. https://doi.org/10.1038/s41467-020-17710-7

Burton PJ, Messier C, Smith DW, Adamowicz WL (2003) Towards sustainable management of the boreal forest. NRC Research Press

Cai WH, Liu Z, Yang YZ, Yang J (2018) Does environment filtering or seed limitation determine post-fire forest recovery patterns in boreal larch forests? Front Plant Sci 9. https://doi.org/10.3389/fpls.2018.01318

Camill P, Clark JS (2000) Long-term perspectives on lagged ecosystem responses to climate change: permafrost in boreal peatlands and the grassland/woodland boundary. Ecosystems 3:534–544. https://doi.org/10.1007/s100210000047

Campos-Ruiz R, Parisien M-A, Flannigan MD (2018) Temporal patterns of wildfire activity in areas of contrasting human influence in the Canadian Boreal Forest. Forests 9:159. https://doi.org/10.3390/f9040159

Chae Y, Kang SM, Jeong S-J, Kim B, Frierson DMW (2015) Arctic greening can cause earlier seasonality of Arctic amplification. Geophys Res Lett 42:536–541. https://doi.org/10.1002/2014GL061841

Chen D, Loboda TV (2018) Surface forcing of non-stand-replacing fires in Siberian larch forests. Environ Res Lett 13:045008. https://doi.org/10.1088/1748-9326/aab443

Chen HYH, Luo Y, Reich PB, Searle EB, Biswas SR (2016) Climate change-associated trends in net biomass change are age dependent in western boreal forests of Canada. Ecol Lett 19:1150–1158. https://doi.org/10.1111/ele.12653

Chu T, Guo X (2014) Remote sensing techniques in monitoring post-fire effects and patterns of forest recovery in boreal forest regions: a review. Remote Sens (Basel) 6:470–520. https://doi.org/10.3390/rs6010470

Chu T, Guo X, Takeda K (2016) Remote sensing approach to detect post-fire vegetation regrowth in Siberian boreal larch forest. Ecol Indic 62:32–46. https://doi.org/10.1016/j.ecolind.2015.11.026

Conard SG, Sukhinin AI, Stocks BJ, Cahoon DR, Davidenko EP, Ivanova GA (2002) Determining effects of area burned and fire severity on carbon cycling and emissions in Siberia. Clim Change 55:197–211. https://doi.org/10.1023/A:1020207710195

Coops NC, Hermosilla T, Wulder MA, White JC, Bolton DK (2018) A thirty year, fine-scale, characterization of area burned in Canadian forests shows evidence of regionally increasing trends in the last decade. PLoS One 13:e0197218. https://doi.org/10.1371/journal.pone.0197218

Curtis PG, Slay CM, Harris NL, Tyukavina A, Hansen MC (2018) Classifying drivers of global forest loss. Science 361:1108–1111. https://doi.org/10.1126/science.aau3445

Cyr D, Gauthier S, Bergeron Y, Carcaillet C (2009) Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front Ecol Environ 7:519–524. https://doi.org/10.1890/080088

de Beurs KM, Henebry GM, Owsley BC, Sokolik IN (2018) Large scale climate oscillation impacts on temperature, precipitation and land surface phenology in Central Asia. Environ Res Lett 13:065018. https://doi.org/10.1088/1748-9326/aac4d0

Decree 188 (2019) Guidance on forest reforestation, composition of forest reforestation project, development order of forest reforestation project and introduction of changes in it. (No. 188). Decree of Ministry on Natural Resources and Ecology of the Russian Federation

de Groot WJ, Cantin AS, Flannigan MD, Soja AJ, Gowman LM, Newbery A (2013) A comparison of Canadian and Russian boreal forest fire regimes. For Ecol Manag 294:23–34. The Mega-fire reality. https://doi.org/10.1016/j.foreco.2012.07.033

Donato DC, Fontaine JB, Campbell JL, Robinson WD, Kauffman JB, Law BE (2006) Post-wildfire logging hinders regeneration and increases fire risk. Science 311:352–352. https://doi.org/10.1126/science.1122855

D'Orangeville L, Houle D, Duchesne L, Phillips RP, Bergeron Y, Kneeshaw D (2018) Beneficial effects of climate warming on boreal tree growth may be transitory. Nat Commun 9:3213. https://doi.org/10.1038/s41467-018-05705-4

Duncan BN, Ott LE, Abshire JB, Brucker L, Carroll ML, Carton J, Comiso JC, Dinnat EP, Forbes BC, Gonsamo A, Gregg WW, Hall DK, Ialongo I, Jandt R, Kahn RA, Karpechko A, Kawa SR, Kato S, Kumpula T, Kyrölä E, Loboda TV, McDonald KC, Montesano PM, Nassar R, Neigh CSR, Parkinson CL, Poulter B, Pulliainen J, Rautiainen K, Rogers BM, Rousseaux CS, Soja AJ, Steiner N, Tamminen J, Taylor PC, Tzortziou MA, Virta H, Wang JS, Watts JD, Winker DM, Wu DL (2020) Space-based observations for understanding changes in the Arctic-Boreal Zone. Rev Geophys 58:e2019RG000652. https://doi.org/10.1029/2019RG000652

El-Guellab A, Asselin H, Gauthier S, Bergeron Y, Ali AA (2015) Holocene variations of wildfire occurrence as a guide for sustainable management of the northeastern Canadian boreal forest. For Ecosyst 2:15. https://doi.org/10.1186/s40663-015-0039-2

Enright NJ, Fontaine JB, Bowman DM, Bradstock RA, Williams RJ (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Front Ecol Environ 13:265–272. https://doi.org/10.1890/140231

Ferster CJ, Eskelson BNI, Andison DW, LeMay VM (2016) Vegetation mortality within natural wildfire events in the Western Canadian Boreal Forest: what burns and why? Forests 7:187. https://doi.org/10.3390/f7090187

Flanagan SA, Hurtt GC, Fisk JP, Sahajpal R, Hansen MC, Dolan KA, Sullivan JH, Zhao M (2016) Potential vegetation and carbon redistribution in Northern North America from climate change. Climate 4:2. https://doi.org/10.3390/cli4010002

Flannigan M, Stocks B, Turetsky M, Wotton M (2009) Impacts of climate change on fire activity and fire management in the circumboreal forest. Glob Chang Biol 15:549–560. https://doi.org/10.1111/j.1365-2486.2008.01660.x

Forbes BC, Fauria MM, Zetterberg P (2010) Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. Glob Chang Biol 16:1542–1554. https://doi.org/10.1111/j.1365-2486.2009.02047.x

Frelich LE, Reich PB, Peterson DW (2017) The changing role of fire in mediating the relationships among oaks, grasslands, mesic temperate forests, and boreal forests in the Lake States. J Sustain For 36:421–432. https://doi.org/10.1080/10549811.2017.1296777

Gauthier S, Bernier P, Kuuluvainen T, Shvidenko AZ, Schepaschenko DG (2015) Boreal forest health and global change. Science 349:819–822. https://doi.org/10.1126/science.aaa9092

Giglio L, Randerson JT, van der Werf GR, Kasibhatla PS, Collatz GJ, Morton DC, DeFries RS (2010) Assessing variability and long-term trends in burned area by merging multiple satellite fire products. Biogeosciences 7:1171–1186. https://doi.org/10.5194/bg-7-1171-2010

Gillett NP, Weaver AJ, Zwiers FW, Flannigan MD (2004) Detecting the effect of climate change on Canadian forest fires. Geophys Res Lett 31. https://doi.org/10.1029/2004GL020876

Gitas I, Mitri G, Veraverbeke S, Polychronaki A (2012) Advances in remote sensing of post-fire vegetation recovery monitoring—a review. Remote Sens Biomass-Princ Appl 1:334

Goetz SJ, Bunn AG, Fiske GJ, Houghton RA (2005) Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. Proc Natl Acad Sci USA 102:13521–13525. https://doi.org/10.1073/pnas.0506179102

Goldammer JG, Furyaev V (2013) Fire in ecosystems of boreal Eurasia. Springer

Guay KC, Beck PSA, Berner LT, Goetz SJ, Baccini A, Buermann W (2014) Vegetation productivity patterns at high northern latitudes: a multi-sensor satellite data assessment. Glob Chang Biol 20:3147–3158. https://doi.org/10.1111/gcb.12647

Guo W, Liu H, Wu X (2018) Vegetation greening despite weakening coupling between vegetation growth and temperature over the boreal region. J Geophys Res Biogeosci 123:2376–2387. https://doi.org/10.1029/2018JG004486

Hanes CC, Wang X, Jain P, Parisien M-A, Little JM, Flannigan MD (2018) Fire-regime changes in Canada over the last half century. Can J For Res 49:256–269. https://doi.org/10.1139/cjfr-2018-0293

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853. https://doi.org/10.1126/science.1244693

Hansen WD, Braziunas KH, Rammer W, Seidl R, Turner MG (2018) It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99:966–977. https://doi.org/10.1002/ecy.2181

Harris RMB, Remenyi TA, Williamson GJ, Bindoff NL, Bowman DMJS (2016) Climate–vegetation–fire interactions and feedbacks: trivial detail or major barrier to projecting the future of the Earth system? Wiley Interdiscip Rev Clim Change 7:910–931. https://doi.org/10.1002/wcc.428

Hart SJ, Henkelman J, McLoughlin PD, Nielsen SE, Truchon-Savard A, Johnstone JF (2019) Examining forest resilience to changing fire frequency in a fire-prone region of boreal forest. Glob Chang Biol 25:869–884. https://doi.org/10.1111/gcb.14550

Helbig M, Wischnewski K, Kljun N, Chasmer LE, Quinton WL, Detto M, Sonnentag O (2016) Regional atmospheric cooling and wetting effect of permafrost thaw-induced boreal forest loss. Glob Chang Biol 22:4048–4066. https://doi.org/10.1111/gcb.13348

Héon J, Arseneault D, Parisien M-A (2014) Resistance of the boreal forest to high burn rates. Proc Natl Acad Sci USA 111:13888–13893. https://doi.org/10.1073/pnas.1409316111

Hoecker TJ, Higuera PE (2019) Forest succession and climate variability interacted to control fire activity over the last four centuries in an Alaskan boreal landscape. Landsc Ecol 34:227–241. https://doi.org/10.1007/s10980-018-00766-8

Hogg EH (Ted), Brandt JP, Michaelian M (2008) Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can J For Res 38:1373–1384. https://doi.org/10.1139/X08-001

Huang J, Tardif JC, Bergeron Y, Denneler B, Berninger F, Girardin MP (2010) Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. Glob Chang Biol 16:711–731. https://doi.org/10.1111/j.1365-2486.2009.01990.x

Humber ML, Boschetti L, Giglio L, Justice CO (2019) Spatial and temporal intercomparison of four global burned area products. Int J Digit Earth 12:460–484. https://doi.org/10.1080/17538947.2018.1433727

IPCC (ed) (2013) Atlas of global and regional climate projections. In: Climate change 2013—The physical science basis. Cambridge University Press, Cambridge, pp 1311–1394. https://doi.org/10.1017/CBO9781107415324.029

Johnstone JF, Chapin FS (2006) fire interval effects on successional trajectory in boreal forests of Northwest Canada. Ecosystems 9:268–277. https://doi.org/10.1007/s10021-005-0061-2

Johnstone JF, Chapin FS III, Foote J, Kemmett S, Price K, Viereck L (2004) Decadal observations of tree regeneration following fire in boreal forests. Can J For Res 34:267–273. https://doi.org/10.1139/x03-183

Johnstone JF, Hollingsworth TN, Chapin FS, Mack MC (2010) Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Glob Chang Biol 16:1281–1295. https://doi.org/10.1111/j.1365-2486.2009.02051.x

Johnstone JF, Rupp TS, Olson M, Verbyla D (2011) Modeling impacts of fire severity on successional trajectories and future fire behavior in Alaskan boreal forests. Landsc Ecol 26:487–500. https://doi.org/10.1007/s10980-011-9574-6

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GL, Schoennagel T, Turner MG (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378. https://doi.org/10.1002/fee.1311

Kasischke ES, Turetsky MR (2006) Recent changes in the fire regime across the North American boreal region—Spatial and temporal patterns of burning across Canada and Alaska. Geophys Res Lett 33. https://doi.org/10.1029/2006GL025677

Kauppi PE, Posch M, Pirinen P (2014) Large impacts of climatic warming on growth of boreal forests since 1960. PLoS One 9:e111340. https://doi.org/10.1371/journal.pone.0111340

Keenan TF, Riley WJ (2018) Greening of the land surface in the world's cold regions consistent with recent warming. Nat Clim Change 1. https://doi.org/10.1038/s41558-018-0258-y

Keenan RJ, Reams GA, Achard F, de Freitas JV, Grainger A, Lindquist E (2015) Dynamics of global forest area: results from the FAO Global Forest Resources Assessment 2015. For Ecol

Manag 352:9–20. Changes in global forest resources from 1990 to 2015. https://doi.org/10.1016/j.foreco.2015.06.014

Kharuk VI, Ranson KJ, Dvinskaya ML, Im ST (2011) Wildfires in northern Siberian larch dominated communities. Environ Res Lett 6:045208. https://doi.org/10.1088/1748-9326/6/4/045208

Kharuk VI, Im ST, Oskorbin PA, Petrov IA, Ranson KJ (2013) Siberian pine decline and mortality in southern Siberian mountains. For Ecol Manage 310:312–320. https://doi.org/10.1016/j.foreco.2013.08.042

Kharuk VI, Dvinskaya ML, Petrov IA, Im ST, Ranson KJ (2016) Larch forests of Middle Siberia: long-term trends in fire return intervals. Reg Environ Change 16:2389–2397. https://doi.org/10.1007/s10113-016-0964-9

Kim J-S, Kug J-S, Jeong S-J, Park H, Schaepman-Strub G (2020) Extensive fires in southeastern Siberian permafrost linked to preceding Arctic Oscillation. Sci Adv 6:eaax3308. https://doi.org/10.1126/sciadv.aax3308

Koven CD (2013) Boreal carbon loss due to poleward shift in low-carbon ecosystems. Nat Geosci 6:452–456. https://doi.org/10.1038/ngeo1801

Krawchuk MA, Cumming SG, Flannigan MD (2009) Predicted changes in fire weather suggest increases in lightning fire initiation and future area burned in the mixedwood boreal forest. Clim Change 92:83–97. https://doi.org/10.1007/s10584-008-9460-7

Kukavskaya EA, Soja AJ, Petkov AP, Ponomarev EI, Ivanova GA, Conard SG (2012) Fire emissions estimates in Siberia: evaluation of uncertainties in area burned, land cover, and fuel consumption. Can J For Res 43:493–506. https://doi.org/10.1139/cjfr-2012-0367

Kukavskaya EA, Buryak LV, Ivanova GA, Conard SG, Kalenskaya OP, Zhila SV, McRae DJ (2013) Influence of logging on the effects of wildfire in Siberia. Environ Res Lett 8:045034. https://doi.org/10.1088/1748-9326/8/4/045034

Kukavskaya EA, Buryak LV, Shvetsov EG, Conard SG, Kalenskaya OP (2016) The impact of increasing fire frequency on forest transformations in southern Siberia. For Ecol Manage 382:225–235. https://doi.org/10.1016/j.foreco.2016.10.015

Kurkowski TA, Mann DH, Rupp TS, Verbyla DL (2008) Relative importance of different secondary successional pathways in an Alaskan boreal forest. Can J For Res 38:1911–1923. https://doi.org/10.1139/X08-039

Kuuluvainen T, Aakala T, Várkonyi G (2017) Dead standing pine trees in a boreal forest landscape in the Kalevala National Park, northern Fennoscandia: amount, population characteristics and spatial pattern. For Ecosyst 4:12. https://doi.org/10.1186/s40663-017-0098-7

Lapointe-Garant M-P, Huang J-G, Gea-Izquierdo G, Raulier F, Bernier P, Berninger F (2010) Use of tree rings to study the effect of climate change on trembling aspen in Québec. Glob Chang Biol 16:2039–2051. https://doi.org/10.1111/j.1365-2486.2009.02048.x

Lara MJ, Genet H, McGuire AD, Euskirchen ES, Zhang Y, Brown DRN, Jorgenson MT, Romanovsky V, Breen A, Bolton WR (2016) Thermokarst rates intensify due to climate change and forest fragmentation in an Alaskan boreal forest lowland. Glob Chang Biol 22:816–829. https://doi.org/10.1111/gcb.13124

Lehtonen I, Venäläinen A, Kämäräinen M, Peltola H, Gregow H (2016) Risk of large-scale fires in boreal forests of Finland under changing climate. Nat Hazards Earth Syst Sci 16:239–253. https://doi.org/10.5194/nhess-16-239-2016

Li Y, Sulla-Menashe D, Motesharrei S, Song X-P, Kalnay E, Ying Q, Li S, Ma Z (2017) Inconsistent estimates of forest cover change in China between 2000 and 2013 from multiple datasets: differences in parameters, spatial resolution, and definitions. Sci Rep 7:8748. https://doi.org/10.1038/s41598-017-07732-5

Lindenmayer D, Thorn S, Banks S (2017) Please do not disturb ecosystems further. Nat Ecol Evol 1:1–3. https://doi.org/10.1038/s41559-016-0031

Liu Z (2016) Effects of climate and fire on short-term vegetation recovery in the boreal larch forests of Northeastern China. Sci Rep 6:37572. https://doi.org/10.1038/srep37572

Liu Z, Yang J, Chang Y, Weisberg PJ, He HS (2012) Spatial patterns and drivers of fire occurrence and its future trend under climate change in a boreal forest of Northeast China. Glob Chang Biol 18:2041–2056. https://doi.org/10.1111/j.1365-2486.2012.02649.x

Liu YY, van Dijk AIJM, de Jeu RAM, Canadell JG, McCabe MF, Evans JP, Wang G (2015) Recent reversal in loss of global terrestrial biomass. Nat Clim Change 5:470–474. https://doi.org/10.1038/nclimate2581

Liu Z, Ballantyne AP, Cooper LA (2019) Biophysical feedback of global forest fires on surface temperature. Nat Commun 10:214. https://doi.org/10.1038/s41467-018-08237-z

MacDonald GM, Larsen CPS, Szeicz JM, Moser KA (1991) The reconstruction of boreal forest fire history from lake sediments: a comparison of charcoal, pollen, sedimentological, and geochemical indices. Quat Sci Rev 10:53–71. https://doi.org/10.1016/0277-3791(91)90030-X

Macias Fauria M, Johnson EA (2008) Climate and wildfires in the North American boreal forest. Philos Trans R Soc B Biol Sci 363:2317–2329. https://doi.org/10.1098/rstb.2007.2202

Malevsky-Malevich SP, Molkentin EK, Nadyozhina ED, Shklyarevich OB (2008) An assessment of potential change in wildfire activity in the Russian boreal forest zone induced by climate warming during the twenty-first century. Clim Change 86:463–474. https://doi.org/10.1007/s10584-007-9295-7

Malvar MC, Silva FC, Prats SA, Vieira DCS, Coelho COA, Keizer JJ (2017) Short-term effects of post-fire salvage logging on runoff and soil erosion. For Ecol Manage 400:555–567. https://doi.org/10.1016/j.foreco.2017.06.031

Marchand W, Girardin MP, Gauthier S, Hartmann H, Bouriaud O, Babst F, Bergeron Y (2018) Untangling methodological and scale considerations in growth and productivity trend estimates of Canada’s forests. Environ Res Lett 13:093001. https://doi.org/10.1088/1748-9326/aad82a

McDowell NG, Allen CD (2015) Darcy’s law predicts widespread forest mortality under climate warming. Nat Clim Change 5:669–672. https://doi.org/10.1038/nclimate2641

Mekonnen ZA, Riley WJ, Randerson JT, Grant RF, Rogers BM (2019) Expansion of high-latitude deciduous forests driven by interactions between climate warming and fire. Nat Plants 5:952–958. https://doi.org/10.1038/s41477-019-0495-8

Melvin AM, Celis G, Johnstone JF, McGuire AD, Genet H, Schuur EAG, Rupp TS, Mack MC (2018) Fuel-reduction management alters plant composition, carbon and nitrogen pools, and soil thaw in Alaskan boreal forest. Ecol Appl 28:149–161. https://doi.org/10.1002/eap.1636

Michaelian M, Hogg EH, Hall RJ, Arsenault E (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest: Aspen mortality following severe drought. Glob Chang Biol 17:2084–2094. https://doi.org/10.1111/j.1365-2486.2010.02357.x

Mokhov II, Chernokulsky AV (2010) Regional model assessments of forest fire risks in the Asian part of Russia under climate change. Geogr Nat Resour 31:165–169. https://doi.org/10.1016/j.gnr.2010.06.012

Mollicone D, Achard F, Marchesini LB, Federici S, Wirth C, Leipold M, Rosellini S, Schulze E-D, Valentini R (2002) A remote sensing based approach to determine forest fire cycle: case study of the Yenisei Ridge dark taiga. Tellus B 54:688–695. https://doi.org/10.1034/j.1600-0889.2002.01338.x

Mollicone D, Eva HD, Achard F (2006) Human role in Russian wild fires. Nature 440:436–437. https://doi.org/10.1038/440436a

Monks SA, Arnold SR, Chipperfield MP (2012) Evidence for El Niño–Southern Oscillation (ENSO) influence on Arctic CO interannual variability through biomass burning emissions. Geophys Res Lett 39. https://doi.org/10.1029/2012GL052512

Moreno-Ruiz JA, García-Lázaro JR, Arbelo M, Riaño D (2019) A comparison of burned area time Series in the Alaskan boreal forests from different remote sensing products. Forests 10:363. https://doi.org/10.3390/f10050363

Moser B, Temperli C, Schneiter G, Wohlgemuth T (2010) Potential shift in tree species composition after interaction of fire and drought in the Central Alps. Eur J For Res 129:625–633. https://doi.org/10.1007/s10342-010-0363-6

Mouillot F, Schultz MG, Yue C, Cadule P, Tansey K, Ciais P, Chuvieco E (2014) Ten years of global burned area products from spaceborne remote sensing—a review: analysis of user needs and recommendations for future developments. Int J Appl Earth Obs Geoinformation 26:64–79. https://doi.org/10.1016/j.jag.2013.05.014

Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik DS (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ Res Lett 6:045509. https://doi.org/10.1088/1748-9326/6/4/045509

Myers-Smith IH, Kerby JT, Phoenix GK, Bjerke JW, Epstein HE, Assmann JJ, John C, Andreu-Hayles L, Angers-Blondin S, Beck PSA, Berner LT, Bhatt US, Bjorkman AD, Blok D, Bryn A, Christiansen CT, Cornelissen JHC, Cunliffe AM, Elmendorf SC, Forbes BC, Goetz SJ, Hollister RD, de Jong R, Loranty MM, Macias-Fauria M, Maseyk K, Normand S, Olofsson J, Parker TC, Parmentier F-JW, Post E, Schaepman-Strub G, Stordal F, Sullivan PF, Thomas HJD, Tømmervik H, Treharne R, Tweedie CE, Walker DA, Wilmking M, Wipf S (2020) Complexity revealed in the greening of the Arctic. Nat Clim Change 10:106–117. https://doi.org/10.1038/s41558-019-0688-1

Novenko EY, Tsyganov AN, Volkova EM, Kupriyanov DA, Mironenko IV, Babeshko KV, Utkina AS, Popov V, Mazei YA (2016) Mid- and Late Holocene vegetation dynamics and fire history in the boreal forest of European Russia: a case study from Meshchera Lowlands. Palaeogeogr Palaeoclimatol Palaeoecol 459:570–584. https://doi.org/10.1016/j.palaeo.2016.08.004

Otoda T, Doi T, Sakamoto K, Hirobe M, Nachin B, Yoshikawa K (2013) Frequent fires may alter the future composition of the boreal forest in northern Mongolia. J For Res 18:246–255. https://doi.org/10.1007/s10310-012-0345-2

Ott LAVRA, Mann PCAD, Van Cleve K (2006) Successional processes in the Alaskan boreal forest. Alsk Chang Boreal For 100

Pacé M, Gadet B, Beguin J, Bergeron Y, Paré D (2019) Drivers of boreal tree growth and stand opening: the case of jack pine on sandy soils. Ecosystems. https://doi.org/10.1007/s10021-019-00425-2

Pachauri RK, Allen MR, Barros VR, Broome J, Cramer W, Christ R, Church JA, Clarke L, Dahe Q, Dasgupta P (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC

Padilla M, Stehman SV, Chuvieco E (2014) Validation of the 2008 MODIS-MCD45 global burned area product using stratified random sampling. Remote Sens Environ 144:187–196. https://doi.org/10.1016/j.rse.2014.01.008

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D (2011) A large and persistent carbon sink in the world's forests. Science 333:988–993. https://doi.org/10.1126/science.1201609

Parisien M-A, Parks SA, Krawchuk MA, Flannigan MD, Bowman LM, Moritz MA (2011) Scale-dependent controls on the area burned in the boreal forest of Canada, 1980–2005. Ecol Appl 21:789–805. https://doi.org/10.1890/10-0326.1

Payette S, Delwaide A (2003) Shift of Conifer boreal forest to Lichen–Heath Parkland caused by successive stand disturbances. Ecosystems 6:540–550. https://doi.org/10.1007/PL00021507

Perrault-Hébert M, Boucher Y, Fournier R, Girard F, Auger I, Thiffault N, Grenon F (2017) Ecological drivers of post-fire regeneration in a recently managed boreal forest landscape of eastern Canada. For Ecol Manage 399:74–81. https://doi.org/10.1016/j.foreco.2017.05.026

Piao S, Wang X, Park T, Chen C, Lian X, He Y, Bjerke JW, Chen A, Ciais P, Tømmervik H, Nemani RR, Myneni RB (2020) Characteristics, drivers and feedbacks of global greening. Nat Rev Earth Environ 1:14–27. https://doi.org/10.1038/s43017-019-0001-x

Polar Research Board, Board on Life Sciences, Division on Earth and Life Studies, National Academies of Sciences, Engineering, and Medicine (2019) Understanding Northern latitude vegetation greening and browning: proceedings of a workshop. National Academies Press, Washington, DC. https://doi.org/10.17226/25423

Ponomarev EI, Kharuk VI, Ranson KJ (2016) Wildfires dynamics in Siberian larch forests. Forests 7:125. https://doi.org/10.3390/f7060125

Potapov P, Hansen MC, Stehman SV, Loveland TR, Pittman K (2008) Combining MODIS and Landsat imagery to estimate and map boreal forest cover loss. Remote Sens Environ 112:3708–3719. https://doi.org/10.1016/j.rse.2008.05.006

Potapov P, Turubanova S, Hansen MC (2011) Regional-scale boreal forest cover and change mapping using Landsat data composites for European Russia. Remote Sens Environ 115:548–561. https://doi.org/10.1016/j.rse.2010.10.001

Potapov P, Hansen MC, Laestadius L, Turubanova S, Yaroshenko A, Thies C, Smith W, Zhuravleva I, Komarova A, Minnemeyer S, Esipova E (2017) The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. Sci Adv 3:e1600821. https://doi.org/10.1126/sciadv.1600821

Potter S, Solvik K, Erb A, Goetz SJ, Johnstone JF, Mack MC, Randerson JT, Román MO, Schaaf CL, Turetsky MR, Veraverbeke S, Walker XJ, Wang Z, Massey R, Rogers BM (2020) Climate change decreases the cooling effect from postfire albedo in boreal North America. Glob Chang Biol 26:1592–1607. https://doi.org/10.1111/gcb.14888

Prince SD, Tucker CJ (1986) Satellite remote sensing of rangelands in Botswana II. NOAA AVHRR and herbaceous vegetation. Int J Remote Sens 7:1555–1570. https://doi.org/10.1080/01431168608948953

Reich PB, Sendall KM, Stefanski A, Rich RL, Hobbie SE, Montgomery RA (2018) Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. Nature 562:263. https://doi.org/10.1038/s41586-018-0582-4

Rocha AV, Blakely B, Jiang Y, Wright KS, Curasi SR (2018) Is arctic greening consistent with the ecology of tundra? Lessons from an ecologically informed mass balance model. Environ Res Lett 13:125007. https://doi.org/10.1088/1748-9326/aaeb50

Rogers BM, Randerson JT, Bonan GB (2013) High-latitude cooling associated with landscape changes from North American boreal forest fires. Biogeosciences 10:699–718. https://doi.org/10.5194/bg-10-699-2013

Rogers BM, Soja AJ, Goulden ML, Randerson JT (2015) Influence of tree species on continental differences in boreal fires and climate feedbacks. Nat Geosci 8:228–234. https://doi.org/10.1038/ngeo2352

Rogers BM, Balch JK, Goetz SJ, Lehmann CER, Turetsky M (2020) Focus on changing fire regimes: interactions with climate, ecosystems, and society. Environ Res Lett 15:030201. https://doi.org/10.1088/1748-9326/ab6d3a

Rolstad J, Blanck Y, Storaunet KO (2017) Fire history in a western Fennoscandian boreal forest as influenced by human land use and climate. Ecol Monogr 87:219–245. https://doi.org/10.1002/ecm.1244

Rowe JS, Scotter GW (1973) Fire in the Boreal Forest. Quatern Res 3:444–464. https://doi.org/10.1016/0033-5894(73)90008-2

Sannikov SN, Goldammer JG (1996) Fire ecology of pine forests of Northern Eurasia. In: Goldammer JG, Furyaev VV (eds) Fire in ecosystems of boreal eurasia, forestry sciences. Springer, Dordrecht, pp 151–167. https://doi.org/10.1007/978-94-015-8737-2_11

Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, Dakos V, van de Koppel J, van de Leemput IA, Levin SA, van Nes EH, Pascual M, Vandermeer J (2012) Anticipating critical transitions. Science 338:344–348. https://doi.org/10.1126/science.1225244

Schroeder TA, Wulder MA, Healey SP, Moisen GG (2011) Mapping wildfire and clearcut harvest disturbances in boreal forests with Landsat time series data. Remote Sens Environ 115:1421–1433. https://doi.org/10.1016/j.rse.2011.01.022

Schulze E-D, Wirth C, Mollicone D, Ziegler W (2005) Succession after stand replacing disturbances by fire, wind throw, and insects in the dark Taiga of Central Siberia. Oecologia 146:77–88. https://doi.org/10.1007/s00442-005-0173-6

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D, Petr M, Honkaniemi J, Lexer MJ, Trotsiuk V, Mairota P, Svoboda M, Fabrika M, Nagel TA, Reyer CPO (2017) Forest disturbances under climate change. Nat Clim Change 7:395

Shuman JK, Foster AC, Shugart HH, Hoffman-Hall A, Krylov A, Loboda T, Ershov D, Sochilova E (2017) Fire disturbance and climate change: implications for Russian forests. Environ Res Lett 12:035003. https://doi.org/10.1088/1748-9326/aa5eed

Shvetsov EG, Kukavskaya EA, Buryak LV (2016) Satellite monitoring of the state of forest vegetation after fire impacts in the Zabaikal region. Contemp Probl Ecol 9:702–710. https://doi.org/10.1134/S1995425516060123

Shvetsov EG, Kukavskaya EA, Buryak LV, Barrett K (2019) Assessment of post-fire vegetation recovery in Southern Siberia using remote sensing observations. Environ Res Lett 14:055001. https://doi.org/10.1088/1748-9326/ab083d

Soja A, Shugart H, Sukhinin A, Conard S, Stackhouse P Jr (2006) Satellite-derived mean fire return intervals as indicators of change in Siberia (1995–2002). Mitig Adapt Strat Glob Chang 11:75–96. https://doi.org/10.1007/s11027-006-1009-3

Soja AJ, Tchebakova NM, French NHF, Flannigan MD, Shugart HH, Stocks BJ, Sukhinin AI, Parfenova EI, Chapin FS, Stackhouse PW (2007) Climate-induced boreal forest change: predictions versus current observations. Glob Planet Change 56:274–296. Northern Eurasia regional climate and environmental change. https://doi.org/10.1016/j.gloplacha.2006.07.028

Spittlehouse DL (2005) Integrating climate change adaptation into forest management. For Chron 81:691–695. https://doi.org/10.5558/tfc81691-5

Splawinski TB, Cyr D, Gauthier S, Jetté J-P, Bergeron Y (2019) Analyzing risk of regeneration failure in the managed boreal forest of northwestern Quebec. Can J For Res 49:680–691. https://doi.org/10.1139/cjfr-2018-0278

Stephens SL, Burrows N, Buyantuyev A, Gray RW, Keane RE, Kubian R, Liu S, Seijo F, Shu L, Tolhurst KG, van Wagtendonk JW (2014) Temperate and boreal forest mega-fires: characteristics and challenges. Front Ecol Environ 12:115–122. https://doi.org/10.1890/120332

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT (2018) Evidence for declining forest resilience to wildfires under climate change. Ecol Lett 21:243–252. https://doi.org/10.1111/ele.12889

Stralberg D, Wang X, Parisien M-A, Robinne F-N, Sólymos P, Mahon CL, Nielsen SE, Bayne EM (2018) Wildfire-mediated vegetation change in boreal forests of Alberta, Canada. Ecosphere 9: e02156. https://doi.org/10.1002/ecs2.2156

Suarez F, Binkley D, Kaye MW, Stottlemyer R (1999) Expansion of forest stands into tundra in the Noatak National Preserve, northwest Alaska. Écoscience 6:465–470. https://doi.org/10.1080/11956860.1999.11682538

Sulla-Menashe D, Woodcock CE, Friedl MA (2018) Canadian boreal forest greening and browning trends: an analysis of biogeographic patterns and the relative roles of disturbance versus climate drivers. Environ Res Lett 13:014007. https://doi.org/10.1088/1748-9326/aa9b88

Svensson J, Andersson J, Sandström P, Mikusiński G, Jonsson BG (2019) Landscape trajectory of natural boreal forest loss as an impediment to green infrastructure. Conserv Biol 33:152–163. https://doi.org/10.1111/cobi.13148

Syphard AD, Sheehan T, Rustigian-Romsos H, Ferschweiler K (2018) Mapping future fire probability under climate change: does vegetation matter? PLoS One 13:e0201680. https://doi.org/10.1371/journal.pone.0201680

Taboada A, Fernández-García V, Marcos E, Calvo L (2018) Interactions between large high-severity fires and salvage logging on a short return interval reduce the regrowth of fire-prone serotinous forests. For Ecol Manage 414:54–63. https://doi.org/10.1016/j.foreco.2018.02.013

Tape KD, Lord R, Marshall H-P, Ruess RW (2010) Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. Écoscience 17:186–193. https://doi.org/10.2980/17-2-3323

Theil H (1950) A rank-invariant method of linear and polynomial regression analysis, Part 3. Presented at the proceedings of Koninalijke Nederlandse Akademie van Weinenschatpen A, pp 1397–1412

Thorn S, Bässler C, Brandl R, Burton PJ, Cahall R, Campbell JL, Castro J, Choi C-Y, Cobb T, Donato DC, Durska E, Fontaine JB, Gauthier S, Hebert C, Hothorn T, Hutto RL, Lee E-J, Leverkus AB, Lindenmayer DB, Obrist MK, Rost J, Seibold S, Seidl R, Thom D, Waldron K, Wermelinger B, Winter M-B, Zmihorski M, Müller J (2018) Impacts of salvage logging on biodiversity: a meta-analysis. J Appl Ecol 55:279–289. https://doi.org/10.1111/1365-2664.12945

Thurner M, Beer C, Ciais P, Friend AD, Ito A, Kleidon A, Lomas MR, Quegan S, Rademacher TT, Schaphoff S, Tum M, Wiltshire A, Carvalhais N (2017) Evaluation of climate-related carbon turnover processes in global vegetation models for boreal and temperate forests. Glob Chang Biol 23:3076–3091. https://doi.org/10.1111/gcb.13660

Tucker CJ, Vanpraet CL, Sharman MJ, Van Ittersum G (1985) Satellite remote sensing of total herbaceous biomass production in the senegalese sahel: 1980–1984. Remote Sens Environ 17:233–249. https://doi.org/10.1016/0034-4257(85)90097-5

Turetsky MR, Kane ES, Harden JW, Ottmar RD, Manies KL, Hoy E, Kasischke ES (2011) Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. Nat Geosci 4:27–31. https://doi.org/10.1038/ngeo1027

Turetsky MR, Benscoter B, Page S, Rein G, van der Werf GR, Watts A (2015) Global vulnerability of peatlands to fire and carbon loss. Nat Geosci 8:11–14. https://doi.org/10.1038/ngeo2325

Veraverbeke S, Rogers BM, Goulden ML, Jandt RR, Miller CE, Wiggins EB, Randerson JT (2017) Lightning as a major driver of recent large fire years in North American boreal forests. Nat Clim Change 7:529–534. https://doi.org/10.1038/nclimate3329

Walker XJ, Baltzer JL, Cumming SG, Day NJ, Ebert C, Goetz S, Johnstone JF, Potter S, Rogers BM, Schuur EAG, Turetsky MR, Mack MC (2019) Increasing wildfires threaten historic carbon sink of boreal forest soils. Nature 572:520–523. https://doi.org/10.1038/s41586-019-1474-y

Ward DS, Shevliakova E, Malyshev S, Lamarque J-F, Wittenberg AT (2016) Variability of fire emissions on interannual to multi-decadal timescales in two Earth System models. Environ Res Lett 11:125008. https://doi.org/10.1088/1748-9326/11/12/125008

Wessels KJ, Prince SD, Zambatis N, MacFadyen S, Frost PE, Zyl DV (2006) Relationship between herbaceous biomass and 1-km2 Advanced Very High Resolution Radiometer (AVHRR) NDVI in Kruger National Park, South Africa. Int J Remote Sens 27:951–973. https://doi.org/10.1080/01431160500169098

Whitman E, Parisien M-A, Thompson DK, Flannigan MD (2018) Topoedaphic and forest controls on post-fire vegetation assemblies are modified by fire history and burn severity in the Northwestern Canadian Boreal Forest. Forests 9:151. https://doi.org/10.3390/f9030151

Whitman E, Parisien M-A, Thompson DK, Flannigan MD (2019) Short-interval wildfire and drought overwhelm boreal forest resilience. Sci Rep 9:1–12. https://doi.org/10.1038/s41598-019-55036-7

Worrall JJ, Rehfeldt GE, Hamann A, Hogg EH, Marchetti SB, Michaelian M, Gray LK (2013) Recent declines of Populus tremuloides in North America linked to climate. For Ecol Manage 299:35–51. https://doi.org/10.1016/j.foreco.2012.12.033

Wotton BM, Nock CA, Flannigan MD (2010) Forest fire occurrence and climate change in Canada. Int J Wildland Fire 19:253–271. https://doi.org/10.1071/WF09002

Wotton BM, Flannigan MD, Marshall GA (2017) Potential climate change impacts on fire intensity and key wildfire suppression thresholds in Canada. Environ Res Lett 12:095003. https://doi.org/10.1088/1748-9326/aa7e6e

Xu L, Myneni RB, Iii FSC, Callaghan TV, Pinzon JE, Tucker CJ, Zhu Z, Bi J, Ciais P, Tømmervik H, Euskirchen ES, Forbes BC, Piao SL, Anderson BT, Ganguly S, Nemani RR, Goetz SJ, Beck PSA, Bunn AG, Cao C, Stroeve JC (2013) Temperature and vegetation seasonality diminishment over northern lands. Nat Clim Change 3:581–586. https://doi.org/10.1038/nclimate1836

Yang J, Pan S, Dangal S, Zhang B, Wang S, Tian H (2017) Continental-scale quantification of post-fire vegetation greenness recovery in temperate and boreal North America. Remote Sens Environ 199:277–290. https://doi.org/10.1016/j.rse.2017.07.022

Young AM, Higuera PE, Duffy PA, Hu FS (2017) Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. Ecography 40:606–617. https://doi.org/10.1111/ecog.02205

Zhang N, Yasunari T, Ohta T (2011) Dynamics of the larch taiga–permafrost coupled system in Siberia under climate change. Environ Res Lett 6:024003. https://doi.org/10.1088/1748-9326/6/2/024003

Zhu Z, Piao S, Myneni RB, Huang M, Zeng Z, Canadell JG, Ciais P, Sitch S, Friedlingstein P, Arneth A, Cao C, Cheng L, Kato E, Koven C, Li Y, Lian X, Liu Y, Liu R, Mao J, Pan Y, Peng S, Peñuelas J, Poulter B, Pugh TAM, Stocker BD, Viovy N, Wang X, Wang Y, Xiao Z, Yang H, Zaehle S, Zeng N (2016) Greening of the Earth and its drivers. Nat Clim Change 6:791. https://doi.org/10.1038/nclimate3004

Zhu C, Kobayashi H, Kanaya Y, Saito M (2017) Size-dependent validation of MODIS MCD64A1 burned area over six vegetation types in boreal Eurasia: large underestimation in croplands. Sci Rep 7. https://doi.org/10.1038/s41598-017-03739-0

A Paleo-perspective on Ecosystem Collapse in Boreal North America

5

Serge Payette

Abstract

The boreal forest covers about one-third of the world's forested area. Ecosystem creation and ecosystem collapse are common components of the long-term evolution of the boreal forest fueled by the ever-changing climatic and geophysical conditions since the last glacial period. After the late Pleistocene characterized by abrupt climatic changes, ecosystem building of the boreal biota prevailed from early- to mid-Holocene times (from 10,000 to 4000 years before present), including forest and peatland growth and expansion from south to north towards the Arctic tundra. Large-scale collapse of the dominant terrestrial ecosystems occurred after the mid-Holocene caused by the progressive decrease of orbitally forced solar radiation. Post-fire deforestation during the late Holocene, especially during the Little Ice Age (particularly from the end of the sixteenth century to the mid-nineteenth century), occurred in the northern part of the boreal forest with the creation of subarctic tundra covering the exposed summits and snow-patch environments on downwind side of ridges. Permafrost also expanded in wetlands with the creation of palsas and extensive peat plateaus. Human-induced post-Little Ice Age warming is unparalleled at the scale of the Holocene and is now significantly impacting the cold-prone ecosystems of the northern part of the boreal forest. Their changes and replacement by novel ecosystems adapted to the new climate are already detectable. Variable tree line advances and shrubification of forest-tundra and Arctic tundra environments across North America and Eurasia are presently the main ecosystem responses, with large-scale permafrost decay in subarctic and Arctic wetlands, to the continuous and increased warming of the twentieth and the twenty-first centuries. Fire,

---

S. Payette (✉)
Department of Biology, Université Laval, Quebec City, QC, Canada

Northern Research Center (Centre d'études nordiques), Université Laval, Quebec City, QC, Canada
e-mail: serge.payette@bio.laval.ca

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_5

the principal disturbance factor of ecosystems after climate is bound to affect profoundly the integrity of most mesic and dry plant communities. It is expected that the fire regime of the northern part and southern part of the boreal forest will cause extensive changes and severe damage to northern ecosystems, more so if precipitation amounts are reduced during this century. Greater damage to the forest is anticipated if this change of the fire regime is accompanied by an increase of human impact.

5.1 Introduction

Human-induced climate change was a little-discussed topic in the early 1970s. At that time international meetings on Quaternary and climate sciences were more focused on the question of when the present interglacial would end and the next full continental glaciation begin (Kukla et al. 1972); the answer was, apparently, about 18,800 years from then (Mörner 1972). Little attention was devoted to the slow warming trend documented since the mid-1800s following the Little Ice Age (Grove 1988). However, a few geophysicists began to recognize the potential impact of future increases in atmospheric carbon dioxide would have on the climate in the following decades and centuries and the 'perpetuation of the present interglacial period' (Mitchell 1972). Whatever the focus, whether on the end of the present interglacial, the next glacial episode or post-Little ice Age warming, the earth surface is continuously reshaped by disturbances that give rise to a series of parallel episodes of ecosystem creation and ecosystem collapse. Every life includes a birth, a more or less long developmental life and an ultimate collapse. The same fundamental process of a lifespan which maintenance depends on the duration of 'stable' environmental condition operates in every ecosystem on the planet earth.

A straightforward definition of collapse refers to 'a transformation of identity, loss of defining features, and/or replacement by a novel ecosystem' (Bland et al. 2018). The decline in populations of keystone ecosystem structures is among the marked changes in local and regional conditions that cause a state of collapse. A collapsed ecosystem is one in which major changes in structural and functional conditions occur either irreversibly or reversibly but in a time- and energy-consuming process (Lindenmayer et al. 2016). As a result, collapsed ecosystems often show a loss of biodiversity in terms of reduced number and variable abundance of species.

The collapse of ecosystems is a natural ecological event in the history of the biosphere. A continuous process of ecosystem creation and extirpation has always existed in terrestrial biomes, from the Equator to the Poles, during the current glacial-interglacial period. To properly address the collapse component of the biosphere we need to consider the spatiotemporal development of the dominant ecosystems in each biome. In this chapter, I focus on the boreal biome covering about one-third of the world's forested area (Fig. 5.1), with an emphasis on the North American boreal forest, and the life history of the dominant ecosystems. The main objective here is to

Fig. 5.1 The global boreal forest

show that ecosystem collapse is a common feature of boreal forest evolution throughout the ages because of the ever-changing geophysical conditions at the earth's surface. Ecosystem collapse after deglaciation, from the late Pleistocene to present time, is addressed hereafter with an emphasis on the influence of climate and associated local and regional disturbances on the long-term evolution of the boreal forest, from its creation several thousand years ago to its present condition. I will also focus on the present human-induced climate change and its considerable impact on boreal ecosystems, particularly at the northern fringe bordering the Arctic tundra. I will show how substantial the building and transformation of northern ecosystems have been over the last centuries, and how this suggests their imminent transformation and replacement by novel ecosystems adjusted to the new climate.

5.2 Ecosystem Collapse During the Late Pleistocene

5.2.1 Abrupt Climatic Changes

Well before the last glaciation, boreal vegetation occurred in the Arctic during the Pliocene-Pleistocene transition, particularly in Greenland and the Canadian Arctic Archipelago (Funder et al. 1985; Bennike and Böcher 1990), and during the Middle Pleistocene interglacials (Past Interglacials Working Group of Pages 2016) as well as the last interglacial (130–100k years ago) in Greenland (Bennike and Böcher 1990). The glacial part of the last glacial-interglacial period was affected recurrently by abrupt climatic changes caused by the spatiotemporal dynamics of continental ice (e.g. the Laurentide and Fennoscandian ice sheets) in close association with the nearby Atlantic Ocean (Bradley 2014). After the Last Glacial Maximum from 26 to 20 ka (Clark et al. 2009), the late Pleistocene was the theater of abrupt climatic changes that, at the time, resulted in the rise and fall of tundra and boreal ecosystems of short duration on both sides of the Atlantic Ocean (Woillard 1978; Levesque et al. 1994; Mayle and Cwynar 1995). Successive creation and destruction of terrestrial ecosystems were common over the last glacial cycle south of the ice border (Fig. 5.2a1). The end of the period of abrupt climatic changes coincided with the Younger Dryas stadial between 13,000 and 11,700 years ago on both sides of the Atlantic Ocean (Mayle and Cwynar 1995; Brauer et al. 2008). Tundra vegetation and boreal forest close to the glacier ice margin formed contiguous communities that replaced each other in a few centuries. The collapse of both vegetation types according to ambient climatic conditions was not severe enough to eradicate the dominant arctic and boreal species; it was rather a reshuffling of plant functional groups according to local environmental conditions (Mayle and Cwynar 1995). With the increase of incoming solar radiation after the Younger Dryas, progressive deglaciation of the Laurentide ice sheet (Broecker et al. 1989; Dyke 2004) and the onset of the Holocene period 11,700 years ago (Berger 1978; Walker et al. 2012; Bradley 2014), tundra vegetation was extirpated from lowland sites and replaced by boreal vegetation (Fig. 5.2a, b).

5.2.2 Human Disturbance

The collapse of several late Pleistocene ecosystems, from open to closed vegetation covers, has often been attributed to human interference through massive extinction of the megafauna. The most likely causes of the collapse are the combined influence of overkilling and habitat alteration coinciding with a time of rapid climatic changes that occurred on several continents (Zimov et al. 1995; Miller et al. 2005; Koch and Barnosky 2006). The continent-scale extinction of the North American megafauna was one of the main driving forces of the collapse of open herbivore-prone treeless habitats and the shift to dense plant covers of herbivore-less boreal and temperate habitats that promoted higher biomass accumulation and increased fire frequency

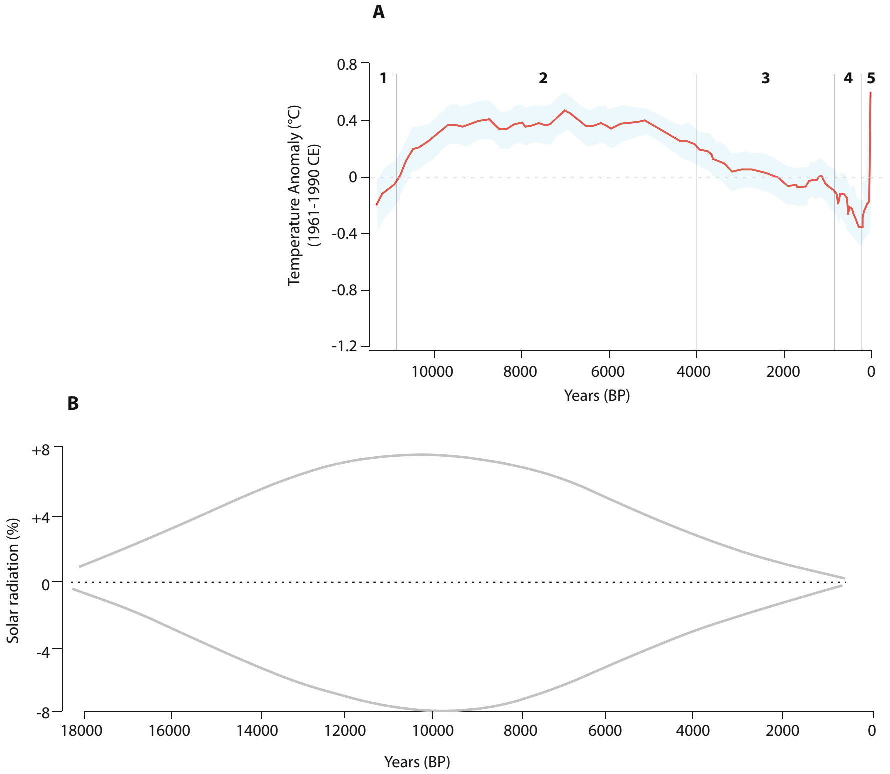


Fig. 5.2 (**A**) Reconstruction of globally stacked hemispheric temperature anomalies for the late Pleistocene and Holocene periods (including one sigma uncertainty in blue). Numbers refer to the following. (1) Late Pleistocene; (2) Early- to mid-Holocene; (3) Late Holocene; (4) Little Ice Age; (5) Warming during the nineteenth to twenty-first centuries. Modified from Marcott et al. (2013). (**B**) Insolation anomalies for the northern hemisphere for summer (upper curve) and winter (lower curve) as a percentage difference from 18,000 years BP (not calibrated) to the present. Modified from Bradley (2014)

(Gill et al. 2009). These events occurred at the transition of the late Pleistocene with the Holocene.

5.3 Ecosystem Building During Early- to Mid-Holocene

The Holocene period is subdivided into three parts (Walker et al. 2012). The first part, the early Holocene, ranged between 11,700 and 8200 years ago, and its end is directly associated with the cooling 8.2K event (Alley and Ágústsdóttir 2005). The second part of the period, the mid-Holocene, started after the 8.2K event and ended about 4200 years ago (Walker et al. 2012). The late Holocene then followed from 4200 years ago to present.

5.3.1 Creation of the Boreal Forest Environment

Most boreal forest ecosystems were developed during the period extending from early- to mid-Holocene, after glacier ice covering the northern part of the northern hemisphere melted (Dyke 2004; Occhietti et al. 2011). Tree migrating from ice-free refugia in Beringia, Siberia and south of the ice margin readily invaded barren soils and tundra communities (Davis 1983; Ritchie et al. 1983; Ritchie 1987; Macdonald and Cwynar 1991; Payette and Lavoie 1994; Kremenetski et al. 1998; Kullman 2002, 2008; Macdonald et al. 2008; Binney et al. 2009), including those in southern Greenland (Fredskild 1991; Normand et al. 2013). Tree spread and forest establishment varied from 6 to more than 26 km century^{-1} for mid- to late successional and early successional trees in Europe (Feurdean et al. 2013), because of proximity of tree sources in late-glacial Beringia (Zazula et al. 2006) and unglaciated southern Europe (Tzedakis et al. 2013; de Lafontaine et al. 2014) and northern Siberia (Kremenetski et al. 1998). On the other side of the Atlantic Ocean and according to radiocarbon-dated macrofossils, the rate of post-glacial spread of Jack pine (*Pinus banksiana*), an early successional tree species, was rather rapid in eastern Canada, 25–30 km century^{-1} during the early Holocene and 10–11 km century^{-1} during the late Holocene (Payette and Frégeau 2019). Biotic velocities of latitudinal tree displacement, as shown here by Jack pine migration (Payette and Frégeau 2019), were indeed faster when climate was warmer during the early Holocene (Ordonez and Williams 2013). Suitable soil conditions, abundance of empty niches and warm climatic conditions associated with solar radiation 8% greater than at present were also major factors for successful forest establishment in remote northern habitats (Berger 1978; Ritchie et al. 1983; Bradley 2014; Fig. 5.2a2, b).

Northern boreal forests located east of Hudson Bay established more recently, about 5000-7000 years ago, because of late deglaciation (Richard et al. 1982; Lamb 1985; Gajewski et al. 1993; Occhietti et al. 2011). This period, from the early Holocene to about 3000–4000 years ago, was one of construction and maintenance of forest ecosystems mainly through post-fire succession (Carcaillet et al. 2001; Fastie and Lloyd 2003; Gavin et al. 2007; de Lafontaine and Payette 2011; Couillard et al. 2013; Payette and Frégeau 2019). Most well-drained hill summits, slopes and valley bottoms covered by alluvial and relatively thick glacial deposits (till) were colonized by conifer and mixed broadleaf-conifer forests able to regenerate freely after stand disturbances. Regeneration failures after the passage of fires were less frequent, and rather unusual given favorable warmth and soil moisture. Forest resilience (Peterson et al. 1998), i.e., the ability of a forest to recover after an environmental disturbance with the same composition, structure and functions, was maximal during this period (Engstrom and Hansen 1985; Lamb 1985; Ritchie 1987; Cwynar and Spear 1991; Carcaillet et al. 2001; Couillard et al. 2013; Frégeau et al. 2015; Fréchette et al. 2018).

5.3.2 Peatland Expansion

Peatlands also developed freely during the early Holocene, immediately after deglaciation in boreal North America and Eurasia (Foster and King 1984; Couillard and Payette 1985; Glaser and Janssens 1986; Foster and Fritz 1987; Charman 2002; Bauer et al. 2003; Kuhry and Turunen 2006; Macdonald et al. 2006; Gorham et al. 2007; Mäkilä and Moisanen 2007; Beaulieu-Audy et al. 2009; Lavoie et al. 2009; Jones and Yu 2010; Rydin and Jeglum 2013; Magnan et al. 2014). Common hydroseral processes (succession of plant communities in wet environments) in boreal peatlands generally proceeded directly as carbon (C) sinks from the minerotrophic stage (fen development) to the ombrotrophic stage (*Sphagnum* bog development) (Glaser and Janssens 1986; Vitt and Chee 1990; Williams et al. 2011), and less frequently without the transitional fen stage in extreme, moist, subarctic environments (Payette 1988). Latitudinal distribution of the two main peatland types shows a neat predominance of bogs in the southern part and fens in the northern part of the boreal biome (Gore 1983). The development of peatlands has been a continuous, progressive process of peat infilling and C sequestration, although at a variable rate depending on local topography and sedimentary conditions (Frolking and Roulet 2007; Weckström et al. 2010; Van Bellen et al. 2011; Schulze et al. 2015). Most peatlands reached their spatial, topographical growth limits from early- to mid-Holocene in northern ice-free refugia and boreal areas that deglaciated early (Macdonald et al. 2006; Jones and Yu 2010), whereas full peatland development was delayed until the millennia following the mid-Holocene in late-deglaciated areas in northeastern North America (Payette 1984; Gorham et al. 2007).

5.3.3 Southern Conifer Forest and Insects

Overall, and except for the cooling event associated with catastrophic drainage of large proglacial lakes to the North Atlantic Ocean 8200 years ago (Alley et al. 1997; Barber et al. 1999), which had no direct significant impact on the boreal biome, forest ecosystems developed freely during the first half of the Holocene. Only south of the boreal forest did a major event that resembled a collapse occurred during the mid-Holocene. This event corresponds to the decline of hemlock (*Tsuga canadensis*), a widespread member of the boreo-temperate tree flora of the eastern North-American forest. The decline was most likely caused by successive insect outbreaks of the spruce budworm (*Choristoneura fumiferana* Clem.) and the hemlock looper (*Lambdina fiscellaria fiscellaria* Guen.) (Bhiry and Filion 1996). Although it occurred within a short period of time, the continent-scale drop of hemlock populations had an impact on the tree composition of temperate forests (Anderson et al. 1986; Bhiry and Filion 1996; Fuller 1998). Except for the two major defoliation events of hemlock decline at 4910 ± 90 and 4200 ± 100 year B.P (Bhiry and Filion 1996), the abundance of spruce budworm populations varied frequently during the Holocene (Simard et al. 2006; Lavoie et al. 2009; Navarro et al. 2018) without causing regeneration damage to conifer forests, except in the late Holocene

(Jasinski and Payette 2005). Spruce budworm is by far the principal agent of biotic disturbance in the North-American boreal forest. Except for the larch sawfly (*Pristiphora erichsonii* Hartig), which defoliates regularly eastern larch (*Larix laricina*), a deciduous conifer in boreal North America (Jardon et al. 1994; Filion et al. 2010), spruce budworm is presently the main defoliator of boreal conifers (with balsam fir, *Abies balsamea*, as the primary host species, and spruces, *Picea* spp., as secondary host species). The insect causes massive tree defoliation and mortality during regional-scale outbreaks (Holling 1992), which have occurred three times over the last 100 years (Blais 1983; Jardon et al. 2003). Outbreaks are closely related to climatic conditions. The northern limit of outbreaks is well south of the range of host species, and warmer climate in this century suggests that outbreak severity and duration will increase in the northern part of the boreal forest in central and eastern Canada (Gray 2008).

5.4 Ecosystem Collapse After the Mid-Holocene

The progressive reduction of solar radiation associated with orbital forcing over the northern hemisphere (Berger 1978) is among the main drivers of continent-scale cooling from the mid-Holocene to the present (Bradley 2014; Fig. 5.2a3, b). Decreasing temperatures generally accompanied by variable precipitation regimes progressively changed the functioning of ecosystems. This period of major ecosystem change is at the origin of the collapse of several forests especially in the northern part of the biome. The onset of large-scale ecosystem collapse generally began after 4000 cal. years BP, in the form of compounding and cascading stand disturbances, often a deadly combination of events mainly caused by climate cooling–fire interactions in the northern part and climate–fire–insect interactions in the southern part of the biome, respectively. Logging, a recent, novel disturbance in the southern boreal forest is another factor that may affect the integrity of the forest ecosystem.

5.4.1 Ecosystem Collapse in the Northern Part of the Boreal Forest

5.4.1.1 Climate–Fire Interactions

After 3500 years before present, the northern part of the boreal biome progressively lost large tracts of forests due to post-fire regeneration failure. Viable seed banks were reduced due to cooler growing seasons, first on the most elevated hilltops near the Arctic tree line and then southward along the main hill slopes. Opening of the forest cover created lichen-shrub tundra communities at the origin of the forest-tundra ecotone (Payette and Gagnon 1985; Asselin and Payette 2005; Williams et al. 2011; Gajewski 2019). Large-scale deforestation of the northernmost parts of the biome and the resulting creation of tundra-like ecosystems continued until the present time, with increased intensity over the last millennium, particularly during the Little Ice Age (Arseneault and Payette 1997). A greater loss of forest cover occurred near the Arctic tree line, accompanied by a shift in conifer stands to lower altitudes and the consequent formation of depressed subarctic tree lines (Payette et al. 2001; Fig. 5.3). Tree removal modified site conditions, reducing the reestablishment of the trees, which further affected the conditions necessary for tree regeneration. A feedback to a possible irreversible state may shift the sites to less complex ecosystems like shrub tundra in which the original forests do not recover (Runyan et al. 2012; Johnstone et al. 2016).

5.4.1.2 Collateral Effects of Forest Collapse

Depending on the intensity and severity of fire disturbances, ecosystem collapse resulting from the shift of forest to tundra communities on hilltops and slopes has been the key process at the origin of novel ecosystems across the forest-tundra ecotone. The forest-to-tundra shift triggered a chain of ecological events exacerbated by the winter environment. Natural deforestation of hilltops profoundly modified the spatial dynamics of the snow cover and the correlative thermal regime. Natural forest removal induces snow deflation and transportation away from the newly formed wind-exposed tundra summits (Fig. 5.4a). Significant changes in wind, temperature and snow conditions (Rouse and Kershaw 1971; Rouse 1976; Arseneault and Sirois 1990) produce a colder environment for tree establishment, survival and growth. Measurements of climatic parameters in a conifer forest and in a treeless post-fire tundra environment at the tree line in boreal Finland show marked ecosystem changes. Fire-induced forest loss increased wind velocity by 60%, lowered evapotranspiration and changed the soil thermal regime due to a snow depth reduced by 20–30 cm, all of which are site conditions that preclude forest recovery (Vajda and Venäläinen 2005). Snow depth diminishes greatly on deforested summits, whereas it increases significantly on lee sides (downwind side of ridges), particularly in north- to southeast-exposed slopes of the North-American Precambrian plateau.

As a result, post-fire collapse of summit forests induced the formation of two novel ecosystems. The first corresponds to a wind-exposed lichen-shrub community retaining only a thin, less-insulating snow cover that causes permafrost to grow and expand as frost-heaved (periglacial) features at the soil surface. The origin of the second ecosystem, a post-fire chionophilous community, often called a snow patch environment, is composed of a mixture of small arctic-alpine and boreal plants adapted to thick snow cover caused by snow drifting down from deforested hilltops (Truchon-Savard et al. 2019; Fig. 5.4a). Thick snow accumulated in snow patches melts late in summer, thus preventing tree establishment. Similar collateral effects of ecosystem transformation also occur in snowier parts of the southern boreal environment. In the current era, extensive stand disturbances including total tree removal due to logging also markedly change local snow dynamics, and cause snow avalanches on steep lee slopes (Germain et al. 2005). Avalanche activity is controlled by woody vegetation that grows to a height sufficiently for reducing snow movement.

5.4.1.3 Extensive Collapse of Woodlands During the Little Ice Age

In addition to the negative impact of fire disturbance, contributing to the reduction in extent of northernmost forests, regional-scale collapse of highland woodlands also

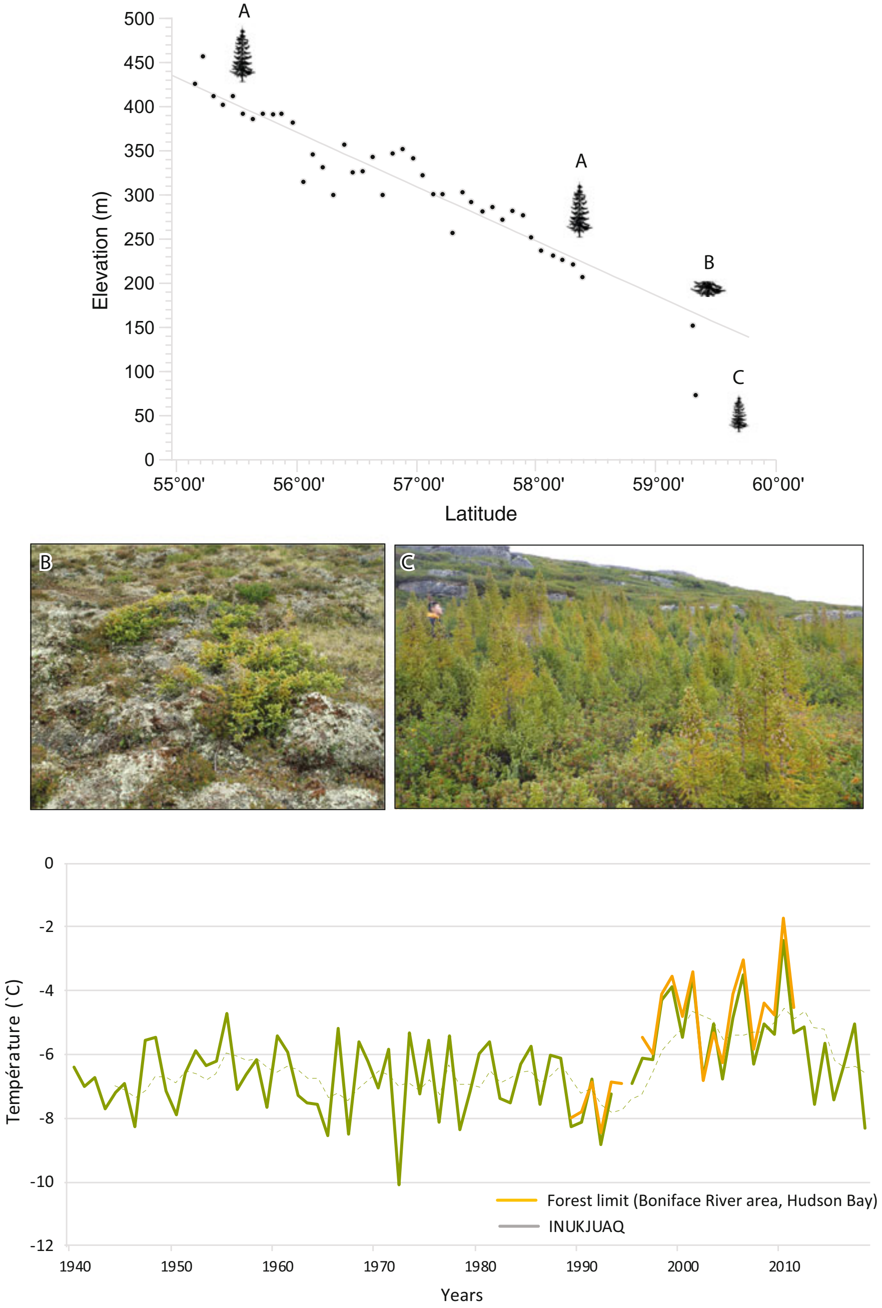


Fig. 5.3 Upper panel: Maximum altitude of conifer (black spruce, *Picea mariana*) forest stands (black circles) according to latitude from the northern boreal forest to the Arctic tree line (modified from Payette et al. 2001) (**A**) and tree species limit in Arctic tundra (**B**, **C**). Middle panel: Shrubby black spruce (**B**) and newly developed 'Arctic tree grove' (**C**) at the northernmost limit of the tree species. Small trees (**C**) are >2.5 m high (see research scientist on the left side of the photo) and are

occurred during the Little Ice Age (Figs. 5.2a4 and 5.4b). Over several hundred km^2, mature white spruce (*Picea glauca*) trees of open forests on the exposed high plateau of northeastern North America (northern Quebec and Labrador) died off over several years, through progressive foliage attrition during severe winters, particularly in the first part of the nineteenth century (Payette 2007). The collapse of highland woodlands was probably due to climatic causes, without interference from other allogenic (abiotic) disturbances. Complete defoliation and frost-killed vegetative buds on the exposed trees were the proximal causes for tree death and the recent shift of highland subarctic woodlands to lichen-shrub tundra communities.

5.4.1.4 Wetland Ecosystem Collapse

Northern peatlands that developed during the first half of the Holocene experienced drastic changes of their surface extent and features during the second half of the period. The main changes were associated with permafrost aggradation, particularly over the last millennium.

Between 9 and 14% of the exposed land surface north of 60°N is underlain by permafrost (Gruber 2012). The tipping point for permafrost aggradation and expansion on exposed hilltops and lowland subarctic peatlands is the drier and colder climate that prevailed during the late Holocene (Bhiry et al. 2007), particularly during the Little Ice Age in northern Quebec (Cyr and Payette 2010). Up-thrusting of the peat layer due to ice growth resulted in the creation of a new ecosystem in which up-lifted, snow-free, dry peat covered by lichens, shrubs, and small trees formed palsas (small permafrost mounds covered by peat; Seppälä 2011) and peat plateaus (large permafrost mounds covered by peat). The surface of peat plateaus is often fragmented into residual palsas (Figs. 5.2a4 and 5.4c, k). More than 75% of the surface of several subarctic peatlands are up-lifted, and the remainder is composed of herbaceous fen vegetation colonized by small conifers. Similar to the chain of events described for the upland woodland/exposed tundra shift, tree loss in wooded peatlands triggered permafrost growth and inception of subarctic ice wedges, one of the iconic features of the frozen Arctic biome (Payette et al. 1986; MacKay 2000; Kokelj et al. 2014; Fig. 5.4d, e). Ice wedges are formed by deep frost cracking into the peat and mineral soil layers (Mackay 1993), and are distributed as polygonal nets on the surface of peat plateaus and palsas. Overall, snow-free conditions prevailing in deforested hilltop sites and exposed peatlands are probably the main factors

◄

Fig. 5.3 (continued) bearing cones. Lower panel: Vertical growth of black spruce stems is directly related to the increased warming between the mid-1990s and twenty-first century (lower panel of this figure) as shown by mean annual temperature (dotted line: 5-year running mean) at Inukjuak weather station (located along the coastal tundra of Hudson Bay; Environment Canada 2019). The superposed temperature curves are from the automated weather stations located at the forest limit and tree line in the Boniface River area (eastern coast of Hudson Bay, northern Canada). Inukjuak mean annual temperature trends: 1940–1993: –6.8 °C; 1995–2018: –5.5 °C; 1995–2012: –5.1 °C; 2013–2018: –6.7 °C. Boniface mean annual temperature trend: 1996–2015: –4.8 °C. Photo C credit: Benoît Tremblay

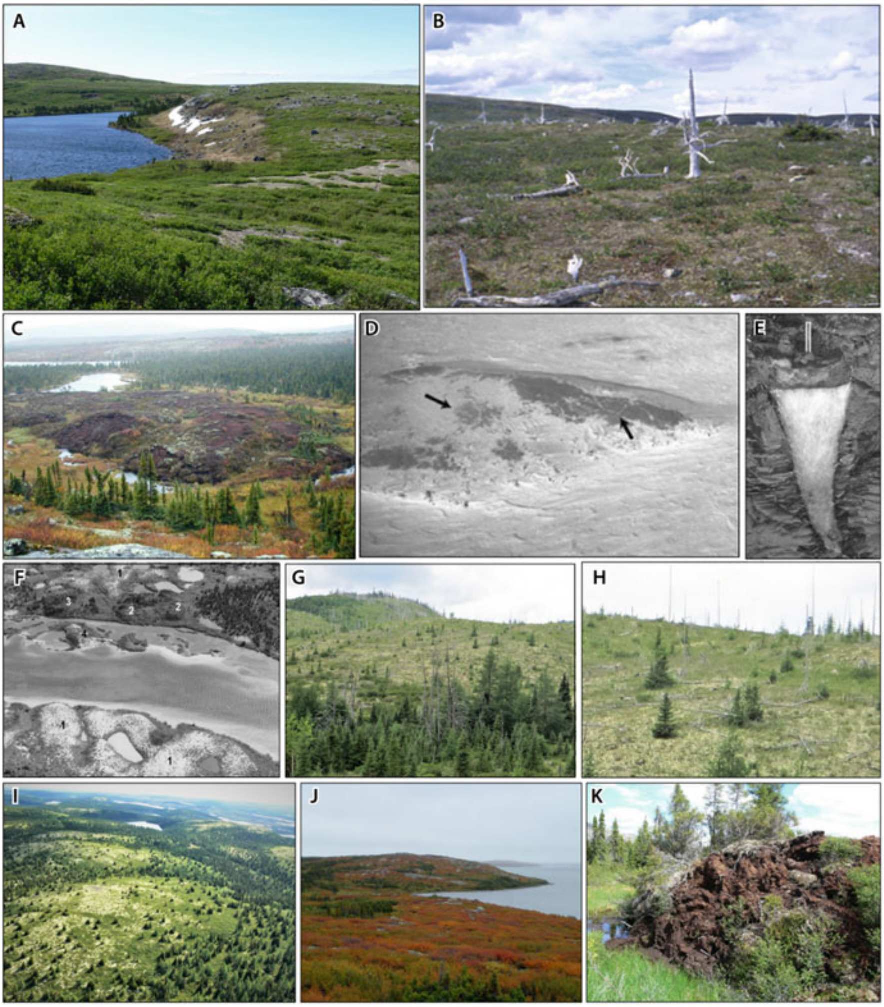


Fig. 5.4 (**A**) Collapse of hilltop forest stands. Deforestation of hilltops and slopes of the northern boreal forest over the last millennium (forest-tundra ecotone near Hudson Bay coast) caused a shift to wind-exposed tundra communities with collateral effects on the thermal soil regime, promoting permafrost growth. The snowless tundra site contrasts with the snowpatch environment formed on the lee side, where large quantities of drifting snow accumulate. Late melting of the snow in summer precludes tree encroachment. Confined, residual forest communities near the lakeshore survived wild fires. (**B**) Collapse of highland woodlands. Well-preserved vertical stems of mature conifer stems (white spruce, *Picea glauca*) of a highland subarctic woodland are standing or lying on the ground. Trees died off through progressive foliage attrition during the very cold winters of the Little Ice Age period, particularly in the first part of the nineteenth century (according to Payette 2007). Only shrubby spruces survived the cold spell. (**C**) Fen peatland disturbed by permafrost growth over the last millennia. The peatland is occupied by a peat plateau about 6.5 m above ground, which indicates the presence of buried ice lenses >7 m thick. The fen has lost more than 90% of its original surface because of permafrost aggradation. Peripheral thermokarst ponds formed because of ice melting. (**D**) Exposed, snow-free surface of a permafrost peatland forming a small island at the centre of a large subarctic lake (Lac à l'Eau Claire, northern Quebec). Arrows show polygonal cracks caused by ice wedge growth. (**E**) Ice wedge 48-cm wide about 1500 years old located on the

responsible for the decreasing borealization of the northern part of the biome during the late Holocene.

5.4.1.5 Changing Water Levels of Subarctic Lakes and Rivers

Subarctic lakes and rivers were also influenced by the drier, snowless and colder climate that prevailed during a large part of the Little Ice Age. Lake and river water levels are controlled by the amount of snow accumulated in subarctic watersheds in winter (Payette and Delwaide 2000, 2004; Vallée and Payette 2007). Significant lowering of water level due to reduced snowfalls during the sixteenth and seventeenth centuries created larger floodplains and lakeshores (Bégin and Payette 1988), which were then disturbed by the growth of mineral palsas (permafrost mounds devoid of a peat layer) (Fig. 5.4f).

5.4.2 Ecosystem Collapse in the Southern Part of the Boreal Forest

5.4.2.1 Shift of Closed-Crown Forests to Woodlands

Other than the common process of post-fire succession underway in the southern boreal forest since early Holocene, there are several cases during the late Holocene, in particular during the last centuries including the twentieth century, when ecosystem resilience failed to return forests to pre-fire composition and structure (de Lafontaine and Payette 2011; Runyan and D'Odorico 2016). Failure of post-fire regeneration occurred in several parts of the southern boreal forest where the dominant closed-crown forests have converted to open-crown forests, i.e., lichen

◄

Fig. 5.4 (continued) permafrost peatland of part **D**. © Nature (1986), 322: 724–727. (**F**) Significant lowering of water level of a subarctic river (northern Quebec) due to reduced snowfall during the sixteenth and seventeenth centuries. The larger floodplain was impacted by permafrost growth in the form of palsas during the Little Ice Age. (1) Mineral palsas; (2) Palsas; (3) Wooded palsa; (4) Degraded floodplain palsas caused by increased water level, especially after the 1950s. (**G**) Post-fire shift of closed-crown conifer forest to lichen woodland (and parkland). Untouched dense forests in background and foreground. The collapse-prone fire occurred in 1991 (southern boreal forest, Quebec), 6 years after a spruce budworm (*Choristoneura fumiferana*) outbreak. (**H**) Enlargement of the collapsed dense forest showing trees standing and lying on the ground. This photo was taken in 2018, 27 years after fire. The dense moss forest has been replaced by a young lichen woodland (parkland) colonized by the lichen *Cladonia mitis*, a post-fire species dominating the sun-exposed ground surface 15–50 years after fire. (**I**) Current expansion of conifer trees on lichen-heath hilltops of the forest-tundra ecotone, above subarctic tree lines. Reforestation of hilltop tundras is underway, at least in the southern part of the ecotone. The forest border (trees >2.5 m) is shown around the lichen hilltops, which are currently colonized by spruce <2.5 m established by seed. (**J**) Shrubification of the northern part of the boreal biome and the low Arctic biome. Shrub expansion includes enlargement of pre-existing thickets, seedling establishment and enhanced vertical growth of branches. Sun-loving lichens are declining, because they are unable to compete with shrubs. Shrub cover is of autumn-coloured dwarf birch (*Betula glandulosa*) foliage at the tree line in northern Quebec. (**K**) Palsa degradation showing exposed peat and associated thermokarst ponds (due to melting of ice lenses in peat and mineral layers), fen trees and herbaceous vegetation, mostly Cyperaceae. Successional terrestrialization triggered by recent warming is underway woodlands and lichen parklands (Payette and Delwaide 2003; Girard et al. 2009; Gonzalez et al. 2013; Tremblay et al. 2013; Payette and Delwaide 2018; Figs. 5.2a3 and 5.4g, h). Different sets of causal factors acting in synergy (Payette et al. 2000; Payette and Delwaide 2003; Jasinski and Payette 2005; Girard et al. 2008, 2009; Côté et al. 2013) explain the process by which closed-crown forest shifted to become lichen woodlands over the last centuries and into the present. Among these factors, recurrent fires at short intervals and light fires that maintain thick blackened organic horizons at the soil surface appear to be the proximal factors involved in the shifting process. The low survival of seedlings in dense forest impacted by fire is one of the main causes explaining the forest-woodland shift. The preponderance of residual, thick blackened organic material at the surface floor of burned spruce-moss forests, caused by low-severity fires, is one key factor for the low survival of seedlings. The number of seedling niches in these sites is largely reduced by the absence of moist ground, in particular *Sphagnum* mossy substrates, which are among the best seedbeds for seed germination and seedling growth (Veilleux-Nolin and Payette 2012; Boiffin and Munson 2013).

The conversion of dense forests to woodlands is currently occurring during the post-fire successional process across the southern boreal forest zone (Fig. 5.5). There is no indication when this conversion will end, given that several recently burned closed-crown forests have been transformed to woodlands (Fig. 5.4g). The collapse of dense forests also is attributed to compounding disturbances that occurred during a short period of time during the twentieth century, as for example, a forest attacked by insect defoliators followed a few years later by fire (Payette et al. 2000; Jasinski and Payette 2005). Although repetitive insect outbreaks and recurrent fires over the last 150 years may have been facilitated by recent warming, there is no clear data available that validates the direct impact of recent climate change on the frequency and severity of these stand disturbances. Adding to the complex dynamics of boreal ecosystems discussed here, large-scale logging nowadays is a relatively new and major disturbance in the boreal forest of North America (Hansen et al. 2013), since it began in the nineteenth century. Post-logging succession has occasionally played a role in the collapse of dense forests (Dussart and Payette 2002). This has been the case when young post-logged stands with a limited seed bank have either been unable to reproduce the original forest, because of successive insect attacks and fires especially during warmer and drier growth seasons of the twentieth century (Payette and Delwaide 2003; Fig. 5.4f, h) or have had deficient advance regeneration (Dussart and Payette 2002). Similar changes of forest types in the mixed boreal forest are occurring presently in western North America where variations in fire severity have changed the course of post-fire succession from coniferous to mixed and deciduous stands (Johnstone and Kasischke 2005).

5.4.2.2 Microclimatic Signatures of Closed-Crown Forests and Woodlands

The microclimatic signature of the main boreal forest types expressed in terms of energy transfer and balance depends on the density of the tree canopy. The main greenhouse effects created by dense tree canopies, like closed-crown forests, are the

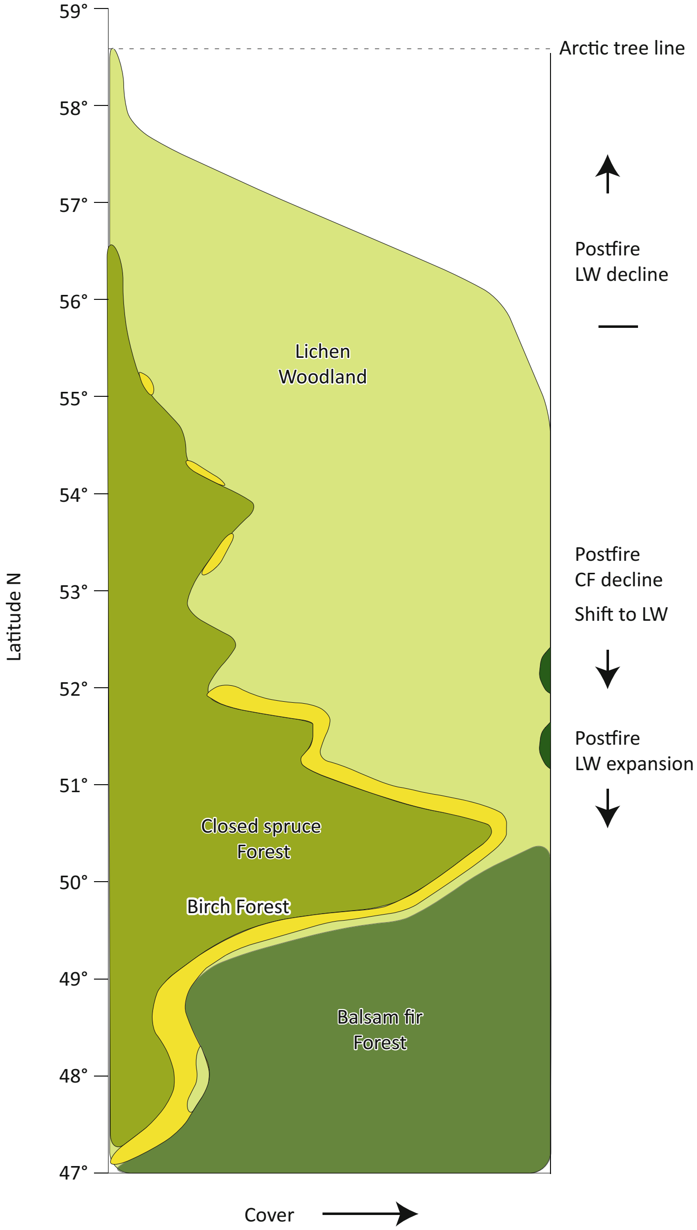


Fig. 5.5 Distribution of lichen woodlands (LW) and other forest types of the boreal forest according to latitude (after Payette and Delwaide 2018). The southward expansion of lichen woodlands at the expense of closed-crown forests (CF) is shown, as well as its decline northward to the Arctic tree line. Birch (white birch, *Betula papyrifera*) forests across the boreal zone may correspond to an alternative stable state closely associated with post-fire generation failure of conifer stands

conservation of daily solar energy inputs far greater than the loss of daily solar energy outputs. These beneficial greenhouse effects on the ecosystem are significantly reduced when closed-crown forests shift to lichen woodlands (Payette and Delwaide 2018). The dissipation of long-wave radiation because of weakened greenhouse effects and greater albedo ultimately culminate in the reduction of the frost-free growth season and increase of frequency and intensity of frost events (Plasse and Payette 2015; Payette and Delwaide 2018). This is particularly the case regarding the microclimatic changes caused by the expansion of pale-coloured lichens on the burned surface of fire-killed forests. Yellow-whitish *Cladonia* lichens significantly increase the albedo of the soil surface.

5.5 Present Post-Little Ice Age Warming and Ecosystem Collapse and Recovery

The coldest conditions of the Holocene were those of the Little Ice Age, and they lasted several hundred years, from the fourteenth century to the second half of the nineteenth century (Grove 1988). Since then, and over the last 150 years, ecosystem recovery in the form of vegetative growth and sexual reproduction of the main boreal species, trees in particular, first proceeded slowly in the late nineteenth to early twentieth century. From then until the mid-twentieth century, ecosystem recovery increased steadily but it has accelerated markedly over the last 30 years (Fig. 5.3). West Greenland and northern Quebec temperatures have increased by 1.0–1.5 °C since the mid-1990s (CEN 2016; Saros et al. 2019). Temperatures have risen continuously since the Little Ice Age, now reaching a global temperature higher than during 90% of the entire Holocene (Marcott et al. 2013). The coldest ecosystems created during the last millennia, and particularly during the Little Ice Age, like permafrost peatlands, snowpatches and post-fire lichen-heath communities derived from former subarctic woodlands, are presently at risk of decline and total extirpation. A large number of these ecosystems are now in the final phase of collapse. Tree regeneration and shrub expansion in terrestrial habitats, and permafrost decay and water variation in wetland habitats are the main components involved in the process of ecosystem collapse and recovery during this short period of major human-caused warming.

5.5.1 Tree Line Advance, Regeneration and Consolidation of Pre-existing Forests of the Forest-Tundra Ecotone

Collapsed ecosystems may recover if the main basic structure of communities is still present, given sufficient time. Depressed tree growth forms during the Little Ice Age in the forest-tundra transition zone, or even before in the nearby Arctic shrub tundra, are presently recovering as ‘normal’ vertical tree stems. Minor advancing Arctic tree lines are currently occurring because of warmer climate east (Lavoie and Payette 1994; Lescop-Sinclair and Payette 1995) and west of Hudson Bay towards the

Yukon and Alaska (Suarez et al. 1999; Danby and Hik 2007a; Mamet et al. 2019). Similar tree line advances have been recorded in Scandinavia (Kullman and Öberg 2009) and Siberia (Esper and Schweingruber 2004; Kharuk et al. 2010). The significant 1.0–1.5 °C increase in annual temperature at the Arctic tree lines in eastern Canada over the last 30 years (Fig. 5.3) has promoted massive seedling establishment along the coasts of Hudson Bay (Caccianiga and Payette 2006) and Ungava Bay (Tremblay et al. 2012), and in southern Labrador (Trant and Hermanutz 2014) and the Northwest Territories of central Canada (Lantz et al. 2019). Most demographic changes at Arctic tree line, however, are related to the consolidation of pre-existing tree populations rather than marked changes in the position of the tree line (Payette and Filion 1985; Szeicz and Macdonald 1995; Danby and Hik 2007b; Trant and Hermanutz 2014; Timoney and Mamet 2019).

A striking example of changing ecosystem attributes associated with current warming is black spruce (*Picea mariana*) stems at the Arctic tree line, which are 2 m taller and 1.6 times larger than the spruce stems that were growing in the same woodlands during the Little Ice Age between the seventeenth and nineteenth centuries (Vallée and Payette 2004). Increased temperature over the last decades caused a significant range shift of vertical stem growth, about 90 km north of the current tree line (Payette and Delwaide 1994; Payette et al. 2001; Fig. 5.3). Shrubby black spruce krummholz located in protected microrefugia of the Arctic tundra are in the process of becoming small tree groves, with cone-bearing stems well above the 2.5 m tree height threshold, thus far north of the natural range of spruce trees. These Arctic outliers are responding readily to climate forcing, most likely because of their large ecological plasticity (Rapoport 1982). Spruce krummholz are currently growing taller and larger and, most likely, represent the new expanding edge of the modern subarctic and Arctic tree lines (Gamache and Payette 2004) (Fig. 5.4i). The scattered black spruce outliers of the shrub tundra probably established through long-distance seed transport over the last millennia, possibly during the post-glacial migration peak of the species, and remained as stunted bushes until the warming during this century. The new ‘Arctic trees’ of the shrub tundra mirror the ongoing expansion of boreal trees above subarctic tree lines of the forest-tundra ecotone (Gamache and Payette 2005; Figs. 5.3 and 5.4i). With the present warming in the northern part of the boreal biome, increased seed germination and seedling establishment are now possible given the fact that the threshold of 800–940 thermal sum degree-days for seed germination is attained yearly at least since the mid-1990s (Sirois 2000; Meunier et al. 2007).

5.5.2 Shrubification of the Northern Part of the Boreal Biome

Under present biome-scale warming, however, tree expansion appears less responsive than deciduous shrub expansion, particularly that of dwarf birch (*Betula glandulosa*) (Fig. 5.4j). Shrubification of the northern part of the boreal biome and the low Arctic biome is no doubts one of the most important ecological events occurring across the North-American continent and Eurasia over the last 50 years

(Forbes et al. 2010; Myers-Smith et al. 2011; Ropars and Boudreau 2012; Tape et al. 2012; Tremblay et al. 2012; Provencher-Nolet et al. 2015; Vowles and Björk 2019). Well-drained soils covered by extensive lichen carpets are among the main types of low-growth vegetation currently impacted by shrub expansion (Fig. 5.4j). The process of shrubification implies not only the enlargement of pre-existing thickets and clones, but also greater vertical growth of individuals and widespread establishment from sexual regeneration (Ropars and Boudreau 2012; Paradis et al. 2016). Increased shrub height promotes greater snow thickness and higher soil temperature during winter and lesser freezing degree-days (Sturm et al. 2005; Paradis et al. 2016). On the other hand, evergreen shrub expansion has no effect on snow cover but acts more specifically on recalcitrant litter that facilitates C accumulation on the soil surface (Vowles and Björk 2019). Densification of the shrub cover over lichen-heath tundra communities of the forest-tundra ecotone will probably facilitate fire spread, given warmer springs and summers in the foreseeable future. Large-scale decline of the lichen cover is presently restricted to treeless sites of the forest-tundra, and not sites where shrub and tree growth exceed the 60% cover threshold, as in dense conifer forests where lichens are but small mats scattered on the forest floor.

5.5.3 Collapse and Recovery of Wetland and Riparian Ecosystems

Permafrost peatlands developed over the last millennium, especially during the Little Ice Age, are presently in a declining stage that is proceeding rapidly in North America and northern Europe (Couillard and Payette 1985; Allard and Seguin 1987; Payette et al. 2004; Marchildon 2007; Sannel and Kuhry 2011; Jolivel and Allard 2013; Bouchard et al. 2014; Jean and Payette 2014; Borge et al. 2016; Jones et al. 2016; Matveev et al. 2016; Treat and Jones 2018; Martin et al. 2019; Pelletier et al. 2019). Rapid permafrost decay over the last 60 years in most frozen peatlands caused the concurrent formation of thermokarst ponds (melting of ice lenses in peat and mineral layers) and herbaceous vegetation, mostly Cyperaceae, through successional terrestrialization (Fig. 5.4k). The main climatic driver for accelerated permafrost decay over the last decades was snow precipitation, which increased from the 1970s to present, and increased annual temperature to well above the mean after the mid-1990s, particularly in northern Quebec (Fig. 5.3). Permafrost decay does not always change carbon-sink peatlands to carbon-source peatlands (thermokarst ponds) because rapid terrestrialization promotes peat accumulation (Payette et al. 2004; Bouchard et al. 2014). High carbon accumulation rates over the last decades are currently occurring in northern peatlands (Crawford et al. 2003; Piilo et al. 2019). Fast permafrost degradation is clearly underway in the northern part of the boreal zone as evidenced by, for example, the northward recession of the permafrost boundary in northern Quebec by about 130 km from the mid-1950s to present (Thibault and Payette 2009).

5.6 Lessons Learned from the Past to Anticipate the Future

The present temperature rise corresponds roughly to the early Holocene climate when ecosystem building was at its maximum. In contrast to how ecosystems completely filled the landscape during that period, the new frontiers for forest expansion are more difficult to reach and cross (Ordonez and Williams 2013), given the heavy periglacial inertia of northern environments formerly occupied by forests and woodlands. Wind-exposed, snowless tundra hilltops of the northern part of the boreal biome are harsh environments for tree establishment. Milder, snowier winters and moister soil conditions are necessary for a safe return of tree species to reforest subarctic tundra. It is rightly postulated from empirical data pertaining to the southern boreal forest that a warmer climate, as predicted for this century, outweighs the negative effect of lower water availability (D'Orangeville et al. 2016). However, outside the temperature window (Nicault et al. 2015), increased precipitation will most probably be the main factor promoting seed germination, seedling survival as well as growth of conifer forests (Girardin et al. 2016) for reforestation of the northern part of the boreal forest.

One of the most important drivers of ecological change that will affect the future boreal forest is the fire regime (Heinselman 1973; Johnson 1992; Payette et al. 1989; Bergeron et al. 2004; Erni et al. 2017). In areas surrounding the most fire-prone sites of the boreal forest in eastern Canada, the fire regime has been very active over the last two centuries with an annual burn rate (or fire rotation) of about 2.1% (Héon et al. 2014; Erni et al. 2017). Moreover, over the second part of the twentieth century, the southern part of the North American boreal forest was characterized by a doubling of annual burnt area and a significant increase in the frequency of >1000 km^2 fire conflagrations (Kasischke and Turetsky 2006). However, this compilation of North American boreal fires did not include the rather large-scale fires that occurred in the northern part of the eastern boreal forest between the 1920s and the 1960s where more than 30% of all fires were > 1000 km^2, all fires most likely caused by long lasting dry and warm conditions (Payette et al. 1989). The recent increase of wildfires fires (over 2002–2005) in northern Russia was caused by human activity (Mollicone et al. 2006). About 80% of all forest-tundra and shrub-tundra fires in this area were <100 ha, because of the reduced amount of combustible material and less frequent fire-prone climatic conditions. Future trends in fire activity (Bergeron et al. 2010) in the northeastern part of the boreal forest are bound to severely limit any possibility of larger burned areas, due to a lack of fuel available. It is also possible that treeless sites in the forest-tundra currently colonized by seedlings and saplings of expanding tree populations could risk losing their tundra status if fire conflagrations increase in size and frequency during this century of warmer climate.

The process of increased tree invasion is triggered presently in the southernmost hilltop tundras of the boreal biome by the positive feedback to warming caused by lower albedo of forest vegetation compared to tundra vegetation (Gamache and Payette 2005). However, more warmth, as expected for the foreseeable decades, is necessary to colonize the subarctic tundra sites. In absence of fire conflagrations, tree expansion and forest rebuilding during this century of excessive warmth will probably have a 'tabula rasa' effect on the structure and diversity of future subarctic ecosystems. The most likely ecosystems to collapse are the genuine cold-prone ecosystems like the snowless lichen-heath tundras, permafrost peatlands and snowpatches, created during the late Holocene. The diversified cryptogamic and vascular flora adapted to these fragile ecosystems are currently at risk of extirpation (Savard and Payette 2013), but have a chance to survive further north in the proximal Arctic tundra. Most ecosystems of the boreal biome of central and eastern North America, which depend largely on the diversified physiography and soils of the Precambrian shield and fertile lowlands, are more at risk than those located to the west, on the less-diversified boreal part of the continent. Fertile, silty soils facilitating tree regeneration dominate the landscape in Alaska, where time lags of 150–200 years in forestation are predicted following climatic warming (Chapin and Starfield 1997). As in central and eastern North America, development of new ecosystems or novel combinations of species following climatic change are expected in boreal Alaska (Chapin and Starfield 1997), probably with a reshuffling of common species of the forest flora. It is not known if partitioning of the flora, including southern boreal species, will proceed rapidly through migration associated with increased temperature northward (Loarie et al. 2009). Global borealization with large-scale collapse of subarctic cold-prone ecosystems is probably the main outcome that the northernmost part of the boreal biome and southern part of the Arctic biome will experience under the warmer climate of this century. However, migration of temperate and southern boreal tree species across the boreal forest and the shrub tundra will lag because of limited dispersal and establishment in already occupied forest areas although less so in forest-tundra and shrub-tundra environments.

Acknowledgements I am most grateful to the funding research agencies of Canada (Natural Sciences and Engineering Research Council of Canada and the Fonds de recherche Nature et Technologies of Quebec) for their long-term support. Ann Delwaide provided excellent laboratory assistance. I thank the editors Pep Canadell and Detlef Schulze for support and constructive comments during revision of the manuscript. Special thanks to my colleague Benoît Tremblay for the 'Arctic trees' photograph shown in Fig. 5.3.

References

Allard M, Seguin MK (1987) The Holocene evolution of permafrost near the tree line, on the eastern coast of Hudson Bay (northern Quebec). Can J Earth Sci 24:2206–2222

Alley RB, Ágústsdóttir AM (2005) The 8k event: cause and consequences of a major Holocene abrupt climate change. Quat Sci Rev 24:1123–1149

Alley RB, Mayewski PA, Sowers T, Stuiver M, Taylor KC, Clark PU (1997) Holocene climate instability: a prominent widespread event 8200 yr ago. Geology 25:483–486

Anderson RS, Davis RB, Miller NG, Stuckenrath R (1986) History of late- and post-glacial vegetation and disturbance around Upper South Branch Pond, northern Maine. Can J Bot 64:1977–1986

Arseneault D, Payette S (1997) Reconstruction of millennial forest dynamics from tree remains in a subarctic tree line peatland. Ecology 78:1873–1883

Arseneault D, Sirois L (1990) Forme et croissance de l’épinette noire (*Picea mariana* (Mill.) B.S.P.) avant et après-feu en toundra forestière. Naturaliste canadien 117:1–7

Asselin H, Payette S (2005) Late Holocene opening of the forest tundra landscape in northern Québec, Canada. Glob Ecol Biogeogr 14:307–314

Barber DC, Dyke A, Hillaire-Marcel C, Jennings AE, Andrews JT, Kerwin MW, Bilodeau G, McNeely R, Southon J, Morehead MD, Gagnon J-M (1999) Forcing of the cold event of 8,200 years ago by catastrophic drainage of Laurentide lakes. Nature 400:344–347

Bauer IE, Gignac LD, Vitt DH (2003) Development of a peatland complex in boreal western Canada: lateral site expansion and local variability in vegetation succession and long-term peat accumulation. Can J Bot 81:833–847

Beaulieu-Audy V, Garneau M, Richard PJH, Asnong H (2009) Holocene palaeoecological reconstruction of three boreal peatlands in the La Grande Rivière region, Québec, Canada. Holocene 19:459–476

Bégin Y, Payette S (1988) Dendrochronological evidence of lake-level changes in the last three centuries in subarctic Québec. Quat Res 30:210–220

Bennike O, Böcher J (1990) Forest-tundra neighbouring the North Pole: plant and insect remains from the Plio-Pleistocene Kap København formation, North Greenland. Arctic 43:331–338

Berger A (1978) Long-term variations of daily insolations and quaternary climatic changes. J Atmos Sci 35:2362–2367

Bergeron Y, Gauthier S, Flannigan M, Kafka V (2004) Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85:1916–1932

Bergeron Y, Cyr D, Girardin MP, Carcaillet C (2010) Will climate change drive 21st century burn rates in Canadian boreal forest outside of its natural variability: collating global climate model experiments with sedimentary charcoal data. Int J Wildland Fire 19:1127–1139

Bhiry N, Filion L (1996) Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity. Quat Res 45:312–320

Bhiry N, Payette S, Robert ÉC (2007) Peatland development at the arctic tree line (Québec, Canada) influenced by flooding and permafrost. Quat Res 67:426–437

Binney HA, Willis KJ, Edwards ME, Bhagwat SA, Anderson PM, Andreev AA, Blaauw M, Damblon F, Haesaerts P, Kienast F, Kremenetski KV, Krivonogov SK, Lozhkin AV, Macdonald GM, Novenko EY, Oksanen P, Sapelko TV, Väliranta M, Vazhenina L (2009) The distribution of late-quaternary woody taxa in northern Eurasia: evidence from a new macrofossil database. Quat Sci Rev 28:2445–2464

Blais JR (1983) Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can J For Res 13:539–547

Bland LM, Rowland JA, Regan TJ, Keith DA, Murray NJ, Lester RE, Linn M, Rodriguez JP, Nicholson E (2018) Developing a standardized definition of ecosystem collapse for risk assessment. Front Ecol Environ 16:29–36

Boiffin J, Munson A (2013) Three large fire years threaten resilience of closed crown black spruce forests in eastern Canada. Ecosphere 4:art. 56

Borge AF, Westermann S, Solheim I, Etzelmüller B (2016) Strong degradation of palsas and peat plateaus in northern Norway during the last 60 years. Cryosphere Discuss 1–31. https://doi.org/10.5194/tc-2016-12

Bouchard F, Francus P, Pienitz R, Laurion I, Feyte S (2014) Subarctic thermokarst ponds: investigating recent landscape evolution and sediment dynamics in thawed permafrost of northern Québec (Canada). Arctic Antarct Alpine Res 46:251–271

Bradley R (2014) Paleoclimatology. reconstructing climates of the quaternary, 3rd edn. Academic, New York

Brauer A, Haug GH, Dulski P, Sigman DM, Negendank JFW (2008) An abrupt wind shift in western Europe at the onset of the Younger Dryas cold period. Nat Geosci 1:520–523

Broecker WS, Kennett JP, Flower BP, Teller JT, Trumbore S, Bonani G, Wolfli W (1989) Routing of meltwater from the Laurentide ice sheet during the Younger Dryas cold episode. Nature 341:318–321

Caccianiga M, Payette S (2006) Recent advance of white spruce (*Picea glauca*) in the coastal tundra of the eastern shore of Hudson Bay (Québec, Canada). J Biogeogr 33:2120–2135

Environment Canada (2019) Historical climate data. Available at http://climate.weather.gc.ca

Carcaillet C, Bergeron Y, Richard PJH, Fréchette B, Gauthier S, Prairie Y (2001) Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? J Ecol 89:930–946

CEN (2016) Données des stations climatiques de la région de la rivière Boniface au Nunavik, Québec, Canada, v. 1.2 (1988-2016). Nordicana D7. https://doi.org/10.5885/45129SL-DBDA2A77C0094963

Chapin FS III, Starfield AM (1997) Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. Clim Change 35:449–461

Charman D (2002) Peatlands and environmental change. Wiley, Chichester, UK

Clark PU, Dyke AS, Shakun JD, Carlson AE, Clark J, Wohlfarth B, Mitrovica JX, Hostetler SW, McCab AM (2009) The last glacial maximum. Science 325:710–714

Côté D, Girard F, Hébert F, Bouchard S, Gagnon R, Lord D (2013) Is the closed crown boreal forest resilient after successive stand disturbances? A quantitative demonstration from a case study. J Veg Sci 24:664–674

Couillard L, Payette S (1985) Évolution holocène d'une tourbière à pergélisol. Can J Bot 63:1104–1121

Couillard P-L, Payette S, Grondin P (2013) Long-term impact of fire on high-altitude balsam fir (*Abies balsamea*) forests in south-central Quebec deduced from soil charcoal. Can J For Res 43:188–199

Crawford RMM, Jeffree CE, Rees WG (2003) Paludification and forest retreat in northern oceanic environments. Ann Bot 91:213–226

Cwynar LC, Spear RW (1991) Reversion of forest to tundra in the central Yukon. Ecology 72:202–212

Cyr S, Payette S (2010) The origin and structure of wooded permafrost mounds at the arctic treeline in eastern Canada. Plant Ecol Divers 3:35–46

Danby RK, Hik DS (2007a) Evidence of recent treeline dynamics in southwest Yukon from aerial photographs. Arctic 60:411–425

Danby RK, Hik DS (2007b) Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. J Ecol 95:352–363

Davis MB (1983) Holocene vegetational history of the eastern United States. In: Wright Jr HE (ed) Late-quaternary environments of the United States. Vol. 2. The holocene. University of Minnesota Press, Minneapolis, MN, pp 166–181

de Lafontaine G, Payette S (2011) Shifting zonal patterns of the southern boreal forest in eastern Canada associated with changing fire regime during the Holocene. Quat Sci Rev 30:867–875

de Lafontaine G, Guerra CAA, Ducousso A, Petit RJ (2014) Cryptic no more: soil macrofossils uncover Pleistocene forest microrefugia within a periglacial desert. New Phytol 204:715–729

D'Orangeville L, Duchesne L, Houle D, Kneeshaw D, Côté B, Pederson N (2016) Northeastern North America as a potential refugium for boreal forests in a warming climate. Science 352:1452–1455

Dussart E, Payette S (2002) Ecological impact of clear-cutting on black spruce-moss forests in southern Québec. Ecosci 9:533–543

Dyke AS (2004) An outline of North American deglaciation with emphasis on central and northern Canada. In: Ehlers J, Gibbard PL (eds) Quaternary glaciations—extent and chronology, Part II. Elsevier, Amsterdam, pp 373–424

Engstrom DR, Hansen BCS (1985) Postglacial vegetational change and soil development in southeastern Labrador as inferred from pollen and chemical stratigraphy. Can J Bot 63:543–561

Erni S, Arseneault D, Parisien M-A, Bégin Y (2017) Spatial and temporal dimensions of fire activity in the fire-prone eastern Canadian taiga. Glob Chang Biol 23:1152–1166

Esper J, Schweingruber FH (2004) Large-scale treeline changes recorded in Siberia. Geophys Res Lett 31:L06202

Fastie CL, Lloyd AH (2003) Fire history and postfire forest development in an upland watershed of interior Alaska. J Geophys Res 108:FFR6-1–FFR6-13

Feurdean A, Bhagwat SA, Willis KJ, Birks HJB, Lischke H, Hickler T (2013) Tree migration-rates: narrowing the gap between inferred post-glacial rates and projected rates. PLoS One 8:e71797

Filion L, Cloutier C, Cournoyer L (2010) Dendroécologie des épidémies de la tenthrède du mélèze (*Pristiphora erichsonii*). In: Payette S, Filion L (eds) La dendroécologie : Principes, méthodes et applications. Presses de l'Université Laval, Québec, QC, pp 437–465

Forbes BC, Macias Faurea M, Zetterberg P (2010) Russian Arctic warming and "greening" are closely tracked by tundra shrub willows. Glob Chang Biol 16:1542–1554

Foster DR, Fritz SC (1987) Mire development, pool formation and landscape processes on patterned fens in Dalarna, central Sweden. J Ecol 75:409–437

Foster DR, King GA (1984) Landscape features, vegetation and developmental history of a patterned fen in south-eastern Labrador, Canada. J Ecol 72:115–143

Fréchette B, Richard PJH, Grondin P, Lavoie M, Larouche AC (2018) Histoire postglaciaire de la végétation et du climat des pessières et des sapinières de l'Ouest du Québec. Gouvernement du Québec, Ministère des Forêts, de la Faune et des Parcs, Direction de la recherche forestière. Forest Research Report n^{o} 179. Quebec, QC

Fredskild B (1991) The genus *Betula* in Greenland: holocene history, present distribution and synecology. Nordic J Bot 11:393–412

Frégeau M, Payette S, Grondin P (2015) Fire history of the central boreal forest in eastern North America reveals stability since the mid-Holocene. Holocene 25:1912–1922

Frolking SE, Roulet NT (2007) Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. Glob Chang Biol 13:1079–1088

Fuller JL (1998) Ecological impact of the mid-Holocene hemlock decline in southern Ontario, Canada. Ecology 79:2337–2351

Funder S, Abrahamsen N, Bennike O, Feyling-Hanssen RW (1985) Forested Arctic: evidence from North Greenland. Geology 13:542–546

Gajewski K (2019) Environmental history of the northwestern Québec treeline. Quat Sci Rev 206:29–43

Gajewski K, Payette S, Ritchie JC (1993) Holocene vegetation history at the boreal-forest-shrub-tundra transition in north-western Quebec. J Ecol 81:433–443

Gamache I, Payette S (2004) Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada. J Ecol 92:835–845

Gamache I, Payette S (2005) Latitudinal responses of subarctic tree lines to recent climate change in eastern Canada. J Biogeogr 32:849–862

Gavin DG, Hallett DJ, Hu FS, Lertzman KP, Prichard SJ, Brown KJ, Lynch JA, Bartlein P, Peterson DL (2007) Forest fire and climate change in western North America: insights from sediment charcoal records. Front Ecol Environ 5:499–506

Germain D, Filion L, Hétu B (2005) Snow avalanche activity after fire and logging disturbances, northern Gaspé Peninsula, Québec, Canada. Can J Earth Sci 42:2101–2116

Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS (2009) Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. Science 326:1100–1103

Girard F, Payette S, Gagnon R (2008) Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. J Biogeogr 35:529–537

Girard F, Payette S, Gagnon R (2009) Origin of the lichen-spruce woodland in the closed-crown forest zone of eastern Canada. Glob Ecol Biogeogr 18:291–303

Girardin MP, Hogg EH, Bernier PY, Kurz WA, Guo XJ, Cyr G (2016) Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. Glob Chang Biol 22:627–643

Glaser PH, Janssens JA (1986) Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. Can J Bot 64:395–415

Gonzalez E, Hébert F, Boucher J-F, Sirois P, Lord D (2013) Lichen-spruce woodland early indicators of ecological resilience following sylvicultural disturbances in Québec's closed-crown forest zone. Am J Plant Sci 4:749–765

Gore AJP (ed) (1983) Ecosystems of the world. Vol. 4B, Mires: swamp, bog, fen and moor. Regional studies. Elsevier, New York

Gorham E, Lehman C, Dyke A, Janssens J, Dyke L (2007) Temporal and spatial aspects of peatland initiation following deglaciation in North America. Quat Sci Rev 26:300–311

Gray DR (2008) The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. Clim Change 87:361–383

Grove J (1988) The little ice age. Methuen, London, UK

Gruber S (2012) Derivation and analysis of a high-resolution estimate of global permafrost zonation. Cryosphere 6:221–233

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853

Heinselman ML (1973) Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat Res 3:329–382

Héon J, Arseneault D, Parisien M-A (2014) Resistance of the boreal forest to high burn rates. Proc Natl Acad Sci USA 111:13888–13893

Holling CS (1992) The role of forest insects in structuring the boreal landscape. In: Shugart HH, Leemans L, Bonan GB (eds) A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, UK, pp 170–191

Jardon Y, Filion L, Cloutier C (1994) Tree-ring evidence for endemicity of the larch sawfly in North America. Can J For Res 24:742–747

Jardon Y, Morin H, Dutilleul P (2003) Périodicité et synchronisme des épidémies de la tordeuse des bourgeons de l'épinette au Québec. Can J For Res 33:1947–1961

Jasinski JPP, Payette S (2005) The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecol Monogr 75:561–583

Jean M, Payette S (2014) Dynamics of active layer in wooded palsas of northern Quebec. Geomorphology 206:87–96

Johnson EA (1992) Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge, UK

Johnstone JF, Kasischke ES (2005) Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. Can J For Res 35:2151–2163

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GLW, Schoennagel T, Turner MG (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378

Jolivel M, Allard M (2013) Thermokarst and export of sediment and organic carbon in the Sheldrake River watershed, Nunavik, Canada. J Geophys Res Earth 118:1729–1745

Jones MC, Yu Z (2010) Rapid deglacial and early Holocene expansion of peatlands in Alaska. Proc Natl Acad Sci USA 107:7347–7352

Jones BM, Baughman CA, Romanovsky VE, Parsekian AD, Babcock EL, Stephani E, Jones M, Grosse G, Berg EE (2016) Presence of rapidly degrading permafrost plateaus in south-central Alaska. Cryosphere 10:2673–2692

Kasischke ES, Turetsky MR (2006) Recent changes in the fire regime across the North American boreal region: spatial and temporal patterns of burning across Canada and Alaska. Geophys Res Lett 33:L09703

Kharuk VI, Im ST, Dvinskaya ML (2010) Forest–tundra ecotone response to climate change in the Western Sayan Mountains, Siberia. Scand J Forest Res 25:224–233

Koch PL, Barnosky AD (2006) Late quaternary extinctions: state of the debate. Annu Rev Ecol Evol Syst 37:215–250

Kokelj SV, Lantz TC, Wolfe SA, Kanigan JC, Morse PD, Coutts R, Molina-Giraldo N, Burn CR (2014) Distribution and activity of ice wedges across the forest-tundra transition, western arctic Canada. J Geophys Res Earth 119:2032–2047

Kremenetski CV, Sulerzhitsky LD, Hantemirov R (1998) Holocene history of the northern range limits of some trees and shrubs in Russia. Arctic Alpine Res 30:317–333

Kuhry P, Turunen J (2006) The postglacial development of boreal and subarctic peatlands. In: Wieder RK, Vitt DH (eds) Boreal peatland ecosystems, Ecological studies 188. Springer, Berlin, pp 25–46

Kukla GJ, Matthews RK, Mitchell JM Jr (1972) Guest editorial: the end of the present interglacial. Quat Res 2:261–269

Kullman L (2002) Boreal tree taxa in the central Scandes during the late-glacial: implications for late-quaternary forest history. J Biogeogr 29:1117–1124

Kullman L (2008) Early postglacial appearance of tree species in northern Scandinavia: review and perspective. Quat Sci Rev 27:2467–2472

Kullman L, Öberg L (2009) Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. J Ecol 97:415–429

Lamb HF (1985) Palynological evidence for postglacial change in the position of tree limit in Labrador. Ecol Monogr 55:241–258

Lantz TC, Moffat ND, Fraser RH, Walker X (2019) Reproductive limitation mediates the response of white spruce (*Picea glauca* (Moench) Voss) to climate warming across the forest-tundra ecotone. Arctic Sci 5:167–184

Lavoie C, Payette S (1994) Recent fluctuations of the lichen-spruce forest limit in subarctic Quebec. J Ecol 82:725–734

Lavoie M, Filion L, Robert ÉC (2009) Boreal peatland margins as repository sites of long-term natural disturbances of balsam fir/spruce forests. Quat Res 71:295–306

Lescop-Sinclair K, Payette S (1995) Recent advance of the arctic treeline along the eastern coast of Hudson Bay. J Ecol 83:929–936

Levesque AJ, Cwynar LC, Walker IR (1994) A multiproxy investigation of late-glacial climate and vegetation change at Pine Ridge pond, southwest New Brunswick, Canada. Quat Res 42:316–327

Lindenmayer DB, Messier C, Sato C (2016) Avoiding ecosystem collapse in managed forest ecosystems. Front Ecol Environ 14:561–568

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field C, Ackerly DD (2009) The velocity of climatic change. Nature 462:24–31

Macdonald GM, Cwynar LC (1991) Post-glacial population growth rates of *Pinus contorta* ssp. *latifolia* in western Canada. J Ecol 79:417–429

Macdonald GM, Beilman DW, Kremenetski KV, Sheng Y, Smith LC, Velichko AA (2006) Rapid early development of circumarctic peatlands and atmospheric CH_4 and CO_2 variations. Science 314:285–288

Macdonald GM, Kremenetski KV, Beilan DW (2008) Climate change and the northern Russian treeline zone. Philos Trans R Soc B 363:2285–2299

Mackay JR (1993) Air temperature, snow cover, creep of frozen ground, and the time of ice-wedge cracking, western Arctic coast. Can J Earth Sci 30:1720–1729

MacKay JR (2000) Thermally induced movements in ice-wedge polygons, western arctic coast: a long-term study. Géographie physique et Quaternaire 54:41–68

Magnan G, Garneau M, Payette S (2014) Holocene development of maritime ombrotrophic peatlands of the St. Lawrence North Shore in eastern Canada. Quat Res 82:96–106

Mäkilä M, Moisanen M (2007) Holocene lateral expansion and carbon accumulation of Luovuoma, a northern fen in Finnish Lapland. Boreas 36:198–210

Mamet SD, Brown CD, Trant AJ, Laroque CP (2019) Shifting global *Larix* distributions: Northern expansion and southern retraction as species respond to changing climate. J Biogeogr 46:30–44

Marchildon C (2007) Évolution spatio-temporelle des palses et des lithalses de la région des rivières Sheldrake et Nastapoka, côte est de la baie d'Hudson, Nunavik. M.Sc. thesis, Laval University, Department of Geography, Québec, QC

Marcott SA, Shakun JD, Clark PU, Mix AC (2013) A reconstruction of regional and global temperature for the past 11,300 years. Science 339:1198–1201

Martin LCP, Nitzbon J, Aas KS, Etzelmüller B, Kristiansen H, Westermann S (2019) Stability conditions of peat plateaus and palsas in northern Norway. J Geophys Res Earth Surf. https://doi.org/10.1029/2018jf004945

Matveev A, Laurion I, Deshpande BN, Bhiry N, Vincent WF (2016) High methane emissions from thermokarst lakes in subarctic peatlands. Limnol Oceanogr 61:S150–S164

Mayle FE, Cwynar LC (1995) Impact of the Younger Dryas cooling event upon vegetation of Atlantic Canada. Ecol Monogr 65:129–154

Meunier C, Sirois L, Bégin Y (2007) Climate and *Picea mariana* seed maturation relationships: a multi-scale perspective. Ecol Monogr 77:361–376

Miller GH, Fogel ML, Magee JW, Gagan MK, Clarke SJ, Johnson BJ (2005) Collapse in Pleistocene Australia and a human role in megafaunal extinction. Science 309:287–290

Mitchell JM Jr (1972) The natural breakdown of the present interglacial and its possible intervention by human activities. Quat Res 2:436–445

Mollicone D, Eva HD, Achard F (2006) Human role in Russian wild fires. Nature 440:436–437

Mörner N-A (1972) When will the present interglacial end? Quat Res 2:341–349

Myers-Smith IH, Forbes BC, Wilmking M et al (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ Res Lett 6:045509

Navarro L, Harvey A-É, Ali A, Bergeron Y, Morin H (2018) A Holocene landscape dynamic multiproxy reconstruction: how do interactions between fire and insect outbreaks shape an ecosystem over long time scales? PLoS One 13:e0204316

Nicault A, Boucher É, Tapsoba D, Arseneault D, Berninger F, Bégin C, DesGranges JL, Guiot J, Marion J, Wicha S, Bégin Y (2015) Spatial analysis of black spruce (*Picea mariana* (Mill.) B.S.P.) radial growth response to climate in northern Québec – Labrador Peninsula, Canada. Can J For Res 45:343–352

Normand S, Randin C, Ohlemüller R, Bay C, Høye TT, Kjær ED, Körner C, Lischke H, Maiorano L, Paulsen J, Pearman PB, Psomas A, Treier UA, Zimmermann NE, Svenning J-C (2013) A greener Greenland? Climatic potential and long-term constraints on future expansions of trees and shrubs. Philos Trans R Soc B 368:20120479

Occhietti S, Parent M, Lajeunesse P, Robert F, Govare É (2011) Late pleistocene–early holocene decay of the Laurentide Ice Sheet in Québec-Labrador. In: Ehlers J, Gibbard PL, Hughes PD (eds) Quaternary glaciations. Extent and chronology. developments in quaternary science, vol 15. Elsevier, Amsterdam, pp 601–630

Ordonez A, Williams JW (2013) Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. Ecol Lett 16:773–781

Paradis M, Lévesque E, Boudreau S (2016) Greater effects of increasing shrub height on winter versus summer soil temperature. Environ Res Lett 11:085005

Past Interglacials Working Group of Pages (2016) Interglacials of the last 800,000 years. Rev Geophys 54:162–219

Payette S (1984) Peat inception and climate change in northern Quebec. In: Mörner NA, Karlén W (eds) Climatic change on a yearly to millennial basis. Reidel, London, pp 173–179

Payette S (1988) Late-Holocene development of subarctic ombrotrophic peatlands: allogenic and autogenic succession. Ecology 69:516–531

Payette S (2007) Contrasted dynamics of northern Labrador tree lines caused by climate change and migration lag. Ecology 88:770–780

Payette S, Delwaide A (1994) Growth of black spruce at its northern range limit in Arctic Quebec, Canada. Arctic Alpine Res 26:174–179

Payette S, Delwaide A (2000) Recent permafrost dynamics in a subarctic floodplain associated with changing water levels, Québec. Arctic Antarct Alpine Res 32:316–323

Payette S, Delwaide A (2003) Shift of conifer boreal forest to lichen-heath parkland caused by successive stand disturbances. Ecosystems 6:540–550

Payette S, Delwaide A (2004) Dynamics of subarctic wetland forests over the past 1500 years. Ecol Monogr 73:373–391

Payette S, Delwaide A (2018) Tamm review: the North-American lichen woodland. For Ecol Manag 417:167–183

Payette S, Filion L (1985) White spruce expansion at the tree line and recent climatic change. Can J For Res 15:241–251

Payette S, Frégeau M (2019) Long-term succession of closed boreal forests at their range limit in eastern North America shows resilience to fire and climate disturbances. For Ecol Manag 440:101–112

Payette S, Gagnon R (1985) Late Holocene deforestation and tree regeneration in the forest-tundra of Québec. Nature 313:570–572

Payette S, Lavoie C (1994) The arctic tree line as a record of past and recent climate changes. Environ Rev 2:78–90

Payette S, Gauthier L, Grenier I (1986) Dating ice-wedge growth in subarctic peatlands following deforestation. Nature 322:724–727

Payette S, Morneau C, Sirois L, Desponts M (1989) Recent fire history of the northern Quebec biomes. Ecology 70:656–673

Payette S, Bhiry N, Delwaide A, Simard M (2000) Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce-moss forest. Can J For Res 30:288–305

Payette S, Fortin M-J, Gamache I (2001) The subarctic forest-tundra: the structure of a biome in a changing climate. BioScience 51:709–718

Payette S, Delwaide A, Caccianiga M, Beauchemin M (2004) Accelerated thawing of subarctic peatland permafrost over the last 50 years. Geophys Res Lett 31:L18208

Pelletier M, Allard M, Lévesque E (2019) Ecosystem changes across a gradient of permafrost degradation in subarctic Québec (Tasiapik valley, Nunavik, Canada). Arctic Sci 5:1–26

Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. Ecosystems 1:6–18

Piilo SR, Zhang H, Garneau M, Gallego-Sala A, Amesbury MJ, Väliranta MM (2019) Recent peat and carbon accumulation following the Little Ice Age in northwestern Québec, Canada. Environ Res Lett 14:075002

Plasse C, Payette S (2015) Frost hollows of the boreal forest: a spatiotemporal perspective. J Ecol 103:669–678

Provencher-Nolet L, Bernier M, Lévesque E (2015) Quantification des changements récents à l'écotone forêt-toundra à partir de l'analyse numérique de photographies aériennes. Ecosci 21:419–433

Rapoport EH (1982) Areography. Geographical strategies of species. The Fundacion Bariloche series. Pergamon, Oxford, UK

Richard PJH, Larouche A, Bouchard MA (1982) Âge de la déglaciation finale et histoire postglaciaire de la végétation dans la partie centrale du Nouveau-Québec. Géographie physique et Quaternaire 36:63–90

Ritchie JC (1987) Postglacial vegetation of Canada. Cambridge University Press, Cambridge, UK

Ritchie JC, Cwynar LC, Spear RW (1983) Evidence from north-west Canada for an early Holocene Milankovitch thermal maximum. Nature 305:126–128

Ropars P, Boudreau S (2012) Shrub expansion at the forest-tundra ecotone: spatial heterogeneity linked to local topography. Environ Res Lett 7:015501

Rouse WR (1976) Microclimate changes accompanying burning in subarctic lichen woodland. Arctic Alpine Res 8:357–376

Rouse WR, Kershaw KA (1971) The effects of burning on the heat and water regimes of lichen-dominated subarctic surfaces. Arctic Alpine Res 3:291–304

Runyan CW, D'Odorico P (2016) Global deforestation. Cambridge University Press, New York

Runyan CW, D'Odorico P, Lawrence D (2012) Physical and biological feedbacks of deforestation. Rev Geophys 50:RG4006

Rydin H, Jeglum JK (2013) The biology of peatlands. Oxford University Press, Oxford, UK

Sannel ABK, Kuhry P (2011) Warming-induced destabilization of peat plateau/thermokarst lake complexes. J Geophys Res 116:G03035

Saros JE, Anderson NJ, Juggins S, McGowan S, Yde JC, Telling J, Bullard JE, Yallop ML, Heathcote AJ, Burpee BT, Fowler RA, Barry CD, Northington RM, Osburn CL, Pla-Rabes S, Mernild SH, Whiteford EJ, Andrews MG, Kerby JT, Post E (2019) Arctic climate shifts drive rapid ecosystem responses across the West Greenland landscape. Environ Res Lett 14:074027

Savard J, Payette S (2013) Origin and plant species diversity of high-altitude tundra summits across the boreal forest zone in eastern Canada. Ecosci 20:283–295

Schulze ED, Lapshina E, Filipov I, Kuhlmann I, Mollicone D (2015) Carbon dynamics in boreal peatlands of the Yenisey region, west Siberia. Biogeosciences 12:7057–7070

Seppälä M (2011) Synthesis of studies of palsa formation underlining the importance of local environmental and physical characteristics. Quat Res 75:366–370

Simard I, Morin H, Lavoie C (2006) A millennial-scale reconstruction of spruce budworm abundance in Saguenay, Quebec, Canada. The Holocene 16:31–37

Sirois L (2000) Spatiotemporal variation in black spruce cone and seed crops along a boreal forest–tree line transect. Can J For Res 30:900–909

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, Romanovsky VE (2005) Winter biological processes could help convert arctic tundra to shrubland. BioScience 55:17–26

Suarez F, Binkley D, Kaye MW, Stoolemyer R (1999) Expansion of forest stands into tundra in the Noatak National Preserve, northwest Alaska. Ecoscience 6:465–470

Szeicz JM, Macdonald GM (1995) Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. J Ecol 83:873–885

Tape KD, Hallinger M, Welker JM, Ruess RW (2012) Landscape heterogeneity of shrub expansion in Arctic, Alaska. Ecosystems 15:711–724

Thibault S, Payette S (2009) Recent permafrost degradation in bogs of the James Bay area, northern Quebec, Canada. Permafrost Periglacial Process 20:383–389

Timoney KP, Mamet S (2019) No treeline advance over the last 50 years in subarctic western and central Canada and the problem of vegetation misclassification in remotely sensed data. Ecoscience 26. https://doi.org/10.1080/11956860.2019.1698258

Trant AJ, Hermanutz L (2014) Advancing towards novel tree lines? A multispecies approach to recent tree line dynamics in subarctic alpine Labrador, northern Canada. J Biogeogr 41:1115–1125

Treat CC, Jones MC (2018) Near-surface permafrost aggradation in Northern Hemisphere peatlands shows regional and global trends during the past 6000 years. Holocene 28:998–2010

Tremblay B, Lévesque E, Boudreau S (2012) Recent expansion of erect shrubs in the Low Arctic: evidence from eastern Nunavik. Environ Res Lett 7:035501

Tremblay P, Boucher J-F, Tremblay M, Lord D (2013) Afforestation of boreal open woodlands: early performance and ecophysiology of planted black spruce seedlings. Forests 4:433–454

Truchon-Savard A, Jean M, Payette S (2019) Black spruce (*Picea mariana*) colonization of subarctic snowpatches in response to warmer climate. J Ecol 107:1154–1166

Tzedakis PC, Emerson BC, Hewitt GM (2013) Cryptic or mystic? Glacial tree refugia in northern Europe. Trends Ecol Evol 28:696–704

Vajda A, Venäläinen A (2005) Feedback processes between climate, surface and vegetation at the northern climatological tree-line (Finnish Lapland). Boreal Environ Res 10:299–314

Vallée S, Payette S (2004) Contrasted growth of black spruce (*Picea mariana*) forest trees at treeline associated with climate change over the last 400 years. Arctic Antarct Alpine Res 36:400–406

Vallée S, Payette S (2007) Collapse of permafrost mounds along a subarctic river over the last 100 years (northern Québec). Geomorphology 90:162–170

Van Bellen S, Garneau M, Booth RK (2011) Holocene carbon accumulation rates from three ombrotrophic peatlands in boreal Quebec, Canada: impact of climate-driven ecohydrological change. The Holocene 21:1217–1231

Veilleux-Nolin M, Payette S (2012) Influence of recent fire season and severity on black spruce regeneration in spruce-moss forests of Quebec, Canada. Can J For Res 42:1316–1327

Vitt DH, Chee WL (1990) The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio 89:87–106

Vowles T, Björk RG (2019) Implications of evergreen shrub expansion in the Arctic. J Ecol 107:650–655

Walker MJC, Berkelhammer M, Björck S, Cwynar LC, Fisher DA, Long AJ, Lowe JJ, Newnham RM, Rasmussen SO, Weiss H (2012) Formal subdivision of the Holocene Series/Epoch: a discussion paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). J Quat Sci 27:649–659

Weckström J, Seppä H, Korhola A (2010) Climatic influence on peatland formation and lateral expansion in sub-arctic Fennoscandia. Boreas 39:761–769

Williams JW, Tarasov P, Brewer S, Notaro M (2011) Late quaternary variations in tree cover at the northern forest-tundra ecotone. J Geophys Res 116:G01017

Woillard GM (1978) Grande Pile peat bog: a continuous pollen record for the last 140,000 years. Quat Res 9:1–21

Zazula GD, Telka AM, Harington CR, Schweger CE, Mathewes RW (2006) New spruce (*Picea* spp.) macrofossils from Yukon Territory: implications for late Pleistocene refugia in eastern Beringia. Arctic 59:391–400

Zimov SA, Chuprynin VI, Oreshko AP, Chapin FS III, Reynolds JF et al (1995) Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. Am Nat 146:765–794

Part II

Temperate and Semi-arid Ecosystems

6 The 2016 Tasmanian Wilderness Fires: Fire Regime Shifts and Climate Change in a Gondwanan Biogeographic Refugium

David M. J. S. Bowman, Dario Rodriguez-Cubillo, and Lynda D. Prior

Abstract

Tasmania is rich in endemic, ancient lineages of plant and animal species, which form distinctive communities. These species are restricted to cool, wet environments where fire is very rare. Although protected in the Tasmanian Wilderness World Heritage Area, these palaeoendemic species are threatened by climate change, which is increasing fire activity because of more dry lightning storms and drought. In January 2016, lightning storms ignited numerous fires which destroyed about 1% of the current distribution of the endemic, slow-growing conifer *Athrotaxis cupressoides*. *A. cupressoides* is fire-sensitive, and burnt stands are unlikely to fully recover because mortality is high, there is limited seedling establishment, and scarring of trunks renders surviving burnt trees more vulnerable to subsequent fires. Securing the survival of palaeoendemics like *A. cupressoides* requires costly management interventions, such as use of firefighting chemicals dropped by aircraft, establishing cut or irrigated firebreaks to protect stands from wildfires, and widespread planned burning to reduce fuel loads in flammable vegetation surrounding palaeoendemic refugia. Such intensive management is at odds with the concept of a self-sustaining 'wilderness'. This has raised profound philosophical questions and ongoing political discussion, about acceptable responses to the impacts of climate change on this world heritage area.

D. M. J. S. Bowman (✉) · D. Rodriguez-Cubillo · L. D. Prior
School of Natural Sciences, University of Tasmania, Hobart, TAS, Australia
e-mail: david.bowman@utas.edu.au; dario.rodriguez@utas.edu.au; lynda.prior@utas.edu.au

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_6

6.1 Introduction

The island of Tasmania lies 200 km south of the Australian mainland and contains one of the largest remaining temperate wilderness areas in the southern hemisphere, with almost a quarter of the island conserved in the Tasmanian Wilderness World Heritage Area (TW WHA) (Press 2016; Mackey et al. 2017). The TWWHA is 15,800 km^2 in extent and conserves most of the southwest and the central plateau of the island (Fig. 6.1) and is inscribed on the World Heritage List for seven natural and cultural heritage criteria (Department of the Environment and Energy 2019). World Heritage listing provides the highest level of protection and resourcing available in Australia. One of the key biological values of this world heritage area is the high concentration of ancient lineages of invertebrate animals and vascular and non-vascular plants that are endemic to Tasmania (Kirkpatrick et al. 1993; Jordan et al. 2016). These species are considered 'palaeoendemics', defined as ancient taxonomic groups of organisms that are geographically confined, usually in regions where biologically important features of ancient environments survive but have been lost elsewhere (Jordan et al. 2016). The Tasmanian palaeoendemic taxa and other temperate Australian rainforest flora have demonstrable Gondwanan linkages, as evidenced by the southern hemisphere biogeography of extant related species that have regionally restricted distributions in New Zealand, New Caledonia, and Patagonia in South America (Balmer et al. 2004; Jordan et al. 2016; Mackey et al. 2017). Further, many of these taxa have fossil evidence of extinct close relatives throughout the Cainozoic and in some cases in the Mesozoic, from sites scattered across the southern hemisphere, including Antarctica (Kershaw and McGlone 1995; Hill and Brodribb 1999).

A significant feature of Tasmanian palaeoendemic plants is that they form distinctive communities, with high aesthetic values and strikingly different from the dominant Australian vegetation, with often deep green hues, unusual plant life forms, and vegetation physiognomy. Good examples include Australia's only winter deciduous tree (deciduous beech, *Nothofagus gunnii*), bolster heaths, and the epiphytic mosses and lichens which clothe rainforest trees (Fig. 6.2). These palaeoendemic plant communities are highly spatially restricted in western Tasmania, occurring in cool, moist environments and typically in topographic settings that afford protection from landscape fires. Thus, the palaeoendemic and other temperate rainforest vegetation persists in a fine-scaled intermix with fire-adapted, sclerophyllous, and open-canopied evergreen vegetation dominated by archetypic Australian genera, such as *Eucalyptus*, *Leptospermum*, *Acacia*, and *Banksia* (Balmer et al. 2004; Pyrke and Marsden-Smedley 2005; Wood and Bowman 2012).

An iconic example of a Tasmanian palaeoendemic is the genus *Athrotaxis* in the conifer family Cupressaceae. *Athrotaxis* is believed to have diverged from other conifers in the Cupressaceae in the Jurassic around 150 mya (Leslie et al. 2012) and is regarded as one of the oldest surviving plant lineages on Earth. *Athrotaxis* is distantly related to redwoods, also understood to be 'living fossils' (Schulz and Stutzel 2007). There are two extant species of *Athrotaxis*: *A. cupressoides* D. Don

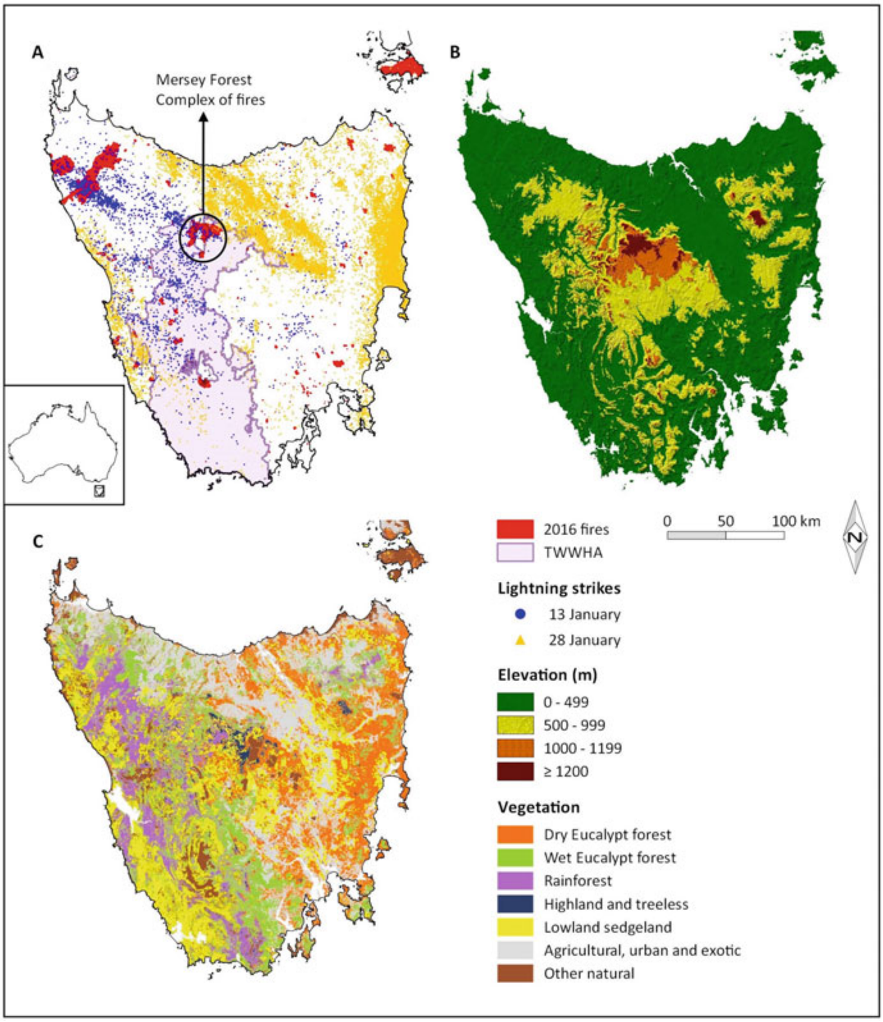


Fig. 6.1 (**a**) The island of Tasmania, showing the Tasmanian Wilderness World Heritage Area (TWWHA), recorded lightning strikes in January 2016, and the areas burnt by wildfires between January and March 2016; (**b**) elevation; and (**c**) vegetation groups (corresponding to those in Table 6.1a)

and *A. selaginoides* D. Don. While the species have distinct morphologies and ecologies they can co-occur and, in some instances, hybridise (Worth et al. 2016a). *A. cupressoides* is a small tree that predominantly occurs at or above the treeline in the western mountains and central plateaux of Tasmania, often in poorly drained areas with deep organic soils. By contrast, *A. selaginoides* is a taller tree, which occurs in temperate rainforests as a canopy emergent in sheltered slopes and valleys in western Tasmania below the treeline. Both are very slow-growing and can

Fig. 6.2 (**a**) Palaeoendemic vegetation in a subalpine area of the TWWHA; (**b**) the long-lived palaeoendemic conifer *Athrotaxis cupressoides*; (**c**) and (**d**) landscape showing stands of *Athrotaxis cupressoides* burnt by the Mersey Forest Complex Fire in the TWWHA in 2016; (**e**) *Sphagnum* moss and organic soils damaged by the fire. (**f**) These fires burnt into topographic refugia, killing the fire-sensitive vegetation. (*Photo credits:* (**a**) and (**b**) Grant Dixon, (**c**)–(**f**) Rob Blakers)

attain ages in excess of 1000 years (Ogden 1978). An unusual feature of the reproductive biology of *A. cupressoides* is the predominance of vegetative reproduction via root suckering, resulting in clonal populations much older than the emergent stems, and possibly originating from seeds that established after deglaciation around 10,000 years ago (Worth et al. 2016b).

Like other Tasmanian palaeoendemics, *Athrotaxis* is intolerant of frequent or intense fire, presumably reflecting the largely fire-free niche in which the species has evolved. Fire regimes in Tasmania changed following the arrival of Aboriginal people, who entered Tasmania via a land bridge in the late Pleistocene (35,000 years ago), well before the height of the last ice age (O'Connell and Allen 2004). Despite continuous occupancy of the Tasmanian landscape, including during periods of abrupt climate change, Aboriginal fire use caused limited damage to

Table 6.1 Total areas of (**a**) vegetation groups and (**b**) selected threatened communities, statewide, and in the Tasmanian Wilderness World Heritage Area (TWWHA)

	Statewide			TWWHA			MFCF
	Area	Area burnt in 2016	%	Area	Area burnt in 2016	%	Area burnt in 2016
(a) Vegetation group (km^2)							
Dry eucalypt forest and woodland	15,895	208	1.3	1625	43	2.7	82
Wet eucalypt forest and woodland	10,934	351	3.2	3629	45	1.2	97
Rainforest and related scrub	7158	87	1.2	3264	9	0.3	12
Highland treeless vegetation	1084	34	3.1	764	33	4.4	34
Lowland sedgeland and grassland	7359	260	3.5	3815	38	1.0	16
Other natural environments	10,053	193	1.9	2615	13	0.5	15
Agricultural, urban, and exotic vegetation	16,240	39	0.2	16	1	8.0	7
Total	68,723	1172	1.7	15,728	183	1.2	262
(b) Selected threatened communities burnt by the Mersey Forest Complex Fires (ha)							
Athrotaxis cupressoides communities[a]	24,355	139	0.57	24,040	139	0.58	139
Athrotaxis selaginoides communities[b]	28,717	2	0.01	17,188	2	0.01	2
Cushion moorland	3162	3	0.08	3020	3	0.08	3
Sphagnum peatland	3478	86	2.46	2740	79	2.86	86

The distributions of these vegetation groups are shown in Fig. 6.1c. The areas burnt in 2016, and as a percentage of each category, are also shown. The area of each vegetation type burnt by the Mersey Forest Complex Fires (MFCF) is also listed. Note that areas in Table 6.1(a) are expressed in km^2, but the areas in Table 6.1(b) are in ha, as they are considerably smaller (1 km^2 = 100 ha)

Areas were calculated by intersecting TasVeg 3.0 (https://listdata.thelist.tas.gov.au/opendata), the TWWHA perimeter (https://data.gov.au), and the 2016 fire boundaries. Note: the total areas presented here, in Press (2016) and AFAC (2016), all differ by up to 10%

[a] Areas are the sum of the three threatened communities containing *A. cupressoides*

[b] Areas are the sum of the three threatened communities containing live *A. selaginoides*

fire-sensitive vegetation compared to the impacts of European colonisation (Bowman and Brown 1986). Importantly, Aboriginal fire management created landscape mosaics of vegetation with different ages since fire and hence fuel loads. Such fire mosaics can impede fires, except under extreme fire weather conditions (Trauernicht et al. 2015). European colonisation, which commenced in 1803, violently disrupted this ancient Tasmanian fire management tradition, resulting in large areas of palaeoendemic vegetation lost due to wildfires. Often, fires were lit or escaped control in the course of pasture management, forest clearing or geological prospecting (Marsden-Smedley 1998). Mapping suggests that around 30% of the range of *A. selaginoides* has been lost in the last 200 years (Brown 1988), and half of the *A. cupressoides* on the central Plateau was burnt in the summer of 1960/1961 by uncontrolled fires set by graziers to renew grasslands during an intense drought (Fig. 6.3) (Johnson and Marsden-Smedley 2002). Fires in this region have also damaged organic soils, which are very slow to recover (Cullen 1995; Bridle et al. 2001; Storey and Comfort 2007).

The well-recognised fire sensitivity of species such as the palaeoendemic conifers has led to the prohibition of campfires (and use of fuel stoves instead) throughout the World Heritage Area (Press 2016). This policy, together with the cessation of pastoralism and a decline in arson, has led to a sharp reduction in human-started fires in the World Heritage Area (AFAC 2016). Unfortunately, ignitions by dry lightning have increased, and since the late 1960s, both the number of fires and total area burnt in the TWWHA have increased, presenting a threat to its integrity (AFAC 2016; Fig. 6.4). In 2016 a series of lightning-ignited fires damaged sensitive vegetation, including *A. cupressoides* populations.

Palaeoendemic species that persist in damp, cool, fire-free refugia in the mountains of Tasmania, such as *Athrotaxis* species, are excellent indicators of anthropogenic climate change for the following reasons. First, dendrochronology of Tasmanian conifers, including *Athrotaxis* species, shows summers have been warming over the last millennium and that this trend has accelerated since the 1950s (Allen et al. 2018). Second, records of lightning-ignited fires show a steady increase in their number and area burnt since the 1990s in western Tasmania. Regardless of the uncertainty of whether lightning has increased in this period (Styger et al. 2018), these data clearly show that landscapes are becoming more receptive to landscape fires because of fuel dryness. Third, analysis of downscaled climate data points to more frequent weather conditions that will support wildfire through this century (Fox-Hughes et al. 2014).

Here, we describe a major fire event that destroyed areas of palaeoendemic vegetation, including *Athrotaxis*, in January 2016. This fire event was caused by the conjunction of extreme drought and lightning storms. We explore the role played by climate change in causing this event, drawing on palaeoecological, historical, climate, and ecological studies. We then consider possible management responses in this globally unique ecosystem, given the reality of increased lightning and anthropogenic landscape fires under a rapidly warming and drying climate, and, more broadly, the philosophical implications of a world heritage Gondwanan refugium threatened by climate change.

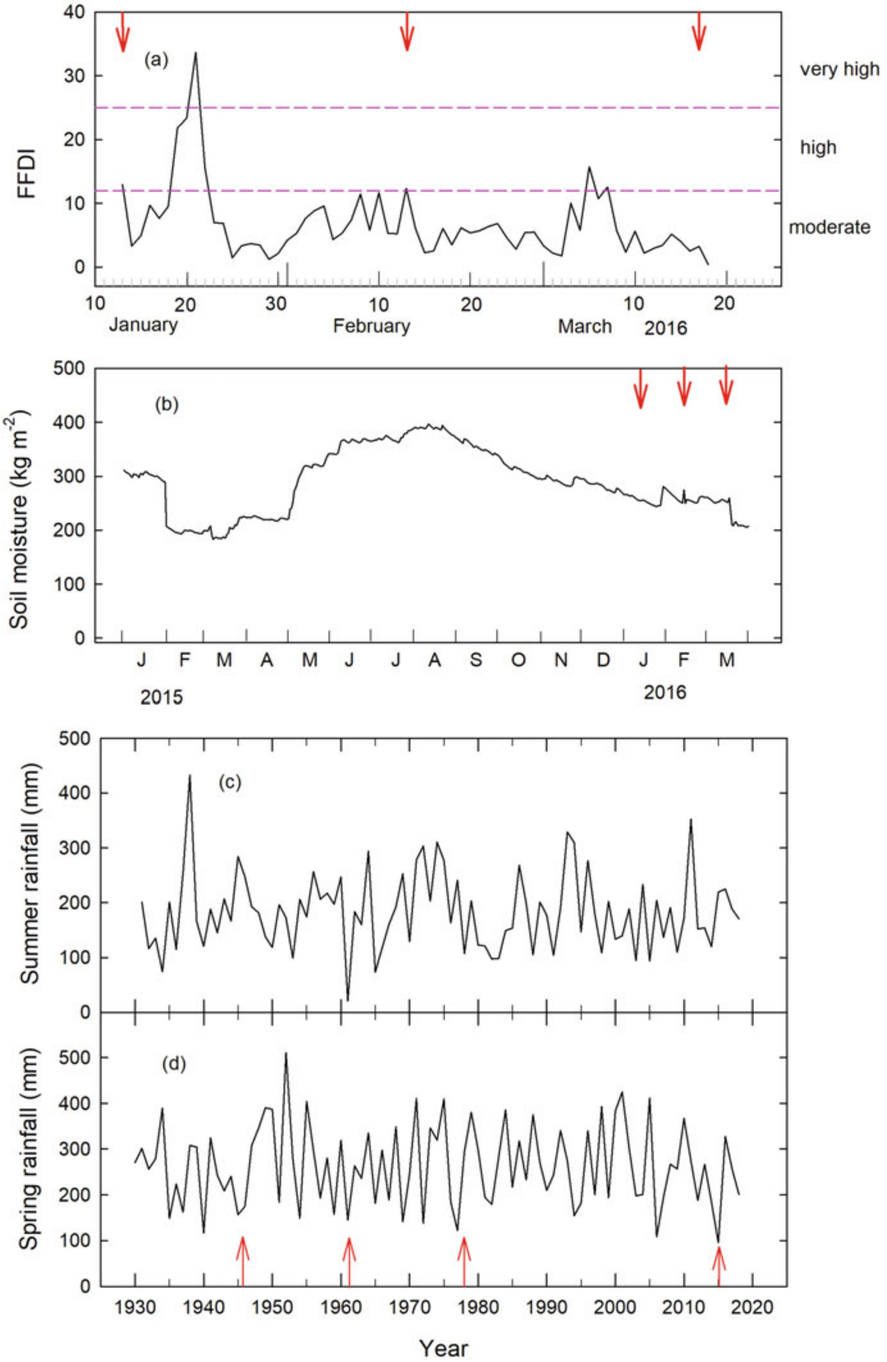


Fig. 6.3 (**a**) Daily maximum forest fire danger index (FFDI) at Liawenee (1057 m elevation) during the period the Mersey Forest Complex Fires burnt in 2016. Values of 12–24 (dashed lines) are regarded as high and 25–49 as very high. The arrows indicate the three electrical storms that

6.2 The 2016 Wilderness Fires

In 2015 Tasmania experienced a severe drought with reduced rainfall throughout the winter followed by the driest spring in 140 years of climate records (Fig. 6.3). Temperatures for Tasmania as a whole were well above average, contributing to the drying: mean maximum temperature in 2015 was 0.28 °C above the annual average, and in the summer of 2015/2016, it was 1.89 °C above the long-term summer average (Bureau of Meteorology archives at http://www.bom.gov.au/climate/current—specifically http://www.bom.gov.au/climate/current/annual/tas/archive/2015.summary.shtml and http://www.bom.gov.au/climate/current/season/tas/archive/201602.summary.shtml). The drying is apparent in the declining soil moisture (Fig. 6.3). Importantly, such extreme dry and warm conditions can cause the typically wet organic 'peat' soils to dry out and become flammable, enabling fire to spread through usually fire-resistant environments in alpine Tasmania.

The drought was associated with two global interannual climate modes both known to affect rainfall and temperature in Australia. First, there was a well-developed El Niño event associated with cool sea surface temperature and slackening easterly winds on the east coast of Australia, known to cause drought on the Australian continent, particularly in the southeast. Second, there were pronounced negative values of the Indian Ocean Dipole, which affects mid-latitude rain bearing winds in the austral spring (Press 2016). Climate change attribution studies using climate change models have shown that the warmth, and to a lesser degree, the dryness can be attributed to the forcing of anthropogenic climate change (Black and Karoly 2016; Karoly et al. 2016).

On the night of 13 January 2016, a massive dry lightning storm ignited more than 80 fires across Tasmania (Press 2016; Fig. 6.1), some of which escalated into major wildfires. A second dry lightning storm on 28 January 2016 and a third on 13 February 2016 also resulted in new ignitions (AFAC 2016). A total of 229 fires burnt in Tasmania between 13 January and 15 March 2016, under generally moderate forest fire danger index (FFDI) conditions (Fig. 6.3). The fires burnt around 125,000 ha of vegetation across Tasmania (AFAC 2016; Fig. 6.1). This included 20,126 ha (1.3%) of the TWWHA (AFAC 2016). The predominant vegetation types burnt by the fires for Tasmania as a whole, and for the TWWHA, were primarily fire-adapted, treeless sedgelands, and eucalypt forests (Table 6.1). Nonetheless, the

---

Fig. 6.3 (continued) ignited fires. (**b**) Soil moisture in the top 1 m of soil adjacent to Lake Mackenzie, in the 15 months up to and including when the fire burnt. This is derived from the Bureau of Meteorology's Barra-VT reanalysis product (https://data.gov.au/dataset/ds-bom-ANZCW0503900566/details?q=). Arrows indicate the electrical storms that ignited the fires. (**c**) Long-term summer (December to February) and (**d**) spring (September to November) rainfall at Meander (Bureau of Meteorology http://www.bom.gov.au/climate/data/index.shtml; station 91,061, with missing values from nearby station 91,267). This station is 16 km from Lake Mackenzie (approx 1100 m elevation) but at only 291 m elevation; however, it has the longest, most complete rainfall record in the area. The arrows indicate the four fires in the historical record that damaged >100 ha of *A. cupressoides* communities

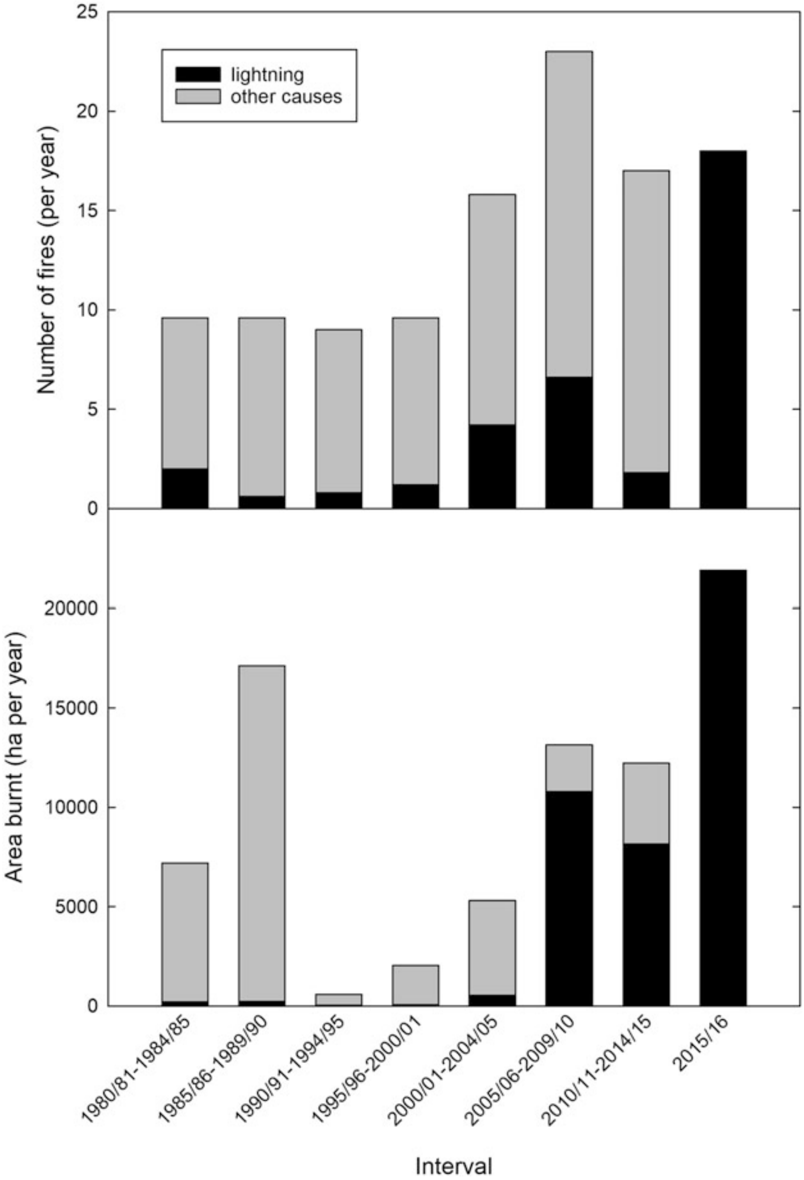


Fig. 6.4 The number of fires and the area burnt by fires started by lightning and those from other causes, in the Tasmanian Wilderness World Heritage Area. Data were averaged over 5-year intervals, except the final bar, which refers to a single year. Data from Styger et al. (2018)

dryness of the fuels also resulted in subalpine areas being burnt by high-severity fires, resulting in widespread stem death and localised combustion of organic soils. Smoke pollution from the fires was associated with adverse effects on human health including hospitalisation for respiratory and cardiovascular illnesses (Edwards et al. 2018). Among the most significant biological impacts was the loss of approximately 141 ha of *A. cupressoides* forest in the Lake Mackenzie area (Senate ECRC 2016). This could have been far worse: a deterioration in fire weather conditions, such as the development of strong, dry northerly winds, during this fire event could have threatened the core refugium of *A. cupressoides* in an area known as the Walls of Jerusalem. The Lake Mackenzie fires were largely quelled by an intense storm that crossed the area in March 2016. A second intense storm crossed the fire ground in May 2016, resulting in a historically significant flood in the lower reaches of the Mersey River.

6.2.1 2016 Fire Impacts on *A. cupressoides* Populations

A post-fire survey of three burnt *A. cupressoides* populations at Lake Mackenzie found that 68% of 3100 stems were killed by the fire (Bowman et al. 2019). There was a humped relationship between survival and stem diameter, with highest survival for stems around 45 cm DBH and poorer survival for smaller and larger stems (Fig. 6.5). This pattern is explicable because smaller stems had thinner bark, and foliage closer to the ground, and were thus more affected by surface fires, whereas larger stems were more vulnerable because they had pre-existing fire scars, which lack a protective layer of bark. Of all sampled living stems, 17% had fire scars, but for stems larger than 50 cm DBH, this value was 79% (Fig. 6.5). The higher mortality of fire-scarred stems suggests a feedback, whereby increased fire frequency leads to increased scarring of trees, which in turn increases stem mortality in future fires. *A. cupressoides* has a long lifespan, with large individual stems over 1000 years old (Ogden 1978), so even very low fire frequency could drive population collapse. Evidence of such local extinction was found in a sediment core, in which four spikes in microscopic charcoal between 6000 and 2500 years ago were each associated with a sharp decline of Cupressaceae pollen, considered a proxy for *Athrotaxis* (Fletcher et al. 2014). The researchers attributed the increased fire activity to the intensification of El Niño in the late Holocene.

There was very limited post-fire regeneration of *A. cupressoides* within a year of the Lake Mackenzie fire, unlike in the more widespread, fire-adapted vegetation elsewhere in Tasmania, where resprouting species are more common (French et al. 2016; Nicholson et al. 2017; Prior et al. 2016). An extensive survey found seedling regeneration or suckering of *A. cupressoides* in some burnt populations, but densities were similar to, rather than higher than, in unburnt plots (Bowman et al. 2019). It is unlikely that regeneration will be sufficient to offset fire-induced mortality of trees and seedlings present at the time of the fire. Previous studies have also noted a post-fire regeneration failure (Kirkpatrick and Dickinson 1984; Cullen and Kirkpatrick 1988). For instance, Holz et al. (2015) noted a dearth of seedlings or saplings in *A. cupressoides* stands killed during the 1960–1961 fire and that they sampled 50 years later. This post-fire recruitment bottleneck is related to the demographic

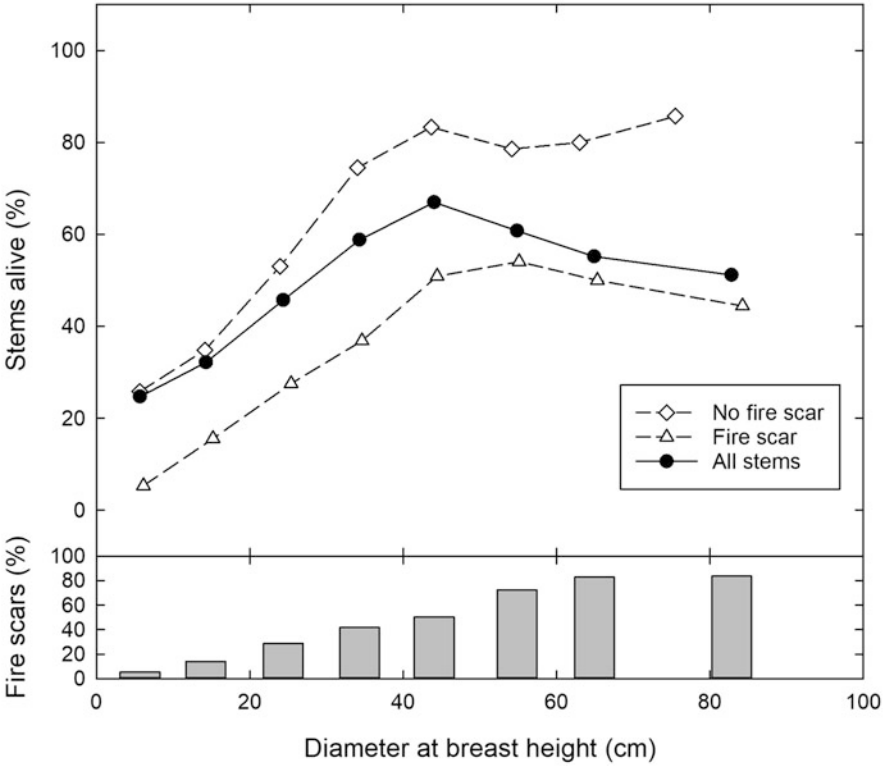


Fig. 6.5 Survival of stems as a function of diameter and whether they had fire scars. Survival was highest at intermediate diameters (around 50 cm). The lower panel shows the percentage of stems with fire scars increased strongly as stem diameter increased; nearly all large stems had been exposed to past fire

attributes of *A. cupressoides*, including the absence of a long-lived seed bank, mast seeding and hence episodic seed crops, poorly protected seeds, limited seed dispersal, inability to resprout from fire-killed stems, and vulnerability to post-fire herbivory (Kirkpatrick and Dickinson 1984; Cullen and Kirkpatrick 1988; Holz et al. 2015). The high fire-induced mortality of adults also affects recruitment because live, mature trees are the only source of seeds or suckers.

The intensity of the Lake Mackenzie fire and hence the susceptibility of *A. cupressoides* stems were not directly determined. However, using the diameter of burnt twigs as a proxy of fire intensity showed it was similar to a wildfire in highly flammable, treeless sedgeland and shrub vegetation in south-western Tasmania, which burnt with an average fire radiative power of 360 MW (French et al. 2016), well below maximum values of more than 1500 MW in fires elsewhere (Ichoku et al. 2008). An experiment using a gas burner simulating very low fire line intensities ($<$ 35 kW m^{-1}) found that 95% of *A. cupressoides* seedlings $<$50 cm tall were completely killed by a short exposure to this flame (Prior et al. 2018).

6.3 Persistence of *A. cupressoides* Under Climate Change

There is palaeoecological, biogeographic, and genetic evidence that palaeoendemics have been able to track the movement of climate refugia through the Quaternary (Mokany et al. 2017). However, under projected climate change, the available niches for *A. cupressoides* will markedly shrink (Fig. 6.6). Currently *A. cupressoides* predominantly occurs between 1100 and 1300 m asl, with the oldest, largest *A. cupressoides* trees found at higher elevations, suggesting that higher areas are the most secure part of its elevation range (Ogden 1978). However, there is little land area above the current upper limit of *A. cupressoides*' range available for it to migrate to, because the few emergent high peaks occupy very small areas (Fig. 6.6).

Species distribution modelling has also highlighted the vulnerability of Tasmanian palaeoendemics to climate change because of the loss of cool, moist refugia critical (Porfirio et al. 2014; Keppel et al. 2015). For example, modelling by Yospin et al. (2015) suggests the current distribution of *Athrotaxis* populations is a legacy of past climates and that attrition will be ongoing, even without further climatic shifts. These models are conservative, because they do not consider the rapid transformative power of fire in changing the species range. Fires trigger a series of feedbacks with the species demography resulting in local extinction of *A. cupressoides* populations. First, a single fire penetrating an unburnt stand can

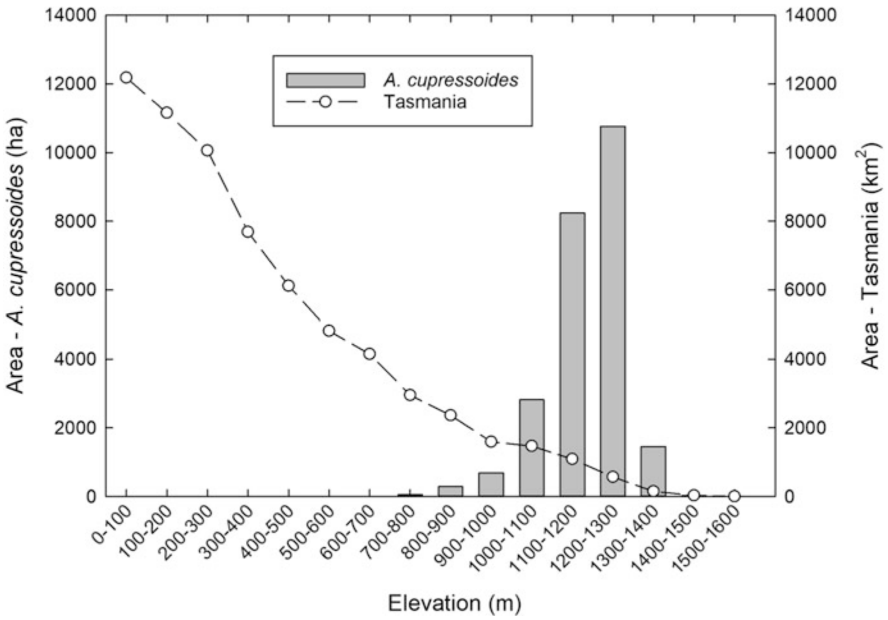


Fig. 6.6 Area occupied by *A. cupressoides* communities (in ha), binned by 100 m elevation classes, compared with that of Tasmania as a whole (in km^2; 1 km^2 = 100 ha). 50% of the area of *A. cupressoides* communities is above 1200 m elevation, compared with only 1% of Tasmania as a whole

kill and damage stems, rendering them more likely to be killed in subsequent fires. The attrition of adults reduces seed production and development of clonal shoots from roots. Burnt stands have a higher likelihood of being burnt because of the increased flammability of understory vegetation in the early post-fire successional stages (Holz et al. 2015). In addition, fires can encourage grass growth, which attracts more herbivores that eat and trample seedlings.

Over longer time scales, landscape fires can eliminate stands of trees and thereby degrade the genetic diversity of the species (Worth et al. 2017), which is already low because of its reliance on clonal reproduction (Worth et al. 2016b). Collectively, the resultant population attrition is an example of the 'interval squeeze' model proposed by Enright et al. (2015). Under this model, climate change both increases the frequency and severity of fire and reduces the ability of plant populations to recover because heat and drought stress lower fecundity, seedling establishment, and growth rates, leading to slower reproductive maturity. Such feedbacks caution against using simple calculations based on post-fire recovery times, which suggest a small fraction (0.1 to 0.2%) of the existing *A. cupressoides* domain can be burnt per year without causing long-term declines in the species range (e.g. Press 2016).

Another important factor affecting fire impact is terrain, which can mitigate the severity of fires, or provide barriers to the progress of fire. A survey of burnt and unburnt stands across the geographic range of *A. cupressoides* found that burnt stands typically occurred in topographic settings exposed to northerly fire bearing winds, more distant from lake edges, and seldom on islands (Bowman et al. 2019). The importance of 'fire refugia' is apparent in the genetic architecture of the species, with the most genetically heterogeneous populations in the sites considered least likely to burn (Worth et al. 2017). Other southern hemisphere relictual conifers have also been shown to persist in fire refugia, for instance, *Widdringtonia cedarbergensis* in South Africa (White et al. 2016), *Callitris sulcata* in New Caledonia (Haverkamp et al. 2015), and *Austrocedrus chilensis* in Patagonia (Landesmann et al. 2015).

Climate change is weakening the effectiveness of topographic refugia for palaeoendemic species such as *A. cupressoides* (Harris et al. 2018). Downscaled climate models predict a steady increase of fire weather throughout the twenty-first century across the geographic range of *A. cupressoides*, driven by warmer temperatures and drier conditions (Fox-Hughes et al. 2014). Concerningly, there is a trade-off between topographic fire protection afforded by rocky areas and increased drought stress because these settings are typically drier than the surrounding landscape (Landesmann et al. 2015). In addition, recent decades have seen a marked increase in the number of, and area burnt by, lightning fires across western Tasmania (Styger et al. 2018) (Fig. 6.4).

Lightning is rare in Tasmania compared with the Australian continent, with <0.5 flashes km^{-2} yr.^{-1}, and its climatology here is little studied (Dowdy and Kuleshov 2014). In January and February 2016, fast-moving cold fronts swept across the west coast of the island causing atmospheric instability and moist convection, resulting in intense lightning activity. However, there was very little precipitation because of drier conditions in the lower atmosphere. The lightning storms tracked across the landscape, igniting fires in vegetation that had dried during a protracted drought. Across the southern hemisphere, there is evidence that lightning-ignited fires are increasing, especially during summers with below average rainfall, typically occurring when westerly winds contract polewards (Mariani et al. 2018). While it is uncertain whether the incidence of lightning has recently increased, the increase in lightning-ignited fires is clear, reflecting more frequent and intense dry periods, during which fuels dry out and become more flammable (Styger et al. 2018) (Fig. 6.4). Analysis of downscaled climate projections suggest lightning activity may decline across Tasmania over this century, but this effect will be counteracted by drying conditions increasing the likelihood of ignition (Love et al. 2016). Clearly a deeper understanding of Tasmanian climate is required to better predict occurrence of dry lightning storms and their coincidence with summer drought.

6.4 Broader Ecological Impacts

Here we have focused on the impact of fire on *Athrotaxis*, largely because, as an iconic, ancient fire-sensitive tree, there is a larger knowledge base and strong motivation to fund research to document fire impacts. It is likely that there are similar demographic impacts for other palaeoendemic conifers and angiosperms, which are known to be highly sensitive to fire and recover poorly (Kirkpatrick and Dickinson 1984). The effects of fire on other biota in these ecosystems, such as endemic invertebrate fauna, are even more poorly known compared to those on vascular plants (Driessen and Kirkpatrick 2017). A critical impact of fire is the destruction of organic soils, which have accumulated extremely slowly through the Holocene and are a keystone feature of these Gondwanan ecosystems (Wood et al. 2011a). Under drought conditions organic soils are highly combustible, and fires can smoulder for months, killing vegetation and exposing the infertile mineral soils below (Hill 1982; French et al. 2016), with adverse hydrological effects (Whinam et al. 2001). Fires can result in a loss of moss beds and the protection they afford to fire-sensitive plants such as *Athrotaxis* and rainforest species (Whinam et al. 2001). Post-fire recovery of vegetation on burnt organic soils is extremely slow and can be interrupted by grazing animals (Bridle et al. 2001). Organic soil can slowly redevelop in the absence of fire after vegetation re-establishes, as has been demonstrated in the Holocene (Fletcher et al. 2014). However, Tasmania is currently climatologically marginal for organic soil development (Brown 2005), and thus burnt soils are most unlikely to be replaced in future warmer and drier climates.

6.5 Anthropocene Management Responses

The Tasmanian 2016 fires resulted in the longest and most costly firefighting campaign in Tasmania's history up to that time (worryingly, at the time of writing, the 2019 wilderness fires, also ignited by dry lightning storms, have eclipsed the 2016 fires in terms of their number, geographic scale, and costs). The 2016 fires were fought with ground-based crews that were helicoptered into remote areas, with some additional aerial suppression (Press 2016). Notably, firefighting chemicals were used for the first time in the TWWHA (Press 2016). Over 40 aircraft, 5600 Tasmanian firefighters, and 1000 firefighters from other Australian States and overseas were involved in the fire campaign. The total cost of the firefighting is estimated to be c. $52.6 million.

It is clear that long-term survival of Tasmanian palaeoendemics is under threat from the synergistic effects of more frequent drought, more extreme fire weather conditions, and more frequent fires ignited by dry electrical storms, all associated with anthropogenic climate change. This presents vexing philosophical and practical questions about the most appropriate management responses in the Tasmanian Wilderness World Heritage Area (Gill 2016; Rickards 2016). One of the core attributes of the TWWHA is that it is a ‘wilderness’, largely free of impacts from industrialised society, and is self-perpetuating, with little need for management interventions. The 2016 fires challenged these ideas, propelling into the social and political consciousness an awareness of the risks posed by climate change and associated increases in fire activity. This was manifest by Australian Commonwealth Government (Senate ECRC 2016) and Tasmanian State Government (Press 2016; DPIPWE 2017) inquiries, a professional review of firefighting (AFAC 2016) and local, national, and international media attention (Gill 2016; Marris 2016).

By definition Tasmanian Wilderness is remote, and the terrain, weather, occurrence of organic soils, and closed canopy vegetation present formidable challenges for fire detection and suppression (Press 2016; AFAC 2016). Clouds and dense canopies can obscure ignitions. Building firebreaks with heavy machinery is rarely possible, given the remote and intractable terrain and wilderness values. Even with helicopters it is difficult and sometimes impossible, to safely insert crews quickly enough to stop the fires spreading before they reach a point where it is no longer practical to put them out. It is also important to note that water bombing can be of limited effectiveness because peat fires can burn underground for many weeks. It is now generally accepted that fire management in the TWWHA must involve increased surveillance of both lightning and fire starts, with rapid attack of uncontrolled fires using ground-based crews and strategic aerial drops of firefighting chemicals (Press 2016; Styger 2018). However, experience from North America has shown that total fire suppression is not achievable even with specialist remote area fire crews and aerial drops of water and firefighting chemicals (Stephens and Ruth 2005; Calkin et al. 2005, 2014). Fire managers in the TWWHA are now using innovative approaches, such as strategically setting up irrigation systems to protect palaeoendemic vegetation under direct threat from fire.

Fuel management of flammable vegetation surrounding palaeoendemic refugia is also essential (Senate ECRC 2016; Kirkpatrick et al. 2018). In remote areas, planned burning is carried out using aircraft without involvement of ground crews (Press 2016). Such planned burning in fire-adapted sedgelands can reduce fire intensity and in some cases block the spread of fires (French et al. 2016). However, this approach requires care and flexibility, and acknowledging that under extreme fire weather conditions, this technique may not effectively limit the spread of fires and carries risk that some fires may escape control. The current reliance on aerial burning of large areas lacks the precision that can be achieved by properly trained crews on foot. Such targeted burning could protect stands of *A. cupressoides* in flammable grasslands, systems that were possibly maintained by Aboriginal landscape burning. It has also been suggested that patch-burning designed to emulate Aboriginal fire management should be implemented, to impede the development of extensive fires (Marsden-Smedley and Kirkpatrick 2000). Compared to aerial burning approaches, crews on the ground have greater situational awareness and can work under a wider range of weather conditions. They are therefore likely to be better able to tailor planned burning to protect threatened vegetation communities, such as small populations of *A. cupressoides* embedded in mosaics of flammable vegetation. This may also involve cutting firebreaks around palaeoendemic vegetation (Press 2016). Improved mapping of stands of *A. cupressoides* was identified as a key requirement following the 2016 fires, as many stands were omitted from existing vegetation maps (Press 2016). Landscape ecology analyses (such as Wood et al. 2011b) are required to identify and prioritise populations of *A. cupressoides* and other threatened communities that are appropriate for such targeted fuel management and identify sites that are likely to persist in fire-resistant refugia (Press 2016).

The vulnerability of palaeoendemic flora to climate change and fire has also prompted the establishment of conservation seed banks. A research programme is under way to discover if seedlings grown from seeds or propagated from cuttings can be established to restore areas of pine burnt and killed in the 2016 fires. Given the projected effects of climate change, there will need to be serious consideration of ex situ conservation programmes for *A. cupressoides*, such as planting seedlings in irrigated, fire-protected cool areas and possibly even excavating entire trees and re-establishing them in botanical gardens in western Tasmania or other regions in the world with climates similar to the Tasmanian mountains.

6.6 Conclusions

The 2016 Tasmanian Wilderness fires highlighted the vulnerability of TWWHA to climate change (Press 2016). The effects of anthropogenic climate change on vulnerable species such as Tasmanian palaeoendemics have been described by a press and pulse model (Harris et al. 2018). According to this model, deteriorating climate conditions can be described as a chronic ‘press’, which stresses ecological systems. Unpredictable, but increasingly frequent, fires act as a ‘pulse’ that can drive the system to local ecological collapse.

The naturally ignited fires of 2016 burnt large areas of flammable vegetation and impacted populations of the palaeoendemic conifer *A. cupressoides*. The event triggered re-evaluation of fire management in the TWWHA, including increased planned burning of flammable vegetation types such as sedgelands and rapid attack of fires using ground crews and aerial drops of firefighting chemicals and establishment of irrigation systems protect vegetation threated by fire. Further consideration of patch-burning, emulating Aboriginal fire management is also required (Marsden-

Smedley and Kirkpatrick 2000). Many of these approaches were trialled following the widespread fires in the TWWHA in January 2019, which were ignited by massive lightning storms. Restoration ecology programmes involving the propagation of seeds from pre-existing seed banks and cuttings is underway in attempt to reverse the population declines of the *A. cupressoides*. Despite these management interventions, the longer-term prognosis for persistence of palaeoendemics like *A. cupressoides* is poor, given both the 'press' of dry climates and the 'pulse' of lightning-ignited fires. Such impacts raise the question of whether the TWWHA should be formally recognised as a world heritage property at risk from climate change-driven fires (UNESCO 1972; Australian National University 2009).

Acknowledgements This research was partially supported by the Australian Research Council (DP110101950) and the Bushfires and Natural Hazards Cooperative Research Centre. We thank Grant Williamson for his help with the geospatial and meteorological analyses.

References

AFAC (2016) A review of the management of the Tasmanian fires of January 2016. Australasian Fire and Emergency Service Authorities Council Limited, East Melbourne, Victoria

Allen KJ, Cook ER, Evans R, Francey R, Buckley BM, Palmer JG, Peterson MJ, Baker PJ (2018) Lack of cool, not warm, extremes distinguishes late 20th Century climate in 979-year Tasmanian summer temperature reconstruction. Environ Res Lett 13:034041. https://doi.org/10.1088/1748-9326/aaafd7

Australian National University (2009) Tasmanian Wilderness. In: Implications of climate change for Australia's world heritage properties: a preliminary assessment. A report to the Department of Climate Change and the Department of the Environment, Water, Heritage and the Arts by the Fenner School of Environment and Society, Australian National University. Canberra, pp. 79–94

Balmer J, Whinam J, Kelman J, Kirkpatrick JB, Lazarus E (2004) Floristic values of the Tasmanian Wilderness World Heritage Area. Nature Conservation Report 2004/3. Department of Primary Industries, Water and Environment, Hobart

Black MT, Karoly DJ (2016) Southern Australia's warmest October on record: the role of ENSO and climate change. Bull Am Meteorol Soc 97(12):S118–S121. https://doi.org/10.1175/bams-d-16-0124.1

Bowman DMJS, Brown MJ (1986) Bushfires in Tasmania: A botanical approach to anthropological questions. Archaeol Ocean 21:166–171

Bowman DMJS, Bliss A, Bowman CJW, Prior LD (2019) Fire caused demographic attrition of the Tasmanian palaeoendemic conifer *Athrotaxis cupressoides*. Austral Ecol 44(8):1322–1339

Bridle KL, Kirkpatrick JB, Cullen P, Shepherd RR (2001) Recovery in alpine heath and grassland following burning and grazing, Eastern Central Plateau, Tasmania, Australia. Arct Antarct Alp Res 33(3):348–356. https://doi.org/10.2307/1552242

Brown PB (1988) Distribution and conservation of King Billy pine. Forestry Commission, Hobart

Brown MJ (2005) Buttongrass moorlands. In: Reid JB, Hill RS, Brown MJ, Hovenden MJ (eds) Vegetation of Tasmania. Aust Biol Res Study, Canberra, pp 286–303

Calkin DE, Gebert KM, Jones JG, Neilson RP (2005) Forest service large fire area burned and suppression expression trends, 1970–2002. J For 103(4):179–183. https://doi.org/10.1093/jof/103.4.179

Calkin DE, Stonesifer CS, Thompson MP, McHugh CW (2014) Large airtanker use and outcomes in suppressing wildland fires in the United States. Int J Wildland Fire 23(2):259–271. https://doi.org/10.1071/wf13031

Cullen P (1995) Land degradation on the Central Plateau, Tasmania. The legacy of 170 years of exploitation. Parks and Wildlife Service, Hobart

Cullen PJ, Kirkpatrick JB (1988) The ecology of *Athrotaxis* D Don (Taxodiaceae). 1. Stand structure and regeneration of *Athrotaxis cupressoides*. Aust J Bot 36(5):547–560. https://doi.org/10.1071/bt9880547

Department of the Environment and Energy (2019) World Heritage Places—Tasmanian Wilderness. http://www.environment.gov.au/heritage/places/world/tasmanian-wilderness

Dowdy AJ, Kuleshov Y (2014) Climatology of lightning activity in Australia: spatial and seasonal variability. Aust Meteorol Oceanogr J 64(2):103–108. https://doi.org/10.22499/2.6402.002

DPIPWE (2017) Assessment of the ecological impacts of the 2016 Mersey Forest Fire Complex, Nature Conservation Report no 17/5. Department of Primary Industries, Parks, Water & Environment, Hobart

Driessen MM, Kirkpatrick JB (2017) The implications of succession after fire for the conservation management of moorland invertebrate assemblages. J Insect Conserv 21:15–37. https://doi.org/10.1007/s10841-016-9948-9

Edwards LJ, Williamson G, Williams S, Veitch MGK, Salimi F, Johnston FH (2018) Did fine particulate matter from the summer 2016 landscape fires in Tasmania increase emergency ambulance dispatches? A case crossover analysis. Fire 1(2):26. Fire 1:article 26. https://doi.org/10.3390/fire1020026

Enright NJ, Fontaine JB, Bowman DMJS, Bradstock RA, Williams RJ (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Front Ecol Environ 13(5):265–272. https://doi.org/10.1890/140231

Fletcher M-S, Wolfe BB, Whitlock C, Pompeani DP, Heijnis H, Haberle SG, Gadd PS, Bowman DMJS (2014) The legacy of mid-Holocene fire on a Tasmanian montane landscape. J Biogeogr 41(3):476–488. https://doi.org/10.1111/jbi.12229

Fox-Hughes P, Harris R, Lee G, Grose M, Bindoff N (2014) Future fire danger climatology for Tasmania, Australia, using a dynamically downscaled regional climate model. Int J Wildland Fire 23(3):309–321. https://doi.org/10.1071/wf13126

French BJ, Prior LD, Williamson GJ, Bowman DMJS (2016) Cause and effects of a megafire in sedge-heathland in the Tasmanian temperate wilderness. Aust J Bot 64(6):513–525. https://doi.org/10.1071/bt16087

Gill N (2016) Rupture in Tasmania. The Monthly. April: https://www.themonthly.com.au/issue/2016/april/1459429200/nicole-gill/rupture-tasmania

Harris RMB, Beaumont LJ, Vance TR, Tozer CR, Remenyi TA, Perkins-Kirkpatrick SE, Mitchell PJ, Nicotra AB, McGregor S, Andrew NR, Letnic M, Kearney MR, Wernberg T, Hutley LB, Chambers LE, Fletcher MS, Keatley MR, Woodward CA, Williamson G, Duke NC, Bowman DMJS (2018) Biological responses to the press and pulse of climate trends and extreme events. Nat Clim Chang 8(7):579–587. https://doi.org/10.1038/s41558-018-0187-9

Haverkamp C, Prior LD, Fogliani B, L'Huillier L, Anquez M, Hua Q, Bowman DMJS (2015) Effect of landscape fires on the demography of the endangered New Caledonian conifer *Callitris sulcata*. Biol Conserv 191:130–138

Hill R (1982) Rainforest Fire in Western Tasmania. Aust J Bot 30:583–589. https://doi.org/10.1071/BT9820583

Hill RS, Brodribb TJ (1999) Turner Review No. 2—Southern conifers in time and space. Aust J Bot 47(5):639–696

Holz A, Wood SW, Veblen TT, Bowman DMJS (2015) Effects of high-severity fire drove the population collapse of the subalpine Tasmanian endemic conifer *Athrotaxis cupressoides*. Glob Chang Biol 21(1):445–458. https://doi.org/10.1111/gcb.12674

Ichoku C, Giglio L, Wooster MJ, Remer LA (2008) Global characterization of biomass-burning patterns using satellite measurements of fire radiative energy. Remote Sens Environ 112 (6):2950–2962. https://doi.org/10.1016/j.rse.2008.02.009

Johnson KA, Marsden-Smedley JB (2002) Fire history of the northern part of the Tasmanian Wilderness World Heritage Area and its associated regions. Pap Proc R Soc Tasmania 136:145–152

Jordan GJ, Harrison PA, Worth JRP, Williamson GJ, Kirkpatrick JB (2016) Palaeoendemic plants provide evidence for persistence of open, well-watered vegetation since the Cretaceous. Glob Ecol Biogeogr 25(2):127–140. https://doi.org/10.1111/geb.12389

Karoly DJ, Black MT, Grose MR, King AD (2016) The roles of climate change and El Nino in the record low rainfall in October 2015 in Tasmania, Australia. Bull Am Meteorol Soc 97(12): S127–S130. https://doi.org/10.1175/bams-d-16-0139.1

Keppel G, Mokany K, Wardell-Johnson GW, Phillips BL, Welbergen JA, Reside AE (2015) The capacity of refugia for conservation planning under climate change. Front Ecol Environ 13 (2):106–112. https://doi.org/10.1890/140055

Kershaw AP, McGlone MS (1995) The Quaternary history of the southern conifers. In: Enright NJ, Hill RS (eds) Ecology of the southern conifers. Melbourne University Press, Melbourne, pp 30–63

Kirkpatrick JB, Dickinson KJM (1984) The impact of fire on Tasmanian alpine vegetation and soils. Aust J Bot 32(6):613–629. https://doi.org/10.1071/bt9840613

Kirkpatrick JB, Hutchinson MN, McQuillan PB (1993) Alpine Ecosystems. In: Smith SA, Banks MR (eds) Tasmanian Wilderness—World Heritage Values. Royal Society of Tasmania, Hobart, pp 73–79

Kirkpatrick JB, Styger JK, Marsden-Smedley JB (2018) Impact of changes in lightning fire incidence on the values of the Tasmanian wilderness world heritage area. Pap Proc R Soc Tasmania 152:27–32

Landesmann JB, Gowda JH, Garibaldi LA, Kitzberger T (2015) Survival, growth and vulnerability to drought in fire refuges: implications for the persistence of a fire-sensitive conifer in northern Patagonia. Oecologia 179(4):1111–1122. https://doi.org/10.1007/s00442-015-3431-2

Leslie AB, Beaulieu JM, Rai HS, Crane PR, Donoghue MJ, Mathews S (2012) Hemisphere-scale differences in conifer evolutionary dynamics. Proc Natl Acad Sci U S A 109(40):16217–16221. https://doi.org/10.1073/pnas.1213621109

Love PT, Fox-Hughes P, Harris R, Remenyi T, Bindoff N (2016) Impact of climate change on weather-related fire risk factors in the TWWHA. Part II report. Tasmanian Government, Hobart

Mackey B, Cadman S, Rogers N, Hugh S (2017) Assessing the risk to the conservation status of temperate rainforest from exposure to mining, commercial logging, and climate change: a Tasmanian case study. Biol Conserv 215:19–29. https://doi.org/10.1016/j.biocon.2017.08.032

Mariani M, Holz A, Veblen TT, Williamson G, Fletcher MS, Bowman DMJS (2018) Climate change amplifications of climate-fire teleconnections in the Southern Hemisphere. Geophys Res Lett 45(10):5071–5081. https://doi.org/10.1029/2018gl078294

Marris E (2016) Blazes threaten iconic trees. Nature 530:137–138

Marsden-Smedley JB (1998) Changes in southwestern Tasmanian fire regimes since the early 1800s. Pap Proc R Soc Tasmania 132:15–29

Marsden-Smedley J, Kirkpatrick JB (2000) Fire management in Tasmania's Wilderness World Heritage Area: ecosystem restoration using Indigenous-style fire regimes? Ecol Manag Restor 1:195–203

Mokany K, Jordan GJ, Harwood TD, Harrison PA, Keppel G, Gilfedder L, Carter O, Ferrier S (2017) Past, present and future refugia for Tasmania's palaeoendemic flora. J Biogeogr 44 (7):1537–1546. https://doi.org/10.1111/jbi.12927

Nicholson A, Prior LD, Perry GLW, Bowman DMJS (2017) High post-fire mortality of resprouting woody plants in Tasmanian Mediterranean-type vegetation. Int J Wildland Fire 26:532–537. https://doi.org/10.1071/WF16211

O'Connell JF, Allen J (2004) Dating the colonization of Sahul (Pleistocene Australia-New Guinea): a review of recent research. J Archaeol Sci 31(6):835–853. https://doi.org/10.1016/j.jas.2003.11.005

Ogden J (1978) Investigations of the dendrochronology of the genus *Athrotaxis* D. Don (Taxodiaceae) in Tasmania. Tree Ring Bull 38:1–13

Porfirio LL, Harris RMB, Lefroy EC, Hugh S, Gould SF, Lee G, Bindoff NL, Mackey B (2014) Improving the use of species distribution models in conservation planning and management under climate change. PLoS One 9(11). https://doi.org/10.1371/journal.pone.0113749

Press AJ (2016) Tasmanian Wilderness World Heritage Area Bushfire and Climate Change Research Project. Tasmanian Government, Hobart

Prior LD, Williamson GJ, Bowman DMJS (2016) Impact of high-severity fire in a Tasmanian dry eucalypt forest. Aust J Bot 64(3):193–205. https://doi.org/10.1071/bt15259

Prior LD, French BJ, Bowman DMJS (2018) Effect of experimental fire on seedlings of Australian and Gondwanan trees species from a Tasmanian montane vegetation mosaic. Aust J Bot 66:511–517. https://doi.org/10.1071/BT18124

Pyrke AF, Marsden-Smedley JB (2005) Fire attributes categories, fire sensitivity, and flammability of Tasmanian vegetation communities. Tasforests 16:35–46

Rickards L (2016) Goodbye Gondwana? Questioning disaster triage and fire resilience in Australia. Aust Geogr 47(2):127–137. https://doi.org/10.1080/00049182.2016.1154496

Schulz C, Stutzel T (2007) Evolution of taxodiaceous Cupressaceae (Coniferopsida). Org Divers Evol 7(2):124–135. https://doi.org/10.1016/j.ode.2006.03.001

Senate ECRC (2016) Responses to, and lessons learnt from, the January and February 2016 bushfires in remote Tasmanian wilderness. Australian Senate Environment and Communications References Committee, Canberra

Stephens SL, Ruth LW (2005) Federal forest-fire policy in the United States. Ecol Appl 15 (2):532–542. https://doi.org/10.1890/04-0545

Storey K, Comfort M (2007) A progress report on the development of rehabilitation priorities for broad scale erosion within the Word Heritage Area on the Central Plateau of Tasmania, 2005–06, Nature Conservation Report 07/01. Department of Primary Industries, Parks, Water and Environment, Hobart

Styger J (2018) The impact of firefighting chemicals on the natural values of the Tasmanian Wilderness World Heritage Area, Consultants report. University of Tasmania, Hobart

Styger J, Marsden-Smedley J, Kirkpatrick J (2018) Changes in Lightning Fire Incidence in the Tasmanian Wilderness World Heritage Area, 1980–2016. Fire 1.:article 38. https://doi.org/10.3390/fire1030038

Trauernicht C, Brook BW, Murphy BP, Williamson GJ, Bowman DMJS (2015) Local and global pyrogeographic evidence that indigenous fire management creates pyrodiversity. Ecol Evol 5 (9):1908–1918. https://doi.org/10.1002/ece3.1494

UNESCO (1972) Convention concerning the protection of the world cultural and natural heritage. Article 11:4. https://whc.unesco.org/en/conventiontext/#Article11.4

Whinam J, Barmuta LA, Chilcott N (2001) Floristic description and environmental relationships of Tasmanian Sphagnum communities and their conservation management. Aust J Bot 49:673–685

White JDM, Jack SL, Hoffman MT, Puttick J, Bonora D, Visser V, February EC (2016) Collapse of an iconic conifer: long-term changes in the demography of *Widdringtonia cedarbergensis* using repeat photography. BMC Ecol 16. https://doi.org/10.1186/s12898-016-0108-6

Wood SW, Bowman DJMS (2012) Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of southwest Tasmania. Landsc Ecol 27:13–28

Wood SW, Hua Q, Bowman DMJS (2011a) Fire-patterned vegetation and the development of organic soils in the lowland vegetation mosaics of south-west Tasmania. Aust J Bot 59:126–136. https://doi.org/10.1071/bt10309

Wood SW, Murphy BP, Bowman DMJS (2011b) Firescape ecology: how topography determines the contrasting distribution of fire and rain forest in the south-west of the Tasmanian Wilderness

World Heritage Area. J Biogeogr 38(9):1807–1820. https://doi.org/10.1111/j.1365-2699.2011.02524.x

Worth JRP, Larcombe MJ, Sakaguchi S, Marthick JR, Bowman DMJS, Ito M, Jordan GJ (2016a) Transient hybridization, not homoploid hybrid speciation, between ancient and deeply divergent conifers. Am J Bot 103(2):246–259. https://doi.org/10.3732/ajb.1500433

Worth JRP, Sakaguchi S, Rann KD, Bowman CJW, Ito M, Jordan GJ, Bowman DMJS (2016b) Gondwanan conifer clones imperilled by bushfire. Scientific Reports 6:article 33930. https://doi.org/10.1038/srep33930

Worth JRP, Jordan GJ, Marthick JR, Sakaguchi S, Colhoun EA, Williamson GJ, Ito M, Bowman DMJS (2017) Fire is a major driver of patterns of genetic diversity in two co-occurring Tasmanian palaeoendemic conifers. J Biogeogr 44(6):1254–1267. https://doi.org/10.1111/jbi.12919

Yospin GI, Wood SW, Holz A, Bowman DMJS, Keane RE, Whitlock C (2015) Modeling vegetation mosaics in sub-alpine Tasmania under various fire regimes. Model Earth Syst Environ 1(3). https://doi.org/10.1007/s40808-015-0019-0

Climate-Induced Global Forest Shifts due to Heatwave-Drought

7

Francisco Lloret and Enric Batllori

Abstract

Episodes of forest mortality attributed to extreme climate variability (e.g. droughts, heatwaves) associated with climate change are increasingly reported in most biomes. The severity and extent of the mortality are also modulated by soils and topography characteristics and the presence of other disturbances such as pests, pathogens, wildfires, windthrow, and past management. Palaeoecological and historical information show that drought-induced forests shifts have occurred in the past in many regions. However, anthropogenic causes are key determinants in current drought-induced transformations of forests to non-forested ecosystems.

The role of forest mortality leading to forest collapse is poorly understood, especially given the lack of long-term ecological surveys. In the short term, we find that an alternate set of species usually takes over the previously dominant tree species in temperate and boreal forests, through gap dynamics.

In our global review, trees are replaced by shrubs in 34% of the cases studied and by grasses in 10% of the cases, pointing to characteristics of forest collapse in the latter more extreme case. Overall these episodes promote a wide array of changes framed in a successional context, usually towards more xeric and herbaceous vegetation. The eventual forest dynamics are largely defined by the

---

F. Lloret (✉)
CREAF, Cerdanyola del Vallès, Spain

Dept. Animal Biology, Vegetal Biology and Ecology, Faculty of Biosciences, Universitat Autònoma Barcelona, Cerdanyola del Vallès, Spain
e-mail: Francisco.Lloret@uab.cat

E. Batllori
CREAF, Cerdanyola del Vallès, Spain

Faculty of Biology, Universitat de Barcelona, Barcelona, Spain
e-mail: e.batllori@creaf.uab.cat

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_7

historical context and particularly by human management, in which to a large extent determines the species pool, forest structure, and regeneration patterns.

Early warning signals of ecosystem shifts based on long-term monitoring and statistics appear essential to anticipate forest collapse. Remote sensing tools constitute a powerful tool for the assessment of changes in forest functional properties. However, when analysing forest dynamics and processes based on biodiversity, the information provided by remote sensing merits further research. We find limited evidence of widespread forest collapse at the global scale, but ongoing mortality events represent a "window to the future" to understand forest resilience in light of increased frequency of climatic extremes.

7.1 Overview of Forest Mortality Episodes at the Global Scale

In 2010, Craig Allen and colleagues' seminal paper (Allen et al. 2010) raised concern about drought-induced tree mortality globally, in almost all forested ecosystems (Fig. 7.1). The causes of the phenomenon were not deeply understood at that time, but it was recognized that drought, often associated with heatwave episodes, was a main driver of the observed forest die-off. The importance of drought severity on global forest mortality affecting all type of forest biomes has been later well established (e.g. Greenwood et al. 2017). It is thus expected that forest mortality will become exacerbated in the future due to climate change. Temperatures are rising, precipitation variability is increasing, and extreme heatwave-drought episodes are becoming more common (Trenberth et al. 2014). The work of Allen et al. (2010) became a milestone for intense international research aimed at elucidating the causes of drought-related tree mortality at different scales (Hartmann et al. 2018). These causes include ecophysiological processes occurring at the tree level (e.g. hydraulic failure, carbon starvation), to biotic interactions (e.g. within stand tree competitive processes or attack and infestation by pests and pathogens) and management legacy at stand and landscape levels (e.g. fire suppression and modification of stand composition and structure) (Allen et al. 2015). However, we are accumulating evidence that extreme drought and heatwaves often interact with other disturbance agents such as insects, pathogens, fire, wind, and snow/ice, which are also becoming exacerbated by climate change (Seidl et al. 2017). In some cases, such as wildfires, interactions with drought episodes are likely to promote ecosystems shifts (Batllori et al. 2017, 2019; Henzler et al. 2018). In other cases, drought episodes are concomitant with pathogens and pests, but their interaction, though plausible (Gaylord et al. 2013), is hard to quantitatively elucidate (e.g. Meddens et al. 2015; Stephenson et al. 2018). In other cases, complex interactions may appear: drought and wind can mutually reinforce their effects (e.g. Usbeck et al. 2010) and, in turn, facilitate the impact of other disturbance agents, such as insects and fire (Seidl et al. 2017). In this chapter, while recognizing the intricated relationship between the different disturbance agents within the context of climate change, we will focus on the consequences of increasing drought and heatwaves to potential forest shifts.

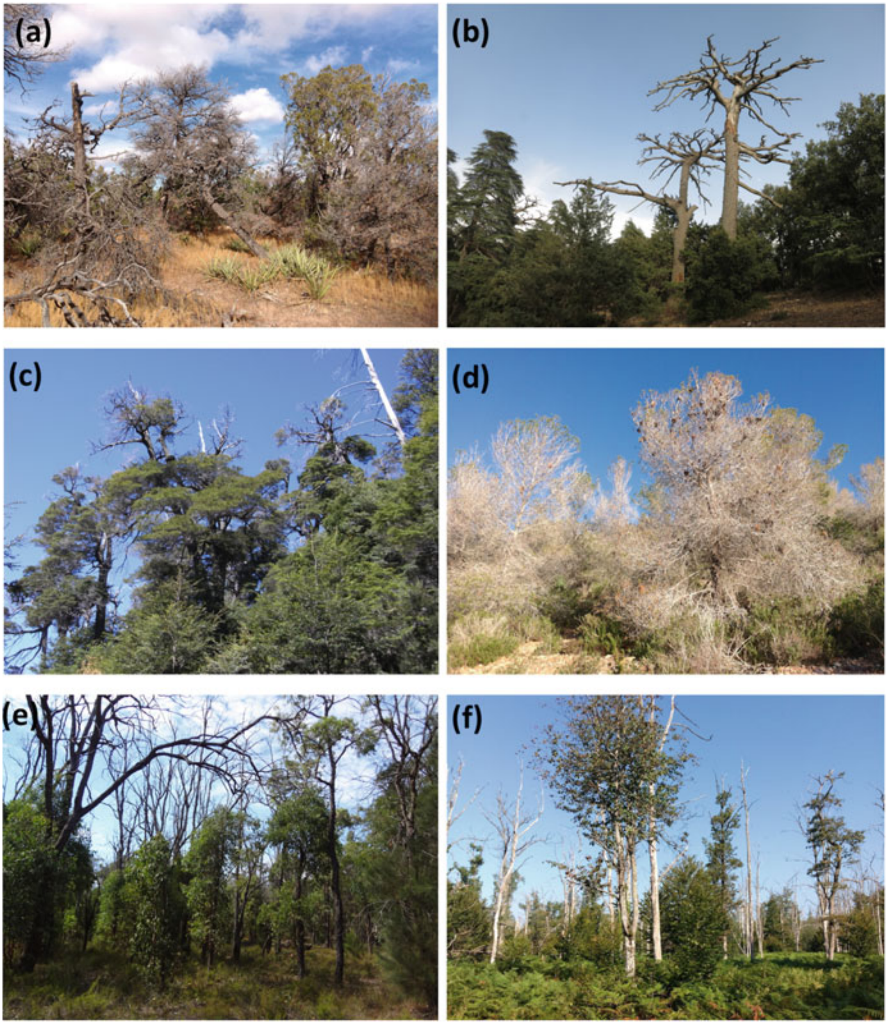


Fig. 7.1 Examples of forest die-off in different forest ecosystems: (**a**) *Pinus edulis* mortality, New Mexico (USA), photo F. Lloret; (**b**) *Cedrus atlantica* mortality, Morocco, photo E. Batllori; (**c**) *Nothofagus dombeyi* mortality, Argentina, photo F. Lloret; (**d**) *Pinus halepensis* mortality, Spain, photo F. Lloret; (**e**) *Eucalyptus marginata* mortality, Northern Jarrah Forest (Australia), photo G. Matusick, (**f**) *Quercus robur* mortality, France, photo F. Lloret

The increasing number of studies regarding drought- and/or heat-induced forest mortality since the initial 89 reported cases in Allen et al. (2010) reflects the raising concern about ecosystem vulnerability to climate-driven forest mortality events. From 2010 to 2018, 2415 research articles related to the subject were published (search in Thomson Reuters Web of Science by keywords (forest *and* (mortality *or* dieoff *or* die-off *or* dieback *or* die-back) and (drought OR heat*)), compared with

1577 published from 1950 to 2009. These works encompass a gradient from natural to managed forests and display a large range of mortality rates, up to 40% year^{-1} (Greenwood et al., 2017). However, the magnitude of the phenomenon in terms of tree mortality rate is hard to determine from the literature because regular surveys are rare, and estimates are often inferred from standing tree mortality. Importantly, forest die-off is not restricted to any given regional climatic conditions, since it occurs from boreal to semi-arid and to tropical forests (Allen et al. 2015), and mortality rates are not significantly different among biomes (Greenwood et al. 2017).

However, not all these reported cases of tree mortality can be defined as forest collapse. In fact, the available information about forest dynamics (Martínez-Vilalta and Lloret 2016; Batllori et al. 2020) and eventual collapse is still scarce, because of the difficulty in dealing with the long-term dimension of the phenomenon in forests ecosystems. In most cases, observed forest mortality is assumed to exceed baseline mortality rates. But mortality episodes can also correspond to pulses in forest dynamics associated with baseline disturbance regimes, which can push ecosystem states backwards or forwards following successional trajectories. Additionally, tree mortality can be buffered by the growth of the surviving surrounding forest or by replantation in highly managed forests. Therefore, in addition to unprecedented and high tree mortality rates synchronically occurring in a short period of time, the magnitude of the phenomenon should also be defined by the spatial distribution and the geographical extent of forest decline and thus its likelihood to ultimately lead to collapse.

The ideas about ecosystem collapse and tipping points have mainly been developed for lacustrine systems, with discrete boundaries and regular mixing that “reset” the system to baseline conditions. In contrast, forests show long-term successional dynamics and diffuse edges and transitions to other ecosystems, making it sometimes difficult to define the areal extent and the temporal scale of the collapse. Indeed, drought-induced tree mortality can exhibit a wide range of spatial patterns (Sommerfeld et al. 2018), from a small, diffuse clustering with scattered spots of dead trees across the landscape as in Central and Southern Europe (e.g. Cailleret et al. 2014; Camarero et al. 2011; Galiano et al. 2010; Rigling et al. 2013) to homogeneously affectations across hundreds of square kilometres in SW North America (Breshears et al. 2005; Meddens et al. 2015), Amazonia (Bonal et al. 2016), California (Jacobsen and Pratt 2018), Australia (Fensham and Holman 1999), and the Sahel (Trichon et al. 2018). These later cases clearly offer examples of current, abrupt forest shifts driven by drought and/or heat, and they may be considered “windows to a future” where forest collapse induced by climate change is likely to occur across vast areas and other biomes. Importantly, forest mortality is not occurring simultaneously around the world, and its spatial heterogeneity can be compared to the temporal mosaics of vegetation recorded in palaeorecords in which vegetation shifts occurred at different time across regions (Williams et al. 2011). The spatial variability of forest mortality is explained because the phenomenon is not exclusively driven by climate.

Ecosystem collapse of forests means that, eventually, the replacing community is unable to maintain the functions carried on by former forests. It occurs, for instance, when the new community shows less productivity, carbon stock, and soil cover, as is the case of savannah-like forests, shrublands, or grasslands. These shifts are associated with changes in species composition, often involving losses of biodiversity, and in the structural characteristics of forests. These changes, in turn, impact ecosystem services, as water provisioning, provided to human societies. So, in general forest mortality events induce changes in energy, water, and nutrient fluxes (Anderegg et al. 2013a). However, it is difficult to integrate the overall balance resulting from changes in fluxes at the ecosystem level and the associated biosphere-atmosphere feedbacks (Hartmann et al. 2018). For instance, transitory pulses of soil nutrients due to litter and woody debris resulting from tree die-off can eventually cause nutrient losses through run-off, with an increase in inorganic forms that ultimately will produce alterations in soil food webs (Xiong et al. 2011). Ecosystem water fluxes are altered as soil water demand by trees is reduced after mortality events, but soil evaporation and understory transpiration tend to increase (Adams et al. 2012). Forest mortality also reduces C uptake (e.g. Ciais et al. 2005; Phillips et al. 2009), but this diminution may be transitory as resilience mechanisms tend to buffer these alterations, for instance, by compensating water use efficiency (Ponce Campos et al. 2013). Importantly, the eventual balance of the changes in ecosystem fluxes induced in forest ecosystems by mortality events will be determined by the functional characteristics of the replacing ecosystem in comparison with the former one. Obviously, all these changes can be highly influenced by management practices, which, depending on their objectives, can have very site-specific outcomes.

Remote sensing technology can be used for extensive and long-term monitoring of key essential ecosystem properties, such as carbon stocks and fluxes following forest mortality (Ciais et al. 2005; Huang et al. 2010). For instance, a combination of ground transects, high-resolution aerial photography, and satellite-based observations documented ~10% tree canopy loss across the entire state of Texas after a record drought in 2011 (Schwantes et al. 2017). Satellite-derived procedures can also be used in detailed, high-resolution surveys at specific sites (Clark et al. 2004; McDowell et al. 2014). They have been applied to describe forest decay in many regions, such as tropical forests (Verbesselt et al. 2016) and mangroves (Galeano et al. 2017), temperate and boreal forests (Lloret et al. 2007; Kharuk et al. 2013; Assal et al. 2016; Byer and Jin 2017; Sommerfeld et al. 2018), and Mediterranean and semi-arid forests and woodlands (Browers et al. 2015; Coates et al. 2015; Garrity et al. 2013; Huang et al. 2010; Trichon et al. 2018). Satellite observations and global monitoring systems have thus the potential to become early warning systems of eventual forest collapse (Rogers et al. 2018; Liu et al. 2019). However, the development of accurate, algorithm-based tools for global assessment of climate-caused disturbances and their consequences is ongoing (McDowell et al. 2014), especially given the difficulties in identifying mechanistic process involving species' demography and composition that will determine eventual ecosystem trajectories.

7.2 Causes of Forest Mortality by Drought

At the scale of individual plants, eventual drought-induced mortality of trees involves interacting physiological processes, mainly hydraulic failure (i.e. xylem embolism and subsequent tissues desiccation caused by high evaporative demand coupled to low soil water supply) and carbon starvation (i.e. depletion of plant carbon compounds due to diminution of photosynthesis resulting from stomata closure, while metabolic C consumption persists) (McDowell et al. 2008; Hartmann et al. 2018). Although important uncertainties about these mechanisms and their relative contribution and interactions still exist (e.g. allocation patterns of C within plants conducting to dead or fatal embolism thresholds) (Anderegg et al. 2015; Hartmann et al. 2018), there is enough evidence to acknowledge the involvement of drought and/or heat in many of the observed events of forest mortality (Fig. 7.2). The magnitude and duration of stressing climatic conditions determine the extent of die-off episodes (McDowell et al. 2008; Greenwood et al. 2017), and the existence of climatic thresholds has been proposed to trigger forest mortality (Huang et al. 2015; Mitchell et al. 2014). However, the multiplicity of causes potentially involved in tree mortality and their interactions, as well as the influence of ecosystem legacies (e.g. species pool, historical management), precludes the establishment of universal rules. Identifying early warning signals of forest collapse is therefore gaining importance as a challenging but strategic, global goal (Cailleret et al. 2016; Kolb 2015; Rogers et al. 2018).

Climate strongly interacts with biotic disturbances, which constitute a major mechanism of forest mortality (Anderegg et al. 2015; Seidl et al. 2017). *Scolytinae* (bark beetles) can cause the death of trees by destroying their vascular system, often associated with fungal infection. This process can be reinforced by drought, because

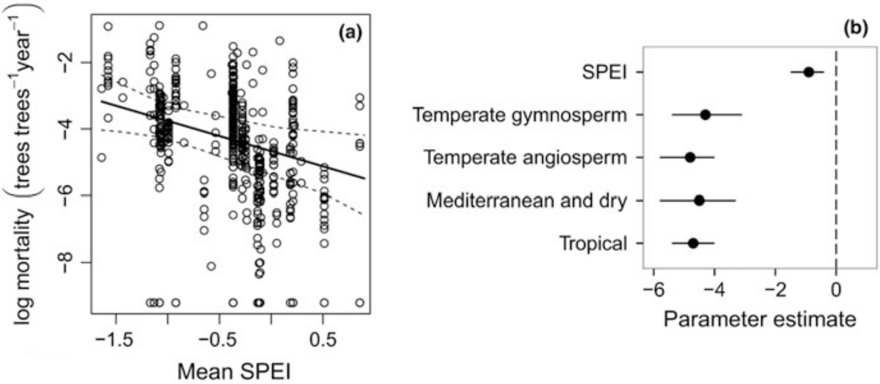


Fig. 7.2 Relationship between annual tree mortality rate (308 species, 30 studies, 27 drought events) and drought (Standardised Precipitation Evapotranspiration Index, SPEI) at a 12-month timescale (Vicente-Serrano et al. 2010) (*left panel*) and the similar contribution of different biomes to the explaining model, indicating the absence of significant differences between biomes (*right panel*). (Figure from Greenwood et al. [2017])

trees stressed by water deficit are often more vulnerable to insect attack (Gaylord et al. 2013), although the ultimate cause of tree death would be the insect attack (Stephenson et al. 2018). Trees infected by insects are a source of propagation, facilitating the attack to healthy trees which in turn become more vulnerable to drought. Infestation can be initiated by wind and snow storms causing treefalls that promote dead tree invasion by insects. In short, a reinforcing feedback between drought and some pests enhances tree mortality (Raffa et al. 2015), and this feedback can be bolstered by other climatic disturbances (Seidl et al. 2017), such as windstorms, which constitute a major agent in some regions (e.g. Europe; Usbeck et al. 2010). Defoliating insects can also cause tree mortality, but they need several growing seasons of continuous infestations to exhaust tree reserves, since trees usually regrow new leaves after the first attacks (Anderegg et al. 2015). Insect-induced mortality may affect vast areas, particularly when concurrent with drought and/or heat (Berner et al. 2017). However, further analyses of the interactions between forest composition, climate, and different pest strategies and life cycles are needed to anticipate future forest vulnerability (Anderegg et al. 2015; De Grandpré et al. 2018; Sánchez-Pinillos et al. 2019).

There are many other factors that contribute to forest mortality, often exacerbating the relationship between climate and tree death. At the landscape scale, topography, geomorphology, and soil characteristics may determine spatial patterns of tree mortality (e.g. Lloret et al. 2004). Abiotic disturbances, such as wildfires, can also interact with drought and heat to challenge forest resilience and promote drastic landscape changes (Johnstone et al. 2016; Batllori et al. 2019). Drought-affected trees may be more vulnerable to fire (van Mantgem et al. 2013), while high temperatures and low relative humidity of air can enhance high-intensity wildfires, fed in turn by higher fuel loads derived from forest die-off (Brando et al. 2014). Additionally, persisting drought conditions can limit forest regeneration after fire (Harvey et al. 2016; Henzler et al. 2018). Finally, intense herbivory pressure combined with drought may also enhance forest mortality, as reported, for instance, by elephants' impact during heavy drought periods in central Africa (Tafangenyasha 1997).

At the local scale, competition between trees, reflected in stand structure, is as a common cofactor of tree mortality (e.g. Bell et al. 2014; Jump et al. 2017), and stands with higher basal area are prone to experience more mortality. Stand structure, species composition, and soil characteristics are influenced by the past legacy of disturbances and succession, which is largely determined by historical management by humans in many ecosystems. In fact, some studies conclude that historical land use, by modifying forest composition and structure, better explains forest decline than climate itself (e.g. Vilà-Cabrera et al. 2011). Therefore, ecosystem legacies constitute a key element to understand current forest response to changing climate (Johnstone et al. 2016) and may explain the emergence of tipping points (der Bolt et al. 2018). In particular, characteristics of the past disturbance regime (including timing, recurrence, extent, and severity of different types of disturbances) are expected to play an important role in the eventual forest response to particular sequences of interacting disturbance episodes (Batllori et al. 2019).

7.3 Historical Perspective of Forest Shifts

From a biogeographical perspective, we expect some correspondence between regional climate and vegetation. Therefore, a key question is how this correspondence is established while climate fluctuates and changes through time. Are there gradual and direct transitions of vegetation composition and structure tightly coupled to climate conditions becoming warmer or drier? Or is there some inertia or resistance allowing vegetation to remain scarcely modified in spite of climate changes, at least for some period of time? Are there tipping points signaling abrupt shifts between vegetation states caused by non-linear responses to environmental changes and by the interactions between several agents, particularly disturbances? Dynamic systems' theory describes non-linear responses that can result in multiple stable states occurring under a given set of environmental variables (Scheffer and Carpenter 2003). However, evidence from terrestrial ecosystems dominated by long-living species is not always straightforward because it requires long timeframes to occur and observe. Thus, information from past climatic transitions can give important insights for these questions.

Palaeorecords provide evidence of past climate-driven forest shifts or collapse even at short time intervals (Fig. 7.3; Williams et al. 2011). However, the temporal resolution of these records is often coarser than our current observation window of forest mortality. Historical ecosystem shifts have been documented in many types of forest-related ecosystems: boreal (Menking et al. 2012), alpine (Tinner and Kaltenrieder 2005), temperate (Tinner and Lotter 2001; Foster et al. 2006; Magny et al. 2012), Mediterranean (Lopez-Blanco et al. 2012), continental forest-grassland ecotones (Williams et al. 2010), tropical savannah-forest ecotones (Rull et al. 2013), tropical montane (Heckmann et al. 2014; Ivory and Russell 2016), peatlands (Swindles et al. 2017), and rainforest (Mayle et al. 2004; Torrescano-Valle and Islebe 2015).

Drought was likely involved in some of these historical ecosystems shifts. This occurred, for instance, in the Great Plains of North America *c*. 8 ka BP involving shifts in prairie forests and C3–C4 grass ecotones (Williams et al. 2010, 2011). But forest collapse may also be related to wetter conditions. In the early Holocene, many areas of central Europe were dominated by *Corylus avellana* woodlands, but *c*. 8.2 ka BP this drought-tolerant species was rapidly replaced by dense canopy forests with *Fagus sylvatica*, *Abies alba*, *Fraxinus excelsior*, *Tilia* spp., *Quercus* spp., and *Ulmus* spp. that outcompeted hazelnut for light after the temperatures decreased ca. 1.5–2 °C and drought stress diminished (Tinner and Lotter 2001). Approximately at the same time many *Larix decidua* forests in the Alps collapsed when climate became cooler (Tinner and Kaltenrieder 2005). Although not involving forests in the strict sense, probably the best recorded case of terrestrial ecosystem collapse occurred in North Africa *c*. 5.5 ka BP, when grassland and woodlands transformed into non-vegetated desert, coupled with climatic aridification, temporally tuned to site-specific conditions (Williams et al. 2011).

Often, past forest collapse appeared associated with other disturbances, such as an increase of wildfires, as shown by charcoal records. Montane forests in Central

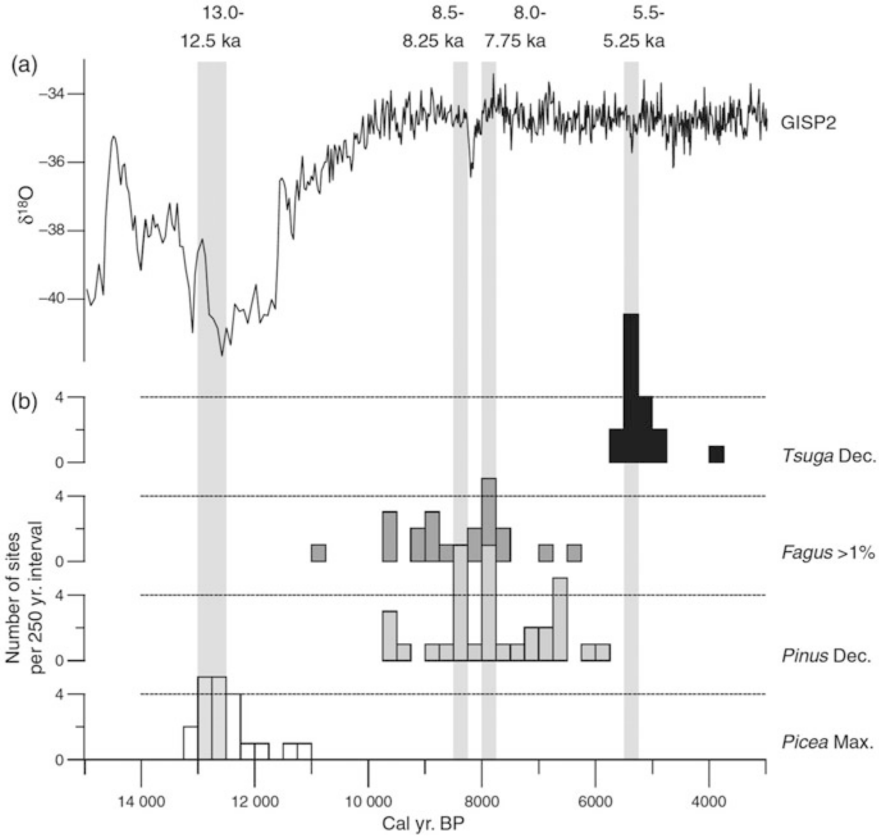


Fig. 7.3 Temporal changes of (**a**) oxygen isotope variations at the GISP2 Greenland ice core in Greenland (Grootes and Stuiver 1997) compared to (**b**) vegetation shifts in New England, USA (Shuman et al. 2009) in the mid-Holocene. (Figure from Williams et al. [2011])

Africa exhibited *c*. 18 ka BP a rapid transformation to initially low vegetation dominated by thicket and grasses after initial warming and drying trends that favoured wildfires and megaherbivores (Ivory and Russell 2016). Later, wetter conditions during the Younger Dryas (10.5 ka BP) promoted encroachment by miombo woodlands (Ivory and Russell 2016). In northeastern South America, the Holocene transformation from rainforest to savannah-like vegetation was determined either by fires or drier climate or by their coupling; further fire intensification led to palm-dominated vegetation, independent of climate conditions (Rull et al. 2013). Pest outbreaks may have also contributed to historical forest collapse. For instance, *Tsuga canadensis* synchronic collapse in northeastern North America 5.5 ka BP has been attributed to outbreaks of the eastern hemlock looper (*Lambdina fiscellaria*), as indicated by chewed leaves collected concurrently to forest decline (Bhiry and Filion 1996). This collapse was, in fact, contemporaneous to regional drought conditions (Foster et al. 2006), supporting a reinforcing feedback between climate and pests. Finally, human activity has historically exacerbated rapid forest declines in many parts of the world. These declines have often been accelerated when coupled to drought periods (Heckmann et al. 2014), which, in turn, may have favoured fires used by humans to transform forests and woodlands into pastures (Lopez-Blanco et al. 2012).

In the first half of the twentieth century, when wide and systematic instrumental records of climate started, drought-induced, extensive forest mortality events were also documented in many locations (Allen et al. 2010), as for instance, northeastern Australia (e.g. Fensham and Holman, 1999; Fensham et al. 2019), New Zealand (Grant 1984), China (e.g. Liang et al. 2003), Europe (e.g. Delatour 1983; Dobbertin et al. 2007), Africa (Tafangenyasha 1997), North America (e.g. Albertson and Weaver 1945; Allen and Breshears 1998; Hogg et al. 2008; Swetnam and Betancour 1998), and South America (e.g. Bonal et al. 2016; Villalba and Veblen 1998). Although the eventual fate of many of these ecosystems has been scarcely assessed, in a few cases the existence of important vegetation shifts has been documented. The 1914–1915 drought in New Zealand resulted in a retreat of ca. 100 m elevation in mountain timberland (Grant 1984), while the extreme drought in 1951–1956 in southwestern North America produced shifts in ecotonal boundaries favouring the expansion of shrublands and grasslands (Allen and Breshears 1998; Swetnam and Betancour 1998). Fensham et al. (2019) proposed that drought-induced die-off may have been a common but largely underestimated disturbance in historical times, as in the Australian savannah with *Eucalyptus* spp. and *Corymbia* spp., where drought-induced tree mortality could be a mechanism driving the intermittent dynamics reported between woodland and grassland-dominated landscapes (Fensham and Holman 1999).

Therefore, ongoing forest mortality events are not new phenomena, as episodes of forest collapse or die-off have also occurred in the past. But how much these phenomena are increasing, how directly they are attributable to human activity, particularly to climate change, and how they are promoting (if they are) the collapse of forest ecosystems are not so easy questions to answer. Uncertainties arise because of the difficulties to obtain, in most cases, baseline estimations of forest mortality and long-term assessments of forest change after the die-off episodes, which is particularly complex in regions where forest landscapes have been strongly modified by human activity (e.g. harvesting, planting, grazing).

7.4 Abrupt Forest Mortality Events and Ecosystem Trajectory

7.4.1 General Trends

One way to analyse ecosystem trajectories and potential forest collapse is to perform field surveys in areas experiencing ongoing episodes of mortality. We have explored stand-level forest change after mortality events, from information directly compiled from authors reporting mortality events worldwide (Batllori et al. 2020). Given the uncertainties of long-term forest dynamics, the focus of this assessment was on

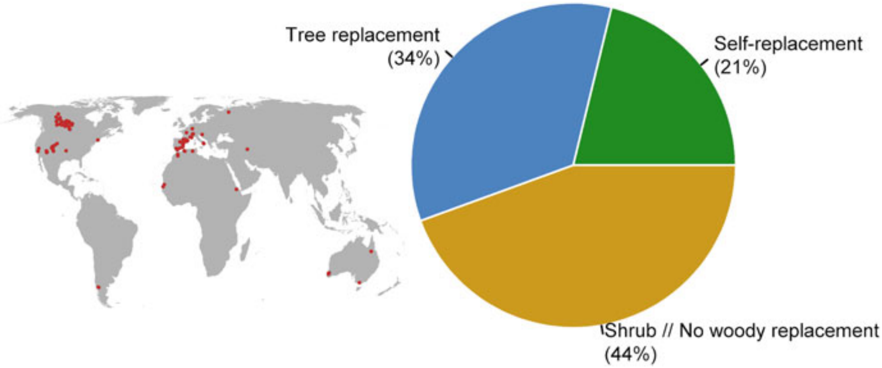


Fig. 7.4 Location of 131 forest sites (*left map*) where replacement patterns after drought-induced forest mortality were characterized and summary of the dominant replacement patterns (*right panel*) showing the proportion of observed post-drought trajectories by vegetation type. Self-replacement refers to the replacement of the pre-drought dominant species with the same species (i.e. by itself), tree replacement refers to replacement by a different tree species and shrub//no woody replacement to replacement by shrublands or no woody replacement, respectively. (Figure adapted from Batllori et al. [2020])

established plants already occupying the gaps opened by dead trees. Those plants in the gaps correspond to small trees or saplings established in the forest understory but also to close neighbouring trees in the overstorey. The rationale behind this approach is to document reliable short-term forest changes rather than uncertain long-term trajectories depending on forest regeneration (i.e. seedlings). Therefore, instead of considering early recruitment stages that are subjected to high and patchy mortality, we assumed that, in the absence of further disturbances, the already established and long-lived tree individuals replacing the dead ones will persist at least for decades (Canham & Murphy 2017) and therefore determine oncoming forest structure and composition. The survey included 131 sites across 5 continents (Fig. 7.4), excluding species-rich tropical forests since those exhibit complex patterns of species turnover after disturbances due to its high diversity (Newbery and Lingenfelder 2008).

The results of our compilation indicate that, following drought-induced mortality, forest species are replaced in the short term by shrubs or herbs in 44% of cases and that self-replacement by the same dominant species only occurs in 21% of cases (Fig. 7.4), many of which involved resprouting genera such as *Quercus*, *Populus*, or *Eucalyptus* (Fig. 7.5). These results provide evidence that drought is a global phenomenon triggering important changes in forests. Nevertheless, the observed changes correspond in some cases to successional pathways, either moving backwards to early successional vegetation, as typically occurs after disturbances, or alternatively killing early- and intermediate-successional species and promoting late successional ones, such as pines which are being replaced by oaks in Europe when grazing levels are low (Rigling et al. 2013). These successional transitions cannot properly be considered ecosystem collapses. Importantly, ecosystem trajectories are largely determined by the available pool of species, which in turn may have been

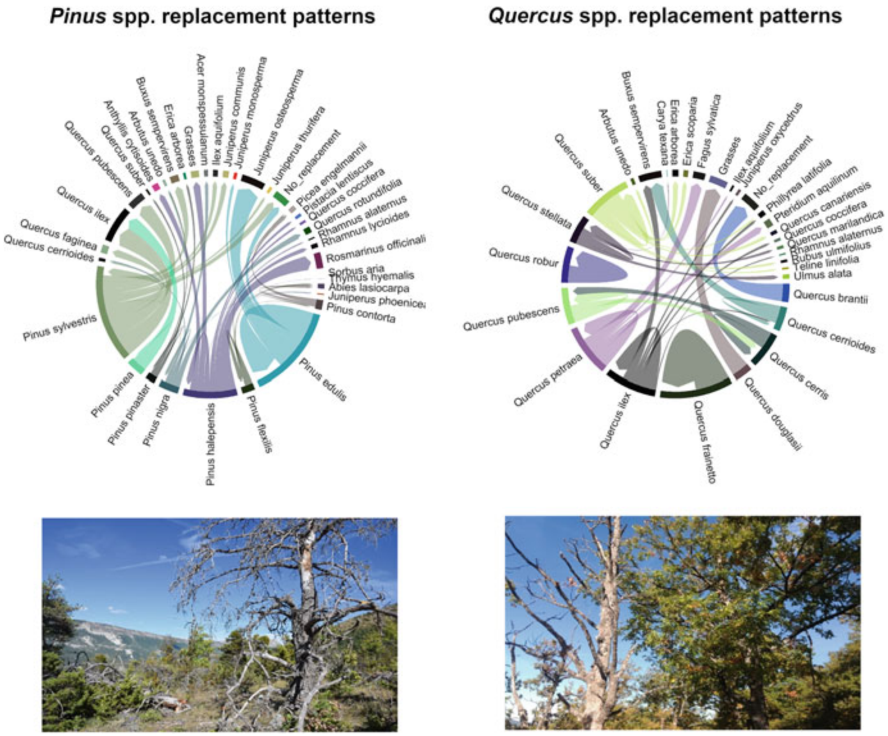


Fig. 7.5 Worldwide replacement patterns at the species level for two major genera (*Pinus* spp., mostly regenerating from seedlings, and *Quercus* spp., in which resprouting is common) of trees affected by drought-induced mortality. The outer level colour bars correspond to the pre-drought dominant and post-drought replacing species, and replacement patterns are depicted by the inner links in each case. Pictures at the bottom depict examples of drought-induced mortality in *Pinus sylvestris* in France (*bottom-left*) and *Quercus frainetto* in Italy (*bottom-right*). (Photo credit: F. Lloret. Data from the provided examples come from sites reported in Batllori et al. [2020])

filtered by previous management and disturbance regime. These results are consistent with preliminary compilation by Martínez-Vilalta and Lloret (2016), in which an approach based on species replacement was formerly proposed.

Forest replacement patterns can initiate trajectories towards communities that exhibit contrasted characteristics in relation to the oncoming climatic conditions. In our compilation, although a majority of post-drought trajectories lead to communities with a more xeric profile (i.e. constituted by species currently living in drier localities and thus a higher tolerance to arid conditions), the opposite (i.e., trajectories to moister communities) also occurs (Fig. 7.6). Shifts to more xeric communities include some well-known cases: *Pinus edulis* was replaced by *Juniperus* spp. and *Purshia tridentata* in southwestern North America (Breshears et al. 2005; Redmond et al. 2015), *Pinus sylvestris* was replaced by *Quercus pubescens* or *Q. ilex* in Europe (Rigling et al. 2013), *Eucalyptus marginata* was replaced by *Corymbia calophylla* in Australia (Matusick et al. 2016), and *Cedrus*

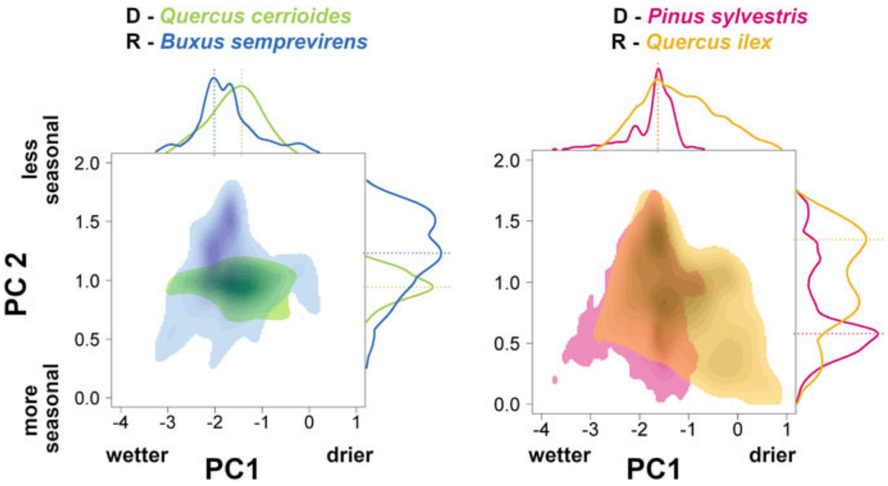


Fig. 7.6 Examples of the bioclimatic characteristics (i.e. bioclimatic niche) of pre-drought dominant species (D) and post-drought replacing species (R) for two cases of forest die-off that resulted in shifts towards more mesic and xeric communities in temperate European forests. Left, *Quercus cerrioides* mortality and right *Pinus sylvestris* mortality. In each plot, the density distribution (i.e. their abundance) of the dominant and replacing species within principal component space (PC1 and PC2 axis) that reflects a gradient from wetter to drier (PC1) and more or less seasonal (PC2) precipitation regimes is depicted. For each species, the abundance along each PC axis and its bioclimatic optima (dotted vertical lines) are shown in the top and right subplots. The bioclimatic optima correspond to the location along each environmental axis where the species is more abundant. Species distribution data were obtained from the Global Biodiversity Information Facility (GBIF; www.gbif.org/) and the climatic data from WorldClim (www.worldclim.org/) and from the Global Evapotranspiration Database (www.cgiar-csi.org). (Figure adapted from Batllori et al. [2020])

atlantica was replaced by, among others, *Quercus rotundifolia* in Africa (Bentouati 2008). Interestingly, shifts to drier communities are associated in some cases (e.g. *P. sylvestris* replacement) with trajectories towards later successional stages dominated by tree species with wide bioclimatic ranges (e.g. *Q. ilex* and *Q. pubescens*). However, trajectories to more mesic communities can also reflect changes towards earlier successional forest stages, as is the case of *Quercus cerrioides* being replaced by *Buxus sempervirens* in southwestern Europe (Fig. 7.6). Shifts towards more mesic communities may also occur when mortality of the forest canopy favours shade-tolerant species growing in the understory, as, for example, the replacement of *Pinus flexilis* by *Abies lasiocarpa* or *Picea engelmannii* in the Rocky Mountains (Smith et al. 2015).

Drought-induced mortality events tend, overall, to trigger changes towards forests dominated by more xeric species. However, post-drought dynamics are also often framed in a successional context and exhibit a wide array of possibilities (Fig. 7.5). The eventual fate of forests is thus defined by the historical context, particularly by human management, which determines species pool, forest structure, and regeneration patterns. Additionally, in combination with drought, other important contributors of forest conversion are pathogens, which can promote changes to shrub-dominated communities (Linares et al. 2010; Matías et al. 2018). Nevertheless, the contribution to forest collapse of insect outbreaks in combination with drought is highly variable. For instance, bark beetles may cause mortality events covering vast extensions and resulting in long-term forest decline, as described in *Pinus edulis* forests of southwestern North America (Breshears et al. 2005), but in other cases outbreaks are followed by self-replacement of the former dominant tree species (Matusick et al. 2016 in Australia; Smith et al. 2015 in the Rocky Mountains).

The assessment above did not include tropical forests due to the difficulties to define post-event trajectories there. The effect of severe drought, often associated with ENSO anomalies, on tree mortality has been widely documented for these forests (e.g. Phillips et al. 2009; Bonal et al. 2016). Although tropical forests seem to have been resilient to past drought events during the Holocene (Mayle and Power 2008), there are some reports of fast shifts to more xeric communities with drier conditions (Condit 1998; Enquist and Enquist 2010); these shifts sometimes involve increasing dominance of lianas (Schnitzer and Bongers 2011). From a functional perspective, other studies have reported shifts in carbon balance, reducing the sink contribution of these forests to the global budget as a result of these events (e.g. Feldpausch et al. 2016). This effect seems buffered by trade-offs involving carbon stocks (Doughty et al. 2015) and spatial heterogeneity (Zuleta et al. 2017), although collateral impacts, such as erosion (Becek and Horwarth 2017) and fires (Brando et al. 2014), can also be important challenge to forest persistence. So, the eventual fate of this highly biodiverse forests shows a variety of responses, from long-term resilience (Meir et al. 2018) to irreversible tipping points (Brando et al. 2014).

7.4.2 Cases of Forest Collapse and Its Relation with Management

When forests are replaced by shrublands or grasslands, trees are unlikely to re-establish, at least in the next decades. In these situations, forests are confronting collapse. Importantly, vulnerable ecosystems often correspond to forests which have previously experienced a history of strong management, often associated with changes in other disturbances such as fire or pests. Management, however, can be an active driver of both forest vulnerability and resilience in the face of climatic extremes, and community trajectories may offer multiple opportunities to reinforce the mechanisms that minimize losses associated with ecosystem collapse (Cobb et al. 2017).

Human management appears as a common key co-driver of forest changes in semi-arid regions where forests grow near their biogeographical edge. In the Sahel, open forests of *Acacia* spp. and *Balanites aegyptiaca*, thickets, and tiger bush formations reflect a long legacy of intense human influence, mostly pastoralism and wood collection, in addition to chronical aridity. There, after the heavy drought of 1968–1984, woody vegetation has not been able to recover in many places, in spite of rainfall returning to past average levels (Gonzalez 2001; Trichon et al. 2018). In fact, recovery of woody vegetation may occur on soils with some capacity of water storage, but continuous decline is consistent with observed surface erosion (Hiernaux et al. 2009). This regional pattern highlights the existence of feedbacks between vegetation and soils, which explain shifts in ecosystem state. Loss of vegetation changes the surface hydrology, shifting from sheet run-off to a network of rills and gullies, in which water bypass the remaining vegetation, thus increasing erosion rate. This process is strongly linked to climatic drought. While moderately degraded sites are able to recover after pulses of rain, this recovery does not happen where vegetation was lost following extreme drought episodes. In fact, at regional scale within Sahel, precipitation thresholds around 200 mm per year can be identified to result in ecosystem collapse in only 20 years (Trichon et al. 2018). The result is an irreversible ecosystem shift at local scale, with consequences in the hydrological regime at watershed scale (e.g. increasing water in streams and in aquifers) (Trichon et al. 2018).

In Ethiopia, dry Afromontane forests dominated by *Juniperus procera* and *Olea europaea* subsp. *cuspidata* have high ecological and economic value in the region. These forests experienced drought-induced mortality in the 1980s, following a previous extreme drought that affected the region in 1973–1974. In addition, local human communities commonly exploited these forests for firewood and construction, exacerbating the effects of drought. Large gaps induced by tree mortality transform the microhabitat (higher ground temperature and less soil moisture) reducing the regeneration of previous dominant trees. Since mortality mostly affected large trees, a reinforcing feedback is established as species' recruitment is also limited by the absence of nurse trees acting as dispersal sinks. Eventually, these forests have been replaced by light-demanding shrubs and herbs following a gradient of increasing aridity at lower elevations. The result is a shift to encroaching light-demanding shrubland which does not show evidences of recovery to the previous forest state (Aynekulu et al. 2011).

In a well-studied case of semi-arid SW North America, large extensions of *Pinus edulis* and *Juniperus monosperma* forests and woodlands experienced dramatic collapse after severe droughts in the 1990s and the early twenty-first century (2000–2003, 2011–2013), accompanied by bark beetle outbreak (Breshears et al. 2005; Cobb et al. 2017) (Fig. 7.1a). The effects on ecosystem functioning are visualized by C loss, which has been estimated to represent ca. 40 times the attributed to wildfire and management in forests of the region (Huang et al. 2010). These forests grew well during the twentieth century as a consequence of fire suppression and the cessation of cattle grazing. They replaced former open *P. ponderosa* forests with grass understory, which were maintained by surface, low-intensity fires, and grazing (Allen et al. 2002). This replacement process was enhanced in the 1950s by drought and bark beetle outbreaks and by a subsequent wet period in which *P. edulis* and *J. monosperma* recruited abundantly. The most recent drought period has also favoured very high-intensity wildfires that burned many of the decayed forests. Post-fire regeneration has been scarce in many sites, leading to a collapse of the relatively dense woodlands of *P. edulis*, moving to savannah-like formation with increasing dominance of juniper, resprouting shrubs (e.g. *Quercus undulata*) and grasslands (Breshears et al. 2005), shifting upwards the ecotone between forests and juniper woodlands (Allen and Breshears 1998).

Bioclimatic regions used to experience seasonal drought periods are also susceptible to drought-induced forest collapse. Extensive crown-collapse in *Eucalyptus marginata*-dominated forest type in SW Australia (Matusick et al. 2016) (Fig. 7.1e) occurred after repeated years of drought and heatwave episodes. Damage mostly occurred on sites with low water holding capacity soils (Cobb et al. 2017). In spite of the ability of dominant species to resprout, this extensive dieback is deeply transforming the forest characteristics, likely for decades, to a high density, low canopy structure, and modifying energy and nutrient fluxes and fire regime (Matusick et al. 2016; Cobb et al. 2017). The interaction between intense drought and human-induced changes in the fire regime as a driver of nonreversible changes is also illustrated in temperate forests from Victoria (SE Australia). Fire removal has favoured fire-sensitive *Allocasuarina* spp. over fire-adapted *Eucalyptus* spp. that were dominant for millennia. Recent droughts further enhanced this replacement since *Allocasuarina* spp. are more drought-tolerant than *Eucalyptus* spp., which nowadays are often unable to re-establish even when the natural fire regime is restored (Zeeman et al. 2014).

In Mediterranean SE Spain, pine planting was a common practice during the 1950–1970s. Particularly, the drought-tolerant *Pinus halepensis* and at less extent *P. pinaster* were extensively planted in poor-soil localities with climatic conditions that can hardly support pine growth (Serra-Diaz et al. 2013). During the decade of the 2010s, extreme drought episodes caused extensive pine mortality (Esteve Selma et al. 2017), often in combination with insect outbreaks of the pine processionary *Thaumetopoea pityocampa* or the homoptera *Matsucoccus feytaudi* (Fig. 7.1d). These plantations show a very impoverished understory and a limited seed production. The result was the loss of forest, particularly in south aspect slopes, which were replaced by a low-stature, open layer of scrubs or herbs, where pine regeneration is jeopardized by seed availability and climatic unsuitability. These transitions are often reinforced by wildfires, which had burned large surfaces of previously planted forests (Pausas et al. 2004). This ecosystem state with low vegetation cover is extremely vulnerable to erosion and water run-off, and, thus, it tends to self-maintain. Here, extreme droughts associated to climate change are moving the ecosystem to an extremely low-structure state, after a temporary, human-enhanced forest state with higher C stocks.

In California, oak open woodlands and chaparral shrublands are also experiencing decline (Coates et al. 2015). In oaklands, herbivores impede oak recruitment, and wildfires and exotic grasses further contribute to the collapse of open forests. In turn, drought-induced recruitment failure, particularly after wildfires, would favour conversion of close chaparral to open scrubland and non-native grasslands (Jacobsen and Pratt 2018). Recent and persistent drought starting in 2012 is also causing important changes in temperate Californian forests. Conifer forests (*Pinus ponderosa*, *P. lambertiana*, *Abies concolor*, *Calocedrus decurrens*) across Sierra Nevada mountains now exhibit high mortality rates, in many cases also associated to bark beetle attacks (Fetting et al. 2019; Pile et al. 2019). Past management plays a relevant role in this decline, given that fire suppression has produced homogenous stand structures with high-density, small trees (McIntyre et al. 2015), which are likely more vulnerable to lower water supply. Ongoing regeneration patterns points to an upward elevation shift of these forests, since drought-tolerant species (*C. decurrens*, *Q. chrysolepis*) are more abundant in the understory, particularly at lower altitudes. This shift is enhanced by the abundance of shrubs and the expansion of forbs and grasses, including some non-native invasive ones, at lower elevations, outcompeting the recruitment of conifers such as *P. ponderosa*. As a result, there is a widespread transformation of low montane mixed conifer forests to sclerophyllous shrublands, enhanced by wildfires (Serra-Diaz et al. 2018) and streamflow increase (Bart et al. 2016) through reinforcing feedbacks. These changes have relevant consequences in the hydrological regime, particularly when shrubs have a small leaf area relative to the replaced tree species, increasing streamflow during wetter years (Bart et al. 2016).

Some forests located at northern latitudes are also subjected to dramatic decline leading to the collapse of former forests. Forests dominated by quaking aspen (*Populus tremuloides*) constitute one of the most widespread forest types in North America. These groves were favoured by past human disturbances such as intensive logging, prescribed fires, crop irrigation, bison elimination, and sheep grazing (Singer et al. 2019). In recent decades sudden aspen decline (SAD) events have been reported to led to fast forest collapse occurring in 3–5 years (Singer et al. 2019). SAD has been found along the whole aspen range but particularly at south-facing aspects in its northern distribution close to boreal regions and at low elevations in its southern edge. Drought plays a major role in this decline (Anderegg et al. 2013b), although predisposing and inciting factors such as shallow soils (Anderegg et al. 2013c) and insect pests and pathogens (Marchetti et al. 2011) significantly contribute to the phenomenon. *Populus tremuloides* groves typically get established after disturbances and self-replace under a regular disturbance regime thanks to its resprouting ability. But in the absence of disturbances, slow successional transitions to mixed conifer forests are prone to occur. Indeed, SAD promotes the shift of aspen forests to formations dominated by drought-tolerant conifers or alternatively the long-term forest replacement by shrubs and grasses (Cobb et al. 2017). Climate projections indicate that increasing heat and drought will further jeopardize aspen forests at their lower and higher elevation limits of distribution, where they would be outcompeted by shrubland and conifers, respectively (Singer et al. 2019). SAD is an example of studied functional shifts in ecosystems, since it has been reported to cause a diminution in C storage of aboveground biomass (Michaelian et al. 2011; Huang and Anderegg 2012), and modification of the biophysical properties (e.g. surface albedo) and the nutrient fluxes (Huang and Anderegg 2014; Cobb et al. 2017).

In southern Siberian forests, drought over the last decades, in combination with insect and root fungi attack, is causing the mortality of different species of conifers (*Abies sibirica*, *Picea obovata*, *Pinus sibirica*) covering thousands of hectares (Kharuk et al. 2013, 2017). Topography plays an important role on soil water availability and temperature, which together with insect outbreaks produce a mosaic of forest-affected patches across the landscape. Although regeneration occurs, it is expected a replacement of the former forests by more drought-tolerant species (e.g. *Pinus sylvestris*, *Larix sibirica*) (Kharuk et al. 2017). But at the steppe ecotone, even these tolerant species growing in open forests are experiencing drought-induced mortality. In these semi-arid forests, a compensatory demographic mechanism appears, since adult mortality enhances regeneration of young trees, unless drought conditions become extreme (Xu et al. 2017).

7.5 Enhancing Resilience

Forest collapse induced by drought/heat emerges when mechanisms promoting resilience fail under the pressure of climatic alterations, which currently are largely caused by anthropogenic activity. In the context of ongoing climate change, collapses may be associated, among others, with (a) episodes of high temperature and low precipitation (i.e. high water deficit), often associated with increasing climatic variability; (b) the pervasive warming trend, which likely produce cumulative effects; or (c) a combination of both (Easterling et al. 2000; Trenberth et al. 2014; Johnstone et al. 2016). Resilience is based on coupled, stabilizing mechanisms that often generates regulation feedbacks that allow the community to "quickly" recover its pre-disturbance characteristics, or alternatively, to reduce the likelihood of state shifts. The idea of promoting resilience of existing ecosystems or facilitating the transition to more resilient but different systems in the face of altered disturbance regimes and climate change is now a powerful strategy in management agendas (Millar et al. 2007; Seidl et al. 2016; Cobb et al. 2017).

7.5.1 Water Demand Strategy

One type of regulatory mechanisms is the optimizing water uptake under situations of hydric deficit. At individual and stand levels, canopy reduction (i.e. leaf loss and tree mortality) represents a regulatory mechanism as it reduces evapotranspirative surface area during periods of high water demand. The losses of plant components can be greater when previous periods of high productivity (e.g. due to favourable climatic conditions) resulted in the building of components with a high demand of resources (Jump et al. 2017). Regardless, if trees survive and maintain enough stocks of resources and bud banks, they would recover when favourable climatic conditions return (e.g. Lloret et al. 2004). However, if unfavourable conditions persist or the frequency and intensity of extreme events increase, these regulatory mechanisms will eventually fail, resilience will be lost, and forests will likely shift to another state. In many cases, reduction of evapotranspiration surface is attained by diminishing stand basal area as a result of competition-induced tree mortality. In this case, forests may gain resilience by remaining with a more open structure, likely maintaining a noticeably part of its functionality, or alternatively being replaced by savannah-like formations. In tropical forests it is hard to detect shifts in species composition given their high natural turnover, but they often simplify its structure by diminishing height and basal area (e.g. Zhou et al. 2014).

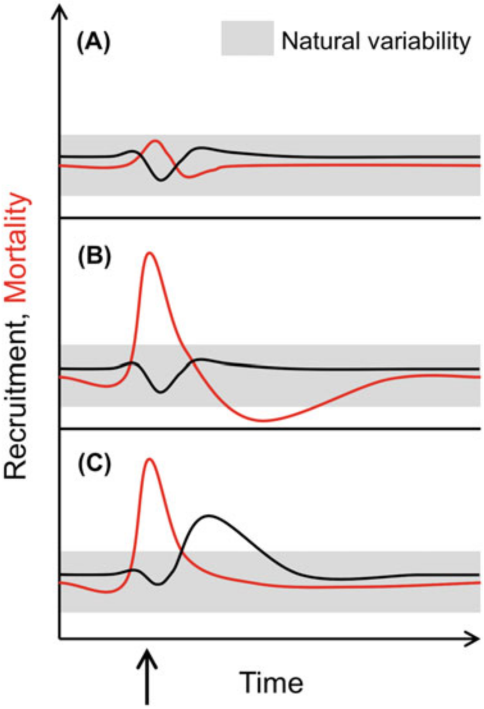
Accordingly, management actions addressed to preventively reduce evapotranspiration surface (e.g. selective thinning) have been proposed (e.g. Grant et al. 2013). A recent meta-analysis shows that forest thinning enhances forest resilience in drought conditions (Sohn et al. 2016). But such practices require caution because leaf production of the remaining stems could compensate transitory leaf losses, and other forest services can also be threatened (Jump et al. 2017). In specific situations, providing more water at the local to the watershed scale can be an option after accurately calculating water balances, since water trade-offs affect different ecosystem and social demands (Grant et al. 2013). Other actions may involve selection of genotypes (at population or species level) with lower water requirement. Maintaining genetic variability in co-occurring populations, i.e. promoting within and between species diversity, may favour functional complementarity and ecosystem resilience in front of water scarcity.

Canopy cover also plays an essential role in the regulatory feedbacks between vegetation and water availability and soil fertility. The more extreme cases, which become paradigmatic examples to describe ecosystem state changes, involve arid systems in which thresholds in vegetation cover reduce water run-off and increase water availability for plants (Rietkerk et al. 2004). Therefore, deprivation of vegetation cover in such arid ecosystems, irrespective of species identity, will favour soil and water losses, which eventually will jeopardize ecosystem functioning. In other biomes, shifts to new forest formations, although having the potential to represent significant biodiversity alterations, will likely result in the maintenance of most ecosystem properties. For instance, loss of forest cover leading to a system dominated by less structured but yet continuous vegetation (e.g. shrubland) will still maintain some essential ecosystem functionalities.

7.5.2 Population and Biodiversity-Based Strategies

Another essential regulatory mechanism of forest resilience involves key demographic processes such as recruitment (Lloret et al. 2012) (Fig. 7.7). Drought-induced leaf loss and eventual tree death reduce competition with understory plants; if those are tree species, they may reoccupy canopy gaps in the long-term, promoting forest resilience. Global patterns of forest dynamics from such a demographic perspective, that is, considering the community regeneration after the mortality event, indicate that pre-existing species may persist after the mortality episode providing a basic demographic element for ecosystem resilience (Martínez-Vilalta and Lloret 2016). However, the temporal persistence of the ecosystem trajectories will only be consolidated if seedling recruitment of arboreal species is successful in the long term. If trees eventually recruit, the reported vegetation-type conversions to shrublands and grasslands could be transitory and in the midterm forest functionality will overall remain, although modifications due to new species composition will

Fig. 7.7 Regulation model of population rates through time (recruitment in black, mortality in orange) to extreme events (*bottom arrow*). From top to bottom, subplots depict (**a**) fluctuation within natural variability, (**b**) high mortality and low recruitment compensated by higher survival of the remaining population, and (**c**) enhanced recruitment after a peak of adult mortality. (Figure from Lloret et al. [2012])



likely appear (Zhang et al. 2018). In consequence, those actions addressed to reinforce regeneration (e.g. by providing seed and seedling banks, reducing recruits mortality from high herbivory pressure, spatial patterning of planting) may support forest resilience.

Coexistence of populations belonging to different species constitutes another regulatory mechanism in the face of environmental fluctuations, extreme events, or directional climatic trends, according to the species' complementary functionality (Loreau and de Mazancourt 2013). Some studies have documented positive relationships between species diversity and essential forest ecosystem functions in front of drought (e.g. Lebourgeois et al. 2013; Hutchinson et al. 2018), although this relationship is not univocal for all forests (Grossiord et al. 2014). There is evidence that tree diversity reduces the impacts of extreme climatic events (Hutchinson et al. 2018; Sousa-Silva et al. 2018). This positive effect can be modulated by past management determining current species composition (Lloret et al. 2007). So, enhancing stand-level tree diversity has been proposed to increase resilience in front of climate change (e.g. Bosela et al. 2019), thus promoting mixed forests compared to monospecific stands. Under great future uncertainty, this strategy would also increase functional diversity, even with low density of distinct functional species (Messier et al. 2019). Importantly, enhancing resilience by forest diversity implies cross-scale landscape management providing connectivity and refuges coupled to topography and microclimate heterogeneity (Fischer et al. 2006; Mori et al.

2017). Within this framework, selection of species or provenances with higher drought tolerance is also in the agenda of forest managers (e.g. Ennos et al. 2019). However, the use of non-native species to reinforce resilience by enhancing diversity should be considered with extreme caution, with the need to accurately assess the suitability of introduced genotypes, and the high risk of introducing non-native pathogens and pests or the loss of native genetic diversity due to genetic flux (e.g. hybridisation) (Ennos et al. 2019).

Biotic interactions are an essential component of biodiversity. Some positive interactions, such as mycorrhizal symbiosis, clearly reinforce forest resilience by enhancing productivity and efficient water and nutrient uptake (Yang et al. 2018). By contrast, antagonistic interactions, involving for instance pests and pathogens, tend to increase forest vulnerability due to positive feedbacks with drought. Thus, when pathogens, insect outbreaks, and herbivory achieve high intensity and extent, they can significantly challenge physiological and demographic mechanisms of resilience (Raffa et al. 2015; Berner et al. 2017). Our knowledge of the complex network of biotic interactions, particularly those involving above and belowground ecosystem components (i.e. soil microbial communities), is rapidly increasing and eventually should be incorporated into strategies to reinforce resilience. Overall, management actions dealing with biodiversity should be selective in their targets, aiming to favour stabilizing interactions and minimizing disruptive ones.

7.5.3 Disturbance Regime-Based Strategy: Wildfires

Disturbance regimes also influence resource and demographic regulatory mechanism. In the case of wildfires, burning reduces evaporative surface, thus temporarily diminishing water demand by vegetation. With low-intensity burning, soil erosion losses are minimized, but high-intensity crown wildfires may cause soil losses, nutrient stock depletion and disruption of demographic regulation by depleting seed and sapling bank and jeopardizing resprouting (Enright et al. 2015). These effects tend to increase under high fire recurrence (Malkisnon et al. 2011). On the other hand, wildfires may have a regulatory effect on populations by promoting the establishment of new cohorts and nutrient recycling (Noss et al. 2006). The multiple positive effects of natural fire regimes are in a balance that is easily disrupted by humans, and altered fire regimes diminish in many cases forest resilience. For instance, fire suppression policies reduce recruitment of some species while increasing evaporative demand as a result of increased stand density. Also, fire suppression derives in higher fuel loads that promote high-intensity crown-fires (Allen et al. 2002; Savage and Mast 2005). The consequences of fire disruptions are particularly complex given that fire regimes are coupled with climate, and both fire and climate are sensitive to human activity from local to global scales (Moritz et al. 2012, Abatzoglou and Williams 2016). So, management of disturbance regimes, such as wildfires, plays an important role in providing forest resilience in front of climate change. Disturbance management implies a delicate case-specific tuning, avoiding catastrophic events but allowing disturbances of limited intensity and extent across mosaic landscapes including both disturbed areas and refuges (Coop et al. 2019).

Compound regimes of wildfires and drought may increase the likelihood of reaching a tipping point by reducing the stored resources as well as seed and bud banks that allow regeneration (Barton and Poulos 2018; Batllori et al. 2017, 2019). For instance, extreme drought conditions may preclude regeneration success after fire, leading to forest collapse or drastic changes in species dominance. Thus, accurate knowledge of the demographic and functional role of fire regime at different scales is important to design an integrative management of this disturbance with the aim of enhancing forest resilience. However, the inherent stochasticity associated to fire occurrence and to climate variability leading to drought, coupled with the wide range of biological responses, makes it difficult to perform precise large-scale predictions of the forest fate.

7.6 Future Prognosis of Forest Collapse

Theory suggests that early warning signals of ecosystem shifts should be discernible under gradual, directional environmental transformation before major changes in the state of ecosystems occur. Such signals could thus be useful to anticipate ecosystem collapse and to design adaptive management strategies (Scheffer et al. 2009; Carpenter et al. 2011). So, a key issue is whether these signals can be detected in forests sufficiently in advance. The early warning signal framework has been well developed and applied in aquatic ecosystems, where the rates of change are fast and shifts can occur several times over short-time windows (e.g. annual cycles of clear and turbid waters in lakes). In terrestrial ecosystems rates of changes are lower. Although early warning signals of individual tree mortality have been inferred from tree ring patterns (Cailleret et al. 2016), this approach is more difficult to apply at the community level as our knowledge on long-term dynamics is much more limited. The phenomenon of critical slowdowns in ecosystem variables is revealing as highly valuable to infer ecosystem shifts (Scheffer et al. 2015), although it is not a necessary condition to infer critical tipping points (Connell and Ghedini 2015; Dakos et al. 2014). Critical slowing down implies that recovery rates after small perturbations become slower when the system is approaching to a tipping point. Empirically, the recovery slowness of the system can be derived after the fluctuations characteristics of any natural environment. Mathematically, this can be detected as increasing temporal autocorrelation and variance in the properties of the system. In principle this approach does not specifically address the behaviour of early warning signals in relation to strong disturbances or environmental fluctuations. A space-for-time substitution analysis where spatial environmental gradients are used to analyse critical thresholds between ecosystem states (Eby et al. 2017; Majumber et al. 2019) may provide tools to integrate critical slowing down and disturbance regimes.

In the midterm, results of the existing forest monitoring networks should allow testing the applicability of resilience indicators to forests under historical disturbance regimes. Importantly, this will directly depend on our understanding on the contribution of major functional traits involved in plants' regeneration after disturbance (i.e. seeding and resprouting). For instance, after fire or extreme drought, resprouter species (e.g. oaks) have provided so far a buffer against post-disturbance forest collapse in some sites dominated by obligate seeder trees (e.g. pines; Karavani et al. 2018). However, increased knowledge is needed on climate-driven alterations of demographic processes for many seedling species (e.g. thresholds of seed production and seedling survival) and to assess the extent of "resprouter exhaustion syndrome", a condition where resprouting ability is limited as a result of stressful pre-disturbance conditions or under too short intervals between disturbance events.

In the current context of increased climatic variability, the interacting effects of multiple disturbances that are directly influenced by climate (e.g. fire, drought, windstorms, pest outbreaks) can be of paramount importance to ecosystem resilience (e.g. Paine et al. 1998; Turner 2010; Buma 2015; Batllori et al. 2019). Ecosystem response to compound disturbance regimes is not simply an additive result of the response to individual disturbance agents. Also, and importantly, specific sequences of events, even under moderate recurrence of individual disturbances, are a strong-enough mechanism to disrupt the resilience of the system (Batllori et al. 2019). Therefore, the effects of interacting disturbance regimes, even if only occurring sporadically over time, can exert a strong influence on the dynamics of ecosystems, further increasing uncertainty in predicting vegetation state under changing climates. Anticipating long-term forest response, resilience and the likelihood of forest collapse will thus require integrating the characteristics of current ecosystem state and thresholds of disturbance into empirically based models of compound disturbance effects.

7.7 Conclusion

Climate trends of increasing aridity and recurrence of extreme drought episodes have occurred in the past, and forests have experienced rapid and profound transformations that have not been always reversible. Human-induced climate change is leading to novel conditions where climate variability in some regions is increasing with longer, more intense, and/or more frequent extreme events, particularly dryness and heat (IPCC 2014, AR5). In addition, humans cause direct, substantial impacts on ecosystems, particularly by modifying fire regimes, introducing antagonistic species and transforming forest composition and structure. Overall, these actions tend to decrease ecosystem resilience by disrupting stabilizing feedbacks. As a result, forest vulnerability and the likelihood of forest collapse are increasing. Recent-past and ongoing forest mortality events associated with episodes of extreme drought and heatwaves represent an invaluable window to the future, as these climatic conditions will become the new normal. Whether the changes we are observing in forests will eventually result in long-term collapse and thus shift to a different state can only be truly resolved by long-term monitoring. Importantly, species composition shifts do not necessarily mean collapse of whole-ecosystem functioning. For instance, species functional complementarity can operate as a resilience mechanism of ecosystem function. Management strategies focused on reducing water demand and reinforcing demographic mechanisms of tree populations' persistence and biodiversity maintenance would enhance the maintenance of current and future forests. Thus, a better understanding of the interrelated mechanisms favouring resilience at different levels (from plant ecophysiology and community assembly to energy and matter balances and feedbacks across landscapes) is essential to acquire tools for maintaining forest biodiversity and services into the future.

Acknowledgements Contribution of T. Aakala, W. R.L. Anderegg, E. Aynekulu, D. P. Bendixsen, A. Bentouati, C. Bigler, C. J. Burk, J. J. Camarero, M. Colangelo, J. D. Coop, R. Fensham, M. L. Floyd, L. Galiano, J. L. Ganey, P. Gonzalez, A. L. Jacobsen, J. M. Kane, T. Kitzberger, J. C. Linares, S. B. Marchetti, G. Matusick, M. Michaelian, R. M. Navarro-Cerrillo, R. B. Pratt; M. D. Redmond, A. Rigling, F. Ripullone, G. Sangüesa-Barreda, Y. Sasal, S. Saura-Mas, M. L. Suarez, T. T. Veblen, A. Vilà-Cabrera, C. Vincke, and B. Zeeman, is recognized, by sharing information about forest regeneration after drought-induced events of forest mortality across temperate and boreal forests of the world. The authors benefited from Spanish Ministry of Economy and Competitiveness (BIOCLIM, CGL2015-67419-R; TIPMED CGL2017-87176-P) and AGAUR, Government of Catalonia (2017 SGR 1001) grants. The authors thank the editors (Pep Canadell and Rob Jackson) and Ernst-Detlef Schulze for their comments on previous versions of the text.

References

Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. Proc Natl Acad Sci 113:11770–11775

Adams HD, Luce CH, Breshears DD, Allen CD, Weiler M, Cody HV, Smith AMS, Huxman TE (2012) Transformative ecosystem change and ecohydrology: Ushering in a new era for watershed management. Ecohydrology 130:126–130

Albertson FW, Weaver JE (1945) Injury and Death or Recovery of Trees in Prairie Climate. Ecol Monogr 15:395–433

Allen CD, Breshears DD (1998) Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. Proc Natl Acad Sci 95:14839–14842

Allen CD, Savage M, Falk DA, Suckling KF, Swetnam TW, Schulke T, Stacey PB, Morgan P, Hoffman M, Klingel J (2002) Ecological restoration of Southwestern ponderosa pine ecosystems: A broad perspective. Ecol Appl 12:1418–1433

Allen CD et al (2010) A global overview of drought and heat induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259:660–684

Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:1–55

Anderegg WRJ, Kane JM, Anderegg LDL (2013a) Consequences of widespread tree mortality triggered by drought and temperature stress. Nat Clim Chan 3:30–36

Anderegg LDL, Anderegg WRL, Abatzoglou J, Hausladen AM, Berry JA (2013b) Drought characteristics' role in widespread aspen forest mortality across Colorado, USA. Glob Chang Biol 19:1526–1537

Anderegg WRL, Plavcova L, Anderegg LDL, Hacke UG, Berry JA, Field CB (2013c) Drought's legacy: Multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. Glob Chang Biol 19:1188–1196

Anderegg WRL et al (2015) Tree mortality from drought, insects, and their interactions in a changing climate. New Phytol 208:674–683

Assal TJ, Anderson PJ, Sibold J (2016) Spatial and temporal trends of drought effects in a heterogeneous semi-arid forest ecosystem. For Ecol Manag 365:137–151

Aynekulu E et al (2011) Dieback affects forest structure in a dry Afromontane forest in northern Ethiopia. J Arid Environ 75:499–503

Bart RB, Tague CL, Moritz MA (2016) Effect of Tree-to-Shrub Type Conversion in Lower Montane Forests of the Sierra Nevada (USA) on Streamflow. PLoS One. https://doi.org/10.1371/journal.pone.0161805

Barton AM, Poulos HM (2018) Pine vs. oaks revisited: conversion of Madrean pine-oak forest to oak shrubland after high-severity wildfire in the Sky Islands of Arizona. For Ecol Manag 414:28–40

Batllori E, De Cáceres M, Brotons L, Ackerly DD, Moritz MA, Lloret F (2017) Cumulative effects of fire and drought in Mediterranean ecosystems. Ecosphere 8:e01906

Batllori E, De Cáceres M, Brotons L, Ackerly DD, Moritz MA, Lloret F (2019) Compound fire-drought regimes promote ecosystem transitions in Mediterranean ecosystems. J Ecol 107:1187–1192

Batllori E et al (2020) Forest and woodland replacement patterns following drought-related mortality. PNAS 117:29720–29729

Becek K, Horwarth AB (2017) Is vegetation collapse on Borneo already in progress? Nat Hazards 85:1279–1290

Bell DM, Bradford JB, Lauenroth WK (2014) Forest stand structure, productivity, and age mediate climatic effects on aspen decline. Ecology 95:2040–2046

Bentouati A (2008) La situation du cèdre de l'Atlas dans les Aurès (Algérie). Forêt Méditerranéenne 29:203–208

Berner LT, Law BE, Meddens AJH, Hicke JA (2017) Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States. Environ Research Lett 12:065005

Bhiry N, Filion L (1996) Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity. Quat Res 45:312–320

der Bolt B et al (2018) Climate reddening increases the chance of critical transitions. Nat Clim Chan 8:478–484

Bonal D, Burban B, Stahl C, Wagner F, Hérault B (2016) The response of tropical rainforests to drought-lessons from recent research and future prospects. Ann For Sci 73:27–44

Bosela M, Kulla L, Roessiger J, Seben V, Dobor L, Buntgen U, Lukac M (2019) Long-term effects of environmental change and species diversity on tree radial growth in a mixed European forest. For Ecol Manag 446:293–303

Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, Coe MT, Siléiro D, Macedo MN, Davidson EA, Nóbrega CC, Alencar A, Soares-Filho BS (2014) Abrupt increases in Amazonian tree mortality due to drought–fire interactions. Proc Natl Acad Sci 111:6347–6352

Breshears DD et al (2005) Regional vegetation die-off in response to global-change-type drought. Proc Natl Acad Sci 102:15144–15148

Browers NC, van Dongen R, Matusick G, Coops NC, Strelein G, Hardy G (2015) Inferring drought and heat sensitivity across a Mediterranean forest region in southwest Western Australia: a comparison of approaches. Forestry 88:454–464

Buma B (2015) Disturbance interactions: Characterization, prediction, and the potential for cascading effects. Ecosphere 6:1–15

Byer S, Jin Y (2017) Detecting drought-induced Tree Mortality in Sierra Nevada Forests with time series of satellite data. Remote Sens 9:929

Cailleret M, Nourtier M, Amm A, Durand-Gillmann M, Davi H (2014) Drought-induced decline and mortality of silver fir differ among three sites in Southern France. Ann For Sci 71:643–657

Cailleret M et al (2016) A synthesis of radial growth patterns preceding tree mortality. Glob Chang Biol 23:1675–1690

Camarero JJ, Bigler C, Linares JC, Gil-Pelegrín E (2011) Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. For Ecol Manag 262:759–769

Canham CD, Murphy L (2017) The demography of tree species response to climate: Sapling and canopy tree survival. Ecosphere 8:e01701

Carpenter SR, Cole JJ, Pace ML, Batt R, Brock WA, Cline T, Coloso J, Hodgson JR, Kitchell JF, Seekell DA, Smith L, Weidel B (2011) Early warnings of regime shifts: a whole-ecosystem experiment. Science 332:1079–1082

Ciais P et al (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533

Clark DB, Soto Castro C, Alfaro Alvarado LD, Read JM (2004) Quantifying mortality of tropical rain forest trees using high-spatial-resolution satellite data. Ecol Lett 7:52–59

Coates AR, Dennison PD, Roberts DA, Roth KL (2015) Monitoring the impacts of severe drought on Southern California Chaparral Species using Hyperspectral and Thermal Infrared Imagery. Remote Sens 7:14276–14291

Cobb RC et al (2017) Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models. Ecosphere 8:e02034

Condit R (1998) Ecological implications of changes in drought patterns: shifts in forest composition in Panama. Clim Chang 39:413–427

Connell SD, Ghedini G (2015) Resisting regime-shifts: the stabilising effect of compensatory processes. Trends Ecol Evol 30:513–515

Coop JD, De Lory TJ, Downing WM, Haire SL, Krawchuk MA, Miller C, Parisien MA, Walker RB (2019) Contributions of fire refugia to resilient ponderosa pine and dry mixed-conifer forest landscapes. Ecosphere 10:e02809

Dakos V, Carpenter SR, van Nes EH, Scheffer M (2014) Resilience indicators: prospects and limitations for early warnings of regime shifts. Phil Trans R Soc Lond B 370:20130263

De Grandpré L, Kneeshaw DD, Perigon S, Boucher D, Marchand M, Pureswaran D, Girardin MP (2018) Adverse climatic periods precede and amplify defoliator-induced tree mortality in eastern boreal North America. J Ecol 107:452–467

Delatour C (1983) Le dépérissements de chênes en Europe. Révue Forestale Française 35:265–282

Dobbertin M, Wermelinger B, Bigler C, Bürgi M, Carron M, Forster B, Gimmi U, Rigling A (2007) Linking Increasing Drought Stress to Scots Pine Mortality and Bark Beetle Infestations. The Scie World J 7(S1):231–239

Doughty CE et al (2015) Drought impact on forest carbon dynamics and fluxes in Amazonia. Nature 519:78–84

Easterling DR et al (2000) Climate extremes: observations, modeling, and impacts. Science 289:2068–2074

Eby S, Agrawal A, Majumder S, Dobson AP, Guttal V (2017) Alternative stable states and spatial indicators of critical slowing down along a spatial gradient in a savanna ecosystem. Glob Ecol Biogeogr 26:638–649

Ennos R, Cottrell J, Hall J, O'Brien D (2019) Is the introduction of novel exotic forest tree species a rational response to rapid environmental change?—A British perspective. For Ecol Manag 32:718–728

Enquist BJ, Enquist CAF (2010) Long-term change within a Neotropical forest: assessing differential functional and floristic responses to disturbance and drought. Glob Change Biol 17:1408–1424

Enright NJ, Fontaine JB, Bowman DMJS, Bradstock RA, Williams RJ (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Front Ecol Environ 13:265–272

Esteve Selma MA, Carreño Fructuoso MF, Moya Perez JM, Montoya P, Fernandez-Martinez J, Perez-Navarro MA, Lloret F (2017) La respuesta de los bosques de *Pinus halepensis* al cambio climático y los eventos de sequía extrema. Modelos preliminares. In: Conesa García C, Perez Cutillas P (eds) Los riesgos ambientales en la Región de Murcia. Ediciones Universidad de Murcia, pp 163–185

Feldpausch TR et al (2016) Amazon forest response to repeated droughts. Glob Biogeochem Cycles 30:964–982

Fensham RJ, Holman JE (1999) Temporal and spatial patterns in drought-related tree dieback in Australian savanna. J Appl Ecol 36:1035–1050

Fensham R, Laffineur RJ, Allen CA (2019) To what extent is drought-induced tree mortality a natural phenomenon? Glob Ecol Biogeogr 28:365–373

Fetting CJ, Mortenson LA, Bulaon BM, Foulk PB (2019) Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. For Ecol Manage 432:164–178

Fischer J, Lindenmayer DB, Manning AD (2006) Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Front Ecol Environ 4:80–86

Foster DR, Oswald WW, Faison EK, Doughty E, Hansen BCS (2006) A climatic driver for abrupt mid-holocene vegetation dynamics and the hemlock decline in New England. Ecology 87:2959–2966

Galeano A, Urrego LE, Botero V, Bernal G (2017) Mangrove resilience to climate extreme events in a Colombian Caribbean Island. Wetl Ecol Manag 25:743–760

Galiano L, Martínez-Vilalta J, Lloret F (2010) Drought-induced multifactor decline of Scots Pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. Ecosystems 13:978–991

Garrity SR, Allen CD, Brumby SP, Gangodagamage C, McDowell NG, Cai DM (2013) Quantifying tree mortality in a mixed species woodland using multitemporal high spatial resolution satellite imagery. Remote Sens Environ 129:54–65

Gaylord ML et al (2013) Drought predisposes pinyon-juniper woodlands to insect attacks and mortality. New Phytol 198:567–578

Gonzalez P (2001) Desertification and a shift of forest species in the West African Sahel. Clim Res 17:217–228

Grant PJ (1984) Drought effect on high-altitude forests, Ruahine Range, North Island, New Zealand. J Bot 22:15–27

Grant GE, Tague CL, Allen CD (2013) Watering the forest for the trees: an emerging priority for managing water in forest landscapes. Front Ecol Environ 11:314–321

Greenwood S et al (2017) Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. Ecol Lett 20:539–553

Grootes PM, Stuiver M (1997) Oxygen 18 / 16 variability in Greenland snow and ice with 103 to 105-year time resolution. J Geophysical Res 102:26455–26470

Grossiord C et al (2014) Tree diversity does not always improve resistance of forest ecosystems to drought. Proc Natl Acad Sci 111:14812–14815

Hartmann H et al (2018) Research frontiers for improving our understanding of drought-induced tree and forest mortality. New Phytol 218:15–28

Harvey BJ, Donato DC, Turner MG (2016) High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob Ecol Biogeogr 25:655–669

Heckmann M, Muiruri M, Boom A, Marchant R (2014) Human–environment interactions in an agricultural landscape: a 1400-yr sediment and pollen record from North Pare, NE Tanzania. Palaeog Palaeoclim Palaeoecol 406:49–61

Henzler J, Weise H, Enright NJ, Zander S, Tietjen B (2018) A squeeze in the suitable fire interval: simulating the persistence of fire-killed plants in a Mediterranean-type ecosystem under drier conditions. Ecol Model 389:41–49

Hiernaux P, Diarra L, Trichon V, Mougin E, Soumaguel N, Baup F (2009) Woody plant population dynamics in response to climate changes from 1984 to 2006 in Sahel (Gourma, Mali). J Hydrol 375:103–113

Hogg EH, Brandt JP, Michaellian M (2008) Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can J For Res 38:1373–1384

Huang CY, Anderegg WRL (2012) Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. Glob Change Biol 18:1016–1027

Huang CY, Anderegg WRL (2014) Vegetation, land surface brightness, and temperature dynamics after aspen forest die-off. J Geophys Res Biogeosciences 119:1297–1308

Huang CY, Asner GP, Barger NN, Neff JC, Floyd ML (2010) Regional aboveground live carbon losses due to drought-induced tree dieback in piñon–juniper ecosystems. Remote Sens Environ 114:1471–1479

Huang K, Yi C, Wu D, Zhou T, Zhao X, Bjanford WJ, Wei S, Wu H, Ling D, Li Z (2015) Tipping point of a conifer forest ecosystem under severe drought. Environ Res Lett 10:024011

Hutchinson C, Gravel D, Guichard F, Potvin C (2018) Effect of diversity on growth, mortality, and loss of resilience to extreme climate events in a tropical planted forest experiment. Sci Rep 8:15443

IPCC (2014) Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press

Ivory SJ, Russell J (2016) Climate, herbivory, and fire controls on tropical African forest for the last 60 ka. Quat Sci Rev 148:101–114

Jacobsen AL, Pratt RB (2018) Extensive drought-associated plant mortality as an agent of type-conversion in chaparral shrublands. New Phytol 219:498–504

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GLW, Schoennagel T, Turner MG (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378

Jump AS, Ruiz-Benito P, Greenwood S, Allen CD, Kitzberger T, Fensham R, Martínez-Vilalta J, Lloret F (2017) Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. Glob Chang Biol 23:3742–3757

Karavani A, Boer MM, Baudena M, Colinas C, Díaz-Sierra R, Pemán J, de Luis M, Enríquez-de-Salamanca A, Resco de Dios V (2018) Fire-induced deforestation in drought-prone Mediterranean forests: drivers and unknowns from leaves to communities. Ecol Monogr 88:141–169

Kharuk VI, Im ST, Oskorbin PA, Petrov IA, Ranson KJ (2013) Siberian pine decline and mortality in southern siberian mountains. For Ecol Manag 310:312–320

Kharuk VI, Im ST, Petrov IA, Dviskaya ML, Fedotova EV, Ranson KJ (2017) Fir decline and mortality in the southern Siberian Mountains. Reg Environ Chang 17:803–812

Kolb TE (2015) A new drought tipping point for conifer mortality. Environ Res Lett 10:031002

Lebourgeois F, Gomez N, Pinto P, Merian P (2013) Mixed stands reduce Abies alba tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. For Ecol Manag 303:61–71

Liang E, Shao X, Kong Z, Lin J (2003) The extreme drought in the 1920s and its effect on tree growth deduced from tree ring analysis: a case study in North China. Ann For Sci 60:145–152

Linares JC, Camarero JJ, Bowker MA, Ochoa V, Carreira JA (2010) Stand-structural effects on *Heterobasidion abietinum*-related mortality following drought events in *Abies pinsapo*. Oecologia 164:1107–1119

Liu Y, Kumar M, Katul GG, Porporat A (2019) Reduced resilience as an early warning signal of forest mortality. Nat Clim Chang 9:880–885

Lloret F, Siscart D, Dalmases C (2004) Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). Glob Chang Biol 10:2092–2099

Lloret F, Lobo A, Estevan H, Maisongrande P, Vayreda J, Terradas J (2007) Woody plant richness and NDVI response to drought events in Catalonia (North Eastern Spain) forests. Ecology 88:2270–2279

Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F (2012) Extreme climatic events and vegetation: The role of stabilizing processes. Glob Chang Biol 18:797–805

Lopez-Blanco C, Giallard MJ, Miracle RM, Vicente E (2012) Lake-level changes and fire history at Lagunillo del Tejo (Spain) during the last millennium: Climate or humans? The Holocene 22:551–560

Loreau M, de Mazancourt C (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol Lett 16:106–115

Magny M, Leroux A, Bichet V, Gauthier E, Richard H, Walter-Simonet AW (2012) Climate, vegetation and land use as drivers of Holocene sedimentation: A case study from Lake Saint-Point (Jura Mountains, eastern France). The Holocene 23:137–147

Majumber S, Tamma K, Ramaswamy S, Guttal V (2019) Inferring critical thresholds of ecosystem transitions from spatial data. Ecology 100:e02722

Malkisnon D, Wittenberg L, Beeri O, Barzolai R (2011) Effects of repeated fires on the structure, composition, and dynamics of Mediterranean Maquis: short- and long-term perspectives. Ecosystems 14:478–488

van Mantgem PJ, Nesmith JCB, Keifer MB, Knapp EE, Flint A, Flint L (2013) Climatic stress increases forest fire severity across the western United States. Ecol Lett 16:1151–1156

Marchetti SB, Worrall JJ, Eager T (2011) Secondary insects and diseases contribute to sudden aspen decline in southwestern Colorado, USA. Can J For Res 41:2315–2325

Martínez-Vilalta J, Lloret F (2016) Drought-induced vegetation shifts in terrestrial ecosystems. Glob Planet Chang 144:94–108

Matías L, Abdelaziz M, Godoy O, Gómez-Aparicio L (2018) Disentangling the climatic and biotic factors driving changes in the dynamics of *Quercus suber* populations across the species' latitudinal range. Div Distrib 25:524–535

Matusick G, Ruthrof KX, Fontaine JB, Hardy GESJ (2016) Eucalyptus forest shows low structural resistance and resilience to climate change-type drought. J Veg Sci 27:493–503

Mayle FE, Power MJ (2008) Impact of a drier Early–Mid-Holocene climate upon Amazonian forests. Phil Trans R Soc Lond B 363:1829–1838

Mayle FE, Beerling DJ, Gosling WD, Bush MB (2004) Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. Phil Trans R Soc Lond B 359:499–514

McDowell NG et al (2008) Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? New Phytol 178:719–739

McDowell N et al (2014) Global satellite monitoring of climate-induced vegetation disturbances. Trends Plant Sci. https://doi.org/10.1016/j.tplants.2014.10.008

McIntyre PJ, Thorne JH, Dolanc CR, Flint AL, Flint LE, Kelly M, Ackerly DD (2015) Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. Proc Natl Acad Sci 112:1458–1463

Meddens AJH, Hicke JA, Macalady AK, Buotte PC, Cowles TR, Allen CD (2015) Tansley insight: patterns and causes of observed pinyon pine mortality in the southwestern United States. New Phytol 206:91–97

Meir P, Mencuccini M, Binks O, Lola da Costa A, Ferreira L, Rowland L (2018) Short-term effects of drought on tropical forest do not fully predict impacts of repeated or long-term drought: gas exchange versus growth. Phil Trans R Soc Lond B 373:1760

Menking KM, Peteet DM, Anderson RY (2012) Late-glacial and Holocene vegetation and climate variability, including major droughts, in the Sky Lakes region of southeastern New York State. Palaeog Palaeocl Plaeoecol 353–355:45–59

Messier C, Bauhus J, Doyon F, Maure F, Sousa-Silva R, Nolet P, Mina M, Aquilue N, Fortin MJ, Puettmann K (2019) The functional complex network approach to foster forest resilience to global changes. Forest Ecosystem 6:21

Michaelian M, Hogg EH, Hall RJ, Arsenault E (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Glob Chang Biol 17:2084–2094

Millar CL, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: Managing in the face of uncertainty. Ecol Appl 17:2145–2151

Mitchell PJ, O'Grady AP, Hayes KR, Pinkard EA (2014) Exposure of trees to drought-induced die-off is defined by a common climatic threshold across different vegetation types. Ecol Evol 4:1088–1101

Mori AS, Lertzman KP, Gustafsson L (2017) Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. J Appl Ecol 54:12–27

Moritz MA, Parisien MA, Barllori E, Krawchuk v DJ, Ganz DJ, Hayhoe K (2012) Climate change and disruptions to global fire activity. Ecosphere 3:article:49

Newbery DM, Lingenfelder M (2008) Plurality of tree species responses to drought perturbation in Bornean tropical rain forest. In: Valk AGVD (ed) Forest Ecology. Springer, pp 147–167

Noss RG, Franklin JF, Baker WL, Schoennagel T, Moyle PB (2006) Managing fire-prone forests in the western United States. Front Ecol Environ 4:481–487

Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. Ecosystems 1:535–545

Pausas JG, Blade C, Valdecantos A, Seva JP, Fuentes D, Alloza JA, Vilagrosa A, Bautista S, Cortina J, Vallejo R (2004) Pines and oaks in the restoration of Mediterranean landscapes of Spain: New perspectives for an old practice—a review. Plant Ecol 171:209–220

Phillips OL et al (2009) Drought sensitivity of the Amazon rainforest. Science 323:1344–1347

Pile LS, Meyer MD, Rojas R, Roe O, Smith MT (2019) Drought impacts and compounding mortality on forest rees in the Southern Sierra Nevada. Forests 10:237. https://doi.org/10.3390/f10030237

Ponce Campos GE et al (2013) Ecosystem resilience despite large-scale altered hydroclimatic conditions. Nature 494:349–352

Raffa W, Kenneth F, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Kolb TE (2015) Responses of tree-killing bark beetles to a changing climate. In: Björkman C, Niemelä P (eds) Climate change and insect pests, CABI Climate Change Series 7, pp 173–201

Redmond MD, Cobb NS, Clifford MJ, Barger NN (2015) Woodland recovery following drought-induced tree mortality across an environmental stress gradient. Glob Chang Biol 21:3685–3695

Rietkerk M, Dekker SC, de Ruiter P, van de Koppel J (2004) Self-Organized Patchiness and Catastrophic Shifts in Ecosystems. Science 305:1926–1929

Rigling A et al (2013) Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Glob Chang Biol 19:229–240

Rogers BM, Solvik K, Hogg EH, Ju J, Masek JG, Michaelian M, Berner LT, Goetz SJ (2018) Detecting early warning signals of tree mortality in boreal North America using multiscale satellite data. Glob Chang Biol 24:2284–2304

Rull V, Montoya E, Nogué S, Vegas-Vilarrúbia T, Safont E (2013) Ecological palaeoecology in the neotropical Gran Sabana region: Long-term records of vegetation dynamics as a basis for ecological hypothesis testing. Persp Plant Ecol Evol Syst 15:338–359

Sánchez-Pinillos M, Leduc L, Ameztegui A, Kneeshaw D, Lloret F, Coll L (2019) Resistance, resilience or change: post-disturbance dynamics of boreal forests after insect outbreaks. Ecosystems 22:886–1901

Savage M, Mast JN (2005) How resilient are southwestern ponderosa pine forests after crown fires? Can J For Res 35:967–977

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648–656

Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter S, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G (2009) Early-warning signals for critical transitions. Nature 461:53–59

Scheffer M, Carpenter SR, Dakos V, van Nes EH (2015) Generic indicators of ecological resilience: inferring the change of a critical transition. Annu Rev Ecol Evol Syst 46:145–167

Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. Ecol Lett 14:397–406

Schwantes AM, Swenson JJ, González-Roglich M, Johnson DM, Domec JC, Jackson RB (2017) Measuring canopy loss and climatic thresholds from an extreme drought along a 5-fold precipitation gradient across Texas. Glob Chang Biol 23:5120–5135

Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA (2016) Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J Appl Ecol 53:120–129

Seidl R et al (2017) Forest disturbances under climate change. Nat Clim Chan 7:395–402

Serra-Diaz JM, Keenan TF, Ninyerola M, Sabaté S, Gracia C, Lloret F (2013) Geographical patterns of congruence and incongruence between correlative species distribution models and a process-based ecophysiological growth mode. J Biogeogr 40:1928–1938

Serra-Diaz JM et al (2018) Disequilibrium of fire-prone forests sets the stage for a rapid decline in conifer dominance during the 21st century. Sci Rep 8:6749

Shuman BN, Newby P, Donnelly JP (2009) Abrupt climate change as an important agent of ecological change in the Northeast U.S. throughout the past 15,000 years. Quat Sci Rev 28:1693–1709

Singer JS, Turnbull R, Foster M, Bettigole C, Frey BR, Downey MC, Covey KR, Ashton MS (2019) Sudden Aspen decline: a review of pattern and process in a changing climate. Forests 10:671. https://doi.org/10.3390/f10080671

Smith JM, Paritsis J, Veblen TT, Chapman TB (2015) Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013. For Ecol Manag 341:8–17

Sohn JA, Saha S, Bauhus J (2016) Potential of forest thinning to mitigate drought stress: a meta-analysis. For Ecol Manag 380:261–273

Sommerfeld A et al (2018) Patterns and drivers of recent disturbances across the temperate forest biome. Nat Commun 9:4355

Sousa-Silva R, Verheyen K, Ponette Q, Bay E, Sioen G, Titeux H, van de Peer T, van Meerbeek K, Muys B (2018) Tree diversity mitigates defoliation after a drought-induced tipping point. Glob Chang Biol 24:4304–4315

Stephenson NL, Das AJ, Ampersee NJ, Bulaon BM, Yee JL (2018) Which trees die during drought? The key role of insect host-tree selection. J Ecol 107:2383–2401

Swetnam TW, Betancour JL (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. J Clim 11:3128–3147

Swindles GT et al (2017) Ecosystem state shifts during long-term development of an Amazonian peatland. Glob Chang Biol 24:738–757

Tafangenyasha C (1997) Tree loss in the Gonarezhou National Park (Zimbabwe) between 1970 and 1983. J Environ Manag 49:355–366

Tinner W, Kaltenrieder P (2005) Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. J Ecol 93:936–947

Tinner W, Lotter AF (2001) Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States (2003–2012). Geology 29:551–554

Torrescano-Valle N, Islebe GA (2015) Holocene paleoecology, climate history and human influence in the southwestern Yucatan Peninsula. Rev Palaeobot Palynol 217:1–8

Trenberth KE et al (2014) Global warming and changes in drought. Nat Clim Chan 4:17–22

Trichon V, Hiernaux P, Walcker R, Mougin E (2018) The persistent decline of patterned woody vegetation: the tiger bush in the context of the regional Sahel greening trend. Glob Chang Biol 24:2633–2648

Turner MG (2010) Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849

Usbeck T, Wohlgemuth T, Dobbertin M, Bürgi A, Pfister C, Rebetez M (2010) Increasing storm damage to forests in Switzerland from 1858 to 2007. Agric For Meteorol 150:47–55

Verbesselt J, Umlauf N, Hirota M, Holmgren M, Van Nes EH, Herold M, Zeileis A, Schffer M (2016) Remotely sensed resilience of tropical forests. Nat Clim Chan 6:1028–1032

Vicente-Serrano SM, Begueria S, Lopez-Moreno JI (2010) A Multiscalar Drought Index Sensitive to Global Warming: the Standardized Precipitation Evapotranspiration Index. J Clim 23:1696–1718

Vilà-Cabrera A, Martínez-Vilalta J, Vayreda J, Retana J (2011) Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula. Ecol Appl 21:1162–1172

Villalba R, Veblen TT (1998) Influences of large-scale climatic variability on episodic tree mortality in Northern Patagonia. Ecology 79:2624–2640

Williams JW, Shuman B, Bartlein PJ, Diffenbaugh NS, Webb IIIT (2010) Rapid, time-transgressive, and variable responses to early Holocene midcontinental drying in North America. Geology 38:135–138

Williams JW, Blois JJ, Shuman BN (2011) Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. J Ecol 99:664–677

Xiong YM, D'Atri JJ, Fu SL, Xia HP, Seastedt TR (2011) Rapid soil organic matter loss from forest dieback in a subalpine coniferous ecosystem. Soil Biol Biochem 43:2450–2456

Xu C, Liu H, Anenkhonov OA, Korolyuk AY, Sandanov DV, Balsanova LD, Naidanov BB, Wu X (2017) Long-term forest resilience to climate change indicated by mortality, regeneration, and growth in semiarid southern Siberia. Glob Chang Biol 23:2370–2382

Yang G, Wagg C, Veresoglou SD, Hempel S, Rillig MC (2018) How soil biota drive ecosystem stability. Trends Plant Sci 23:1057–1067

Zeeman BJ, Lunt ID, Morgan JW (2014) Can severe drought reverse woody plant encroachment in a temperate Australian woodland? J Veg Sci 25:928–936

Zhang T, Niinemets Ü, Sheffield J, Lichstein JW (2018) Shifts in tree functional composition amplify the response of forest biomass to climate. Nature 556:99–102

Zhou G et al (2014) Substantial reorganization of China's tropical and subtropical forests: Based on the permanent plots. Glob Chang Biol 20:240–250

Zuleta D, Duque A, Cardenas D, Muller-Landau HC, Davies SJ (2017) Drought-induced mortality patterns and rapid biomass recovery in a terra firme forest in the Colombian Amazon. Ecology 98:2538–2546

8

Extreme Events Trigger Terrestrial and Marine Ecosystem Collapses in the Southwestern USA and Southwestern Australia

Katinka X. Ruthrof, Joseph B. Fontaine, David D. Breshears,
Jason P. Field, and Craig D. Allen

Abstract

We outline the multiple, cross-scale, and complex consequences of terrestrial and marine ecosystem heatwaves in two regions on opposite sides of the planet: the southwestern USA and southwestern Australia, both encompassing Global Biodiversity Hotspots, and where ecosystem collapses or features of it have occurred in the past two decades. We highlight ecosystem shifts that have clearly demonstrated a substantial change from a baseline state over time, although not necessarily across their entire distribution, with evidence of collapse at local scales. Responses to temperature extremes, such as heatwaves, encompass

---

K. X. Ruthrof (✉)
Environmental and Conservation Sciences, Murdoch University, Murdoch, WA, Australia

Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia
e-mail: k.ruthrof@murdoch.edu.au

J. B. Fontaine
Environmental and Conservation Sciences, Murdoch University, Murdoch, WA, Australia
e-mail: j.fontaine@murdoch.edu.au

D. D. Breshears
School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA

Department of Ecology and Evolutionary Biology via joint appointment, University of Arizona, Tucson, AZ, USA
e-mail: daveb@arizona.edu

J. P. Field
School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA
e-mail: jpfield@arizona.edu

C. D. Allen
U.S. Geological Survey, Fort Collins Science Centre, New Mexico Landscapes Field Station, Los Alamos, NM, USA

© Springer Nature Switzerland AG 2021
J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_8

processes at all scales, including *population level* (e.g. altered demography such as survival, recruitment, and fecundity, together resulting in structural changes), *community level* (e.g. species compositional shifts), and *ecosystem level* (e.g. carbon loss), as well as physical properties altered by vegetation loss (e.g. microclimate, fire behaviour on land). These changes impact all trophic levels with foundational species losses (such as seagrasses, kelp, and trees), flowing through to vertebrates (such as sea turtles, penguins, and cockatoos). Where extensive collapse has occurred, shifts in microclimate could affect important biosphere-to-atmosphere feedbacks including fluxes of energy, carbon, and water. Such extensive changes usually do not occur in isolation and frequently interact with other disturbance processes such as fire, storms, pathogen and pest outbreaks, and anthropogenic stressors. Interactions may alter the likelihood, extent, or severity of subsequent disturbances (linked disturbances) as well as condition the ecological response and recovery (compound disturbances). In addition, if ecosystem collapse is extensive enough (e.g. tree die-off), those changes also can impact climate and ecosystems elsewhere via ecoclimate teleconnections. Increasing rates of climatic extremes will drive a host of direct and indirect feedbacks certain to produce large-scale shifts in ecological functioning at unprecedented rates. Understanding how, why, and where these shifts will occur will be critical for effective ecosystem management and climate change mitigation.

8.1 Introduction

We are increasingly witnessing unprecedented abrupt ecosystem changes across the globe, in both marine and terrestrial systems, across trophic levels and at multiple scales, including well-documented events such as coral bleaching and forest die-off (Hughes et al. 2017; Allen et al. 2010; Ruthrof et al. 2018). These dynamics with many characteristics of ecosystem collapses can occur quickly (months to seasons) and can affect thousands of hectares and millions of individual organisms. While the loss of key species is often captured by the media (e.g. coral bleaching, mangrove loss, fruit bat mass mortality events) and is useful for highlighting examples and losses of charismatic or iconic species, an understanding of the broader consequences is often lacking. Broader implications include changes in ecological functioning and the services they provide. Heatwave events are becoming more frequent and longer-lasting (Meehl and Tebaldi 2004; Oliver et al. 2018), which could lead to large-scale ecological transitions and shifts in planetary functioning—land surface to atmospheric feedbacks, including fluxes of energy, carbon cycling, nutrient cycling, water balance, evaporation, and partitioning of evapotranspiration.

The underlying factors involved in ecosystems reaching critical thresholds of survival, or inability to recover, or indeed transition to alternative states, include climate change-driven, long-term trends and extreme events, management legacies, and interacting effects. Indirect impacts from collapse events can include changes to pests and pathogen populations (Seaton et al. 2015), changes in fungal populations (Hopkins et al. 2018), and shifts in fauna dependent on vulnerable communities (Prugh et al. 2018). Indirect impacts could also result in the loss of key species due to compromised demographic performance as climate events interact with fire frequency (Enright et al. 2015) or altered fire seasonality (Miller et al. 2019, 2020). We may have now reached an important point in time where changes in climate patterns are increasingly affecting ecosystems that have undergone external pressure or disturbances from land use and climate change. The emergence of more frequent and longer-lasting climatic extremes in the coming decades (IPCC 2018) can produce large-scale and abrupt shifts in ecological functioning and persistence at historically unprecedented rates. At present, we have already observed the local or regional loss of iconic species such as fruit bats in eastern Australia (Welbergen et al. 2014), mangroves in Australia's north (Duke et al. 2017), or giant sequoias (*Sequoiadendron giganteum*) in California (Stephenson et al. 2018).

Here we outline the multiple, cross-scale, and complex consequences of heatwave associated with examples of large-scale ecosystem collapses (with temporary or permanent consequences) in two regions on different continents and hemispheres—the southwestern USA and southwestern Australia. They contain Global Biodiversity Hotspots (Myers et al. 2000) and are comprised of structurally similar ecosystem types and include Mediterranean-type forests, woodlands and shrublands, and temperate marine systems.

8.1.1 Progressively Intense Ecological Stresses: From Drought to Warming to Heatwaves

Large-scale ecosystem changes are often driven by extreme events, and here we focus specifically on heatwaves and drought, individually or in combination with one another. These extreme events can impact both terrestrial and marine ecosystems and their biota (Kala et al. 2016; Ruthrof et al. 2018). For terrestrial ecosystems, droughts are one of the key drivers. Drought can drive rapid, landscape scale changes in ecotones (Allen and Breshears 1998). More importantly, these changes can be exacerbated by warmer temperatures accompanying drought—'global change-type drought' or 'hotter drought' (Breshears et al. 2005b; Allen et al. 2015). These hotter drought events have had impacts on forests globally (Allen et al. 2010, 2015; IPCC 2014; Hartmann et al. 2018). However, protracted higher temperatures alone are not the only temperature-related driver. Some recent ecological changes have been tied to heatwaves, i.e. shorter and acute high-temperature periods. For example, tree mortality in southwestern Australia has been linked to heatwaves (Matusick et al. 2013; Ruthrof et al. 2015; Steel et al. 2019). In the austral summer of 2010–2011, a number of heatwave events followed a dry winter, triggering mass defoliation of patches of forest canopy in southwestern Australia, with long-lasting consequences for forest structure (Matusick et al. 2016; Steel et al. 2019). Additionally, legacy effects of prior drought appear to exacerbate tree mortality and crown die-off in response to acute events such as the 2010–2011 heatwaves in southwestern Australia (Matusick et al. 2018). These pulsed heatwave effects, which can occur atop chronic drought, have affected multiple terrestrial plant species at subcontinental scales, for example, forest tree species *Eucalyptus marginata* and *Corymbia calophylla*, woodland tree species *Eucalyptus gomphocephala* and *Banksia attenuata*, and subshrub species *Beaufortia elegans* and *Eremaea beaufortioides* (Ruthrof et al. 2018). Additionally, fauna can simultaneously be impacted, as evident in the recent sudden death of 23,000 spectacled flying foxes (*Pteropus conspicillatus*, approximately one-third of the population) in North Queensland when temperatures exceeded 42 °C in November 2018, and an additional 10,000 bats of another species (black flying foxes, *Pteropus alecto*) also succumbed to the heatwave during the same time (BBC: *How one heatwave killed 'a third' of a bat species in Australia*).

Heatwaves also affect marine ecosystems, and global events have caused extensive coral bleaching over the past 30 years (Goreau et al. 2000; Berkelmans et al. 2004; Hughes et al. 2018a, b). For example, in the Great Barrier Reef, less than 9% of scored reefs showed *no* bleaching in 2016, compared to 42% in 2002 and 44% in 1998 (Hughes et al. 2018b). Additionally, other marine heatwave impacts include reduced cover of kelp and encrusting coralline algae, and tropicalization of fish communities (Wernberg et al. 2013; Wernberg 2021; Ruthrof et al. 2018). In summary, both terrestrial and marine systems are sensitive to temperature changes, both for gradual, chronic higher temperatures, especially when accompanying drought for terrestrial ecosystems, and for sudden, acute heatwaves, with or without concurrent drought.

Heatwave events are increasing in frequency and duration on land and in marine systems (Meehl and Tebaldi 2004; Oliver et al. 2018) (Fig. 8.1). The terrestrial land area affected by heatwaves globally is expected to quadruple by 2040 (Coumou and Robinson 2013). Increased heating may not cause droughts per se, but when droughts do occur, they will likely set in more quickly and be more intensive (Trenberth et al. 2014). Both global aridity changes up to 2010 and model predictions suggest widespread and intensive droughts will occur in the next 30–90 years over many land areas (Dai 2013). The meteorological thresholds (e.g. vapour pressure deficit, temperature, and precipitation) correlated with record drought that killed ~10% of all tree canopy cover across Texas are projected by climate models to become at least more regularly occurring by the end of this century (Schwantes et al. 2017). In marine ecosystems, global average marine heatwaves have increased in frequency by 34% and duration by 17%, resulting in a 54% increase in annual marine heatwave days globally (Oliver et al. 2018).

8.1.2 Legacy Effects, Disturbance Interactions, and Order of Events

Events such as heatwaves and droughts do not occur in isolation. Increasingly, science and management communities recognize the need to address interacting disturbances (region-specific and general disturbance interactions; Allen 2007; Buma et al. 2013; Enright et al. 2014). Spanning marine and terrestrial

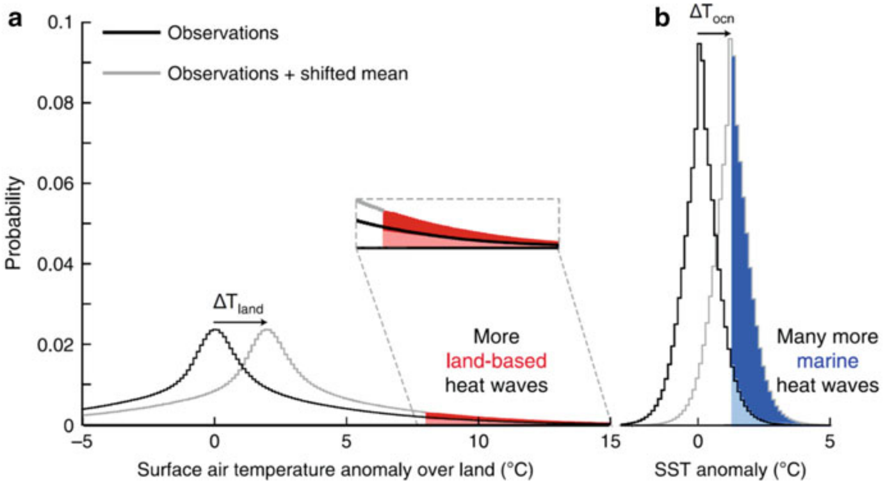


Fig. 8.1 The effect of a shift towards a warmer climate on the probability of land-based and marine heatwaves and hence more land-based heatwaves and many more marine heatwaves. (**a**) The observed distribution of the linearly detrended and deseasonalized local daily surface air temperature anomalies over land and (**b**) the observed distribution of local daily sea surface temperature anomalies (modified from Frölicher and Laufkötter (2018)). A rightward shift in the mean necessarily increases the likelihood and magnitude of heatwaves by historic standards

environments, climate change-driven events (e.g. coral bleaching and forest die-off) are occurring at an increasing frequency and extent which increases the likelihood they coincide with other ecosystem disturbances such as fire, cyclones, and other natural and anthropogenic disturbances. Interactions among these events often produce ecological 'surprises' (Paine et al. 1998) and may lead to altered ecosystem states, loss of foundational species, and impaired ecosystem services (Miao et al. 2009; Silverio et al. 2019; Walden et al. 2019). Predicting and anticipating these interactions is a rapidly developing area of research and management where understanding disturbance sequence, as well as distinguishing between event probability and ecological impact, becomes crucial. Our toolbox for management options needs to adapt rapidly (Cobb et al. 2017).

Interactions may alter the likelihood, extent, or severity of subsequent disturbances (linked disturbances) as well as alter the ecological response and recovery (compound disturbances). For instance, in terrestrial ecosystems, Matusick et al. (2018) showed that the probability of tree mortality and crown die-off increased following an acute heatwave event compounded by a long-term chronic drought. Linked disturbances are illustrated by cases where drought-induced forest die-off increased fire potentials via elevated fuel loads (Ruthrof et al. 2016), and fire behaviour was more intense when fire followed a defoliating hailstorm (Gower et al. 2015). Such cases could readily also manifest as compound disturbances if the first event (drought or hailstorm) impacts postfire survival, regrowth, or regeneration of vegetation via, for example, elevated mortality of particular size classes or loss of seed stores (e.g. case studies (Buma et al. 2013; Buma 2015; Gower et al. 2015). This was illustrated in a case where hail damaged trees and plants had lower resprouting (trees) or reduced recruitment (serotinous shrubs) when a fire followed an intense, defoliating hailstorm, thereby potentially altering species composition and structure (Gower et al. 2015). Similarly, evidence and a conceptual model show how the interplay of fire with a warming and drying climate depresses population persistence in fire-prone shrublands of Western Australia (Enright et al. 2015).

Human activities beyond climate change also have elevated the likelihood of interactive disturbances. For example, in forest ecosystems legacies of fire exclusion or harvest may have impaired capacity to respond to drought or heatwaves, thereby representing a compound disturbance (Johnstone et al. 2016). Historic fire suppression (post-1910) and two regionally wet climate periods (1905–1922 and 1978–1995) in the southwestern USA have facilitated widespread build-up of forest densities and fuel loads. With the recurrence of drought conditions and warmer temperatures since the late 1990s, the overgrown forests in the southwestern USA have been subject to wildfires and tree mortality episodes of unprecedented extent and severity and shifts in vegetation patterns (Allen 2007; Allen et al. 2014). Further examples of human-mediated disturbance interactions abound. Grassy weed invasions through the western USA and Mediterranean-type climate regions globally have altered fire frequencies (D'Antonio and Vitousek 1992; Fusco et al. 2019), often with increased frequencies exceeding the capacity of indigenous plant species to regenerate (i.e. sagebrush *Artemisa tridentata* in western USA). Similarly, elevated rates of intentional burning (prescribed fire), or altered fire seasonality (Miller et al. 2019) may also drive impacts when in conjunction with drought, weeds, or other climatic events (Brooks et al. 2004; Gower et al. 2015; Ruthrof et al. 2016). Major uncertainties exist regarding the effects of disturbance sequence or the time required between events to ensure resilience (though see Enright (2014) for evidence of fire-fire resilience) and remain an important area for future investigation.

If extensive enough, terrestrial vegetation change is expected to alter not only local climate but also climate teleconnections and thereby vegetation elsewhere, a process known as an ecoclimate teleconnection (Stark et al. 2016). For example, simulated complete tree die-off in various regions of the USA impacts climate and gross primary productivity in disparate regions (Swann et al. 2018), and wholesale mortality of trees across Western North America reduces gross primary productivity across Siberia (Garcia et al. 2016). The study by Swann et al. (2018) simulated die-off events from 13 of the most forested regions in the USA and discovered that, for instance, die-off in the Pacific Southwest had a large and widespread negative effect on forest productivity in midwestern and eastern USA.

Similar to some of the examples above for terrestrial ecosystems, interacting factors also occur in marine ecosystems. For example, following the marine heatwave in 2011 in Western Australia's Shark Bay, flooding directly afterwards injected sediments into the marine system causing high turbidity which, on top of heat stress, led to widespread and drastic defoliation in a temperate foundation species of seagrass (*Amphibolis antarctica*; Fraser et al. 2014). High sea surface temperatures (SSTs) increased the seagrass demand for carbon, which could not be met through photosynthesis due to the turbid floodwaters, which reduced light availability and which resulted in plants having a negative carbon balance (Fraser et al. 2014). Thus, disturbances such as extreme climatic events can interact and become synergistic drivers causing complex and severe ecological responses.

8.1.3 Ecosystem Collapses in Southwestern Australia and the USA

Among the regions that already have experienced consequences of extreme climatic events, southwestern Australia and the southwestern USA stand out. Both have experienced marine and terrestrial heatwave events and their similar climates (largely Mediterranean) and climate change predictions (warming and drying of the terrestrial portions make them ideal to compare). Some of the best-studied examples of ecosystem collapses to extreme climatic events include those profiled elsewhere in this book, and we provide a few examples below, illustrating a breadth of impacts across southwestern Australia and southwestern USA (Table 8.1). We focus on examples that have demonstrated a quantitative and substantial change from a baseline state over time, and not necessarily across the entire distribution, but have clear evidence of collapse at local scale. Both regions have experienced extreme climate events straddling land and sea, as well as inland climate extremes and both contain Global Biodiversity Hotspots (Myers et al. 2000).

8.2 Southwestern USA Case Study

8.2.1 Terrestrial Drivers and Ecosystem Responses in the Southwestern USA

Climate across the southwestern USA region ranges from Mediterranean along the coast (dry to wet from South to North) and semi-arid to arid inland due to the rain shadows generated by large N-S mountain ranges (Sierra Nevada, Cascades). Higher-elevation portions of the interior west are wetter and support conifer-dominated forests. Projections of climate change suggest that the southwestern USA will become warmer everywhere and drier throughout via reduced winter rainfall (Diffenbaugh and Field 2013). Extreme drought impacted the Californian region in the last decade, with the 2012–2014 period being the driest in 1200 years and coincident with record high temperatures (Griffin and Anchukaitis 2014) (Fig. 8.2a). Between 1950 and 2020, inland urban areas of Los Angeles County have shown a strong increasing trend in heatwave frequency, duration, and intensity (Hulley et al. 2020). The 2012–2014 drought was nearly a one in 10,000-year event, while the 2012–2015 drought had an almost incalculable return period and is completely without known precedent (Robeson 2015). Although precipitation is the key driver of drought variability, anthropogenic warming has substantially increased the overall likelihood of extreme droughts in California (Williams et al. 2015).

Table 8.1 Summary of some of the effects of hotter conditions, with and without drought, in southwestern Australia and southwestern USA

	Terrestrial heatwave/drought		Marine heatwave	
Trophic level	Southwestern Australia	Southwestern USA	Southwestern Australia	Southwestern USA
1	Tree mortality (Matusick et al. 2013; Challis et al. 2016; Bader et al. 2014) Canopy die-off (Matusick et al. 2012; Matusick et al. 2013; Matusick et al. 2016; Ruthrof et al. 2015) Shrub mortality (Ruthrof et al. 2018) Rhizosphere fungal community shifts (Hopkins et al. 2018) Changes in fuels and increases in fire potentials (Ruthrof et al. 2016) Changes in carbon dynamics (Walden et al. 2019) Midstorey die-off (Steel et al. 2019)	Tree water stress (Williams et al. 2013; Asner et al. 2016) Tree mortality (Breshears et al. 2005a; Young et al. 2017; Fettig et al. 2019) Foliage dieback in giant sequoias (Stephenson et al. 2018) Decreased abundance in Yellow pincushions and Arabian schismus (Prugh et al. 2018) Increased abundance of a native forb, red maids (Prugh et al. 2018) Increased high severity fire activity (Williams et al. 2013; Allen 2014)	Kelp cover decrease, encrusting coralline algae decrease (Wernberg et al. 2013) Turf forming algae cover increase (Wernberg et al. 2013) Coral bleaching and loss (Moore et al. 2012) *Acropora*/*Montipora* coral cover decrease (Depczynski et al. 2013) Turf forming algae cover increase (Smale and Wernberg 2013) Encrusting coralline and non-coralline algae cover decrease (Smale and Wernberg 2013) Massive carbon loss following seagrass loss (Arias-Ortiz et al. 2018)	Copepod species not previously been (or only rarely) observed (Leising et al. 2015) Harmful algal bloom (Ryan et al. 2017)
2	Wood-boring insect outbreak (Seaton et al. 2015)	Mountain pine beetle and western pine beetle colonization (Fettig et al. 2019) Decreased abundance in Wind scorpions, and Spiders (Prugh et al. 2018)	Tropicalization of fish communities (Wernberg et al. 2013) Mass fish kills and lobster behaviour change (Pearce et al. 2011)	High abundances of northern anchovy and sardine larvae and previously unrecorded fish species off Washington and Oregon (Leising et al. 2015)

(continued)

Table 8.1 (continued)

	Terrestrial heatwave/drought		Marine heatwave	
Trophic level	Southwestern Australia	Southwestern USA	Southwestern Australia	Southwestern USA
		Increase abundance of six beetle and an ant species (Prugh et al. 2018)	Green turtle health decline (Thomson et al. 2015) Invasive tropical mussel spawning event (McDonald 2012)	Salmon distribution change (Bond et al. 2015) Tropical species of pigmy killer whales seen much further north (Kintisch 2015) Starfish mortality (Greene 2016)
3	Cockatoo abundance reduction at roost sites (Byrne et al. 2015)	Bird species decline with drought-induced tree mortality (Roberts et al. 2019) Decreased abundance of the California ground squirrel, the San Joaquin kit fox, the giant Kangaroo rat, Western meadowlark, barn owl, blunt-nosed leopard lizard, (Prugh et al. 2018) Increased abundance of a reptile, the common side-blotched lizard, two birds: the killdeer, the greater roadrunner and a rodent, the short-nosed kangaroo rat (Prugh et al. 2018)	Penguin breeding success reduction (Cannell et al. 2012)	Seabird mortality (Jones et al. 2018) Sea Lion mortality (Greene 2016). Decreased weights and growth rates in pups (Leising et al. 2015)

In California, a Global Biodiversity Hotspot, approximately 10.6 million ha of forest containing up to 888 million large trees, experienced measurable loss in canopy water content during drought in 2012–2015, and severe canopy water loss of more than 30% occurred over 1 million ha, affecting up to 58 million large trees (Asner et al. 2016). Estimates indicate as many as 129 million trees died from

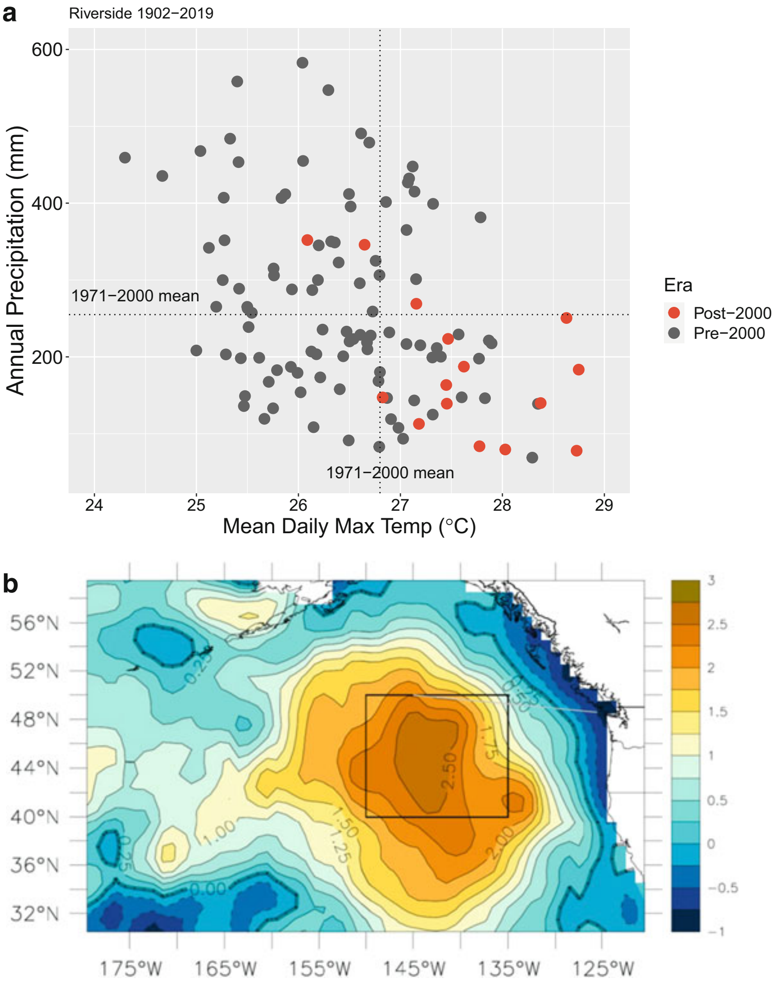


Fig. 8.2 (**a**) Annual precipitation (mm) and mean daily maximum temperatures (°C) in Riverside, California, 1902–2019 (NOAA dataset), (**b**) sea surface temperature anomalies (°C) in the NE Pacific Ocean for February 2014. Anomalies are calculated relative to the mean from 1981 to 2010. (Modified from Bond et al. (2015))

drought and insects in the drought of 2012–2016 in the Sierra Nevada, California, alone (North et al. 2019).

A wide range of other taxa also responded to drought and heat conditions in California between 2012 and 2015. Some 85 species (25%) were classified as losers (decreased in abundance during and following the heat conditions), 12 (4%) were winners (increased in abundance), and 239 (71%) did not have a significant response to drought at the $\alpha = 0.05$ level (Prugh et al. 2018). Short-term water deficits resulted in plant mortality, and longer-term deficits affected carnivorous animals.

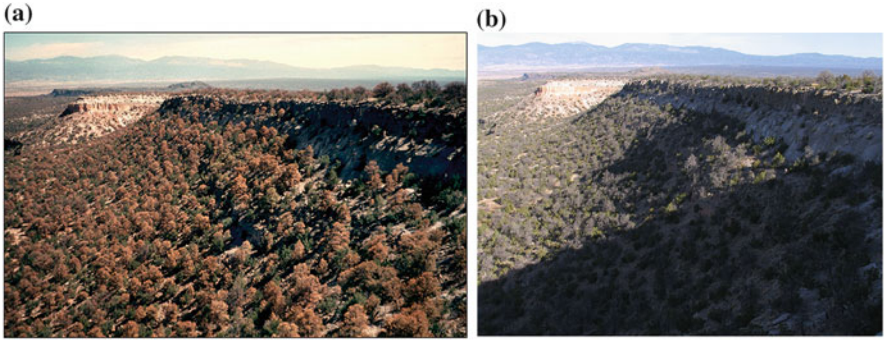


Fig. 8.3 Drought- and heat-induced woodland die-off in pinyon-juniper woodland in the Jemez Mountains of northern New Mexico, USA. Photos showing (**a**) an oblique landscape view of dying *Pinus edulis*, October 2002 (Photo credit: C.D. Allen); (**b**) repeat photo in March 2006 showing grey skeletons of the dead *Pinus edulis* trees, with surviving green *Juniperus monosperma*. (Photo credit: C.D. Allen)

Cross-trophic scale interactions are also important. For example, drought has shown to indirectly promote the long-term persistence of locally rare species by stressing dominant species throughout the food web (Prugh et al. 2018).

Prior to this recent event, the first documentation of regional-scale tree die-off from hotter drought quantified regional-scale die-off across southwestern North American woodlands in 2002–2003 in response to drought and bark beetle infestations (Breshears et al. 2005a). After 15 months of depleted soil water content, >90% of the dominant, overstory tree species (*Pinus edulis*) died. The die-off was reflected in changes in a remotely sensed index of vegetation greenness (Normalized Difference Vegetation Index, NDVI) across the region, extending over 12,000 km^2. The study suggests the large potential for such die-off occurrences to be more severe and extensive under future global change-type drought (drought under warmer conditions, Breshears et al. 2005a). Ecotone shifts can result from regional-scale tree die-off (Fig. 8.3). A first contemporary high-resolution documentation of a shift from drought-induced, sudden tree die-off revealed a rapid landscape scale shift of a woody ecotone in northern New Mexico in the 1950s, where the ecotone between semi-arid ponderosa pine forest and pinyon-juniper woodland shifted by 2 km or more and within <5 years through the mortality of ponderosa pine in response to a severe drought (Allen and Breshears 1998). Importantly, this relatively rapid shift in composition has persisted for 40 years. Flow-on effects included fragmentation (the number of forest fragments increased from 20 to 42 between 1954 and 1963) and erosion rates, which remain high at ~4 mm/yr. (Allen and Breshears 1998).

8.2.2 Marine Drivers and Ecosystem Responses in Southwestern USA

In the marine system off the coast of the southwestern USA, an unusual and extensive mass of warm sea surface temperature (SST) in the Pacific Ocean off the west coast of North America is referred to as 'The Blob' (Bond et al. 2015) (Fig. 8.2b). Maximum SSTs of >6 °C were recorded off southern California (Frölicher and Laufkötter 2018). It was first reported in 2013 and continued to spread through 2016 in three distinct phases (Kintisch 2015). The largest temperature anomalies were the greatest observed in the region for the month of February since the 1980s and possibly as early as 1900 (Bond et al. 2015). Underlying drivers included strongly positive anomalies in sea level pressure (SLP), which suppressed the loss of heat from the ocean to the atmosphere and lead to weak cold advection in the upper ocean (Bond et al. 2015). There are no studies available that have explored how much more probable the occurrence of The Blob was made by climate change. However, its occurrence is consistent with long-term increase of the frequency and intensity of marine heatwaves and offers an opportunity to study the impacts on the marine ecosystem (Kintisch 2015).

'The Blob' in the Pacific Ocean off the west coast of North America has been associated with a wide range of ecological impacts and 'rearranging food webs', including altering nutrient movements and hence phytoplankton blooms, a drop in copepod populations, mortality of sea lions (Greene 2016), starvation of the zooplanktivorous seabird Cassin's Auklets (Jones et al. 2018), starfish mortality (Greene 2016), and a harmful algal bloom (Ryan et al. 2017). Warm water species were sighted further north in 2013–2015 than ever before, including birds, fish, invertebrates, marine mammals, and reptiles (Cavole et al. 2016). In addition, warm water anomaly in the NE Pacific led to the closing of commercial and recreational fisheries due to the harmful algal bloom that occurred and resulted in millions of dollars in losses (Cavole et al. 2016). Higher water temperatures could also increase the risk of invasive species. In Bodega Bay, California, for instance, introduced species were shown to tolerate higher temperatures than native species, which led the authors to suggest that increasing temperatures associated with climate change could disproportionately negatively affect native species (Sorte et al. 2010).

Marine drivers of abrupt ecosystem changes are also related to terrestrial drivers of change. More specifically, 'The Blob' is thought to affect weather in the continental Pacific Northwest, which is downwind. The extra mixed layer heat of The Blob persisted over the summer of 2014 and may have contributed significantly to the unusually warm summer (and in some locations record high temperatures) observed in the continental Pacific Northwest, specifically in Washington state (Bond et al. 2015). The Blob also likely contributed to thunderstorms and lightning activity and one of the biggest wildfires in the Washington State's history during the summer of 2014 (Kintisch 2015).

8.3 Southwestern Australian Case Study

8.3.1 Terrestrial Drivers and Ecosystem Responses in Southwestern Australia

The southwestern portion of Australia has experienced a chronic background temperature increase of ~1 °C over the last 30 years (Bates et al. 2008; Andrys et al. 2017). There has also been a chronic, long-term average decline in rainfall of close to 14% for the period 1975–2004, compared with the mid-1900s-1974 (Bates et al. 2008) (Fig. 8.3a). The trend in total annual rainfall for 1970–2019 for much of the southwestern portion of Western Australia is a reduction of 10–40 mm per decade (BOM 2020). In addition to this chronic warming and drying, an acute drought in 2010 (40–50% below average annual rainfall), and a series of heatwave days occurred, the latter with the highest number of days on record since 1960 (Ruthrof et al. 2018) (53 days >35 °C) occurred in the summer of 2010-2011 (Fig. 8.4a, b). The terrestrial maximum temperatures in the region were 2 °C higher than the long-term March average over the period 1971–2000 baseline. The number of heatwave days in 2011 was the highest, and the Standardized Precipitation Evapotranspiration Index (SPEI) was the lowest on record since 1960 (Ruthrof et al. 2018). These can be viewed as *stacked* meteorological disturbances: the combination of (1) a long-term (chronic) decline in rainfall and gradual increase in average temperature; (2) a severe drought in 1 year, 2010 (acute event); and (3) heatwaves in the summer of 2010-2011, resulted in die-off events in multiple forest and woodland types, across many taxa, thus, making the stacked *meteorological* disturbance highly *ecologically* relevant.

A wide range of terrestrial taxa responded to the heatwave event in 2011 (Ruthrof et al. 2018). The ecological effects were abrupt, synchronous, and included mortality, demographic shifts, and altered species distributions such as tree die-off, reduced counts of an endangered terrestrial bird species, a significant reduction in breeding success in marine penguins, and outbreaks of terrestrial wood-boring insects (Ruthrof et al. 2018). For example, canopy die-off occurred across a range of forest and woodland types, including *Eucalyptus marginata*, *Corymbia calophylla* (Matusick et al. 2013; Hoffmann et al. 2019, Fig. 8.5), *Banksia attenuata*, *Banksia menziesii* (Bader et al. 2014; Challis et al. 2016), and *Eucalyptus gomphocephala* (Matusick et al. 2012). Within drought-affected patches of the Northern Jarrah Forest containing *E. marginata* and *C. calophylla*, 74% of measured stems (≥1 cm DBH) had dying or recently killed crowns, and stem mortality was 26% (Matusick et al. 2013). Projections at the time suggested that over 16,000 ha of the Northern Jarrah Forest had experienced die-off. Die-off sites were larger and more densely clustered in xeric areas (Andrew et al. 2016) with shallower soils and lower water holding capacity, close to rock outcrops, at high elevations, or on steep slopes (Brouwers et al. 2013). After 49 months post-die-off, affected forest sites were still significantly different in terms of structure, including a 23% lower tree diameter, 33% lower basal area, 40% lower canopy height, and a 30% increase in stem density

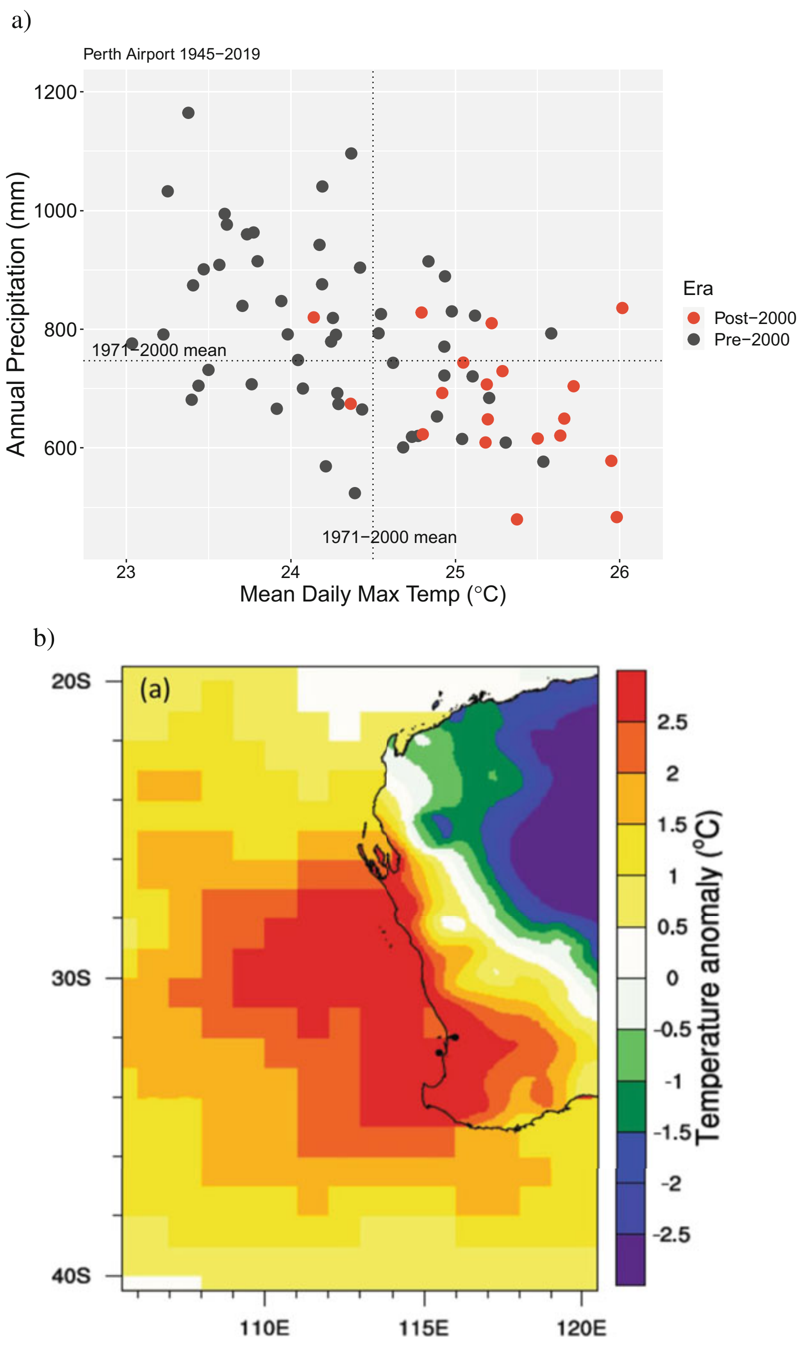


Fig. 8.4 (**a**) Annual precipitation and mean annual maximum temperature for the Perth Airport 1945–2019 (BOM dataset, J. Fontaine, http://www.bom.gov.au/climate/averages/tables/cw_009021.shtml). The period since 2000 has been substantially warmer and drier than in the past, including 6 of 7 years since 2010 being the warmest in the record. (**b**) Temperature anomalies for

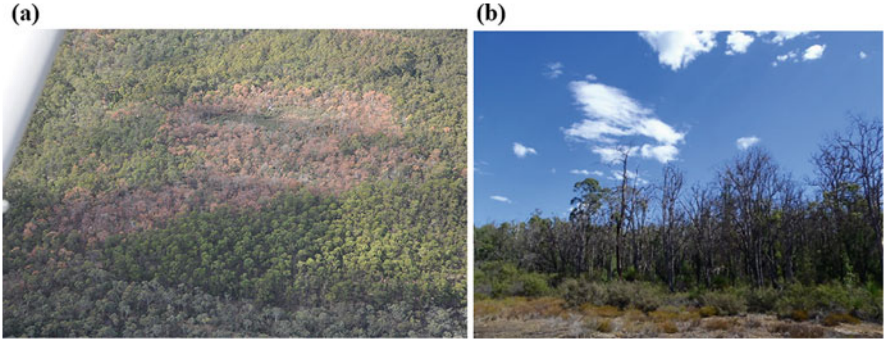


Fig. 8.5 Drought- and heatwave-induced forest die-off in the Northern Jarrah Forest in southwestern Australia. Photos showing (**a**) an aerial photo (Photo credit: G. Matusick), (**b**) a die-off, drought-affected site. (Photo credit: K.X. Ruthrof)

as the trees resprouted (Matusick et al. 2016), suggesting complex dynamics and alternate ecosystem states (Cobb et al. 2017).

Climate change events that severely impact foundational species will reverberate through trophic levels of affected ecosystems. Direct impacts such as altered thermal and light environments certainly have impacts, but the biotic implications such as reduced food availability, increased predation risk, pest outbreaks, disease, and others are likely to be of substantial magnitude. For example, in the Northern Jarrah Forest, drought-affected trees with lower tissue moisture were associated with an outbreak of a longhorned borer, *Phoracantha semipunctata* (a Cerambycidae) (Seaton et al. 2015, 2020), which in turn was targeted for feeding on by an endangered bird, Carnaby's cockatoo (*Calyptorhynchus latirostris*) (K. Ruthrof, unpublished data). Other effects were also catalogued, for instance, fine fuel loads and standing dead wood in the same forest substantially increased, and potential fire spread rates were predicted to be 30% greater in die-off plots (Ruthrof et al. 2016). In addition, die-off plots had different rhizosphere fungal communities compared with control plots (Hopkins et al. 2018). Importantly, die-off plots had more arbuscular mycorrhizal fungi (AM) and fewer ectomycorrhizal fungi (ECM), which could lead to lower levels of fungal inoculum in the soil, resulting in less favourable conditions for seedling establishment.

←

Fig. 8.4 (continued) Western Australia in early 2011, maximum temperature anomaly over land from gridded observations for March 2011 relative to March 1971–2000. Sea surface temperature (SST) anomaly from a combined in situ and satellite-derived product for March 2011 relative to 1971–2000. (Modified from Ruthrof et al. (2018))

8.3.2 Marine Drivers and Ecosystem Responses in Southwestern Australia

For the marine system, in 2011 there was a near-record strength Leeuwin Current (which is calculated using the monthly Fremantle sea levels, FMSL, and was at the highest level in three decades) and one of the strongest La Niña events on record (Pearce and Feng 2013), which delivers warm tropical water to the southwest of Australia. Sea surface temperatures (SSTs) were abnormally high for that time of year (Fig. 8.4b), and these were embedded with a long-term increase in mean SST for Western Australia (Zinke et al. 2014). The SSTs for March 2011 were 2–2.5 °C higher compared with the long-term March average over the period 1971–2011, and close to the coast, weekly temperatures were 3–3.5 °C above long-term averages (1990–2010) for that time of year (Ruthrof et al. 2018).

A wide range of taxa responded to the unprecedented marine heatwave events of early 2011 in Western Australia, spanning 14 degrees of latitude and including two marine World Heritage Areas (Ruthrof et al. 2018). There were significant and abrupt (i.e. occurring within 1–2 seasons) impacts in response to the marine heatwave compared pairwise with baseline datasets, including mortality, demographic shifts, and altered species distributions (Ruthrof et al. 2018). Of major concern was the extensive loss of habitat forming kelp (Smale and Wernberg 2013; Wernberg et al. 2013, 2016; Wernberg 2021); for example, Wernberg et al. (2013) documented a decline from ~80 to ~50% kelp cover across multiple sites in temperate waters. Alongside kelp loss, other encrusting algae (also associated with higher latitude, cooler waters) suffered declines lost while tropical fish species expanded their ranges polewards (Wernberg et al. 2013). Nearshore Western Australia is renowned for its seagrass meadows and species richness. During the 2010–2011 marine heatwave, the most widespread and foundational species, *Amphibolis antarctica*, suffered losses across its range with large declines documented and described as ‘catastrophic’ (>90% decline; Thompson et al. 2015) with flow-on effects to higher trophic levels. In tropical waters, coral bleaching and mortality were also reported with 72–92% bleaching and just 1–6% survival of corals reported from the Ningaloo reef (Depczynski et al. 2013), the western equivalent of the better-known barrier reef off of eastern Australia. Little penguins, a widespread species but with a range edge population approximately 50 km south of Perth, experienced exceptionally poor breeding success with the long-term persistence of the population in question (Cannell et al. 2012). Other, more qualitative, yet also wide-ranging impacts were also noted and included mass fish deaths, altered lobster (*Panulirus cygnus*) behaviour (Pearce et al. 2011), and an invasive tropical mussel spawning event (McDonald 2012).

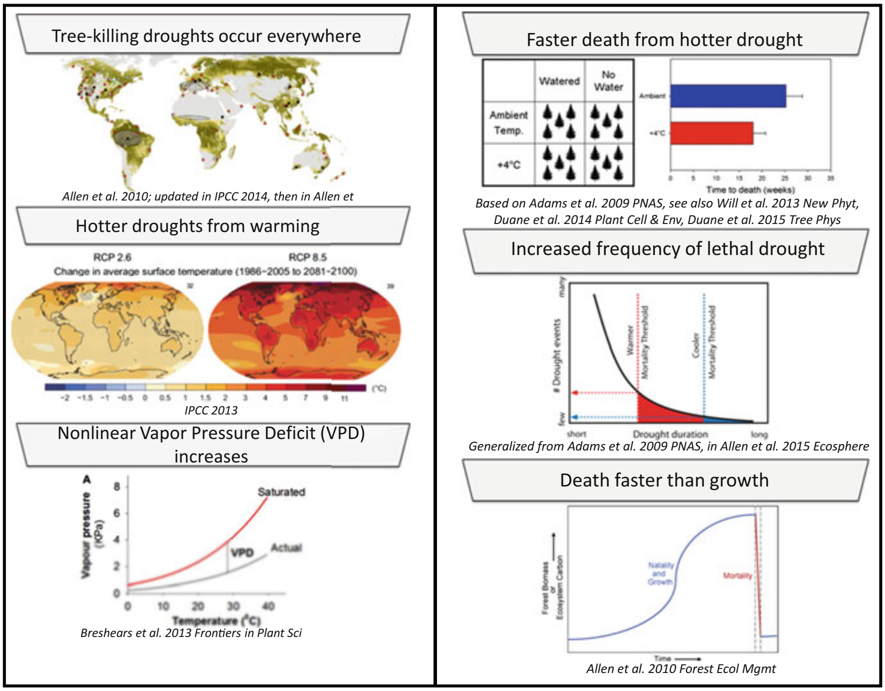
8.4 Ecological Implications

When foundational species that are key modifiers of the environment, structurally, in terms of microclimate, or as habitat modifiers—such as trees in terrestrial systems and corals, kelp and seagrass in marine systems—undergo mass mortality, most other ecosystem services are impacted (Breshears et al. 2011; Arias-Ortiz et al. 2018; Hughes et al. 2018a). During the 2011 marine heatwave in Australia, the seagrass *Amphibolis antarctica* experienced extensive dieback in some areas of Shark Bay, which corresponded with a decline in the health status of the green turtle (*Chelonia mydas*) in the preceding 2 years (Thomson et al. 2015). In terrestrial systems, similar reverberating impacts of tree loss have been associated with reduced carbon storage (Walden et al. 2019), elevated fire potentials (Ruthrof et al. 2016), altered microbial communities (Hopkins et al. 2018), and other undesirable shifts.

Forests sustain global biogeochemical cycles, regulate climate, and provide ecosystem processes and services through the production of fibre, provision of water, and other economic or cultural resources (Cobb et al. 2017). Forests sequester carbon (Anderegg et al. 2013) and alter water and energy fluxes, which together play an important role in regulating the climate. Understanding the drivers, patterns, and severity of changes to these functions is essential to minimizing their broad ranging impacts (Cobb et al. 2017). It is critical to quantify the consequences to above- and below-ground carbon dynamics and storage from die-off events to determine the current and future mitigation potential of forests (Walden et al. 2019). Following the forest die-off in southwestern Australia, there was an estimated significant loss of live standing carbon (49.3 ha^{-1}) and subsequently a significant increase in the dead standing carbon pool at 6 months post-disturbance event (Walden et al. 2019). In southwestern USA, approximately 95.1 million bone-dry tons (BDT) of dead biomass resulted from the 2012–2017 drought-induced forest mortality in California, with a lower bound of 26.2 million BDT (Tubbesing et al. 2020).

A changing climate and increasingly frequent disturbance events such as fire could see even such resilient resprouting forests become carbon sources rather than carbon sinks (Walden et al. 2019). In the marine system, a large quantity of carbon may have been released during the 2011 heatwave, in Shark Bay, Western Australia. An estimated 36% of the seagrass meadows were damaged during the heatwave, and 2–9 $TgCO_2$ was estimated to be released during the following 3 years (Arias-Ortiz et al. 2018). Given that terrestrial and marine heatwaves are predicted to increase with climate change, conservation of these primary producing ecosystems is essential to avoid adverse marine/terrestrial-atmospheric feedbacks.

A synthesis of drought impacts on terrestrial forest ecosystems identified several factors pointing to increased ecological impacts in terrestrial ecosystems as global change, particularly climate change, intensifies (Allen et al. 2015). Many of the drivers of change are accelerating, and the impact and their inevitable interaction as time between events for recovery shrink. Here, we use these same factors and scan across evidence from marine and terrestrial systems to identify drivers as well as those specific to each system (Fig. 8.6). Many of the high confidence factors for


Tree-killing droughts occur everywhere

Allen et al. 2010; updated in IPCC 2014, then in Allen et

Hotter droughts from warming

IPCC 2013

Nonlinear Vapor Pressure Deficit (VPD) increases

Breshears et al. 2013 Frontiers in Plant Sci

Faster death from hotter drought

Based on Adams et al. 2009 PNAS, see also Will et al. 2013 New Phyt, Duane et al. 2014 Plant Cell & Env, Duane et al. 2015 Tree Phys

Increased frequency of lethal drought

Generalized from Adams et al. 2009 PNAS, in Allen et al. 2015 Ecosphere

Death faster than growth

Allen et al. 2010 Forest Ecol Mgmt

Fig. 8.6 Drivers of tree mortality and forest die-off known with high confidence that indicate high likelihood of progressive increases in lethal events with continued warming (based on Allen et al. 2015). These high confidence factors include (*left column, top to bottom*) droughts occur everywhere, hotter droughts occur with warming—the most pervasive and consistent climate change, atmospheric demand in terms of vapour pressure deficit, increases with temperature during drought; (*right column, top to bottom*) trees consistently die faster during drought when temperatures are greater; there are more short droughts than long droughts, so if trees die faster with warming, there is a non-linear increase in lethal events amplified by drought frequency distribution, and tree mortality can occur rapidly relative to regeneration and growth to adulthood. Many of these high confidence factors are also applicable to other organisms, both marine and especially terrestrial

hotter drought drivers of tree mortality and forest die-off are also applicable to other organisms, both marine and especially terrestrial (Table 8.2).

8.4.1 Prognosis for the Future

Ecosystems adjust and change in response to chronic and acute climate events and will continue to do so in the future with climate change. For some ecosystems, changes might be characterized by canopy decline and thinning; in other sites whole stands may suddenly collapse. More vulnerable sites may alter species composition to species that are resilient, or not be able to support a forest, and shift to novel ecosystems composed of shrublands or heathlands with fundamentally different

Table 8.2 Drivers of vulnerability in terrestrial and marine ecosystems that are known with high confidence (modified from Allen et al. 2015)

Drivers with high confidence	Terrestrial ecosystem		Marine ecosystem	
	SWWA	SWUS	SWWA	SWUS
1. Extreme events such as drought and heatwaves (on land) and heatwaves (in water) eventually occur everywhere	√	√	√	√
2. Chronic warming produces hotter extreme events	√	√	√	√
3. Atmospheric moisture demand increases non-linearly with temperature during drought (on land)	√	√	NA	NA
4. Mortality can occur faster in hotter extremes, consistent with fundamental physiology	√	√	√	√
5. Shorter extremes occur more frequently than longer extremes and can become lethal under warming, increasing the frequency of lethal drought non-linearly	√	√	√	√
6. Mortality happens rapidly relative to growth intervals needed for ecosystem recovery	√	√	√	√

properties (fire regimes, carbon storage, hydrology, etc.). Some research in the Northern Jarrah Forest of southwestern Australia, for example, suggests that some locations, such as drier areas within the forest with low water holding capacity (Brouwers et al. 2013), may be more vulnerable than others and may be susceptible to future drought events (Andrew et al. 2016). Such areas, with continued climate change-type drought may be dominated by short, multi-stemmed individuals, following the replacing large trees and hence transforming the ecosystem structure from a tall forest, to a shorter and dense multi-stemmed condition (Matusick et al. 2016). This structural change, moving away from larger trees, is particularly concerning as they have a key ecological role and have the largest biomass and storage of carbon (Choat et al. 2018; Walden et al. 2019).

In marine ecosystems, sea surface temperature is increasing in Western Australia (Pearce and Feng 2007; Wilson et al. 2019), as it is in many regions around the globe (Lima and Wethey 2012). Globally, the frequency of heatwaves has increased since 1980 and severe heat stress is now expected every 6 years (Hughes et al. 2018a). Moreover, further increases in marine heatwave events may reduce the time that communities have to recover, altering community composition in favour of heat tolerant and rapid growing taxa, which may lead to community-wide tropicalization of temperate reefs in the future (Verges et al. 2014; Thomson et al. 2015; Wernberg et al. 2013).

It is difficult to predict how ecosystems will respond to more intense, more frequent, and longer heat extremes. The high number of cases of heat (in marine systems) or heat-compounded drought-induced ecosystem responses (on land) is posing an increasingly difficult challenge to environmental managers. As discussed above, extreme events are frequently intertwined or compounded with other drivers of ecosystem change, such as altered land use, fire, invasive species, etc., making management decisions increasingly complex (Cobb et al. 2017).

8.5 Managing Ecosystem Collapse and Future Research

Conservation, protection, and managing threatening processes have traditionally been central to the managers toolbox. However, in a rapidly changing environment, active on-ground intervention techniques such as restoration are becoming increasingly necessary and even an effective management strategy where vegetation (onshore and offshore) has already been lost (Statton et al. 2018). Given the potential risks of sudden ecosystem changes, managers urgently need adaptation strategies to improve the resistance and resilience of ecosystems to projected increases in climate stress. There are some commonalities in opportunities for management intervention that could be attempted, as outlined for forest ecosystems (Cobb et al. 2017). These commonalities came about because the responses of a range of forests can fall into a number of broad categories: single-state transitions, ecological cascades, and multi-pathway trajectories (Fig. 8.7), which could respond similarly to management intervention techniques.

In forests, for example, management intervention activities could include no action, thinning forest stands to reduce competition, logging, burning, and/or selection of appropriate species to match expected climate changes, for example, for improved drought resistance (Cobb et al. 2017). The broad term of ‘forest thinning’, for example, includes many silvicultural treatments aimed at altering age or size class distributions, species composition, and density and has been a tool in various drought-induced forest collapse studies. However, thinning can increase mortality vulnerability via enhanced understorey growth that provides tree pathogen inoculum sources or enhancing pest populations by increasing slash or increasing windthrow (see case studies in Cobb et al. 2017). Therefore, each of the forest management techniques aimed to enhance resilience to extreme climatic events would need to be set within an adaptive management framework to inform longer-term management (Fig. 8.8).

Another approach involves determining genetic adaptation to climate that may assist in intervention techniques such as restoration (Hoffmann et al. 2019), i.e. assisted gene flow. In terrestrial systems, species from drier and warmer areas may have enhanced physiological tolerance to drought through resistance to xylem cavitation and thus can maintain functioning during hot conditions (Poot and Veneklaas 2013). For instance, *Corymbia calophylla*, a key forest species in south-western Australia, from warmer regions exhibit higher drought tolerance (P50leaf) compared with those from cool regions (Blackman et al. 2017). In marine systems, the patchiness of seagrass loss following heatwave events, such as that recorded in Shark Bay, Western Australia in 2011, as well as differences in salinity across the Bay, may point to adaptation and resilience among meadows. From this, heatwave-resistant genotypes could be identified for use in restoration, as well as mapping

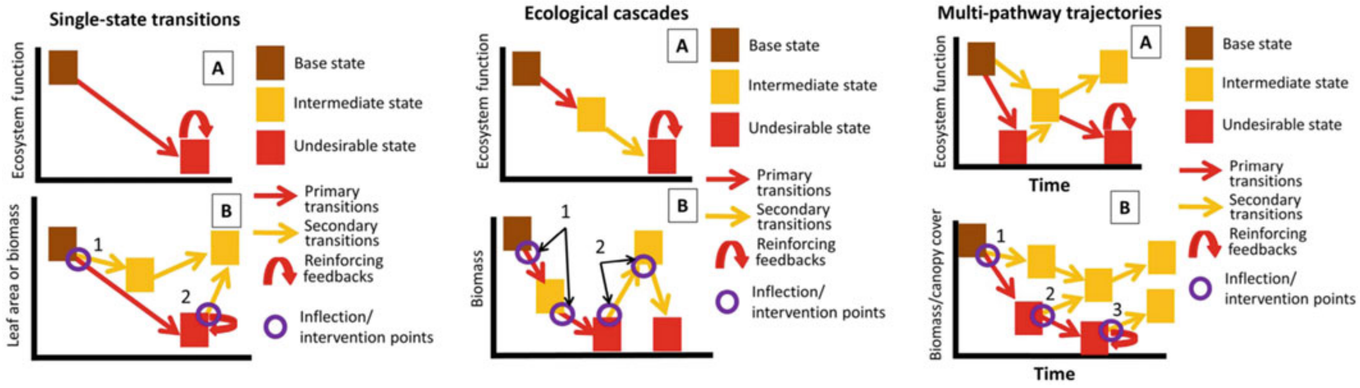


Fig. 8.7 Types of transitions and trajectories in a range of forest ecosystems: single-state transitions, ecological cascades, and multi-pathway trajectories. (Modified from Cobb et al. (2017))

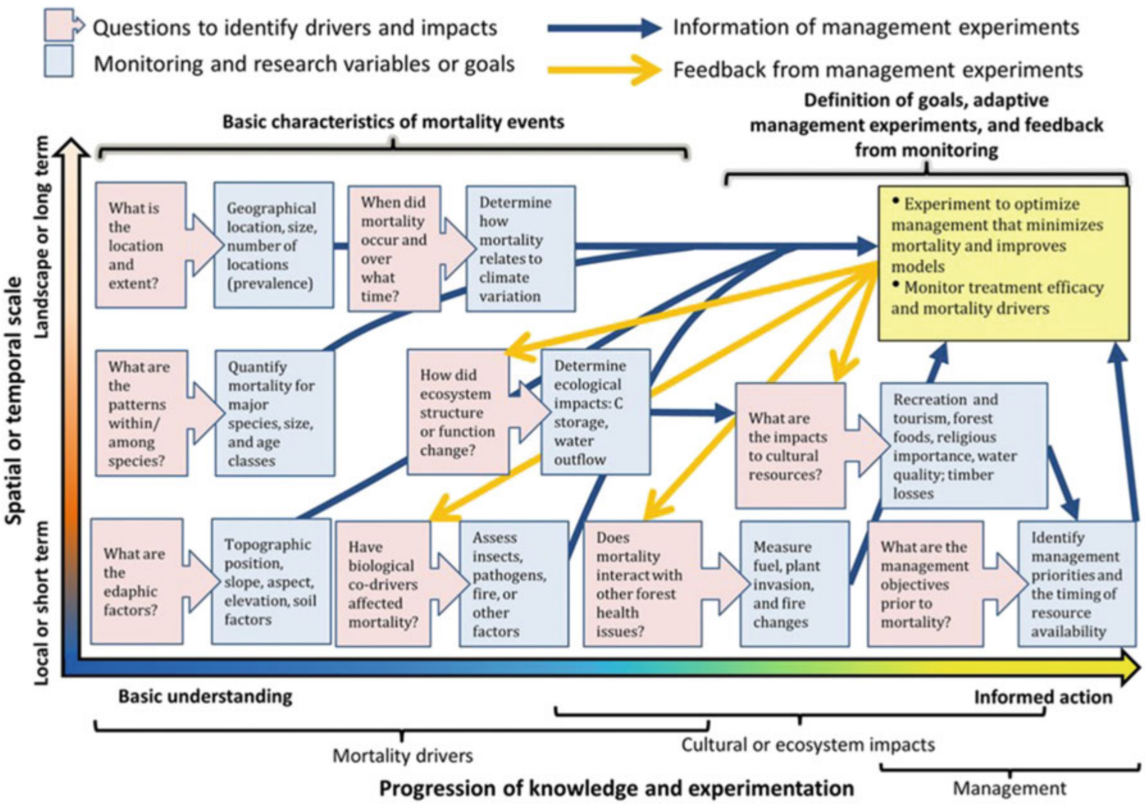


Fig. 8.8 A framework for understanding mortality drivers and identifying useful intervention in an adaptive management framework (Cobb et al. 2017)

vulnerable genotypes for conservation actions (Arias-Ortiz et al. 2018). Elsewhere, research on the exchange of heat-tolerant genotypes across latitudes for corals is proving fruitful, with one study reporting an up to tenfold increase in survival odds of coral larvae under heat stress when parents originated from a high-temperature, lower-latitude location (Dixon et al. 2015). Thus, climate-adjusted provenancing (Prober et al. 2015) or assisted gene migration, across terrestrial and marine systems, may help maintain ecosystem structure, composition, and function into a hotter future (Hoffmann et al. 2019).

Given the speed at which ecosystem changes are occurring in many regions, there are a multitude of knowledge gaps that need to be filled in order to be able to predict for, and manage, abrupt ecosystem changes. Suggestions for future work include (a) clear definitions and naming of both terrestrial and marine heatwaves for better public awareness. For example, a clear quantitative definition of marine heatwaves will facilitate global comparisons and enable better synthesis and a mechanistic understanding of the role of heatwaves in marine ecosystems (Hobday et al. 2016); (b) better and continuous funding for terrestrial and marine heatwaves to better establish long-term monitoring datasets, critical in capturing longer-term ecological impacts of heatwaves, as well as the complex interactions by multiple stressors; (c) development of more cross community/government/industry/researcher collaborative projects; (d) determine how die-off in marine and terrestrial systems and secondary effects such as microbial shifts affect recruitment and population development; (e) better ecological tracking and monitoring of responses to extreme events (i.e. the interconnectedness or relationships between taxa and their environment), rather than biological tracking of individual species; (f) more fully examine disturbance interactions in terms of order and frequency—these have important consequences for taxa response, resistance, and resilience (Hobday et al. 2016; Cannell et al. 2019).

In conclusion, we have already seen multiple examples of terrestrial and marine systems collapse or key trophic levels collapse, which are likely to rapidly escalate as warming progresses. We need to seriously consider reducing net greenhouse gas emissions and work towards internationally agreed targets to prevent further and more complete ecosystem collapse events. Ecosystem collapse is most likely to result from the interaction of multiple disturbances, and extreme climatic events; the latter are predicted to increase in frequency and intensity into the future. Ecosystem collapses will drive changes in ecological processes and impact important biosphere-to-atmosphere feedbacks including fluxes of energy, carbon, and water. Such extensive changes usually do not occur in isolation, and if ecosystem collapse is extensive enough (e.g. tree die-off), those changes have also impacted climate and ecosystems elsewhere via ecoclimate teleconnections. Increasing rates of climatic extremes will drive a host of direct and indirect feedbacks certain to produce large-scale shifts in ecological functioning at unprecedented rates. Understanding how, why, and where these shifts will occur will be critical for management and climate change mitigation.

Acknowledgements The authors thank Dr Shaun Wilson for edits on an earlier draft.

References

Allen CD (2007) Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. Ecosystems 10(5):797–808. https://doi.org/10.1007/s10021-007-9057-4

Allen CD (2014) Forest ecosystem reorganization underway in the southwestern USA—does this foreshadow widespread forest changes in the Anthropocene? Vol RMRS-P-71. USDA Forest Service, RMRS-P-71

Allen CD, Breshears DD (1998) Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. PNAS 95(25):14839–14842. https://doi.org/10.1073/pnas.95.25.14839

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259(4):660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Allen RB, Hurst JM, Portier J, Richardson SJ (2014) Elevation-dependent responses of tree mast seeding to climate change over 45 years. Ecol Evol 4(18):3525–3537. https://doi.org/10.1002/ece3.1210

Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6(8(129)):1–55. https://doi.org/10.1890/ES15-00203.1

Anderegg WRL, Kane JM, Anderegg LDL (2013) Consequences of widespread tree mortality triggered by drought and temperature stress. Nat Clim Chang 3(1):30–36. https://doi.org/10.1038/nclimate1635

Andrew ME, Ruthrof KX, Matusick G, Hardy GES (2016) Spatial configuration of drought disturbance and Forest gap creation across environmental gradients. PLoS One 11(6):18. https://doi.org/10.1371/journal.pone.0157154

Andrys J, Kala J, Lyons TJ (2017) Regional climate projections of mean and extreme climate for the southwest of Western Australia (1970–1999 compared to 2030–2059). Clim Dyn 48:1723–1747. https://doi.org/10.1007/s00382-016-3169-5

Arias-Ortiz A, Serrano O, Masque P, Lavery PS, Mueller U, Kendrick GA, Rozaimi M, Esteban A, Fourqurean JW, Marba N, Mateo MA, Murray K, Rule MJ, Duarte CM (2018) A marine heatwave drives massive losses from the world's largest seagrass carbon stocks. Nat Clim Chang 8(4):338. https://doi.org/10.1038/s41558-018-0096-y

Asner GP, Brodrick PG, Anderson CB, Vaughn N, Knapp DE, Martin RE (2016) Progressive forest canopy water loss during the 2012–2015 California drought. Proc Natl Acad Sci U S A 113(2): E249–E255. https://doi.org/10.1073/pnas.1523397113

Bader MKF, Ehrenberger W, Bitter R, Stevens J, Miller BP, Chopard J, Ruger S, Hardy G, Poot P, Dixon KW, Zimmermann U, Veneklaas EJ (2014) Spatio-temporal water dynamics in mature Banksia menziesii trees during drought. Physiol Plant 152(2):301–315. https://doi.org/10.1111/ppl.12170

Bates BC, Hope P, Ryan B, Smith I, Charles S (2008) Key findings from the Indian Ocean climate initiative and their impact on policy development in Australia. Clim Chang 89(3–4):339–354. https://doi.org/10.1007/s10584-007-9390-9

Berkelmans R, De'ath G, Kininmonth S, Skirving WJ (2004) A comparison of the 1998 and 2002 coral bleaching events on the great barrier reef: spatial correlation, patterns, and predictions. Coral Reefs 23(1):74–83. https://doi.org/10.1007/s00338-003-0353-y

Blackman CJ, Aspinwall MJ, Tissue DT, Rymer PD (2017) Genetic adaptation and phenotypic plasticity contribute to greater leaf hydraulic tolerance in response to drought in warmer climates. Tree Physiol 37(5):583–592. https://doi.org/10.1093/treephys/tpx005

BOM (2020) Australian Bureau of Meteorology. http://www.bom.gov.au/climate/change/index.shtml#tabs=Tracker&tracker=trend-maps&tQ=map%3Drain%26area%3Dwa%26season%3D0112%26period%3D1970. Accessed 20 April 2020

Bond NA, Cronin MF, Freeland H, Mantua N (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys Res Lett 42(9):3414–3420. https://doi.org/10.1002/2015gl063306

Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J, Anderson JJ, Myers OB, Meyer CW (2005a) Regional vegetation die-off in response to global-change-type drought. Proc Natl Acad Sci U S A 102(42):15144–15148. https://doi.org/10.1073/pnas.0505734102

Breshears DD, Nyhan JW, Davenport DW (2005b) Ecohydrology monitoring and excavation of semiarid landfill covers a decade after installation. Vadose Zone J 4(3):798–810. https://doi.org/10.2136/vzj2004.0038

Breshears DD, Lopez-Hoffman L, Graumlich LJ (2011) When ecosystem services crash: preparing for big, fast, patchy climate change. Ambio 40(3):256–263. https://doi.org/10.1007/s13280-010-0106-4

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. Bioscience 54 (7):677–688

Brouwers N, Matusick G, Ruthrof K, Lyons T, Hardy G (2013) Landscape-scale assessment of tree crown dieback following extreme drought and heat in a Mediterranean eucalypt forest ecosystem. Landsc Ecol 28(1):69–80. https://doi.org/10.1007/s10980-012-9815-3

Buma B (2015) Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6(4). https://doi.org/10.1890/ES15-00058.1):70

Buma B, Brown CD, Donato DC, Fontaine JB, Johnstone JF (2013) The impacts of changing disturbance regimes on serotinous plant populations and communities. Bioscience 63 (11):866–876. https://doi.org/10.1525/bio.2013.63.11.5

Byrne M, Barrett G, Blythman M, Finn H, Williams M (2015) Cocky count: a community-based survey for Carnaby's black-cockatoo (*Calyptorhynchus latirostris*) and Forest red-tailed black-cockatoo (*Calyptorhynchus banksii naso*). BirdLife Australia, Floreat

Cannell BL, Chambers LE, Wooller RD, Bradley JS (2012) Poorer breeding by little penguins near Perth, Western Australia is correlated with above average sea surface temperatures and a stronger Leeuwin current. Mar Freshw Res 63(10):914–925. https://doi.org/10.1071/mf12139

Cannell BL, Thomson PG, Schoepf V, Pattiaratchi CB, Fraser MW (2019) Impacts of marine heatwaves. In: Techera E, Winter G (eds) Marine extremes: ocean safety, marine health and the blue economy. Routledge, Chapter 8

Cavole LM, Demko AM, Diner RE, Giddings A, Koester I, Pagniello C, Paulsen ML, Ramirez-Valdez A, Schwenck SM, Yen NK, Zill ME, Franks PJS (2016) Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific. Oceanography 29(2):273–285. https://doi.org/10.5670/oceanog.2016.32

Challis A, Stevens JC, McGrath G, Miller BP (2016) Plant and environmental factors associated with drought-induced mortality in two facultative phreatophytic trees. Plant Soil 404 (1–2):157–172. https://doi.org/10.1007/s11104-016-2793-5

Choat B, Brodribb TJ, Brodersen CR, Duursma RA, Lopez R, Medlyn BE (2018) Triggers of tree mortality under drought. Nature 558(7711):531–539. https://doi.org/10.1038/s41586-018-0240-x

Cobb RC, Ruthrof KX, Breshears DD, Lloret F, Aakala T, Adams HD, Anderegg WRL, Ewers BE, Galiano L, Grunzweig JM, Hartmann H, Huang CY, Klein T, Kunert N, Kitzberger T, Landhausser SM, Levick S, Preisler Y, Suarez ML, Trotsiuk V, Zeppel MJB (2017) Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models. Ecosphere 8(12):17. https://doi.org/10.1002/ecs2.2034

Coumou D, Robinson A (2013) Historic and future increase in the global land area affected by monthly heat extremes. Environ Res Lett 8(3):6. https://doi.org/10.1088/1748-9326/8/3/034018

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Dai AG (2013) Increasing drought under global warming in observations and models. Nat Clim Chang 3(1):52–58. https://doi.org/10.1038/nclimate1633

Depczynski M, Gilmour JP, Ridgway T, Barnes H, Heyward AJ, Holmes TH, Moore JAY, Radford BT, Thomson DP, Tinkler P, Wilson SK (2013) Bleaching, coral mortality and subsequent survivorship on a west Australian fringing reef. Coral Reefs 32(1):233–238. https://doi.org/10.1007/s00338-012-0974-0

Diffenbaugh NS, Field CB (2013) Changes in ecologically critical terrestrial climate conditions. Science 341(6145):486–492. https://doi.org/10.1126/science.1237123

Dixon GB, Davies SW, Aglyamova GA, Meyer E, Bay LK, Matz MV (2015) Genomic determinants of coral heat tolerance across latitudes. Science 348(6242):1460–1462. https://doi.org/10.1126/science.1261224

Duke NC, Kovacs JM, Griffiths AD, Preece L, Hill DJE, van Oosterzee P, Mackenzie J, Morning HS, Burrows D (2017) Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. Marine Freshwater Res. https://doi.org/10.1071/MF16322

Enright NJ, Fontaine JB, Lamont BB, Miller BP, Westcott VC (2014) Resistance and resilience to changing climate and fire regime depend on plant functional traits. J Ecol 102(6):1572–1581. https://doi.org/10.1111/1365-2745.12306

Enright NJ, Fontaine JB, Bowman DMJS, Bradstock RA, Williams RJ (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Front Ecol Environ 13:265–272. https://doi.org/10.1890/140231

Fettig CJ, Mortenson LA, Bulaon BM, Foulk PB (2019) Tree mortality following drought in the central and southern Sierra Nevada, California. US Ecol Manage 432:164–178. https://doi.org/10.1016/j.foreco.2018.09.006

Fraser MW, Kendrick GA, Statton J, Hovey RK, Zavala-Perez A, Walker DI (2014) Extreme climate events lower resilience of foundation seagrass at edge of biogeographical range. J Ecol 102(6):1528–1536. https://doi.org/10.1111/1365-2745.12300

Frölicher TL, Laufkötter C (2018) Emerging risks from marine heat waves. Nat Commun 9(4). https://doi.org/10.1038/s41467-018-03163-6

Fusco EJ, Finn JT, Balch JK, Nagy RC, Bradley B (2019) Invasive grasses increase fire occurrence and frequency across US ecoregions. https://doi.org/10.1073/pnas.1908253116

Garcia ES, Swann ALS, Villegas JC, Breshears DD, Law DJ, Saleska SR, Stark SC (2016) Synergistic ecoclimate teleconnections from forest loss in different regions structure global ecological responses. PLoS One 11(11):e0165042. https://doi.org/10.1371/journal.pone.0165042

Goreau T, McClanahan T, Hayes R, Strong A (2000) Conservation of coral reefs after the 1998 global bleaching event. Conserv Biol 14(1):5–15. https://doi.org/10.1046/j.1523-1739.2000.00011.x

Gower K, Fontaine JB, Birnbaum C, Enright NJ (2015) Sequential disturbance effects of hailstorm and fire on vegetation in a Mediterranean-type ecosystem. Ecosystems. https://doi.org/10.1007/s10021-10015-19886-10025

Greene CH (2016) North America's iconic marine species at risk due to unprecedented ocean warming. Oceanography 29(3):14–17. https://doi.org/10.5670/oceanog.2016.67

Griffin D, Anchukaitis KJ (2014) How unusual is the 2012-2014 California drought? Geophys Res Lett 41(24):9017–9023. https://doi.org/10.1002/2014gl062433

Hartmann H, Moura CF, Anderegg WRL, Ruehr NK, Salmon Y, Allen CD, Arndt SK, Breshears DD, Davi H, Galbraith D, Ruthrof KX, Wunder J, Adams HD, Bloemen J, Cailleret M, Cobb R, Gessler A, Grams TEE, Jansen S, Kautz M, Lloret F, O'Brien M (2018) Research frontiers for improving our understanding of drought-induced tree and forest mortality. New Phytol 218(1):15–28. https://doi.org/10.1111/nph.15048

Hobday A, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver E, Benthuysen J, Burrows MT, Donat MG, Feng M, Holbrook NJ, Moore PJ, Scannell HA, Sen Gupta A, Wernberg T (2016) A hierarchical approach to defining marine heatwaves. Progress Oceanogr 141:227–238. https://doi.org/10.1016/j.pocean.2015.12.014

Hoffmann AA, Rymer PD, Byrne M, Ruthrof KX, Whinam J, McGeoch M, Bergstrom DM, Guerin GR, Sparrow B, Joseph L, Hill SJ, Andrew NR, Camac J, Bell N, Riegler M, Gardner JL, Williams SE (2019) Impacts of recent climate change on terrestrial flora and fauna: some emerging Australian examples. Austral Ecol 44(1):3–27. https://doi.org/10.1111/aec.12674

Hopkins AJM, Ruthrof KX, Fontaine JB, Matusick G, Dundas SJ, Hardy GES (2018) Forest die-off following global-change-type drought alters rhizosphere fungal communities. Environ Res Lett 13(9):13. https://doi.org/10.1088/1748-9326/aadc19

Hughes TP, Kerry JT, Alvarez-Noriega M, Alvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs JPA, Hoogenboom MO, Kennedy EV, Kuo CY, Lough JM, Lowe RJ, Liu G, Cculloch MTM, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global warming and recurrent mass bleaching of corals. Nature 543(7645):373. https://doi.org/10.1038/nature21707

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359(6371):80. https://doi.org/10.1126/science.aan8048

Hughes TP, Kerry JT, Simpson T (2018b) Large-scale bleaching of corals on the great barrier reef. Ecology 99(2):501–501. https://doi.org/10.1002/ecy.2092

Hulley GC, Dousset B, Kahn BH (2020) Rising trends in heatwave metrics across Southern California. Earth's Future 8:e2020EF001480. https://doi.org/10.1029/2020EF001480

IPCC (2014) Climate change 2014: impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge and New York, NY

IPCC (2018) Global warming of 1.5°C. In: Masson-Delmotte V, Zhai P, Pörtner H-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T (eds) An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. World Meteorological Organization, Geneva, p 32

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GLW, Schoennagel T, Turner MG (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14(7):369–378. https://doi.org/10.1002/fee.1311

Jones T, Parrish JK, Peterson WT, Bjorkstedt EP, Bond NA, Ballance LT, Bowes V, Hipfner JM, Burgess HK, Dolliver JE, Lindquist K, Lindsey J, Nevins HM, Robertson RR, Roletto J, Wilson L, Joyce T, Harvey J (2018) Massive mortality of a planktivorous seabird in response to a marine heatwave. Geophys Res Lett 45(7):3193–3202. https://doi.org/10.1002/2017gl076164

Kala J, De Kauwe MG, Pitman AJ, Medlyn BE, Wang YP, Lorenz R, Perkins-Kirkpatrick SE (2016) Impact of the representation of stomatal conductance on model projections of heatwave intensity. Sci Rep 6(7). https://doi.org/10.1038/srep23418

Kintisch E (2015) The Blob' invades Pacific, flummoxing climate experts. Science 348 (6230):17–18. https://doi.org/10.1126/science.348.6230.17

Leising AW, Schroeder ID, Bograd SJ, Abell J, Durazo R, Gaxiola-Castro G, Bjorkstedt EP, Field J, Sakuma K, Robertson RR, Goericke R, Peterson WT, Brodeur R, Barcelo C, Auth TD, Daly EA, Suryan RM, Gladics AJ, Porquez JM, McClatchie S, Weber ED, Watson W, Santora JA, Sydeman WJ, Melin SR, Chavez FP, Golightly RT, Schneider SR, Fisher J, Morgan C, Bradley R, Warybok P (2015) State of the California current 2014–15: impacts of the warm-water "blob". Calif Coop Ocean Fish Invest Rep 56:31–68

Lima FP, Wethey DS (2012) Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nat Commun 3:13. https://doi.org/10.1038/ncomms1713

Matusick G, Ruthrof KX, Hardy G (2012) Drought and heat triggers sudden and severe dieback in a dominant mediterranean-type woodland species. Open Journal of Forestry 2:183–186. https://doi.org/10.4236/ojf.2012.24022

Matusick G, Ruthrof KX, Brouwers NC, Dell B, Hardy GS (2013) Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. Eur J For Res 132(3):497–510. https://doi.org/10.1007/s10342-013-0690-5

Matusick G, Ruthrof KX, Fontaine JB, Hardy GES (2016) Eucalyptus forest shows low structural resistance and resilience to climate change-type drought. J Veg Sci 27(3):493–503. https://doi.org/10.1111/jvs.12378

Matusick G, Ruthrof KX, Kala J, Brouwers NC, Breshears DD, Hardy GES (2018) Chronic historical drought legacy exacerbates tree mortality and crown dieback during acute heatwave-compounded drought. Environ Res Lett 13(9):14. https://doi.org/10.1088/1748-9326/aad8cb

McDonald JI (2012) Detection of the tropical mussel species *Perna viridis* in temperate Western Australia: possible association between spawning and a marine heat pulse. Aquat Invasions 7 (4):483–490. https://doi.org/10.3391/ai.2012.7.4.005

Meehl GA, Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st century. Science 305(5686):994–997. https://doi.org/10.1126/science.1098704

Miao S, Zou CB, Breshears DD (2009) Vegetation responses to extreme hydrological events: sequence matters. Am Nat 173(1):113–118. https://doi.org/10.1086/593307

Miller RG, Tangney R, Enright NJ, Fontaine JB, Merritt DJ, Ooi MKJ, Ruthrof KX, Miller BP (2019) Mechanisms of fire seasonality effects on plant populations. Trends in Evolution and Ecology. https://doi.org/10.1016/j.tree.2019.07.009

Miller RG, Tangney R, Enright NJ, Fontaine JB, Merritt DJ, Ooi MKJ, Ruthrof KX, Miller BP (2020) Fire seasonality mechanisms are fundamental for understanding broader fire regime effects. Trends in Evolution and Ecology. https://doi.org/10.1016/j.tree.2020.08.002

Moore JAY, Bellchambers LM, Depczynski MR, Evans RD, Evans SN, Field SN, Friedman KJ, Gilmour JP, Holmes TH, Middlebrook R, Radford BT, Ridgway T, Shedrawi G, Taylor H, Thomson DP, Wilson SK (2012) Unprecedented mass bleaching and loss of coral across 12 degrees of latitude in Western Australia in 2010–11. PLoS One 7(12):11. https://doi.org/10.1371/journal.pone.0051807

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772):853–858. https://doi.org/10.1038/35002501

North MP, Stevens JT, Greene DF, Coppoletta M, Knapp EE, Latimer AM, Restaino CM, Tompkins RE, Welch KR, York RA, Young DJN, Axelson JN, Buckley TN, Estes BL, Hager RN, Long JW, Meyer MD, Ostoja SM, Safford HD, Shive KL, Tubbesing CL, Vice H, Walsh D, Werner CM, Wyrsch P (2019) Tamm review: reforestation for resilience in dry western US forests. For Ecol Manag 432:209–224. https://doi.org/10.1016/j.foreco.2018.09.007

Oliver ECJ, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV, Benthuysen JA, Feng M, Sen Gupta A, Hobday AJ, Holbrook NJ, Perkins-Kirkpatrick SE, Scannell HA, Straub SC, Wernberg T (2018) Longer and more frequent marine heatwaves over the past century. Nat Commun 9:12. https://doi.org/10.1038/s41467-018-03732-9

Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. Ecosystems 1(6):535–545. https://doi.org/10.1007/s100219900049

Pearce A, Feng M (2007) Observations of warming on the Western Australian continental shelf. Mar Freshw Res 58(10):914–920. https://doi.org/10.1071/mf07082

Pearce AF, Feng M (2013) The rise and fall of the "marine heat wave" off Western Australia during the summer of 2010/2011. J Mar Syst 111:139–156. https://doi.org/10.1016/j.jmarsys.2012.10.009

Pearce A, Lenanton R, Jackson G, Moore J, Feng M, Gaughan D (2011) The "marine heat wave" off Western Australia during the summer of 2010/11. Fisheries Research Division Western Australian Fisheries and Marine Research Laboratories, North Beach

Poot P, Veneklaas EJ (2013) Species distribution and crown decline are associated with contrasting water relations in four common sympatric eucalypt species in southwestern Australia. Plant Soil 364(1–2):409–423. https://doi.org/10.1007/s11104-012-1452-8

Prober SM, Byrne M, McLean EH, Steane DA, Potts BM, Vaillancourt RE, Stock WD (2015) Climate-adjusted provenancing: a strategy for climate-resilient ecological restoration. Frontiers of Ecology and Evolution 3(65). https://doi.org/10.3389/fevo.2015.00065

Prugh LR, Deguines N, Grinath JB, Suding KN, Bean WT, Stafford R, Brashares JS (2018) Ecological winners and losers of extreme drought in California. Nat Clim Chang 8(9):819. https://doi.org/10.1038/s41558-018-0255-1

Roberts LJ, Burnett R, Tietz J, Veloz S (2019) Recent drought and tree mortality effects on the avian community in southern Sierra Nevada: a glimpse of the future? Ecol Appl. https://doi.org/10.1002/eap.1848

Robeson SM (2015) Revisiting the recent California drought as an extreme value. Geophys Res Lett. https://doi.org/10.1002/2015GL064593

Ruthrof KX, Matusick G, Hardy GESJ (2015) Early differential responses of co-dominant canopy species to sudden and severe drought in a Mediterranean-climate type forest. Forests 6:2082–2091. https://doi.org/10.3390/f6062082

Ruthrof KX, Fontaine JB, Matusick G, Breshears DD, Law DJ, Powell S, Hardy G (2016) How drought-induced forest die-off alters microclimate and increases fuel loadings and fire potentials. Int J Wildland Fire 25(8):819–830. https://doi.org/10.1071/wf15028

Ruthrof KX, Breshears DD, Fontaine JB, Froend RH, Matusick G, Kala J, Miller B, Mitchell PJ, Wilson SK, van Keulen M, Enright NJ, Law DJ, Wernberg T, Hardy G (2018) Subcontinental heat wave triggers terrestrial and marine, multi-taxa responses. Sci Rep 8(9). https://doi.org/10.1038/s41598-018-31236-5

Ryan JP, Kudela RM, Birch JM, Blum M, Bowers HA, Chavez FP, Doucette GJ, Hayashi K, Marin R, Mikulski CM, Pennington JT, Scholin CA, Smith GJ, Woods A, Zhang Y (2017) Causality of an extreme harmful algal bloom in Monterey Bay, California, during the 2014–2016 Northeast Pacific warm anomaly. Geophys Res Lett 44(11):5571–5579. https://doi.org/10.1002/2017gl072637

Schwantes AM, Swenson JJ, González-Roglich M, Johnson DM, Domec JC, Jackson RB (2017) Measuring canopy loss and climatic thresholds from an extreme drought along a 5-fold precipitation gradient across Texas. Glob Chang Biol 23:5120–5135. https://doi.org/10.1111/gcb.13775

Seaton S, Matusick G, Ruthrof KX, Hardy G (2015) Outbreak of *Phoracantha semipunctata* in response to severe drought in a Mediterranean Eucalyptus Forest. Forests 6(11):3868–3881. https://doi.org/10.3390/f6113868

Seaton S, Matusick G, Ruthrof KX, Hardy G (2020) Within-tree distribution and survival of the *Eucalyptus* longhorned borer *Phoracantha semipunctata* (Coleoptera: Cerambycidae) in a Mediterranean-type ecosystem. Insects 11(4):225. https://doi.org/10.3390/insects11040225

Silverio DV, Brando PM, Bustamante MMC, Putz FE, Marra DM, Levick SR, Trumbore SE (2019) Fire, fragmentation, and windstorms: a recipe for tropical forest degradation. J Ecol 107(2):656–667. https://doi.org/10.1111/1365-2745.13076

Smale DA, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species. Proc R Soc B-Biol Sci 280(1754):9. https://doi.org/10.1098/rspb.2012.2829

Sorte CJB, Williams SL, Zerebecki RA (2010) Ocean warming increases threat of invasive species in a marine fouling community. Ecology 91(8):2198–2204. https://doi.org/10.1890/10-0238.1

Stark SC, Breshears DD, Garcia ES, Law DJ, Minor DM, Saleska SR, Swann ALS, Villegas JC, Aragão LEOC, Bella EM, Borma LS, Cobb NS, Litvak ME, Magnusson WE, Morton JM, Redmond MD (2016) Toward accounting for ecoclimate teleconnections: intra-and inter-continental consequences of altered energy balance after vegetation change. Landsc Ecol 31:181–194. https://doi.org/10.1007/s10980-015-0282-5

Statton J, Dixon KW, Irving AD, Jackson EL, Kendrick GA, Orth RJ, Sinclair EA (2018) Decline and restoration ecology of Australian seagrasses In: Larkum AWD (ed) Seagrasses of Australia. Springer. https://doi.org/10.1007/978-3-319-71354-0_20

Steel E, Fontaine JB, Ruthrof KX, Burgess TI, Hardy G (2019) Changes in structure of over and midstory tree species in a Mediterranean-type forest after an extreme drought-associated heatwave. Austral Ecol. https://doi.org/10.1111/aec.12818

Stephenson NL, Das AJ, Ampersee NJ, Cahill KG, Caprio AC, Sanders JE, Williams AP (2018) Patterns and correlates of giant sequoia foliage dieback during California's 2012-2016 hotter drought. For Ecol Manag 419:268–278. https://doi.org/10.1016/j.foreco.2017.10.053

Swann ALS, Laguë MM, Garcia ES, Field JP, Breshears DD, Moore DJP, Saleska SR, Stark SC, Villegas JC, Law DJ (2018) Continental-scale consequences of tree die-offs in North America: identifying where forest loss matters most. Environ Res Lett 13(5):055014. https://doi.org/10.1088/1748-9326/aaba0f

Thomson JA, Burkholder DA, Heithaus MR, Fourqurean JW, Fraser MW, Statton J, Kendrick GA (2015) Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. Glob Change Biol 21(4):1463–1474. https://doi.org/10.1111/gcb.12694

Trenberth KE, Dai AG, van der Schrier G, Jones PD, Barichivich J, Briffa KR, Sheffield J (2014) Global warming and changes in drought. Nat Clim Chang 4(1):17–22. https://doi.org/10.1038/nclimate2067

Tubbesing CL, Lara JD, Battles JJ, Tittmann PW, Kammen DM (2020) Characterization of the woody biomass feedstock potential resulting from California's drought. Sci Reports 10:1096. https://doi.org/10.1038/s41598-020-57904-z

Verges A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, Heck KL, Booth DJ, Coleman MA, Feary DA, Figueira W, Langlois T, Marzinelli EM, Mizerek T, Mumby PJ, Nakamura Y, Roughan M, van Sebille E, Sen Gupta A, Smale DA, Tomas F, Wernberg T, Wilson SK (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B-Biol Sci 281(1789):10. https://doi.org/10.1098/rspb.2014.0846

Walden LL, Fontaine JB, Ruthrof KX, Matusick G, Harper RJ, Hardy G (2019) Carbon consequences of drought differ in forests that resprout. Glob Change Biol. 25:1653-1664. https://doi.org/10.1111/gcb.14589

Welbergen J, Booth C, Martin J (2014 Killer climate: tens of thousands of flying foxes dead in a day. The Conversation. https://theconversation.com/killer-climate-tens-of-thousands-of-flying-foxes-dead-in-a-day-23227. Accessed 17 Nov 19

Wernberg T (2021) Marine heatwave drives collapse of kelp forests in Western Australia. In Canadell JG, Jackson RB (ed) Ecosystem collapse

Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Chang 3(1):78–82. https://doi.org/10.1038/nclimate1627

Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA, Wilson S (2016)

Climate-driven regime shift of a temperate marine ecosystem. Science 353(6295):169–172. https://doi.org/10.1126/science.aad8745

Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM, Swetnam TW, Rauscher SA, Seager R, Grissino-Mayer HD, Dean JS, Cook ER, Gangodagamage C, Cai M, McDowell NG (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. Nat Clim Chang 3(3):292–297. https://doi.org/10.1038/nclimate1693

Williams AP, Seager R, Abatzoglou JT, Cook BI, Smerdon JE, Cook ER (2015) Contribution of anthropogenic warming to California drought during 2012–2014. Geophys Res Lett 42 (16):6819–6828. https://doi.org/10.1002/2015gl064924

Wilson S, Kendrick A, Wilson B (2019) The North-Western margin of Australia. In: Sheppard C (ed) World seas: an environmental evaluation (2nd edition). Volume II: the Indian Ocean to the Pacific. p Chapter 14. https://doi.org/10.1016/B978-0-08-100853-9.00019-1

Young DJN, Stevens JT, Earles JM, Moore J, Ellis A, Jirka AL, Latimer AM (2017) Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol Lett 20 (1):78–86. https://doi.org/10.1111/ele.12711

Zinke J, Rountrey A, Feng M, Xie SP, Dissard D, Rankenburg K, Lough JM, McCulloch MT (2014) Corals record long-term Leeuwin current variability including Ningaloo Nino/Nina since 1795. Nat Commun 5(9). https://doi.org/10.1038/ncomms4607

Part III

Tropical and Temperate Coastal Ecosystems

9 Processes and Factors Driving Change in Mangrove Forests: An Evaluation Based on the Mass Dieback Event in Australia's Gulf of Carpentaria

Norman C. Duke, Lindsay B. Hutley, Jock R. Mackenzie, and Damien Burrows

Abstract

A vast area of more than 80 km^2 (6–10% of total) of mangrove forests bordering Australia's Gulf of Carpentaria died *en masse* in late 2015 and early 2016. The dieback occurred over a number of months in synchrony across more than 1500 km of exposed Gulf shorelines. There are serious concerns about the implications of such an event given the important ecological and economic services provided by mangrove ecosystems, and the challenges to policy and management of such an abrupt loss of natural resources at both local and regional scales. In this chapter, we begin by structuring and quantifying the distinct and complex mix of processes involved in the natural establishment, growth, and development of mangrove stands in the context of enhanced environmental variability. Based on these findings, we develop a new evaluation framework to explain the severe response observed in late 2015 in mangroves of the Gulf of Carpentaria. We explore in detail the multiple drivers involved in the event and address the complex question of the role of climate change. These analyses and other observations about this unique event are brought together to assist the ongoing development and implementation of effective management policy, starting with monitoring programs at national and local scales. While this is a work in progress, these findings already provide unequivocal evidence that

---

N. C. Duke (✉) · J. R. Mackenzie · D. Burrows
Centre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Townsville, QLD, Australia
e-mail: norman.duke@jcu.edu.au; jmackenzie@earthwatch.org.au; damien.burrows@jcu.edu.au

L. B. Hutley
Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT, Australia
e-mail: Lindsay.Hutley@cdu.edu.au

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*, Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_9

mangroves are vulnerable and acutely sensitive to extreme variations in sea level and climate change.

9.1 Introduction

Mangrove vegetation, along with saltmarsh and saltpans, make up tidal wetlands which together exist almost exclusively within the upper intertidal zone of temperate and tropical shorelines (Tomlinson 2016). These habitats are largely recognised as environmentally resilient. This observation is reinforced in part in the literature, where the broad distributional ranges of mangrove habitats extend across extremely different climatic zones, from arid desert regions to the wet humid tropics. Furthermore, across this range, the habitat maintains similar structural characteristics with often closed canopies sharing common aspects of functionality, faunal communities and ecosystem benefits. For more than 50 million years, tidal wetland habitats are believed to have persisted (Duke 2017) maintaining their adherence to the tidal zone throughout time—despite sometimes dramatic circumstances, such as changes in sea level of tens of metres. The mere presence today of this relatively small group of plants in the intertidal zone clearly demonstrates the success of their survival and life history strategies. But, this tightly constrained existence, coupled with their narrow genetic diversity, further implies there must be tightly defined environmental limits beyond which the habitat cannot survive. These plants, like all others, are defined by their essential and unique characteristics: salt tolerance and their viviparous propagules, allowing them to occupy this particularly specialised niche across space and time.

Overall, mangrove habitat is limited by sea level and temperature at a global scale (Duke et al. 1998). Plants of the tidal wetland niche are primarily limited to the upper tidal zone, determined by species-specific survival limits often displayed in their distinct zonation patterns. Mangroves and saltmarsh plants flourish within relatively narrow zones determined by the ecological limits of each species where each has conformed to the defining environmental factors present. Beyond these limits the plants cannot exist; importantly, they must also be responsive and adaptable to change.

As environmental factors rapidly change, so the mangroves must relocate if they are to survive and persist. This relocation is limited further by the growth conditions of each species along with their reproductive, dispersal and establishment capabilities. This involves either the relocation of habitat into newly created unoccupied space, or its retreat once the current space becomes inhospitable. For mangrove habitats, relocation equates to instances of either expansion via seedling recruitment, or retreat with dieback. In this way, we aim to further define and quantify the distinct and unusual processes involved in the establishment, growth and development of tidal wetlands. Such an extended understanding of the processes involved will then be used to explain the responses observed when the habitat comes under stress.

With this chapter, we examine key factors influencing tidal wetlands along with the responses of the ecosystem as environmental conditions alter. Our aim has been to link observed processes of change to the key responsible drivers. We specifically draw on the recent instance of severe environmental change associated with the unprecedented mass dieback of mangroves in Australia's remote Gulf of Carpentaria in 2015–2016 (Duke et al. 2017). This event affected a vast region of coastal tidal wetlands and warranted considerable attention. Detailed additional investigations are currently underway by various groups including that by the James Cook University TropWATER Centre funded by the National Environmental Science Program (Fig. 9.1a, b). The current situation is evaluated, but first, we review the factors that define the habitat of mangroves and tidal wetlands.

9.2 Dynamic Processes Influencing Tidal Wetlands and Mangroves

The tidal wetland habitat comprises mangroves, tidal saltmarsh and saltpans (Duke et al. 2019). Key features of this habitat are defined and characterised in a series of four conceptual models (Figs. 9.2, 9.3, 9.4, and 9.5) each describing different levels of a nested framework that provides a ranking of environmental drivers and connections needed to understand and explain observed relationships and the responses of tidal wetlands and mangroves when specific environmental factors change. Using this framework, we describe the drivers that operate at different spatial and temporal scales (Table 9.1).

9.2.1 Level 1: Global Setting of Tidal Wetlands: Site Geomorphology, Sea Level and Climate

The primary determining physical factors for tidal wetland habitat are dominated by sea level, tidal range, slope, and sediment type (Fig. 9.2). Factors influencing mangrove plant diversity, structure and cover are otherwise described in Level 2 (Fig. 9.3). In general, habitat features depend on the extent of soft, unconsolidated sediments between mean sea level and high water levels in order to define the presence, zonation and overall areas of the tidal wetland ecosystem along shoreline and estuarine reaches (Duke 2006; Duke et al. 1998). Accordingly, changes to any of these factors will have profound impacts on the habitat, forcing the affected vegetation to either expand or retreat, depending on the direction, trend and rate of change of these factors, and specifically sea level.

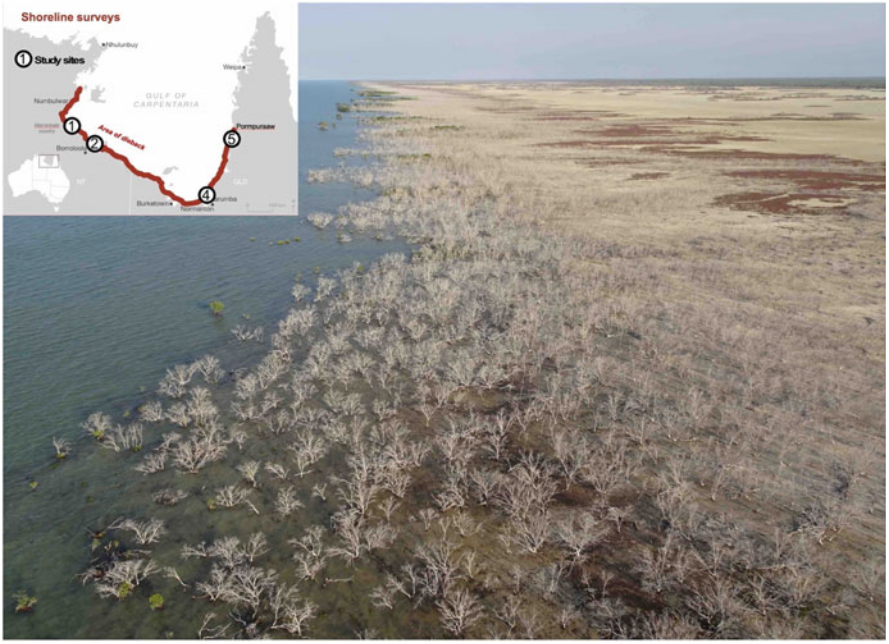


Fig. 9.1 (**a**) Around 8000 ha of shoreline fringing mangroves were killed between late 2015 and early 2016 along ~1500 km around the Gulf of Carpentaria. This picture shows some of the dead shoreline 3 years after (Limmen Bight shoreline at location 1, Northern Territory, 2018). These trees are believed to have died when normally flooding tides were temporarily lowered with a 20 cm drop in sea level associated with the particularly severe El Niño event. The inset shows the extent of the impacted shoreline along with four study site locations (1 and 2 in the Northern Territory, 4 and 5 in Queensland) where detailed investigations focused on vegetation, fauna and topography. Credit: Norman Duke. (**b**) Paired views of seaward fringe mangrove areas in Australia's Gulf of Carpentaria in non-impacted (left images) and impacted (right images) areas following the mass dieback event in late 2015 exemplified in shorelines between Limmen Bight River and McArthur River, Northern Territory, as: **A** and **B** represented in vegetation cover indices pre- and post-impact from satellite imagery (source: National Map)—note, yellow squares mark the location of the green fraction timeline for site 1A (Fig. 9.15); **C** and **D** in aerial surveys of the seaward mangrove fringe observed in June 2016; and **E** and **F** in field studies in 2016 and 2018, respectively (Credit: NC Duke)

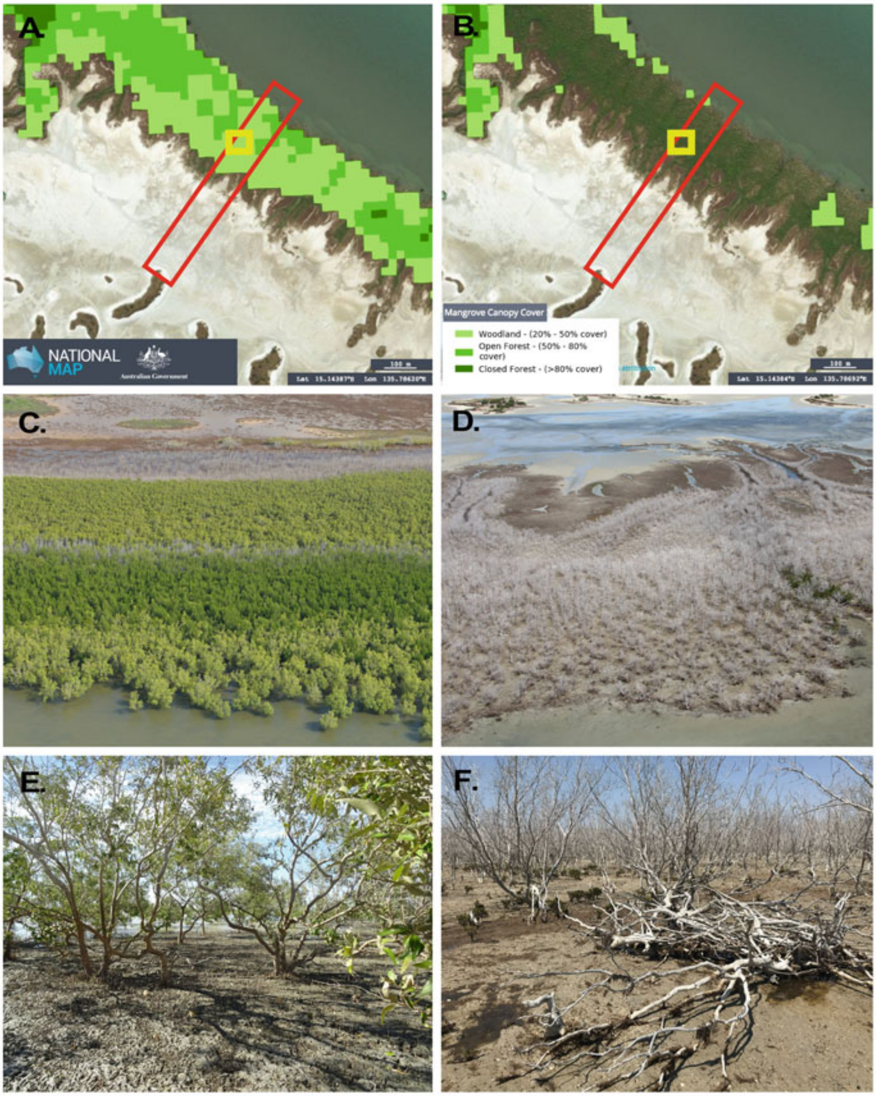


Fig. 9.1 (continued)

9.2.2 Level 2: Composition of Dominant Vegetation Types of Tidal Wetlands: Regional Influences of Temperature and Rainfall

Two key factors, temperature and rainfall, strongly influence the diversity, biomass, presence and relative area of mangrove and tidal saltmarsh in any tidal wetland setting (Fig. 9.3; Duke 1992)—as defined in Level 1. At a regional scale, higher

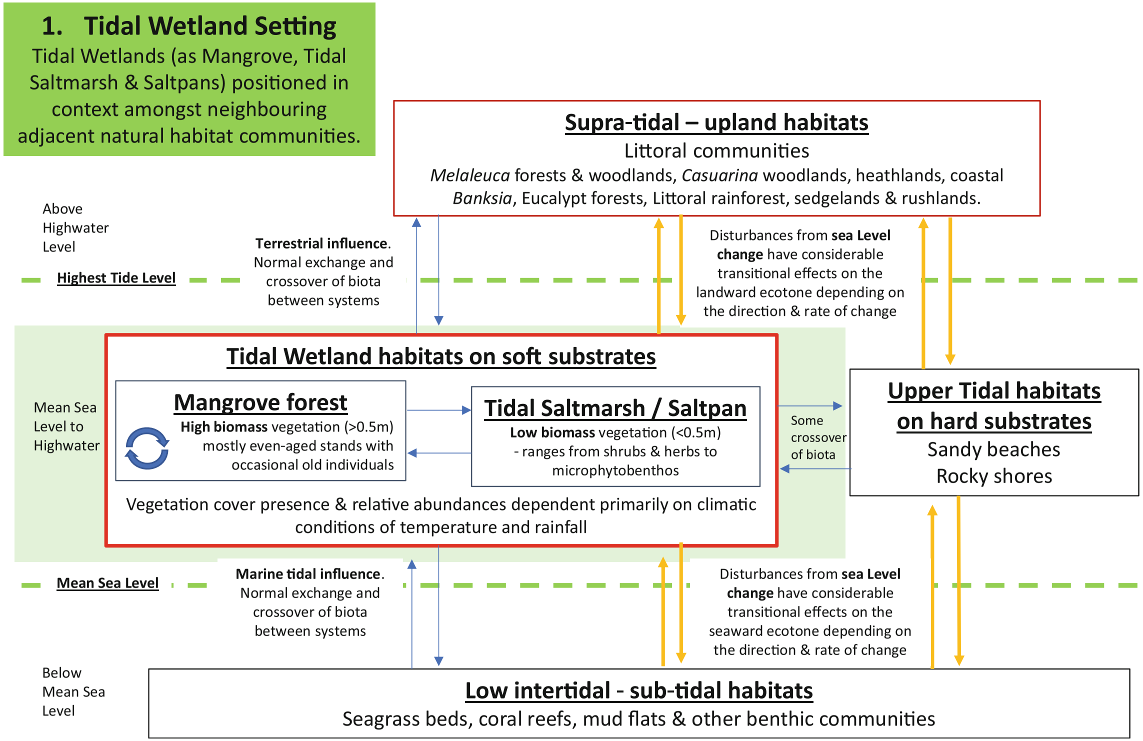


Fig. 9.2 Level 1 schematic conceptual model sets the global physical context for tidal wetlands (red box) amongst neighbouring natural shoreline habitats (Duke et al. 1998; Duke 2006). Blue and yellow arrows respectively signify natural exchanges of biota between habitats and shifts due to disturbances at landward and seaward margins

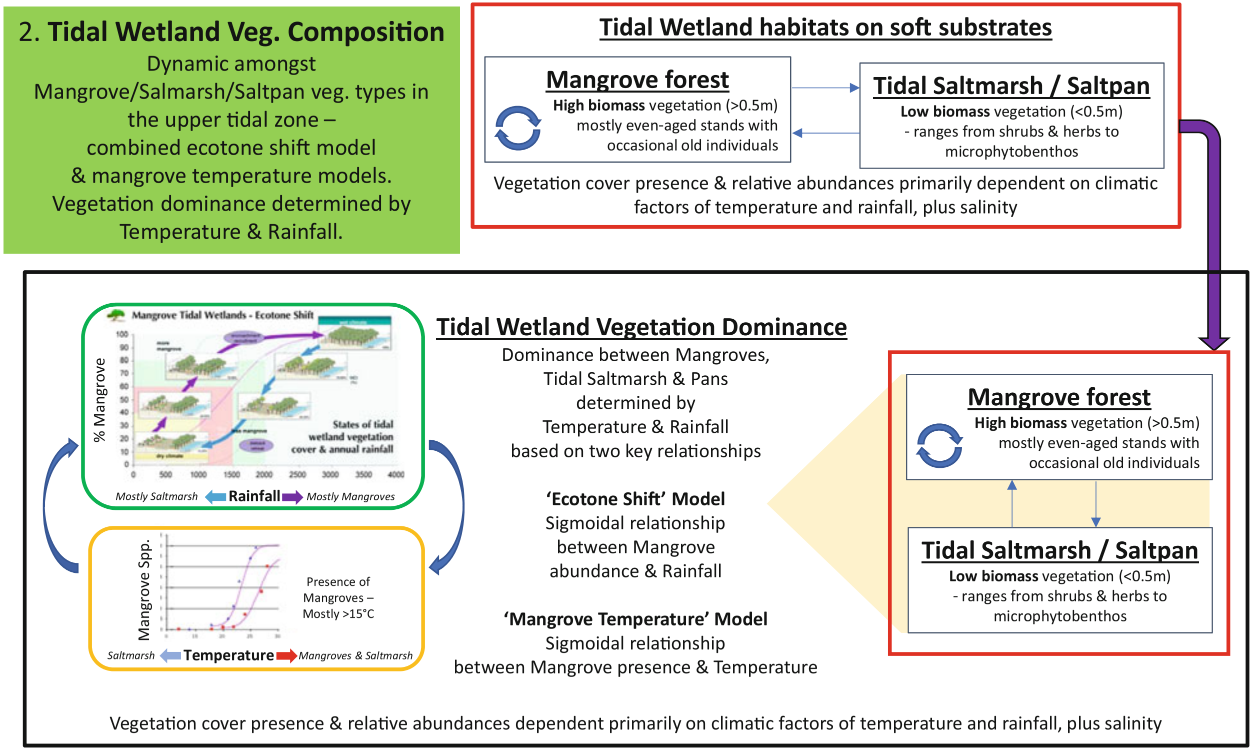


Fig. 9.3 Level 2 schematic conceptual model showing regional climate influences shaping tidal wetlands (red box) with the complex influences of climate variables, particularly temperature (yellow box) and rainfall (green box) (see Duke et al. 2019)

moisture conditions and higher temperatures tend to favour mangrove dominance. The relative abundance of tidal wetland vegetation components (tidal saltmarsh, saltpan and mangroves) is largely determined by local levels of temperature and rainfall—within the constraints defined in the Level 1 schematic (Fig. 9.2). The presence of mangrove species tends to be restricted to sites with higher temperatures while shorter saltmarsh plants, less constrained by temperature, are favoured in temperate settings in the absence of taller mangroves blocking available light. In addition, biomass and biodiversity are also affected, with mangrove and saltmarsh plant types more abundant where temperature and moisture conditions are moderate to maximal (Duke 1992; Duke et al. 2019). There are two distinct relationships for these factors. The models separately define relationships between biodiversity in particular, with either temperature or rainfall. The extent, composition and biomass of tidal wetland vegetation are all primarily influenced by temperature and rainfall. At this time, these influences are best characterised by two separate models for either temperature or rainfall that respectively define each relationship and the relative abundances of mangrove and saltmarsh-saltpan.

A third factor, salinity as the dilution of seawater, is influenced by both temperature and rainfall. This factor can be added to better define and explain the processes involved. While temperature influences relationships with latitude, and rainfall influences distributions across tidal profiles, salinity primarily influences occurrences along estuarine reaches upstream.

9.2.3 Level 3: Sustainable Turnover and Replenishment of Mangrove Forests: Small-Scale, Natural Disturbance Driving Forest Re-establishment, Development and Regeneration

Mangrove habitat is based on the stable structure of living organisms, analogous to coral reefs and forests generally. For this structure to be sustained through time, mangroves must be replaced naturally in an ongoing regenerative process (Fig. 9.4). Mangrove forests have well-developed adaptations and strategies for successfully achieving long-term survival in their specialised niche, including advanced propagule development, buoyant dispersal, enhanced establishment, rapid growth, efficient stand development and turnover. There are tolerances and limits to these capabilities, and once exceeded, the ecosystem and habitat are likely to collapse and become dysfunctional (Duke 2001).

The conceptual model for this third level of tidal wetland processes has been structured around the forest development model—establishment, stand growth, maturity and senescence (Duke 2001; Amir and Duke 2019). The features added relate to those that dominate and influence mangrove forests, like the importance of small gap creation and their restoration. For example, to explain the lack of mangrove forests in senescent conditions, it was proposed these forests were normally replaced before they exceeded advanced maturity. The schematic helps explain the vulnerability of this process by showing the importance of small gap creation events.

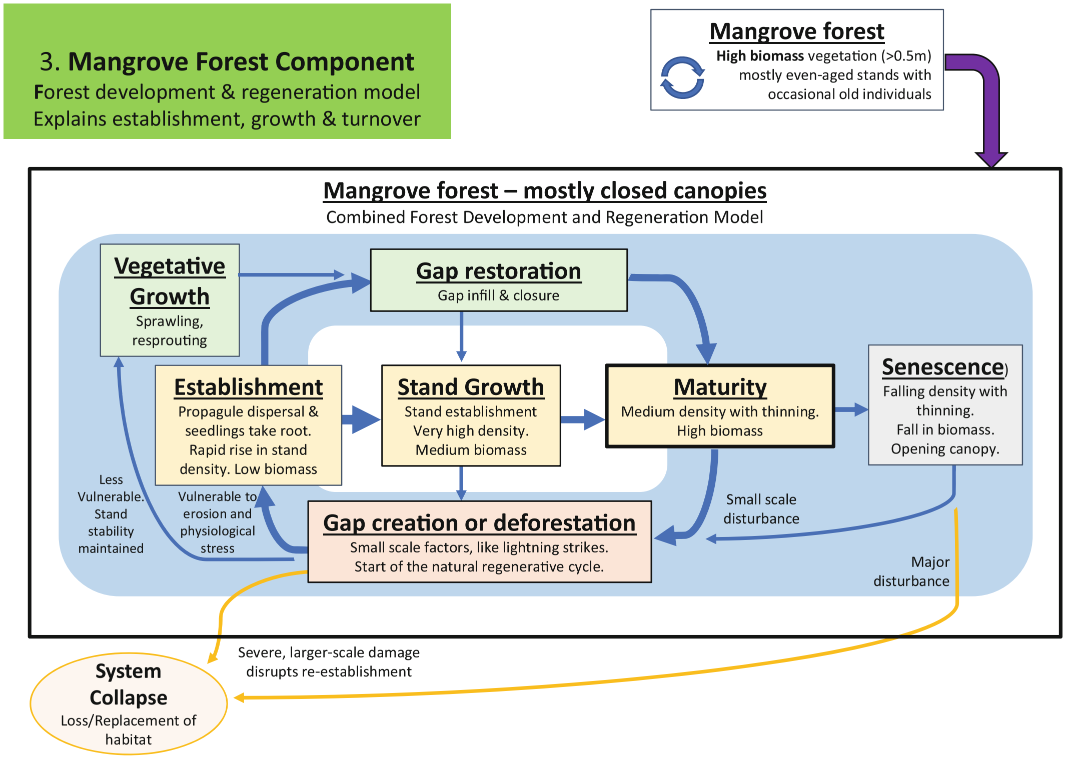


Fig. 9.4 Level 3 schematic conceptual model. The model of sustainable replenishment of mangrove forests has been adapted from a forest development and regeneration model with a notable emphasis on gap creation and restoration (adapted from Duke 2001)

Therefore, while gap creation helps maintain forest vigour and fitness with the maximal presence of healthy mature trees, when the disturbance frequency intensifies this drives higher rates of gap creation leading to the overwhelming of habitat regeneration processors. In this scenario, the mangrove habitat will collapse because there is insufficient time for recovery.

Figure 9.4 also describes a difference in recovery trajectories based on the severity of damage. While gap creation often involves tree death, there are occasions when a gap might be filled and recover by the ingrowth-expansion of surrounding surviving trees. In this case, recovery might be relatively rapid, occurring within a number of years. However, small gap recovery involves the establishment of seedlings and the growth of saplings where gap closure is often much slower, taking one or two decades.

The cause of light gaps in mangrove forests appears mostly to be due to lightning strikes (Amir and Duke 2019), although this remains to be proven. Other causes include herbivore or pathogen attacks, microbursts (small scale, intense downdrafts of wind), root burial from deposited sediments leading to tree death, timber harvesting and large oil spill contamination (Duke 2016).

9.2.4 Level 4: Severe Drivers of Change and Replacement of Tidal Wetland Habitat: Large-Scale Disturbance-Recovery Dynamics Influenced by Human and Natural Drivers

Locally, tidal wetland habitats have highly developed strategies and adaptations supporting their ability to regenerate (Fig. 9.5). When the habitat is disturbed by more extreme conditions exceeding ambient levels, as with catastrophic storms, human cutting, or large oil spills (Duke 2016; Duke et al. 1998), then there is an innate habitat response towards either recovery and re-establishment, or collapse with habitat loss when it fails. This dynamic response is initiated by a larger-scale disturbance event, and the subsequent processes in response incorporate the innate recovery processes of mangrove forests and tidal saltmarsh vegetation.

Severe damage to these tidal wetland components results in both sexual and asexual recovery processes being activated. Both can occur, but there are significant differences as asexual recovery (resprouts) can result in a rapid return to pre-damaged conditions and this pathway is the least disruptive. By contrast, the much slower sexual recovery is essentially the default strategy (depending on the dominant species present) should asexual recovery not be feasible, or the habitat setting has been transformed limiting germination.

Regeneration via sexual recovery takes an order of magnitude longer than asexual pathways (Duke 2016). This is because there is a reliance on the full reproductive development cycle of the affected vegetation, including floral development, fertilisation, seedling production, dispersal, plant establishment, and growth to maturity. During this process, possibly taking decades, the habitat remains vulnerable and at great risk from further disturbance affecting immature plants less able to resist and buffer the exposed conditions following disturbance. Stands undergoing

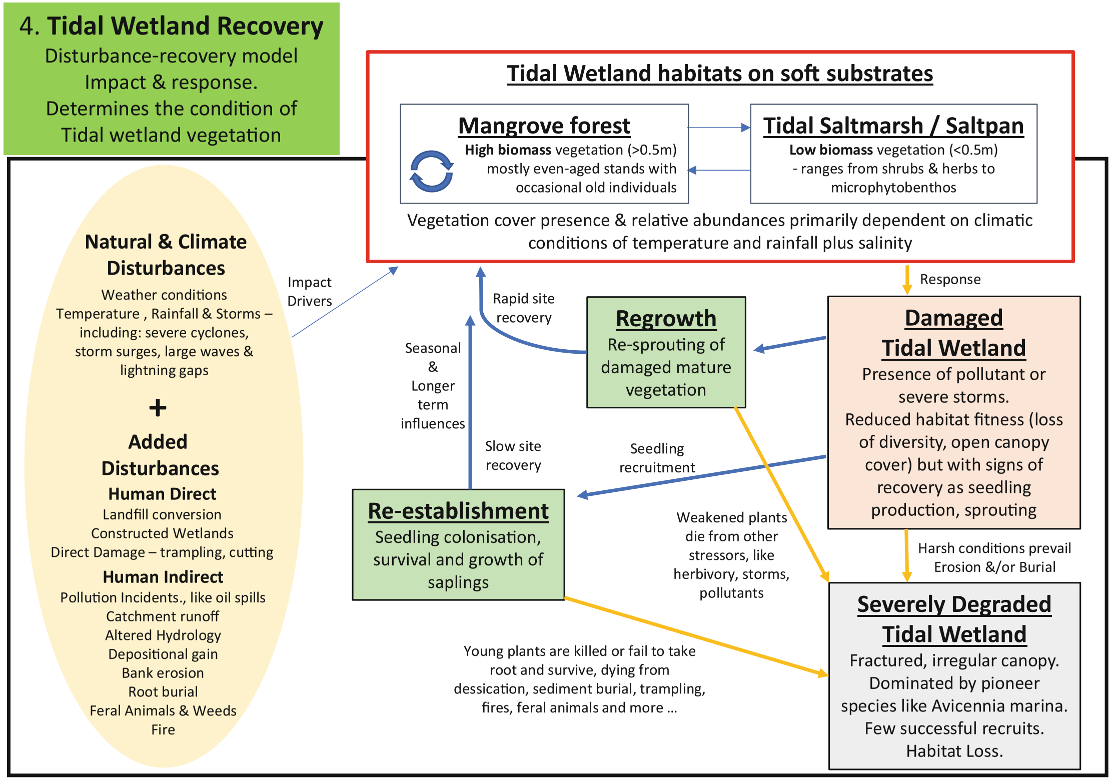


Fig. 9.5 Level 4 schematic conceptual model showing largely localised influences on tidal wetlands (red box) and their recovery processes initiated by various types of severe disturbances due to natural and human impacts. Blue arrows depict regenerative steps while yellow arrows describe initial impacts and degenerative processes (adapted from Duke 2016)

Table 9.1 Four levels of the factors driving key processes that define the occurrence, extent and character of vegetation types inhabiting tidal wetlands, including mangroves, tidal saltmarsh and saltpans. Blank spaces indicate overall influences from other process levels

	Regional drivers, Local impacts		Disturbance and responses	
	Level 1	Level 2	Level 3	Level 4
Physical factors	Shoreline topographic setting plus sea level	Climate variability—spatially & temporally	Regional mangrove forest replenishment with small-scale disturbances	Larger-scale, localised disturbances exceeding ambient range
Sea-level ambient range	Defined between MSL to HAT, mostly	Prevailing influences	Progressive plus fluctuating	Inundation, exposure, loss and gains due to flooding &/or encroachment
Slope	Various from gentle to steep	Prevailing influences	Slow spatial change	High rates of spatial change
Soil condition	Unconsolidated, occasionally coarse & hard	Prevailing influences	Soil stability influences	Loss or gain due to erosion scouring & burial deposition
Temperature		Latitude-related climatic zones	Extremes in evapotranspiration reduce habitat resilience	High- or low-temperature stress reduces biodiversity
Rainfall		Along tidal profile as groundwater, tidal inundation & direct rainfall	Incremental shift towards high or low biomass vegetation	Wet or dry conditions reduce biodiversity with dramatic impacts on
Salinity		Upstream estuarine flows & tides	Incremental shift towards high or low biomass vegetation	Hypersaline to hyposaline extremes reduce biodiversity
Storm severity			Cyclone—high winds, large waves cause plant damage & death in small patch areas	Cyclone—high winds, large waves cause plant damage & death across broad areas
Flooding events			Inundation, erosion, burial cause plant damage & death in small patch areas	Inundation, erosion, burial cause plant damage & death across broad areas
Pollutant incident			Toxic/smothering oil spill, chemical, nutrients cause plant damage & death in small patch areas	Toxic/smothering oil spill, chemical, nutrients cause plant damage & death across broad areas

Direct damage			Harvest, trampling, landfill of small patch areas	Harvest, trampling, landfill of broad areas
Lightning strike			Tree death and recovery in small mangrove canopy patch gaps	Tree death and recovery in compounded Level 3 areas.
Herbivore damage			Plant death and recovery in small patch gaps	Plant death and recovery of broad areas.
Pathogen attack			Plant death and recovery in small patch gaps	Plant death and recovery of broad areas
Temporal circumstances—timing, frequency	Ambient	Ambient	Regular or episodic	Episodic
Vegetation most affected	Tidal wetlands generally (L1 Model), but knowledge of influences on mangroves are better established	Tidal wetlands generally (L2 Model), but knowledge of influences on saltmarsh species are less known	Mangroves primarily (L3 Model)—small-scale saltmarsh turnover likely impacted by comparable disturbances	Tidal wetlands generally (L4 Model), broad-scale impacts largely dominated by mangrove vegetation as the higher biomass structural component

such recovery are continually vulnerable to large waves, strong winds, severe flooding, erosive currents, extreme desiccation, and these factors are often now combined with direct human pressures from pollutants, disrupted drainage, boat wash, cutting and access damage.

As with most tropical forests, mangrove stands comprise a canopy mosaic of different recovery phases from establishment to near maturity with stands distinguished by damaged and dead individuals along with varying growth stages to maturity. Figure 9.6 shows these two contrasting pathways and their respective periods of vulnerability leading to either habitat recovery or collapse. The distinction between recovery trajectories highlights the great importance of maintaining stand stability, if at all possible. Measures of damage severity and extent can support informative modelling of likely habitat recovery.

The type of drivers causing damage effect the rate and pathway to recovery. While all have distinguishable impacts, recovery processes differ when drivers include persistent detrimental effects of harmful pollutants like oil spillage (Duke 2016), agricultural pesticides (Duke et al. 2005) and excess nutrients (Lovelock et al. 2015). By contrast, physical damage from storms and large waves has no persistent detrimental factors limiting their recovery (cs. Duke et al. 2017).

9.3 Climate and Natural Drivers of Key Environmental Changes Along Mangrove Shorelines

The state, condition and health of shorelines can be classified and quantified according to a series of indicators as potential drivers of change (Fig. 9.6). Their consideration provides an improved ability to monitor change affecting tidal wetlands on a broad scale. These data can be used to monitor habitat conditions associated with identified drivers, as well as providing an assessment benchmark for local and national management priorities.

An assessment protocol quantifying these processes compliments pre-existing mapping of coastal environment and tidal wetland habitats using remote sensing of oblique and vertical imagery. In the following section and in reference to Fig. 9.6, a selection of major drivers of change are described. In consideration of our case study evaluation of the cause of mangrove dieback in the Gulf of Carpentaria, we focus particularly on drivers related largely to climate and natural processes affecting tidal wetlands and shorelines (Duke 2014), acknowledging that each are indirectly affected by anthropogenic greenhouse gas emissions.

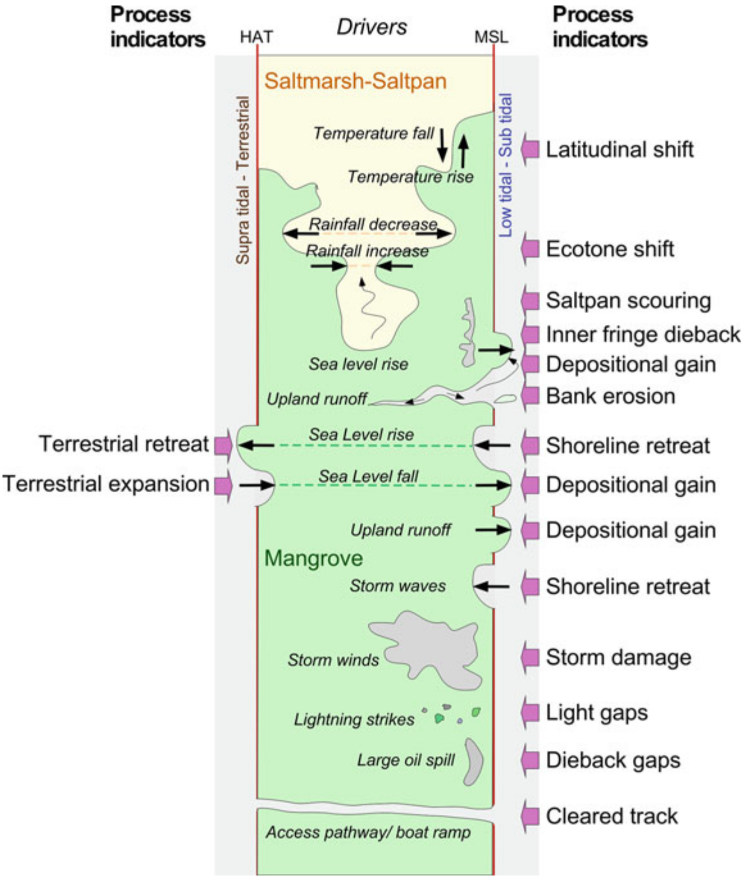


Fig. 9.6 An illustrative schematic showing process response indicators associated with respective drivers acting at the more obvious ecotone locations across the tidal profile

9.3.1 Shoreline Erosion and Seafront Retreat: Severe Storms, Sea Level Rise

Cause Storm conditions coupled with progressively rising sea levels cause incremental and progressive loss of shoreline mangrove habitat.

Indicator Loss of foreshore and shoreline mangrove vegetation marked by fallen and eroded dead trees and exposed stumps, eroded peat mat, and uprooted mobilised stem wood. Instances often also have a lack of seedlings and regrowth recovery, along with the close proximity of depositional sediment banks and berm ridges (see Fig. 9.7).

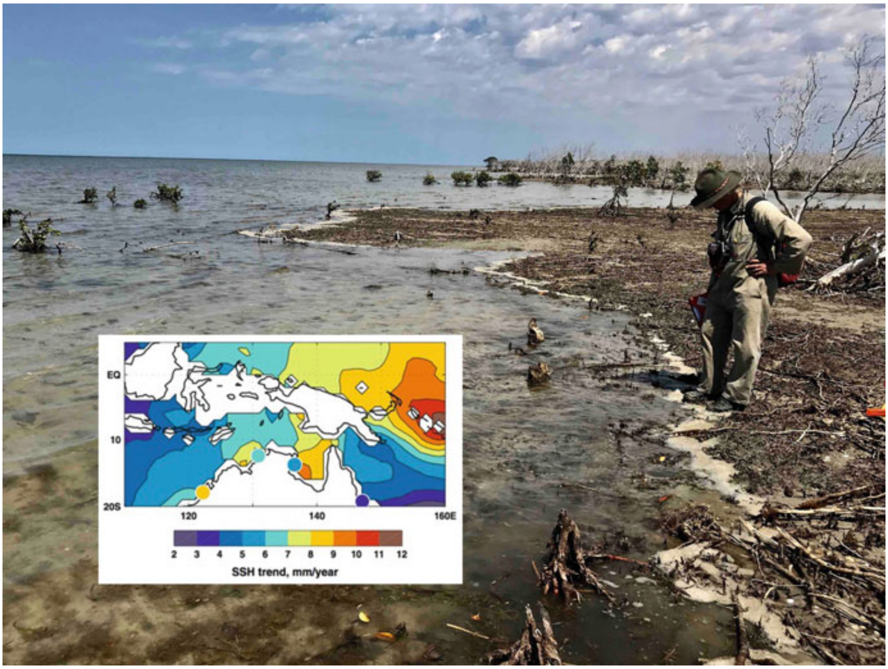


Fig. 9.7 Shoreline erosion occurs when sea edge trees are lost, as seen in the Gulf of Carpentaria (Limmen Bight shoreline at location 1 (Fig. 9.1), Northern Territory, in 2018). Surviving plants are unable to resist strong winds and waves that regularly buffet exposed shorelines. Seedling re-establishment is seemingly too slow and unable to keep up. This can be due to a change in Level 1 processes associated with rising sea levels, but at a local scale similar impacts may be due to Level 4 processes, like cyclones. INSET. Sea level trends estimated from satellite altimeter data from January 1993 to December 2007 in the region. Comparable sea level data from tide gauge data from the National Tidal Centre are indicated by the coloured circles (Image credit: NC Duke)

Impact A loss of shoreline mangrove vegetation not only represents the loss of habitat and ecosystem benefits, but also identifies locations currently experiencing unsustainable rates of change. Such eroded shorelines are highly vulnerable to further imminent disruptive events because they lack the normal protection of exposure-adapted, frontal tree species. Mangrove tree structural types differ in growth form depending on their position along the tidal profile and where they are established. Once matured, these trees are unable to change and adapt further. Exposed seafront positioned trees develop sturdy support structures extending the complex tangle of prop roots of *Rhizophora* species (also see Fig. 9.8). When the same species grow in the middle of a forest, they have significantly fewer prop roots and support structures. In these circumstances, inner trees redirect their growth and structure into gaining maximal crown height in response to light competition. When exposed to shoreline erosion, the inner trees offer little or no benefit in terms of protection for shorelines, or themselves. The only way shoreline mangroves can be re-established is with new recruits growing in exposed conditions. In regions experiencing high rates of sea level rise, this may not be possible! Such shorelines are highly vulnerable.

Process Level This factor relates to the Level 4 (Fig. 9.5) disturbance processes combined with an unusual change in a Level 1 (Fig. 9.2) setting driver, namely sea level. The impacts of rising sea levels are likely to be more severe when combined with severe storms, and any other factors causing damage to protective shoreline vegetation.

9.3.2 Estuarine Bank Erosion: Flood Events, Sea Level Rise

Cause The banks of estuarine channels are regularly inundated by seawater and drained with each tidal cycle. Depending on tide levels, higher flow rates can cause severe erosion. Tidal flow rates are amplified further during periodic flood runoff events. These processes cause significant bank erosion, restructuring of channel margins and mobilisation of sediments. The alternate condition in part is described as depositional gain.

Indicator Eroded banks are steep slopes, showing bare and crumbling earth faces, slumped bank sections with intact vegetation, along with general remnants of collapsed and undermined vegetation like fallen trees, uprooted and inundated plants as seen in many Gulf estuaries (Fig. 9.8).

Fig. 9.8 Bank erosion is normal where it occurs as the alternate response to depositional gain (Fig. 9.11). The two responses account for the slow but natural shift of riverine channels as they meander and migrate across lower estuarine tidal flood plains (Limmen River lower estuary, Northern Territory, in 2017). However, when one exceeds the net effect of the other, this imbalance indicates Level 4 process changes associated with factors like rising sea levels causing increases in tidal volume of estuarine systems (Image credit: NC Duke)

Impact Lost mangrove habitat represents a loss of ecosystem benefits. Also significant is the loss of bank stability much as mentioned with Shoreline Erosion. Such estuarine banks are highly vulnerable.

Process Level This factor mostly relates to a Level 4 process. However, because of rising sea levels, a Level 1 process, there is a greater level of impact delivered by the increased frequency of flooding from the catchment.

9.3.3 Terrestrial Retreat: Upland Erosion, Sea Level Rise

Cause When sea levels rise progressively over time, there is continual pressure on high intertidal shorelines behind tidal wetland habitat and bordering the verge of supratidal vegetation. This upward pressure is caused by saltwater encroachment and higher tidal inundation levels during seasonal and daily highwater tidal peaks.

Indicator There are two notable effects that represent these types of changes: (1) erosion along the upper intertidal edge as a shallow eroded ledge (Fig. 9.9), and as scouring of small runoff tributaries; and (2) death of established supratidal vegetation, like dead *Melaleuca*, *Casuarina* and *Eucalyptus* trees. These effects are

Fig. 9.9 Terrestrial retreat, coupled with saline intrusion, is marked by erosion and dieback of supratidal terrestrial vegetation, and encroachment of mangrove seedlings (Mule Creek area, Northern Territory in 2017). This impact is considered an indicator of changes to Level 1 processes, notably rising sea levels. Impacted sites are likely greatest in areas of flatter terrain (Image credit: NC Duke)

combined with mangrove encroachment which may be scored separately, but dead mature terrestrial trees are more visible than newly established mangrove seedlings, as seen in upper tidal shorelines throughout the southern Gulf (Fig. 9.9).

Impact This impact mostly concerns the loss of supratidal vegetation and the possible expansion of mangrove areas. The ongoing erosion and death of terrestrial vegetation however makes it difficult for the re-establishment of bank stability along this major ecotone. These areas are highly vulnerable with added pressures on seedling establishment.

Process Level This factor mostly relates to a Level 4 process with an unusual change in a Level 1 character. This is driven by rising sea levels.

9.3.4 Saltpan Scouring: Pan Erosion, Sea Level Rise

Cause When unusual and progressively higher levels of tidal waters flood across tidal saltpans, sediments can be sheet eroded, scoured and transported into tidal channels. An associated driver with this one might be Terrestrial Retreat Erosion.

Indicator Scoured saltpan surfaces marked with drainage lines coupled with a lack of saltmarsh vegetation across the saltpan surface, as seen in the Gulf (Fig. 9.10).

Fig. 9.10 Surface sheet erosion is a consequence of additional water in an estuary (Limmen River upstream, Northern Territory in 2017). As with terrestrial retreat, saline intrusion, and mangrove encroachment, this impact is associated with rising sea levels as a Level 1 process (Image credit: NC Duke)

Impact The loss of saltmarsh habitat is significant. There is also a further supply of fine sediments finding their way into the estuary and likely further contributing to depositional gain. In extreme instances, saltmarsh vegetation including natural layers of microphytobenthos has been unable to re-establish so the whole inundated area is actively scoured leaving bare sediments and pools of residual tidal waters.

Process Level This factor mostly relates to a Level 4 process with an unusual change in a Level 1 character. This is driven by rising sea levels coupled with wide gentle sloping profiles.

9.3.5 Depositional Gain: Flood Events, Sea Level Rise

Cause Depositional gain is particularly evident along estuarine channels where seedlings colonise accreting banks. When sediments are flushed downstream from catchment areas disturbed by flooding erosion, they are usually deposited towards the river mouth and along lower estuarine channel margins. The depositional materials often emerge as large mudbanks and form mangrove ‘islands’ when colonised naturally by mangrove vegetation. Mangroves appear to colonise these banks after mud banks exceed mean sea level elevations—the mangrove ‘sweet spot’ zone.

Indicator Newly recruited mangrove seedling and sapling stands growing on shallow muddy banks generally towards the lower estuarine reaches towards the mouth of riverine estuaries (Fig. 9.11). Various key mangrove genera are involved including mostly: *Avicennia*, *Rhizophora*, *Aegialitis*, *Aegiceras* and *Sonneratia*. In general, depositional gain is indicative of the combination of sediment transport processes including catchment runoff and the reworking of deltaic sediments, as seen in the Gulf (Fig. 9.11).

Impact With the increase in mangrove plants, there is a gain for mangrove habitat. But, these new habitats will take many decades to achieve the roles provided by mature stands. As such, this process is likely offset by bank erosion upstream, which is generally seen as the active alternate condition to depositional gain along typical estuarine meanders.

Process Level This factor mostly relates to Level 4 with an unusual change in a Level 1 character. It occurs mainly because of increased flooding across areas of largely unconsolidated sediments, coupled with rising sea levels.

Fig. 9.11 Depositional gain occurs when mangrove seedlings and saplings occupy accreting mudbanks exceeding elevations above mean sea level. Because this additional sediment deposition can be associated with periodic flood events, the expanding vegetation canopy is often stepped and incremental (near Leichardt River mouth, QLD. In 2017. This feature is indicative of a Level 4 process related to larger flood events (Image credit: NC Duke)

9.3.6 Severe Storm Damage: Mangrove Dieback, Cyclonic Winds, Large Waves

Cause Storm conditions bring heavy seas, strong winds and scouring currents that often cause significant and extensive damage to tidal wetland and mangrove habitat. A key agent of such destructive weather conditions is tropical cyclones (Fig. 9.12). The resulting impacts are usually localised in timing and severity, as recorded by the tracks over the last 20 years in the Gulf of Carpentaria (Fig. 9.13).

Indicator Loss of saltmarsh vegetation and loss of mangroves as defoliated uprooted broken trees as well as the loss of canopy cover (Fig. 9.12). For mangroves, both the re-established younger plants and the degradation state of dead trees are indicative of when the damage occurred.

Impact Habitat damage and losses reduce the fitness of tidal wetlands. As a consequence, the ecosystem services are also lost. It is important to quantify such indirect consequences. One key example the likely effects on local fisheries, or any loss of shoreline protection with erosion.

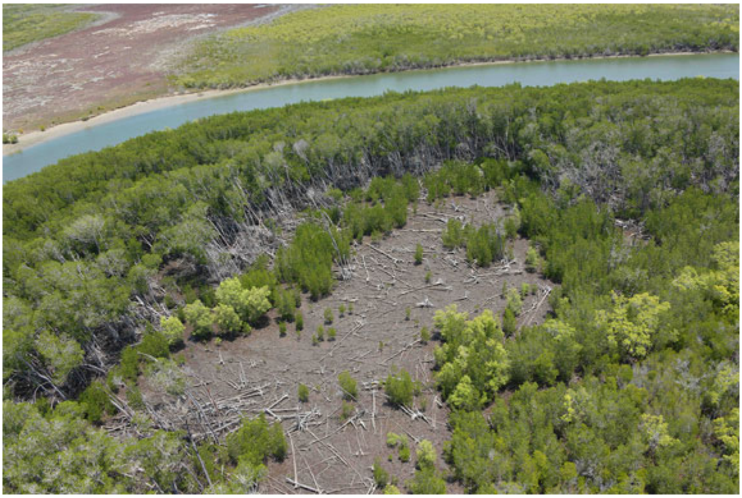


Fig. 9.12 Cyclones often cause severe damage to mangrove forests. Note that where more resilient, exposure-adapted, edge trees remained intact, damaged areas may recover but only after several decades after seedling re-establish amongst the dead and damaged trees (Rose River lower estuary, Northern Territory in Dec 2017; damaged possibly by TC Winsome in Feb 2001, a 981 hPa storm). This impact is a Level 4 natural process (Image credit: NC Duke)

Process Level This factor mostly relates to Level 4 and it occurs mainly because of occasional extreme sea level lows and severe storms coupled with a shoreline weakened by rising sea levels.

9.3.7 Light Gaps: Lightning Strikes, Herbivore Attacks, Mini Tornados

Cause When severe storm weather includes lightning strikes, it causes notable and distinctive damage to mangrove forests in the form of discrete, circular light gaps (Fig. 9.14). These gaps are typically 50–100 m^2 in area. The impacts are unlike other storm damage where trees die standing and unbroken. As gaps mature, the dead trees deteriorate, seedlings establish and grow, and eventually after about 2–3 decades, the gap fills. This process may explain how mangrove forests naturally regenerate and sustain their existence in such a wide selection of locations.

Indicator These relatively small circular light gaps are observed in mangrove forest canopies worldwide. It is important to recognise that gaps will be at a particular stage towards recovery and closure depending on when they were created (Fig. 9.14). Only for 1–8-year-old gaps will the original trees be recognisable as the ones that started the process. While the number of gaps is considered an indicator of storm

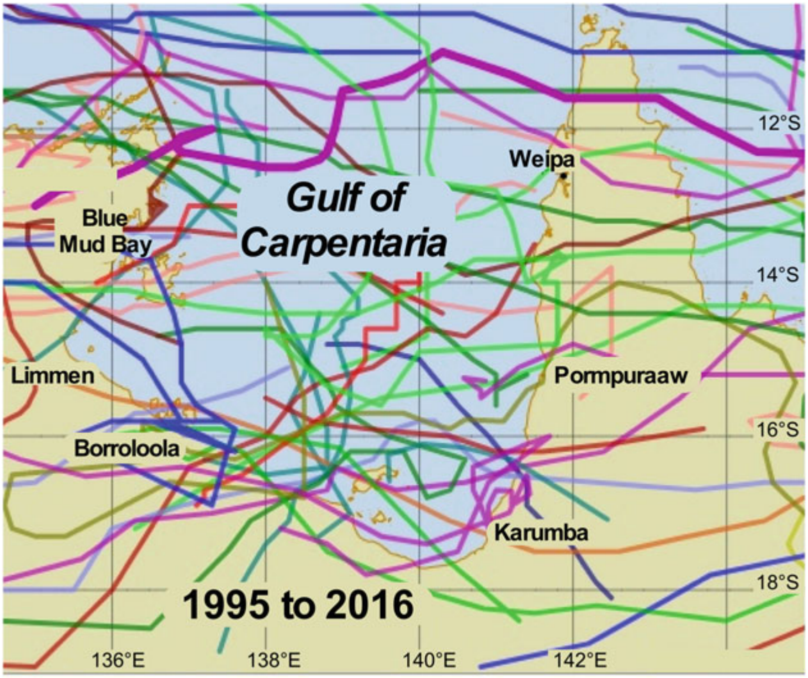


Fig. 9.13 Cyclones are a common feature in the Gulf of Carpentaria. This figure shows tracks of cyclones in the region during the last 20 years, roughly 1–2 each year. Overall, there is a regional net influence, but the impacts delivered by these events are mostly localised as Level 4 damaging processes. This is exemplified further where some shorelines have been notably less affected during this time (BOM 2020)

frequency, the net effect appears to influence the stand age of mangrove forests which curiously lack old senescent stands (Duke 2001).

Impact Light gaps are considered fundamental to forest replacement and turnover. It is notable that the frequency of gap creation is likely dependent on storm severity. As such, as this might increase in any particular area then this will have a profound effect on forest turnover rates. At higher levels of impact, these forests are predicted to be unable to sustain the natural processes involved in their replacement. At this point, mangrove forests would enter a state of ecosystem collapse as the stand becomes fragmented and dysfunctional.

Process Level This factor mostly relates to Level 3 (Fig. 9.4) and it occurs because gap creation is coupled with the increased severity of damaging factors like storms.

Fig. 9.14 Light gaps are caused by lightning strikes killing small patches (~50 m^2) of mangrove trees in amongst otherwise undamaged surrounding mangrove forests. The creation of such gaps is believed to be the chief driver of Level 3 processes responsible for their natural turnover and replacement (Duke 2001; Image credit NC Duke)

9.3.8 Zonal Retreat: Local-Scale Patterns of Single, Dual and Triple Zones of Concurrent Upper Zone Dieback

Cause Zonal retreat describes the relocation of the vegetative habitat of the intertidal zone to higher or lower elevations with respect to the change in water level. For example, tidal wetlands affected by rising sea levels involve concurrent recruitment and expansion into upland habitat with corresponding dieback and loss of mature mangroves at the low water's edge. By contrast, a temporary drop in sea level was experienced in the Gulf of Carpentaria (Duke et al. 2017; Harris et al. 2018) forcing a severe stress response in plants left stranded at higher elevations.

Indicator When a band of mangrove vegetation dies suddenly at the upper ecotone fringe with saltmarsh vegetation, this may be indicative of a sudden drop in sea level. This might be caused by tectonic uplift, severe ENSO events, or it might be due to subsidence, or simply changes in barometric pressure.

Impact Habitat loss reduces the fitness of tidal wetlands and in consequence, the ecosystem benefits may also be lost, like their value to local fisheries or their role in the protection of shorelines from erosion.

Process Level This factor mostly relates to Level 4 where it concerns the unusual and sudden change in a Level 1 character.

9.4 The Synchronous, Large-Scale Mass Dieback of Mangroves in Australia's Remote Gulf of Carpentaria

Observations of driving factors mentioned above describe a range of processes likely to be responsible for the occurrence and condition of tidal wetland habitats, including mangroves in the Gulf of Carpentaria (Fig. 9.1a, b; Table 9.2). Key questions include how severely has the Gulf coastline been impacted and what factors had contributed to such a sudden event? Was this instance of large-scale dieback influenced or caused by climate change, and what is the expectation of its re-occurrence?

Laurance et al. (2011) suggested salt marshes and mangroves were in Australia's top ten most vulnerable ecosystems, with sea level rise, extreme weather events and changes to water balance and hydrology ranked as the three most likely threats. These predictions appear to be broadly accurate as in late 2015 and early 2016, the vast area of more than 80 km^2 of mangrove forests bordering Australia's Gulf of Carpentaria died *en masse* with no known precedent for such a simultaneous and widespread occurrence (Duke et al. 2017). The dieback was extensive and it occurred in synchrony across more than 1500 km of exposed shorelines from Queensland to the Northern Territory (see Fig. 9.15). Canopy vegetation condition expressed as a fractional green cover derived from Landsat and Sentinel-2 data for each of eight sites at four locations spread across the Gulf (Fig. 9.1; see insert). Each time series shows localised changes in cover between 1987 and 2018, highlighting the event in late 2015 when the synchronous mass dieback occurred. This shows unequivocal evidence of a singular, regional-scale impact that defines this mass dieback event.

Table 9.2 A brief summary of environmental observations associated with the 2015 mass mangrove dieback event in Australia's Gulf of Carpentaria (Duke et al. 2017), updated in 2018

General observations	Observed impact	Likely cause	Recovery or degradation	Consequences
Mangrove condition—extent	Dieback of 8000 ha widespread over 1500 km	Regional applied factors	3 years post event, degradation appears to outweigh recovery	Likely to influence fisheries catches, enhanced sediment mobilisation
Mangrove condition—timing	Dieback occurrence synchronous	Single unusual event	Negative localised influences of severe storms and flooding	Shorelines habitats at risk where they share threats
Mangrove condition—biodiversity	Dieback of multiple mangrove species	Setting factor like species zonation	Recovery and degradation rates of wood and roots vary for each species	Some species are at risk of local extinction
Mangrove condition—tidal elevation	Dieback at higher elevation zones and of taller plants	Factor related to tidal elevation	Because taller trees affected most, there is reduced erosion and exposure resilience of surviving stands	The loss of entire foreshore fringing stands, likely to take many decades to recover, if at all
Extreme events—natural variability	No widespread severe storms, cyclones, tsunamis, flooding, etc.	Not applicable	Subsequent cyclones and flooding are likely to cause severe damage to natural recovery	Disturbances likely to alter ecosystem replacement and turnover processes
Extreme events—anthropogenic	No widespread oil spills or other pollutant or sediment discharges	Not applicable	Not applicable	Reduced resilience of shoreline habitats
Extreme events—temperature climate and weather	Likely to be related but limited direct evidence	Extreme high temperatures	No subsequent events of comparably high temperatures	Vulnerable to future extreme high-temperature events
Extreme events—rainfall climate and weather	Likely to be related but limited direct evidence	Prolonged drought and extreme low rainfall	No subsequent events of comparably low rainfall	Vulnerable to future periods of low rainfall
Extreme events—sea level rise	Likely to be related but limited direct evidence	Rising sea levels up to 3×'s the global average	Rising sea levels are likely to affect recovery trajectories	Saline inundation, erosion of terrestrial edge habitats plus scouring of saltmarsh-saltpan
	Very likely related	Temporary sea level	No subsequent events	Damage to shoreline integrity

(continued)

Table 9.2 (continued)

General observations	Observed impact	Likely cause	Recovery or degradation	Consequences
Extreme events—sea level drop		drop of 20 cm Sept–Dec 2015		and exposure resilience

Supplemental source: Hope et al. (2016)

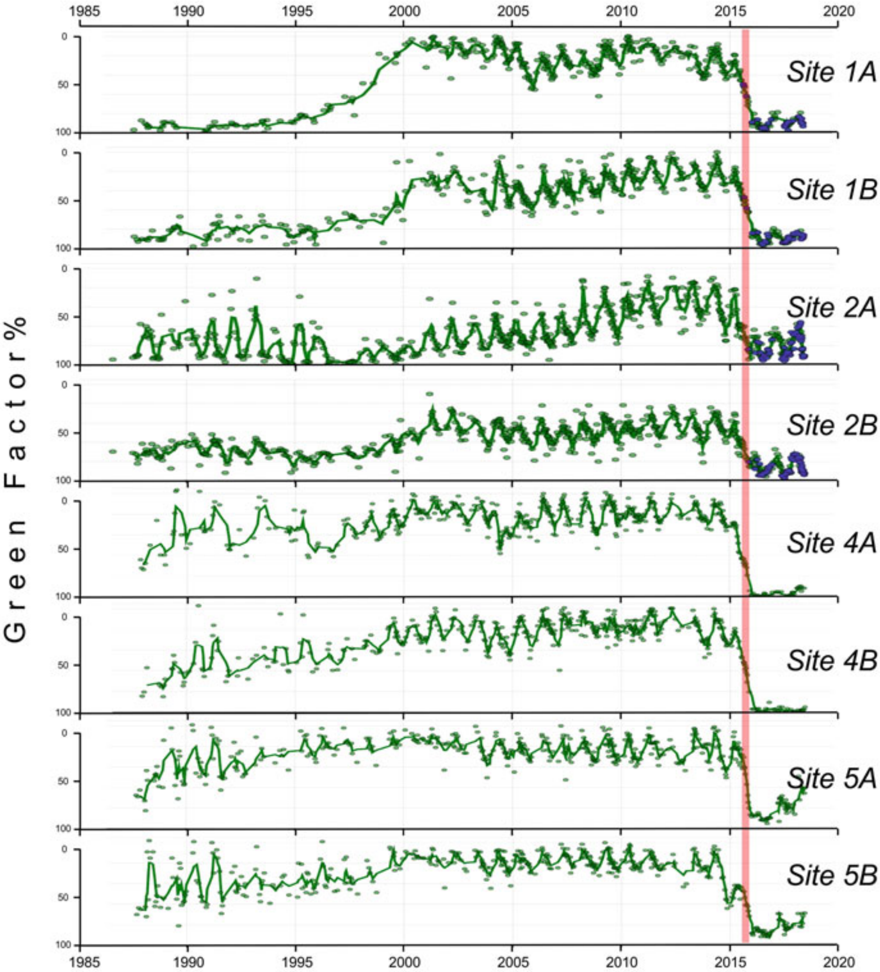


Fig. 9.15 Time series plots of green fractional (Bokeh) cover estimates from Landsat and Sentinel-2 for the four field locations in the Northern Territory (site locations 1 and 2, Fig. 9.1a) and Queensland (site locations 4 and 5, Fig. 9.1) during 1987–2017. The red line indicates the synchronous timing of the late 2015 mass dieback event. The widespread impact was indicative of a dramatic change in a Level 1 factor (see Fig. 9.2)

Box. Mangrove Diversity in the Area of Mass Dieback of Mangroves
Mangrove plant species diversity is relatively low compared to other tropical forest habitats because of the harsh environmental limitations imposed by regular saline inundation. There are around 80 species and hybrids known worldwide (Duke 2017); 46 of these occur in Australia and 25–28 in Australia's Gulf of Carpentaria (Duke 2006). These numbers are further reduced in the southern Gulf with just 12–16 species in this semi-arid (mean annual rainfall ~700 mm) area where the mass dieback of mangroves occurred (Duke et al. 2017). Each of these variations in diversity is directly attributed to levels of rainfall with fewer species in drier regions (Tomlinson 2016). These depressed levels of diversity exemplify that this Gulf area is normally under considerable environmental stress. As such, it is perhaps not surprising therefore that such an area was the first known for a mass impact on mangroves caused by a particularly extreme fluctuation in mean sea level.

With the death of so many mangroves, erosion of the shoreline was expected to follow. But, by how much, and how long before this might be observed? Would there be any recovery? The occurrence of such a large-scale disturbance to shoreline mangroves has raised serious concerns about the consequences for shoreline mangroves and the growing risks these habitats face as the threatening pressures escalate (Harris et al. 2018; Bergstrom et al. 2021). This places a growing urgency towards gaining a better understanding of the key drivers of such a major disturbance event and to ask how had these pressures impacted this mangrove ecosystem to such an extent.

Having established that the mass dieback event was very likely in response to an extreme climate event (Duke et al. 2017), questions were focused on verification as well as the likely implications for policy and management. Local managers facing the consequence of losing significant beneficial natural resources were considered justified in their concern. More informed and targeted strategies would appear to be required to minimise future impacts affecting the social and economic well-being of human communities living in coastal areas generally, and especially along the remote Gulf shoreline. We outline key deductions and lessons learned in reviewing these deductions regards the mass dieback event in the context of other large-scale disturbances.

Our deductions must be prefaced by the manifest realisation that tidal wetland ecosystems are vulnerable and sensitive to both moderate and extreme fluctuations in climate and weather (cs., Duke et al. 2019). Our goal therefore at this time has been to better define the disturbances and risks faced by these unique ecosystems, and to do this by referring to the four process levels involved (Figs. 9.2, 9.3, 9.4, and 9.5) to qualify and possibly quantify the factors identified (Table 9.2). This evaluation is helped also by considering some of the major stochastic processes associated with this event, as recorded in imagery collected during field and aerial surveys of the impacted areas of the Gulf (Fig. 9.16). The image shows the often-complex overlap

Fig. 9.16 An extreme instance of compounded 'classes/types' of temporal and spatial processes observed along shorelines of the Gulf of Carpentaria in December 2017. Note that among other things, foreshore erosion and retreat have left remnants of earlier foreshore mangrove stands marked by short dead stumps, sediments mobilised in various ways, a chenier ridge of drift sands, along with the extensive 2015 dieback of the uniform stand of dead mangroves behind the ridge (Image credit: NC Duke)

of temporal and spatial processes present along this broad shoreline. In the case shown, the processes included:

1. Earlier dieback 20–30 years prior to 2017—visible as dead stumps towards the seaward margin
2. Shoreline sediment mobilisation and shoreline retreat
3. Chenier ridge development with sediment trapped by remnant dead trunks
4. Development of mangroves behind the chenier ridge
5. Channel formation behind the mangrove fringe with root development and sediment trapping raising the mangrove topographical profile
6. Channels prevent further upland migration of mangroves.
7. Shoreline retreat and mangrove regrowth determined by ambient sea level conditions
8. The zone of 2015 mangrove dieback

These and other processes need to be reasonably defined and where possible accounted for. While the circumstances do not necessarily follow standard geomorphological description, they do show the influence of exposure and sediment condition. With such matters in mind, a systematic compilation is being undertaken to more fully describe the location and frequency of at least the more common and widespread factors, especially for the 2015 dieback damage. At this time, it is possible to broadly focus on the key factors involved.

9.4.1 Likely Causal Factors Observed Along the Impacted Shoreline

The dieback event was strongly linked to the severe El Niño of 2015–2016, the third most severe event in Australia's instrumental climate record (Hope et al. 2016; Harris et al. 2017). Arguably the key factor responsible for the mass dieback appears to have been a temporary 20 cm drop in sea level that reduced levels of tidal inundation (Duke et al. 2017). The drop in sea level was also co-incident with above-average air temperatures and drought conditions with over 4 years of below-average monsoonal rains (see Fig. 9.17).

The impacts of these short term 'pulse' events (rapid drop in sea level, elevated temperatures, monsoonal failure) were amplified by a longer-term climatic 'press' driven by decades of air and ocean warming (Harris et al. 2018; Bergstrom et al. 2021). Weather data gathered from eight meteorological stations spread across the Gulf south coast region (Numbulwar, Ngukurr, Borroloola, Centre Island, Macarthur River Mine, Mornington Island, Burketown, Normanton) showed mean temperatures rose by around 0.9 °C over the previous 50 years, and that temperatures during late 2015 exceeded all previous records—as shown in the plot (Fig. 9.17a). While concurrent rainfall levels were mostly below average over the 4 years previous to 2015, over the last 50 years there was no distinguishable trend in mean rainfall (Fig. 9.17b).

There was, however, a significant long-term rise in sea level recorded across three monitoring stations (Milner Bay on Groote Island, Karumba and Weipa; see Fig. 9.17c). This trend had a mean 3.65 mm/year rise in sea level over the previous 25 years (9.1 cm over the period). These data were detrended based on this rise to further emphasise the unusually low sea levels at the time of the mass dieback in 2015. The reduced sea levels were a notable consequence of the particularly severe El Niño event depicted in Southern Oscillation Index measures (Fig. 9.17d).

Sea levels are particularly sensitive to changes in climatic conditions, including atmospheric wind forcing (Wyrtki 1984, 1985). When a severe El Niño event occurs, such as the 2015–2016 event, the prevailing wind field collapses (Freund et al. 2019). In southern tropical latitudes, this results in prevailing south-easterly trade winds being reversed by strong westerly winds. These unusual atmospheric conditions force warm surface waters from the western to the eastern side of the Pacific Ocean for as long as the El Niño conditions last. The resulting sea levels in the western Pacific can be notably lower (up to 20 cm), and in the eastern Pacific, they will be correspondingly higher and warmer. During these times also, there are often an unusually large number of tropical cyclones.

Severe El Niño conditions bring large changes to sea level and extreme climatic conditions like drought and heatwave. Together, they have a strong influence on

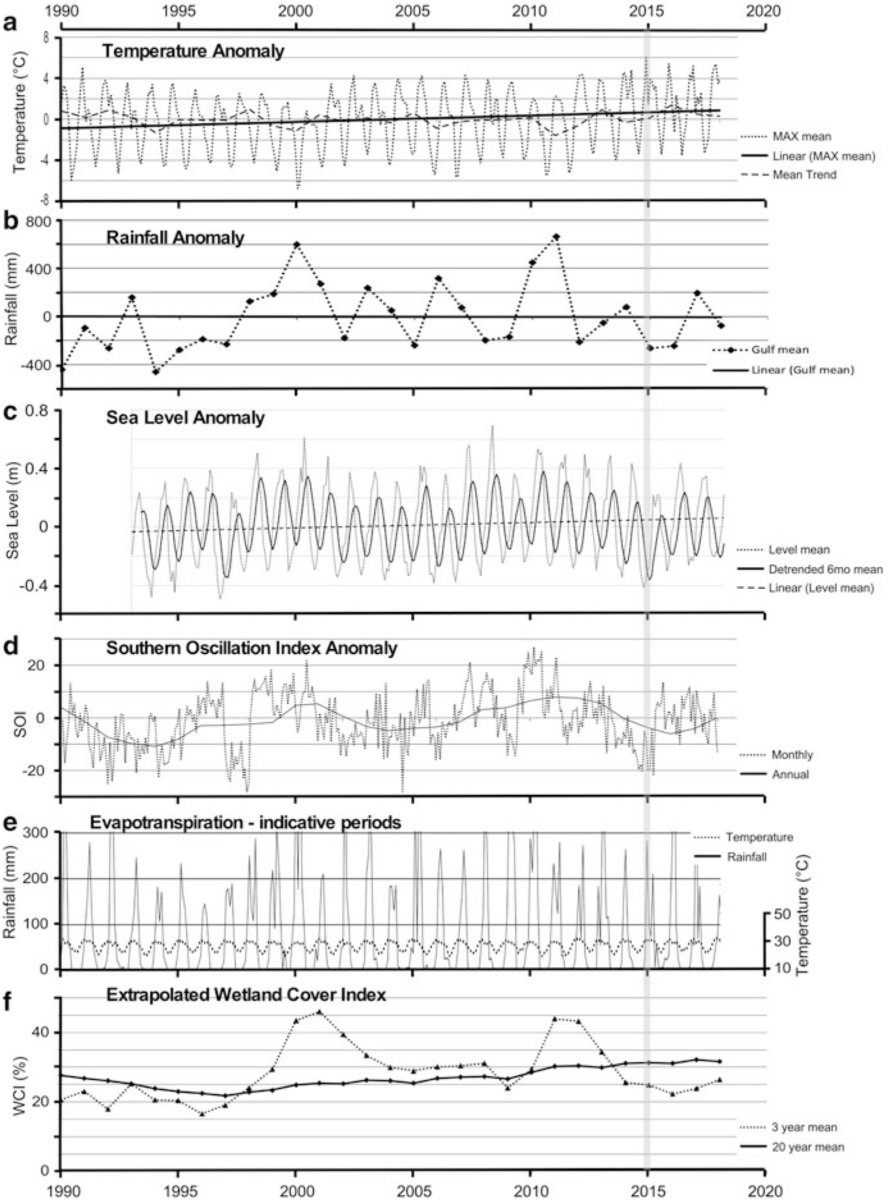


Fig. 9.17 The condition of climate and environmental factors up to and after the 2015 mangrove dieback event (grey vertical line) in the Gulf of Carpentaria. Data were sourced online mostly from the Australian Bureau of Meteorology (BOM 2020). Factors showing anomalies were calculated using the 1990–2019 reference period, including (top to bottom): (**a**) temperature monthly and annual mean maxima plus the overall trend; (**b**) rainfall annual means plus the overall trend; (**c**) sea level monthly means, the overall trend, and the detrended six-monthly means; (**d**) the Southern Oscillation Index monthly and annual means; (**e**) indicative levels of evapotranspiration shown as periods when the temperature exceeded rainfall at respective scales; and (**f**) wetland cover index levels deduced from its rainfall correlate (see Duke et al. 2019) using 3- and 20-year running means

mangrove forests. These tidal habitats are already under extreme pressure from steadily rising sea levels. The 2015–2016 mass dieback of mangroves has therefore been considered a classic ‘press-pulse’ response as described by Harris et al. (2018) for this and other ecosystems across Australia, both marine and terrestrial. Available moisture, vapour pressure, temperature and sea level across the Gulf of Carpentaria up to and during the dieback period were all consistent with a failure in the monsoon’s normal arrival that year (Harris et al. 2018). These were likely to have influenced the widespread occurrence of hypersaline sediment porewater, resulting in severe mortality of mangroves as conditions exceeded plant tolerances. These conditions are likely to have resulted in the rapid decline seen in mangrove cover during November–December 2015 (Fig. 9.15) which persisted into the dry season of 2016. Apparently, similar circumstances were reported by Lovelock et al. (2017) for mangrove stands on the semi-arid Western Australian coastline, except that the drop in sea levels was not as large as that experienced along the Gulf. Nevertheless, low sea levels had corresponded with the 2015–2016 ENSO event, resulting in enhanced soil salinity, some loss of mangrove cover and slow recovery. In this instance, the impacted area was two orders of magnitude smaller than the event in the Gulf of Carpentaria.

The observations from the Gulf of Carpentaria reveal a complex interplay of at least four environmental factors, (namely a sea level drop, a lengthy drought, low rainfall and a heatwave), which are associated with the severe El Niño event. The combination of drivers forced a severe short-term response while under the longer-term influence of prevailing climatic conditions (namely, rising sea levels caused by rising temperatures). In this way, the climatic press was amplified by an extreme pulse event (Harris et al. 2018), notably where it forced exceedance of the physiological and ecological tolerance of these plants driving the vulnerable habitat they make up, into a significantly degraded state—perhaps irreversibly.

Mangroves of the semi-arid, wet-dry tropical Gulf of Carpentaria coastline exist at or near the upper limit of their zonal distribution positions in terms of tolerance of seasonal aridity, air and sea surface temperatures, and porewater salinity. They were therefore highly susceptible to this particular climate press. At the time of the mass dieback, spatially averaged, mean air temperatures and sea surface temperatures had increased by 1.64 and 1.56 °C, respectively since 1910.

At a local stand scale, mangrove species distributions were notably coupled to their periods of regular tidal flooding. Tidal inundation levels were reduced by abnormally low sea levels for the Gulf of Carpentaria during the latter months of 2015 (Fig. 9.17c), a consequence of the extreme El Niño conditions at the time, with its derived effect of high barometric pressures and prevailing winds (Harris et al. 2017).

These climatic conditions can be compared to a previous instance of a short-term (less than 5 month) drop in sea level as notably observed with the very severe 1982–1983 El Niño event (Lukas et al. 1984; Wyrtki 1984, 1985; Oliver and Thompson 2011). On that occasion, however, no record of mangrove condition was reported, so we do not know if they were impacted or not. What we do know is that the 1982–1983 pulse event did not appear to have coincided with equivalent amplified temperatures as observed with the 2015–2016 event, nor was it accompanied by monsoonal rainfall failure.

In order to understand the cause of such mass dieback of mangroves, it is important to know if there have been any earlier similar events. There is compelling evidence to suggest there have been.

If we refer again to Fig. 9.15 with its Green Fraction plots from sites across the Gulf of Carpentaria for the period from 1987 to 2017, note that there were synchronously depressed levels of canopy cover during the late 1980s and early 1990s, and these levels gradually increased to more or less maximal levels by 2000. After that time, canopy cover remained at relatively high levels until the abrupt drop in 2015–2016. Notably, during this period, there were no comparably severe El Niño events since 1997–1998 (BOM 2020). What is apparent in these plots is that there was a steady increase in canopy cover from very low levels starting in 1987. The question is why were the levels were generally low during that time? While there are a number of factors to consider, this feature is consistent with there being a similarly significant event of synchronous, mass mangrove dieback across the Gulf with the very severe El Niño event in 1982–1983. The likely impact of the intervening 1997–1998 event might also be depicted in these plots where there was a notable, but less pronounced drop in canopy cover at that time. This implies that the 1997–1998 event may have had a lesser impact.

These findings are of great relevance and importance, warranting further detailed investigations. There is a great need to gain a more complete understanding of the ecosystem processes involved, as well as delivering effective management guidelines and models to predict the likelihood and timing of future events. Should there have been similar past dieback events with different associated factors, then it makes it possible to develop and refine predictive models by focusing on the specific climate variables responsible in each case. For example, was a drop in sea level the primary factor causing mass dieback, or was it a combination of factors? Further studies are needed to establish the historic variability in climate in relation to mangrove cover across the Gulf. This relies in part on matching remote sensing data (satellite, historic airborne photography) with climatic conditions during each instance of mass mangrove dieback should that be the case.

Another important climate variable is rainfall. Mangroves require freshwater input from rainfall delivered directly, or as catchment runoff, tidal flooding, or groundwater flows. However, since the southern hemisphere wet season anomaly of 2010–2011, the Gulf of Carpentaria coastline had experienced significantly below average mean annual rainfalls (Fig. 9.17b). The wet seasons of 2014–2015 and 2015–2016 yielded rainfall anomalies of –586 and –295 mm in the Borroloola area of the southern Gulf coastline. In this 'pulse period', monsoons were of short duration, inducing low cloud cover, high radiation levels, elevated air temperatures (Fig. 9.17a), vapour pressure deficits and high evaporation rates (Hope et al. 2016). Had these stressors become particularly acute leading into the late dry season of 2015 (Oct to Nov)—the period when the mass dieback event became prominent? The evidence is inconclusive.

Firstly, note that low rainfall levels (Fig. 9.17b) had not resulted in mangrove dieback on previous occasions when rainfall conditions were similarly low, like during the mid-1990s. Furthermore, note the indicative evapotranspiration periods (Fig. 9.17e) also had no specific correlative links to the mass dieback event. Secondly, this observation was supported further by estimates derived using the equation for estimating wetland cover index, as the percentage of mangrove cover versus the total area of tidal wetlands (Duke et al. 2019). During the past 25 years, while the proportion of mangrove extent had risen overall from ~20% to just more than 30% (Fig. 9.17f), then the downward pressure of recent drier weather conditions could be placed in a larger context, where it is considered unlikely to have had a strong influence on the mass dieback of mangroves in 2015–2016.

9.4.2 Linking Specific Factors with the Dieback Event

In view of the evidence available, we evaluated the processes and factors likely to cause the 2015 mass dieback of mangroves in Australia's Gulf of Carpentaria. The key points in our approach are summarised in Table 9.3, based mostly on the information and data listed in Table 9.1. These observations describe features of the dieback event with its impact and dramatic environmental response. The key primary features were: the occurrence of dieback over a broad geographic area; its synchronous occurrence; and, its involvement with multiple mangrove species (Table 9.3). These observations were used to justify ruling out a number of key processes, including those in Levels 3 and 4 as replenishment and localised factors, supported by the lack of evidence for large-scale, human-related extreme events. The investigation into the cause was thus directed towards the two other level influences.

It was considered feasible that Level 1 and 2 processes might have been jointly responsible for the mass dieback event. Both had substantive evidence to justify their further serious consideration (Table 9.3) based on changes in climate as well as sea level. But, there was at least one of the Level 2 climate variables that warranted further critical consideration. As mentioned, an equation describing the significant relationship between mangrove cover and observed annual rainfalls over the previous 20–30 years (Duke et al. 2019) could be applied in this case to estimate areas for comparison with observed areas (Fig. 9.17f). For the Gulf dieback event in 2015, the derived annual estimates of wetland cover index varied between 28.14 and 28.86% during the 2013–2016 period. By comparison, those measured from available mapping data at the time (Duke et al. 2017) were around 27.1%. This meant that the observed extremes in rainfall did not appear to account for the overall losses observed, of around 6% of the regions' mangrove cover. Therefore, the dieback response did not appear to be caused primarily by the short-term low rainfall levels recorded preceding the mass dieback event in late 2015. It appears that moisture levels due to rainfall had been maintained within the normal range for these generally resilient trees.

Accordingly, Level 2 processes were excluded as the most likely primary causes since the unusual climatic variables surrounding the dieback event had not have been

Table 9.3 Deductions from the environmental forensic evaluation of the 2015 mass mangrove dieback event in Australia's Gulf of Carpentaria (Duke et al. 2017), based on the four levels of influencing processes that define the occurrence, extent and character of tidal wetlands

	Regional drivers, local impacts		Disturbance and responses	
	Level 1	Level 2	Level 3	Level 4
Evidence observed	Shoreline topographic setting plus sea level	Climate variability	Regional mangrove forest replenishment with small-scale disturbances	Localised disturbances exceeding ambient range
Mass dieback widespread—synchronous occurrence, not species specific	Likely	Likely	Small-scale human & natural factors excluded	Local human & natural factors excluded—no severe weather event, no large oil spill, etc.
Highest records of air temperature	Likely	Period of high moisture stress. Unlikely primary factor, as temperatures not beyond survival range & not specifically synchronous with mass dieback.	Excluded	Excluded
Prolonged drought period	Likely	Period of high moisture stress. Unlikely primary factor, as deduced Wetland Cover Index from longer-term rainfall data indicated no dieback & event not specifically synchronous with dieback	Excluded	Excluded
Higher elevation zones—dieback of taller vegetation mostly	Severe moisture stress at higher tidal inundation zones	Co-factor moisture stress—primary influence unlikely	Excluded	Excluded
Temporary drop of 20 cm in sea level	Apparent severe moisture stress associated with	Co-factor moisture stress—excluded as the	Excluded	Excluded

(continued)

Table 9.3 (continued)

	Regional drivers, local impacts		Disturbance and responses	
	Level 1	Level 2	Level 3	Level 4
Evidence observed	Shoreline topographic setting plus sea level	Climate variability	Regional mangrove forest replenishment with small-scale disturbances	Localised disturbances exceeding ambient range
correlated. with synchronous mass dieback	lack of tidal flooding into higher elevation zones	likely primary factor		

sufficient to explain the severe response. As such, it was considered unlikely therefore that the mass dieback would have occurred had it not been for the temporary 20 cm drop in sea level. This left at least one significant remaining question regarding the cause. Was the drop in sea level alone sufficient to have triggered the event? Or, had the impact of the temporary drop in sea level been enhanced by the extreme climatic conditions at the time? In either case, the co-occurrence of Level 1 and 2 influences was certainly notable for the 2015 mass dieback event—so at this time, such a likelihood cannot be ruled out.

9.4.3 Did Human-Induced Climate Change Play a Role in the 2015–2016 Dieback of Mangroves?

Whether this instance of a climate-related impact is related to human-induced climate change is not yet fully clear. This is because the mass dieback has so far only been reported as a one-off event. This means that the relationship with any particular factors remains inconclusive. As such, the dieback event could simply be a unique and unusual combination of detrimental factors—a situation rarely, if ever, to be repeated. However, as stated above, there are tantalising new observations and evidence suggesting there might be at least one other past occurrence. This possibly is extremely important for several reasons, like better understanding the cause, and it is now being fully investigated.

What is clear at this time is that the ‘press’ component of the multiple drivers identified so far are associated with the general thrust of anthropogenic climate change, specifically warming and its derivative driver, sea level rise. And, we can be reasonably confident that the warming trend will continue for the foreseeable future. So, human-induced climate change is implicated.

The ‘pulse’ component was driven by a drop in sea level, resulting from the severe 2015–2016 El Niño event. And, while it had been established that climate change had intensified ENSO periods in recent decades, with stronger El Niño and

La Niña events with their lower frequency, we have recently become aware that there are different types of ENSO periods, with Central Pacific events becoming more common with climate change, and Eastern Pacific events becoming fewer but more intense (see Cai et al. 2018). In a more recent account (Freund et al. 2019), the authors described some of these complexities in their statement 'in 2014/2015, the "failed" El Niño was categorized by our classification scheme as a Central Pacific event, whereas the following year, 2015/2016, another event closely resembled a canonical Eastern Pacific event that resulted in one of the strongest in the past 400 years'.

So, are El Niño events influenced by global climate change? The evidence at hand leaves some lingering doubts, but climate records over the past century confirm that the three most severe El Niños occurred during the last 30 years (BOM 2020). This is consistent with the idea that global warming in recent decades (see IPCC 2018) has led to more severe El Niño events. And, with more severe events, there is a strong likelihood of respectively larger sudden drops in sea level, and more damage to mangrove forests.

Having focused on the damage to mangrove forests, it is appropriate now to consider the recovery processes necessary for these forests to survive. And, where damaging events are more frequent or more severe, these habitats still need time to recover to preserve their beneficial ecosystem services like carbon sequestration, shoreline protection and fishery habitat. These recovery processes mostly involve: flowering and germination; production of mature propagules; dispersal to suitable sites; establishment despite tidal flushing, waves and predators; and, growth into mature individuals in preferably closed forest stands. There are quite a few vulnerable steps, but most of all, it takes time for the new stand to gain functionality and sustainability. And, judging by the apparent canopy recovery curve depicted in Fig. 9.15 (1987–2000 for the Gulf sites)—supported in other field studies (e.g. Duke et al. 1997; Duke 2001)—such recovery takes upward of two decades. Should there be accumulative impacts—this includes impacts from additional factors like more intense tropical cyclones (at 2 per year on average for 1975–2015 in the Gulf; also see: BOM 2020) and the growing pressures of sea level rise (notably 8–9 mm/year for 1993–2007 in the southern Gulf, being 2–3 times the global average; see Church et al. 2009)—these combined pressures further inhibit habitat recovery. The scenarios are illustrated in the Level 4 schematic (Fig. 9.5) where the longer-term trajectory for repeated, large-scale disturbances to mangroves inevitably leads to their severely degraded state (marked by low diversity, fragmented structure and poor functionality)—a state of effective ecosystem collapse (described by Duke et al. 2007).

9.5 Current Recommendations for Management Strategies

In this section, we discuss the appropriate and most effective management strategies to best deal with incidents like the mass dieback of Gulf mangroves. There are three chief considerations to bring focus to such actions: (a) to reduce the risk of such events happening again; (b) to facilitate recovery of damaged stands; and (c) to facilitate the transition of damaged habitat to an alternate environmental state, if recovery to the past state is not possible.

Our recommendations for addressing these requirements regards mangrove and saltmarsh-saltpan habitat, referred to here as tidal wetland habitat, is to follow a carefully considered series of interlinking tasks outlined in the following points:

1. Apply local risk minimisation by reducing localised pressures on threatened tidal wetland habitat: by removing feral animals like wild pigs (*Sus scrofa*), especially where they dig up young mangrove seedlings along the supratidal ecotone edge; by controlling grazing livestock (like cattle, horses, goats, camels, deer) near tidal wetlands; by preventing severe rangeland fires especially those close to tidal wetlands; by eradicating invasive weeds like rubber vine (*Cryptostegia grandiflora*); by preventing spillage or release of toxic chemicals or other pollutants as either airborne or with the water, likely to reach tidal wetlands.
2. Apply regional risk minimisation by reducing national and global pressures where they threaten tidal wetland habitat: by reducing levels of atmospheric carbon to stop rising temperatures, sea level and detrimental changes in rainfall; by finding ways to reduce carbon emissions; by rewarding those who show leadership in this endeavour.
3. Make accurate area maps to describe the extent of impacted and non-impacted tidal wetland habitat: by mapping healthy and damaged areas using satellite data and imagery of mangrove, dead mangroves, saltmarsh and saltpans, biomass and tree height; by mapping elevation levels using data like LIDAR to define habitat relevant contours of mean sea level (MSL) and highwater (HAT) levels; by historical mapping to identify and quantify past areas of each vegetation type and specifically defining ecotone edges.
4. Make accurate area maps to describe the changes taking place to areas of impacted and non-impacted tidal wetland habitat using each of the methods listed in (3).
5. Conduct condition monitoring to learn more about the ongoing health of tidal wetland habitat: by supporting indigenous ranger groups, community groups and researchers to conduct regular surveys measuring current status and comparing with the past condition; by using aerial surveys and boat-based surveys to complement satellite mapping; by scoring the severity and extent of a broad range of habitat responses to the various drivers of change including obviously human-influenced factors like altered hydrology, vegetation clearing, pollution, landfill, rock walls, along with more natural factors, like drought dieback, shoreline erosion, storm damage, saltpan scouring, terrestrial retreat and light gaps.
6. Develop models for the prediction of future events likely to impact tidal wetland habitat, using various types of data sources: by using accurate vegetation data on diversity, tree loss and seedling establishment for development of forest growth and recovery models; by mapping sediment elevation to describe changes in displacement and mobilisation of sediments—sites of erosion and deposition;

climate data for identification of climate factors known to influence forest development, growth and replacement processes, like temperature, rainfall, period length of drought conditions, sea level, southern oscillation index, evapotranspiration.

7. Facilitation of recovery: by careful consideration and evaluation of a range of mitigation intervention methods, like the removal of dead timber, planting seedlings, channelling to improve drainage, alterations to slope and topography, addition of nutrients and other chemical agents. In general, the rule is that no intervention should be applied unless some advantage can be demonstrated. If mitigation works, like planting, are instigated then it is essential that scientifically robust monitoring continues for 3 or more years afterwards and the results published (as per Duke 1996).
8. Develop and implement a strategy for mitigation and monitoring of tidal wetlands at State and National levels: by applying the above recommendations.

9.6 A Regional Mitigation and Monitoring Strategy for Tidal Wetlands

There is a demonstrable need for a regional shoreline resource inventory where the presence and condition of the many natural assets and resources spread along national shorelines can be displayed and quantified. Furthermore, there is a compelling case also for a companion product for registering the many notable environmental impacts occurring along these shorelines caused by damaging events at specific dates and locations.

Our evidence shows that a number of appreciable events, like the mass dieback of mangroves in Australia's Gulf of Carpentaria, had gone undetected for months or years after they occurred. And, there are likely to be many more unreported incidents. For example, during a 2017 survey of the northern sector of the Great Barrier Reef shoreline, it was discovered that two cyclones, 2 and 3 years earlier, had severely damaged and killed up to 600 ha of dense shoreline fringing mangroves near the Starcke River in far north-eastern Queensland (Duke and Mackenzie 2018). There are important questions about how such a large impact had gone undetected for so many years. This is highly relevant given the great level of concern for coral reefs where their condition in the region had noticeably worsened in recent years. The consequences of such a devastating impact on shoreline mangroves are expected to have broad and significant longer-term detrimental influences on reefal environments when sediments become mobilised as mangrove benefits of buffering and shoreline protection deteriorate.

In summary, such observations demonstrate notable inadequacies in current State and National shoreline monitoring efforts. And, it is of great concern that essential awareness of such damaging incidents along the Australian shoreline generally may be lost, or at best delayed from public acknowledgement. What is needed is an effective strategy with a standard and robust methodology for gathering detailed shoreline data for public display.

So, there is one overall lesson to be taken from our assessment presented in this chapter. This is a strong case for developing and implementing a national shoreline monitoring strategy. This can be seen as a fundamental environmental management opportunity. It would be an important outcome also for the identification and quantification of specific prioritisation issues regards future damaging events affecting shorelines around the country. The strategy could be usefully developed around the identification of indicative environmental responses to specific drivers of change. Each indicator can be scored, quantified, located and assessed for its severity and extent based on its multiple occurrences along the vast Australian shoreline.

The lasting value of such a resource would be in its quantification of habitat conditions as well as its identification of emerging environmental issues like the often-notable shoreline damage caused by severe cyclones, large oil spills, sea level rise or extreme fluctuations in mean sea level. This might then be compared systematically against the baseline status of habitat conditions established on a regional scale at the commencement of such a program. Report card scores might also be derived covering specific shoreline sections.

A targeted use of the monitoring strategy might also be to track longer-term change as either recovery takes place, or deterioration continues. In either case, the knowledge gained would be essential for developing national priorities for shoreline mitigation intervention projects. In any case, such knowledge would be used in the development of strategies for the protection and conservation of shoreline resources for each State and around the country.

These arguments and observations support the need for an effective national shoreline monitoring strategy. State and Federal environmental managers of national coastal resources and assets in Australia could use more comprehensive knowledge about the extent and condition of shoreline habitats, as well as the threats, drivers and risks faced by these natural resources. Such a knowledge base is considered essential for best management practice for the protection of shoreline habitats facing escalating changes in climate, higher temperatures, more severe storm impacts and rising sea levels.

9.7 Vulnerability of Impacted Shorelines with Key Risks and Consequences

Our evaluation of the 2015 mass dieback of Gulf mangroves was made in the context of the fundamental processes influencing the drivers of key environmental components. This approach delivered a relatively robust understanding of not only why there was such a dramatic environmental response in the Gulf event, but also whether it might be possible to predict future occurrences. The evidence presented and particularly the processes responsible for environmental changes provide the basis for developing reliable indicators of likely responses. As one example, the wetland cover index could be applied more in the prediction of risks and changes due to longer-term changes in at least one key factor, namely rainfall (Duke et al. 2019). It is expected that relationships with other climate as well as physical factors, plus disturbance factors, might also contribute to a future predictive capability for better management of vulnerable shoreline ecosystems.

What is clear is the conclusion that the Gulf mass dieback event was seemingly unprecedented. No earlier instances of comparable dieback have been documented elsewhere, nor in the Gulf during the assessment period of 1987–2019. However, this observation has one notable caveat where we have new untested evidence, implying there may have been an earlier event in the region. This potentially significant earlier event may have taken place during the prior severe El Niño of 1982–1983 when a comparable drop in sea level was reported for the Gulf (Wyrtki 1984, 1985). While no observations were made at the time regarding the impact on mangrove forests, some historical imagery appears to support this hypothesis (Duke et al. 2021a, b). If this is proven true, an assessment of the associated climatic conditions along with the other variables would greatly enhance the development of a robust and reliable predictor of possible future occurrences.

Such a well-informed understanding of natural ecosystem responses of tidal wetlands is needed for more effective mitigation actions likely to deliver reliable, effective and lasting outcomes. In any case, we have usefully identified a unique and unusual vulnerability of tidal wetlands habitats with their likely extreme responses to future environmental changes.

Our deliberations have also shed further light on the growing number of implications for associated coastal marine habitats like corals and seagrasses as well as mangroves. There are also related questions to be asked regards vulnerable mobile marine fauna, including commercial fishery species like mud crabs, barramundi and prawns (Plaganyi et al. 2020). In addition, coastal water quality is recognised as a significant environmental management issue where severe runoff through estuarine ecosystems like mangroves might contribute to the unusually large amounts of sediments, nutrients and harmful agricultural chemicals moving into coastal waters and amongst other sensitive nearshore habitats, like seagrass beds and the Great Barrier Reef.

The buffering role of coastal mangroves and tidal wetlands is essential knowledge for the minimisation of risks to nearshore habitats. There is increasing awareness also of the benefits of mangrove and tidal wetland estuarine ecosystems, their condition and status. This supports the growing urgency in developing a better understanding of the key drivers of disturbance events, and to better understand how these detrimental pressures might combine to take these ecosystems down a trajectory towards collapse. While there is precedent for the recovery of shoreline ecosystems (Duke and Khan 1999), recent events demonstrate that disturbances are likely to re-occur too frequently for existing recovery processes (cs. Duke et al. 2007).

Acknowledgements Research on the mass mangrove dieback in Australia's Gulf of Carpentaria was supported with funding from the Australian Government's National Environmental Science Program and the Northern Territory Government.

References

Amir AA, Duke NC (2019) Distinct characteristics of canopy gaps in the subtropical mangroves of Moreton Bay, Australia. Estuar Coast Shelf Sci 222:66–80. https://doi.org/10.1016/j.ecss.2019.04.007

Bergstrom DM, Wienecke BC, van der Hoff J, Hughes L, Lindemayer DL, Ainsworth TD, Baker CM, Bland L, Bowman DMJS, Brooks ST, Canadell JG, Constable A, Dafforn KA, Depledge MH, Dickson CR, Duke NC, Helmstedt KJ, Johnson CR, McGeoch MA, Melbourne-Thomas J, Morgain R, Nicholson EN, Prober SM, Raymond B, Ritchie EG, Robinson SA, Ruthrof KX, Setterfield SA, Sgro CM, Stark JS, Travers T, Trebilco R, Ward DFL, Wardle GM, Williams KJ, Zylstra PJ, Shaw JD (2021) Ecosystem collapse from the tropics to the Antarctic: an assessment and response framework. Glob Chang Biol (online):1–12. https://doi.org/10.1111/gcb.15539

BOM (2020) Australian Bureau of Meteorology, Canberra. online access, March 2020. http://www.bom.gov.au/cyclone/climatology/trends.shtml

Cai W, Wang G, Dewitte B, Wu L, Santoso A, Takahashi K, Yang Y, Carréric A, McPhaden MJ (2018) Increased variability of eastern Pacific El Niño under greenhouse warming. Nature 564:201–206

Church JA, White NJ, Hunter JR, McInnes K, Mitchell W (2009) Sea level. In: Poloczanska ES, Hobday AJ, Richardson AJ (eds) A marine climate change impacts and adaptation report card for Australia 2009. Online, NCCARF

Duke NC (1992) Mangrove floristics and biogeography. In: Robertson AI, Alongi DM (eds) Tropical mangrove ecosystems, coastal and Estuarine studies series. American Geophysical Union, Washington, DC, pp 63–100. 329 pages

Duke NC (1996) Mangrove reforestation in Panama: an evaluation of planting in areas deforested by a large oil spill. In Field CD (ed) Restoration of mangrove ecosystems. International Society for Mangrove Ecosystems, Okinawa, and International Tropical Timber Organization, Yokohama, pp 209–232

Duke NC (2001) Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. Wetlands Ecol Manag 9:257–269

Duke NC (2006) Australia's Mangroves. The authoritative guide to Australia's mangrove plants. University of Queensland and Norman C Duke, Brisbane, 200 pages

Duke NC, Meynecke J-O, Dittmann S, Ellison AM, Anger K, Berger U, Cannicci S, Diele K, Ewel KC, Field CD, Koedam N, Lee SY, Marchand C, Nordhaus I, Dahdouh-Guebas F (2007) A world without mangroves? Science 317:41–42. https://doi.org/10.1126/science.317.5834.41b

Duke NC (2014) Mangrove coast. In: Harff J, Meschede M, Petersen S, Thiede J (eds) Encyclopedia of marine geosciences. Springer, Dordrecht, pp 412–422

Duke NC (2016) Oil spill impacts on mangroves: recommendations for operational procedures and planning based on a global review. Mar Pollut Bull 109(2):700–715

Duke NC (2017) Mangrove floristics and biogeography revisited: further deductions from biodiversity hot spots, ancestral discontinuities and common evolutionary processes. In: Rivera-Monroy VH, Lee SY, Kristensen E, Twilley RR (eds) Mangrove ecosystems: a global biogeographic perspective. Structure, function and services, vol 2. Springer, pp 17–53

Duke NC, Khan MA (1999) Structure and composition of the seaward mangrove forest at the Mai Po Marshes Nature Reserve, Hong Kong. In: Lee SY (ed) The mangrove ecosystem of Deep Bay and the Mai Po Marshes, Hong Kong. Hong Kong University Press, Hong Kong, pp 83–104. Proceedings of the international workshop on the mangrove ecosystem of Mai Po and Deep Bay, 3–20 Sept 1993, Hong Kong

Duke NC, Mackenzie J (2018) East Cape York Report 2017. Final Report: East Cape York Shoreline Environmental Surveys. Report to the Commonwealth of Australia. Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER) Publication 17/67, James Cook University, Townsville, 144 pp

Duke NC, Pinzón ZS, Prada MC (1997) Large-scale damage to mangrove forests following two large oil spills in Panama. Biotropica 29(1):2–14

Duke NC, Ball MC, Ellison JC (1998) Factors influencing biodiversity and distributional gradients in mangroves. Glob Ecol Biogeogr Lett Mangrove Spec Issue 7:27–47

Duke NC, Bell AM, Pedersen DK, Roelfsema CM, Bengtson Nash S (2005) Herbicides implicated as the cause of severe mangrove dieback in the Mackay region, NE Australia — serious implications for marine plant habitats of the GBR World Heritage Area. Mar Pollut Bull 51:308–324

Duke NC, Kovacs JM, Griffiths AD, Preece L, Hill DJE, Oosterzee P v, Mackenzie J, Morning HS, Burrows D (2017) Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. Mar Freshwat Res 68(10):1816–1829

Duke NC, Field C, Mackenzie JR, Meynecke J-O, Wood AL (2019) Rainfall and its hysteresis effect on relative abundances of tropical tidal wetland mangroves and saltmarsh-saltpans. Mar Freshwat Res 70(8):1047–1055

Duke NC, Mackenzie J, Kovacs J, Staben G, Coles R, Wood A, Castle Y (2021a) Assessing the Gulf of Carpentaria mangrove dieback 2017-2019. NESP Final Report, Volume 1: Aerial Surveys. National Environmental Research Program (NESP), Commonwealth of Australia. Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER) Publication 20/20. James Cook University, Townsville, 181 pp

Duke NC, Mackenzie J, Hutley L, Staben G, Bourke A (2021b) Assessing the Gulf of Carpentaria mangrove dieback 2017-2019. NESP Final Report, Volume 2: Field Studies. National Environmental Research Program (NESP), Commonwealth of Australia. Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER) Publication 20/21. James Cook University, Townsville, 133 pp

Freund MB, Henley BJ, Karoly DJ, McGregor HV, Abram NJ, Dommenget D (2019) Higher frequency of Central Pacific El Niño events in recent decades relative to past centuries. Nat Geosci 12:450–455

Harris T, Hope P, Oliver E, Smalley R, Arblaster J, Holbrook N, Duke N, Pearce K, Braganza K, Bindoff N (2017) Climate drivers of the 2015 Gulf of Carpentaria mangrove dieback. Australia, NESP Earth Systems and Climate Change Hub: 31 pages. JCU TropWATER Report #17/57

Harris RM, Beaumont LJ, Vance T, Tozer C, Remenyi TA, Perkins-Kirkpatrick SE, Mitchell PJ, Nicotra AB, McGregor S, Andrew NR, Letnic M, Kearney MR, Wernberg T, Hutley LB, Chambers LE, Fletcher M, Keatley MR, Woodward CA, Williamson G, Duke NC, Bowman DM (2018) Linking climate change, extreme events and biological impacts. Nat Clim Change 8 (7):579–587

Hope P, Wang G, Lim E-P, Hendon HH, Arblaster JM (2016) What caused the record-breaking heat across Australia in October 2015? Bull Am Meteorol Soc 97(12):1–5

IPCC (2018) Special report on global warming of 1.5°C. http://ipcc.ch/report/sr15/

Laurance WF, Dell B, Turton SM, Lawes MJ, Hutley LB, McCallum H, Dale P, Bird M, Hardy G, Prideaux G, Gawne B, McMahon CR, Yu R, Hero J-M, Schwarzkopf L, Krockenberger A, Setterfield SA, Douglas M, Silvester E, Mahony M, Vella K, Saikia U, Wahren C-H, Xu Z, Smith B, Cocklin C (2011) The ten Australian ecosystems most vulnerable to tipping points. Biol. Conserv 144:1472–1480

Lovelock CE, Cahoon DR, Friess DA, Guntenspergen GR, Krauss KW, Reef R, Rogers K, Saunders ML, Sidik F, Swales A, Saintilan N, Thuyen LX, Triet T (2015) The vulnerability of Indo-Pacific mangrove forests to sea-level rise. Nature 526:559–563

Lovelock CE, Feller IC, Reef R, Hickey S, Ball MC (2017) Mangrove dieback during fluctuating sea levels. Sci Rep 7(1680):1–8

Lukas R, Hayes SP, Wyrtki K (1984) Equatorial sea level response during the 1982–1983 El Niño. J Geophys Res 89(C6):10425–10430

Oliver ECJ, Thompson KR (2011) Sea level and circulation variability of the Gulf of Carpentaria: influence of the Madden-Julian Oscillation and the adjacent deep ocean. J Geophys Res Oceans 116:C02019. https://doi.org/10.1029/2010JC006596

Plaganyi E, Deng RA, Hutton T, Kenyon R, Lawrence E, Upston J, Miller M, Moeseneder C, Pascoe S, Blamey L, Eves S (2020) From past to future: understanding and accounting for recruitment variability of Australia's redleg banana prawn (Penaeus indicus) fishery. ICES J Mar Sci. Online 14 pages. https://doi.org/10.1093/icesjms/fsaa092

Tomlinson PB (2016) The botany of mangroves, 2nd edn. Cambridge University Press, Cambridge

Wyrtki K (1984) The slope of sea level along the equator during the 1982-83 El Niño. J Geophys Res 89(C6):10,419–10,424

Wyrtki K (1985) Sea level fluctuations in the Pacific during the 1982-83 El Niño. Geophys Res Lett 12(3):125–128

Recurrent Mass-Bleaching and the Potential for Ecosystem Collapse on Australia's Great Barrier Reef

10

Morgan S. Pratchett, Scott F. Heron, Camille Mellin, and Graeme S. Cumming

Abstract

Coral reefs are extremely vulnerable to human-induced climate change. Most notably, increasing ocean temperatures are causing increasing incidence and severity of mass coral bleaching. There have been three major episodes of mass-bleaching on Australia's Great Barrier Reef (GBR) in just the last 5 years, corresponding with extreme temperatures in 2016, 2017 and 2020. Recurrent episodes of mass-bleaching are compounding upon pre-existing disturbances and pressures to suppress coral cover and undermine key ecosystem processes, which may ultimately result in ecosystem collapse. The potential for ecosystem collapse on the GBR is already apparent based on transformation in coral assemblages and system-wide declines in coral recruitment in the immediate aftermath of recent mass-bleaching episodes, which are unlikely to be restored with accelerating changes in environmental conditions, and increasing incidence of large-scale and severe mass-bleaching episodes. Significant improvements in the management of anthropogenic pressures and disturbances are fundamental for conserving

---

M. S. Pratchett (✉) · G. S. Cumming
ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia
e-mail: morgan.pratchett@jcu.edu.au; graeme.cumming@jcu.edu.au

S. F. Heron
ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia

Physics and Marine Geophysics Laboratory, College of Science and Engineering, James Cook University, Townsville, QLD, Australia
e-mail: scott.heron@jcu.edu.au

C. Mellin
The Environment Institute and School of Biological Sciences, University of Adelaide, Adelaide, SA, Australia
e-mail: a1183033@adelaide.edu.au

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_10

the GBR, but averting ecosystem collapse requires immediate and effective action to redress global climate change.

10.1 Introduction

Changing environmental conditions caused by human-induced climate change pose a substantial threat to species, communities and ecosystems (Thomas et al. 2004; Hoegh-Guldberg and Bruno 2010; Pecl et al. 2017; Newbold 2018). The physiological and behavioural responses of individual organisms to changing environmental conditions (Walther et al. 2002; Dillon et al. 2010; Nagelkerken and Munday 2016) affect population viability and abundance, biological interactions and the distribution of species. These may in turn have more general impacts on ecosystem structure and function. Critically, climate change has contributed to widespread and accelerated degradation across many different ecosystems (Hoegh-Guldberg et al. 2007; Thomson et al. 2014; Bergstrom et al. 2015; Wernberg et al. 2016; Iknayan and Beissinger 2018; Sharma et al. 2019), such that many ecosystems are now facing relatively rapid, pronounced and lasting changes in structure and function.

Human-induced climate change is caused by sustained increases in greenhouse gas emissions (Rosenzweig et al. 2008) that drive slow but persistent changes in underlying environmental conditions (Henson et al. 2017). In contrast, the effects of climate change on natural systems may appear abrupt, due to threshold effects and self-reinforcing feedbacks (Turner et al. 2020). Persistent changes in underlying environmental conditions are also conflated by corresponding increases in environmental variability and the incidence and severity of anomalous or extreme conditions (Turner et al. 2020). On coral reefs, mass-bleaching of reef-building corals is one of the most apparent effects of climate change (Glynn 1991; Eakin et al. 2010; Hughes et al. 2018a) and is inexorably linked to the occurrence of heatwaves (e.g., Heron et al. 2016; Skirving et al. 2019; Sully et al. 2019). Marine heatwaves and corresponding mass-bleaching episodes will become more frequent and severe with increasing ocean temperatures (Smale et al. 2019). The responses of corals to heatwaves are also conditional upon prior exposure to extreme conditions (Pratchett et al. 2013; Hughes et al. 2019a) and the broader context of environmental pressures and disturbances (Hoegh-Guldberg et al. 2007; Wooldridge and Done 2009).

Coral reefs are particularly vulnerable to climate change owing to the temperature sensitivity of reef-building corals (Jokiel and Coles 1990; Hoegh-Guldberg 1999). The interaction between corals and their symbiotic dinoflagellates (Symbiodiniaceae) and the photosynthetically derived nutrients provided to the coral host are compromised at elevated temperatures (Iglesias-Prieto et al. 1992). Declines in the concentration or pigmentation of Symbiodiniaceae lead to apparent paling of the coral host, and severe or prolonged bleaching results in starvation and mortality of the coral (Hoegh-Guldberg 1999). While coral bleaching is moderated by nutrient conditions and light intensity (Morris et al. 2019; Bollati et al. 2020), large-scale (e.g., pan-tropical) incidence of simultaneous bleaching across many coral colonies and species (Eakin et al. 2019) is undeniably linked to extreme thermal stress. Links between mass-bleaching and apparent warming of the world's oceans were first proposed in the early 1990s (Jokiel and Coles 1990; Glynn 1991). However, it is was not until the first documented global mass-bleaching in 1998 that there was widespread recognition of and concern about the threat posed by global climate change to coral reefs (Walther et al. 2002; Sheppard 2003). Since 1998, there have been several episodes of global mass-bleaching (Eakin et al. 2019) and climate change is now one of the foremost threats to coral reefs (Hughes et al. 2018a). Most notably, successive years of extreme temperatures in 2015–2017 resulted in unprecedented incidence of successive years of mass-bleaching at many locations throughout the world (Hughes et al. 2017; Harrison et al. 2018; Head et al. 2019; Smith et al. 2019), with significant effects on coral assemblages and reef ecosystems.

Hard (scleractinian) corals are fundamental to the structure and function of coral reef ecosystems, contributing to (1) reef accretion (Perry et al. 2013), (2) habitat structure (Graham et al. 2006; Alvarez-Filip et al. 2009), as well as (3) carbon fixation and nutrient cycling (Goreau et al. 1979; Wild et al. 2004; Cole et al. 2008). Extensive coral loss, caused by mass coral bleaching and/or other increasing disturbances and pressures (Bellwood et al. 2019), will not only affect the ecological structure of benthic habitats (Norström et al. 2009), but also have significant and far-reaching effects on critical ecosystem functions and services. Most notably, extensive coral loss is linked to significant declines in reef-associated organisms (Stella et al. 2011; Pratchett et al. 2018), and these effects are further exacerbated by the inevitable decomposition and disintegration of dead corals (Idjadi and Edmunds 2006; Rogers et al. 2014). Recent and pronounced declines in the health and abundance of corals (and corresponding changes in structure of reef habitats) have been linked to declines in fisheries productivity (Bell et al. 2013; Rogers et al. 2014), biodiversity (Wilson et al. 2006; Stuart-Smith et al. 2018), and carbonate production (Perry et al. 2013; Perry and Morgan 2017). There is also increasing evidence of broad-scale changes in ecosystem processes (Graham et al. 2015; Hughes et al. 2019b), which will limit coral recovery and are indicative of fundamental changes in ecosystem function. Taken together, rapid and pronounced changes in the identity of formerly coral-dominated habitats, with significant and lasting consequences for biodiversity and productivity, suggest that increasing effects of climate change may lead to the collapse of coral reef ecosystems.

This chapter highlights recent impacts of climate change on Australia's Great Barrier reef (GBR), which has experienced unprecedented incidence and severity of coral bleaching. The corresponding ecological changes within this system (and specifically, within shallow reef environments that are normally dominated by reef-building corals) are considered within the context of multiple and diverse cumulative disturbances (e.g., Mellin et al. 2019a). Importantly, the effects of climate change on coral reefs do not operate independently of other major disturbances and anthropogenic pressures. Rather, marked changes in environmental conditions (and specifically, the incidence and severity of thermal anomalies) are compounding upon perennial threats to coral reef assemblages to greatly conflate and accelerate changes in the structure and function of these systems. Changes in ecosystem structure and function associated with increasing disturbances are fundamental in assessing the resilience and conversely, the potential for ecosystem collapse (Cumming and Peterson 2017) of the GBR. In what follows, we first lay out a set of criteria for collapse. We then discuss trends in coral reef ecosystems along the GBR before undertaking a more detailed discussion of whether the GBR ecosystem is collapsing and outline necessary steps to defer or prevent ecosystem collapse.

10.2 Considering the Criteria for Collapse of Coral Reefs

Evaluating the potential for collapse of coral reefs requires a clear definition of collapse. There are many different forms of ecological change, with different consequences for human societies. If we consider ecological change along a spectrum from mild to severe, collapse occupies the far right-hand segment of that continuum; it is distinct from such phenomena as population fluctuations, gradual declines, extinctions that occur at baseline rates, and some kinds of regime shift. For example, a lake that shifts from clear water to eutrophic under the influence of phosphorus loading has not necessarily collapsed; indeed, the changes it has experienced may be fully reversible. Collapse has been variously defined in the ecological literature (e.g., Mullon et al. 2005, Pinsky et al. 2011) but in essence, it can be recognised by four major attributes (as reviewed by Cumming and Peterson 2017):

(i) Collapse involves a loss of identity and the disappearance of key actors (e.g., species, trophic levels), system components (e.g., oceanic currents) and interactions (e.g., predation, competition and genetic exchange). A significant reduction in the area of coral cover, for example, may indicate reef degradation but is not enough on its own to qualify as collapse. Collapse on reefs might, for example, be signalled by the loss of species that are essential for the persistence of reefs as we know them, such as key habitat-forming corals (Johns et al. 2014; Ortiz et al. 2014; Alvarez-Filip et al. 2013) or apex predators (Sandin et al. 2008; Estes et al. 2011).

(ii) Loss of identity should occur rapidly relative to the regeneration times and turnover rates of identity-defining components of the system. Population dynamics define a characteristic temporal scale at which a given ecosystem operates. If, for example, the interval between successive marine heatwaves is less than the time required for population recovery, coral species that are highly susceptible to bleaching are likely to go extinct (Hughes et al. 2018a). Collapse implies rapid change that is difficult to adapt to; it is not the same as a gradual decline, which may offer many more opportunities for persistence.

(iii) Collapse involves substantial losses of 'capital', which in the case of an ecosystem equates to biomass, species and structures. 'Substantial' depends on the criteria used to define system identity. For example, coral reef ecosystems might collapse due to widespread loss of topographic complexity (Graham et al. 2006; Alvarez-Filip et al. 2009) or extensive depletion of fish stocks (Jackson et al. 2001). Analyses of collapsed fisheries typically use the term to describe reductions of >95% of pre-collapse biomass. For example, Newfoundland Cod spawner biomass declined to 99% below pre-collapse levels (Myers et al. 1997). Keith et al. (2013) adopted thresholds of 80–90% in a range of variables when defining ‘critically endangered’ ecosystems.

(iv) Collapse has lasting consequences that persist longer than a single generation or much longer than the typical dynamics of the system, though it may be irreversible. Collapse changes system dynamics and influences recovery times. For example, suppression of coral recruitment following widespread and severe coral depletion on the GBR (Hughes et al. 2019b) contributes to evidence of recent or impending ecosystem collapse.

These criteria provide a conceptual frame of reference against which to assess on-going changes along the GBR and consider the potential for ecosystem collapse.

10.3 Background Trends on the Great Barrier Reef

Coral reef ecosystems have been subject to a long-history of anthropogenic disturbances (McCulloch et al. 2003; Pandolfi et al. 2003; Duarte et al. 2020), and degradation of many coral reef ecosystems was already apparent in the 1960s and 1970s (Bruno and Selig 2007). This was long before the implementation of rigorous and standardised monitoring programs to assess the status and trends of coral reef ecosystems, which focus attention on specific causes of localised coral mortality (Sweatman et al. 2011; De’ath et al. 2012). Standardised monitoring was implemented on Australia’s Great Barrier Reef in the 1980s (Sweatman et al. 2011) and has been fundamental in demonstrating the ecological benefits of contemporary management arrangements (Emslie et al. 2015) and the factors structuring coral reef assemblages and habitats (Sweatman 2008; De’ath et al. 2012). The long-term monitoring program (LTMP) involves recurrent (often annual) surveys of coral and fish assemblages in shallow reef environments, characterising the status and trends on permanent transects in specific habitats (Emslie et al. 2011) and the entire perimeter of individual reefs (Sweatman et al. 2011).

Systematic monitoring on the GBR (especially since the mid-1990s) shows an apparent decline in overall coral cover (Sweatman et al. 2011; De’ath et al. 2012; Mellin et al. 2019a). Long-term trends in average coral cover vary greatly among reefs (Cheal et al. 2008; Wilson et al. 2009) and regions (Osborne et al. 2011), mostly in accordance with spatiotemporal patterns in the occurrence of major disturbances, such as cyclones and population irruptions of the coral-feeding crown-of-thorns starfish. To assess the relative contribution of different disturbances, recent coral mortality recorded in each year and at each reef was ascribed to one of several different agents (Osborne et al. 2011) or the documented occurrence of specific disturbances between successive surveys (De’ath et al. 2012). Both these approaches poorly account for inherent patchiness in the impacts of large-scale disturbances (Pratchett 2010; Puotinen et al. 2016) or their simultaneous

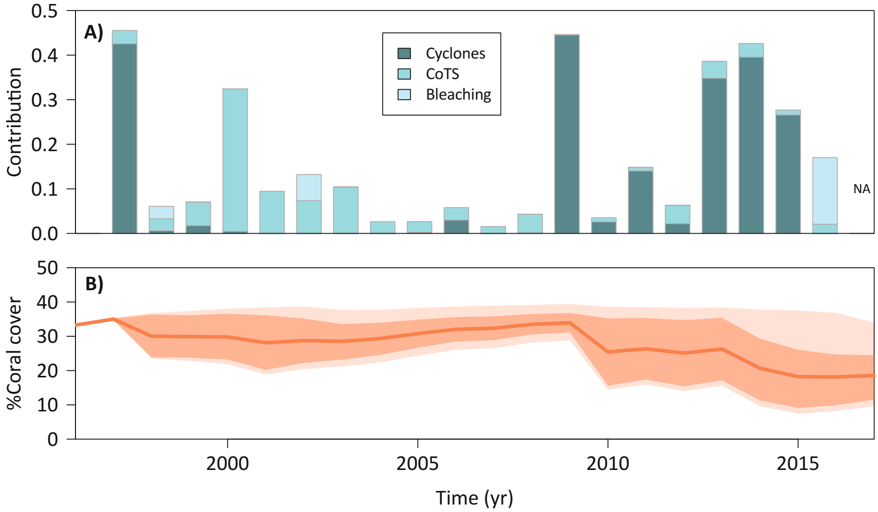


Fig. 10.1 Cumulative impact of major disturbances on the Great Barrier Reef and regional trends in coral cover between 1996 and 2016. (**a**) Relative contribution of cyclones, population irruptions of CoTS and mass coral bleaching to the regional decline in coral cover. (**b**) Mean predictions of coral cover averaged across the entire Great Barrier Reef; envelopes indicate the 95% confidence interval across a total of 1000 model simulations (light hue), the interquartile range (medium hue) and the mean trajectory (dark continuous line). Reproduced (with permission) from Mellin et al. (2019a)

occurrence (Mellin et al. 2019a). More importantly, they do not consider the roles of chronic disturbances and changing environmental conditions (e.g., declining water quality) that undermine the recovery capacity of coral assemblages (Wakeford et al. 2008; Ortiz et al. 2018; MacNeil et al. 2019; Mellin et al. 2019a). Nonetheless, coarse-level attributions between documented coral loss and purported agents of coral mortality highlight the significant spatial and temporal incidence of major acute disturbances (De'ath et al. 2012), if only at select reefs that are monitored (Mellin et al. 2020).

Documented declines in the average coral cover across the GBR from 1985 to 2015 coincided with very intense cyclonic storms ('cyclones') and recurrent population irruptions of the crown-of-thorns starfish (CoTS), *Acanthaster* cf. *solaris* (De'ath et al. 2012; Mellin et al. 2019a; Fig. 10.1). The spatial impact of individual cyclones is generally restricted to within 50 km of the cyclone track (Puotinen 2004). Cyclones generally cross the GBR perpendicular to the coastline. However, very large, intense or slow moving cyclones can impact reefs hundreds of kilometres away from the track (Puotinen et al. 2020) and some have unusually destructive tracks (Cheal et al. 2017). There has been particularly high incidence of intense (category 4–5) cyclones since 2009 (Puotinen et al. 2016; Cheal et al. 2017), which collectively affected much of the GBR. Severe cyclones also have dramatic effects on the structure and function of coral reef ecosystems (Cheal et al. 2017; Wilson et al. 2006), causing rapid and extensive coral loss while altering physical habitat structure (e.g., Beeden et al. 2015; Madin et al. 2018). By comparison, feeding activities of high densities of CoTS result in much more protracted, but often substantial, coral mortality (Pratchett et al. 2014) and leave dead coral colonies structurally intact (Wilson et al. 2006). Population irruptions of CoTS have been documented across a wide range of Indo-Pacific reefs since the late 1950s (Pratchett et al. 2014) and are regularly associated with punctuated coral loss (Bruno and Selig 2007). The GBR has the dubious distinction of being the only location where regular and recurrent population irruptions appear to occur, at approximately 15–17 year intervals (Babcock et al. 2020). These irruptions stem from gradual increases in the densities of CoTS on mid-shelf reefs north of Cairns (and mostly north of Cooktown), which then propagate north and south (Vanhatalo et al. 2016). Very high densities of CoTS, capable of causing extensive coral depletion, tend to be restricted to mid-shelf reefs (Vanhatalo et al. 2016), but may occur along the entire length of the GBR, and occasionally coincide with other major disturbances (Mellin et al. 2019a).

Modelling based on LTMP transect data (Mellin et al. 2019a) suggests that average coral cover on the GBR has declined from 33.3% (IQR: 33.1–33.4%) in 1996 to 18.6% (IQR: 11.5–24.5%) in 2017. Aside from cyclones and CoTS, mass coral bleaching was also recorded, but was a minor contributor to coral mortality, at least up until 2016 (Fig. 10.1). There are also many other disturbances operating at a wide range of spatiotemporal scales (see also Bellwood et al. 2019; Matthews et al. 2019) that do not necessarily cause pronounced levels of coral mortality but still contribute to declining coral cover by constraining coral recovery (Ortiz et al. 2018; MacNeil et al. 2019; Mellin et al. 2019a). Most importantly, poor water quality greatly limits the capacity of coral assemblages to cope with recurrent disturbances, especially on near-shore reefs (MacNeil et al. 2019; Mellin et al. 2019b). It is possible that coral assemblages may have been able to withstand recurrent episodes of perennial disturbances (such as cyclones) over recent decades, were it not for chronic effects of human exploitation and coastal development (e.g., Ortiz et al. 2018). Even so, these ecosystems must now also cope with increasing disturbances associated with climate change (Hughes et al. 2017, 2019a; Vercelloni et al. 2020).

10.4 Climate Change and Mass Coral Bleaching

Mass coral bleaching is the most obvious (but by no means the only) effect of climate change on coral reefs (Hoegh-Guldberg 1999) and has occurred at fairly regular intervals on the GBR since 1980 (Donner et al. 2018). The extent and severity of bleaching recorded on the GBR has increased from 1980 to 2020 (Fig. 10.2). However, the most severe episode of mass-bleaching occurred in 2016 based on the proportion of reefs surveyed that had severe (>30% of corals bleached) and extreme (>60% of corals bleached) levels of coral bleaching (Hughes et al. 2017, unpublished data).

Bleaching *severity* is measured in many different ways and at different scales (e.g., Hoogenboom et al. 2017; Hughes et al. 2017, 2018b), depending on whether

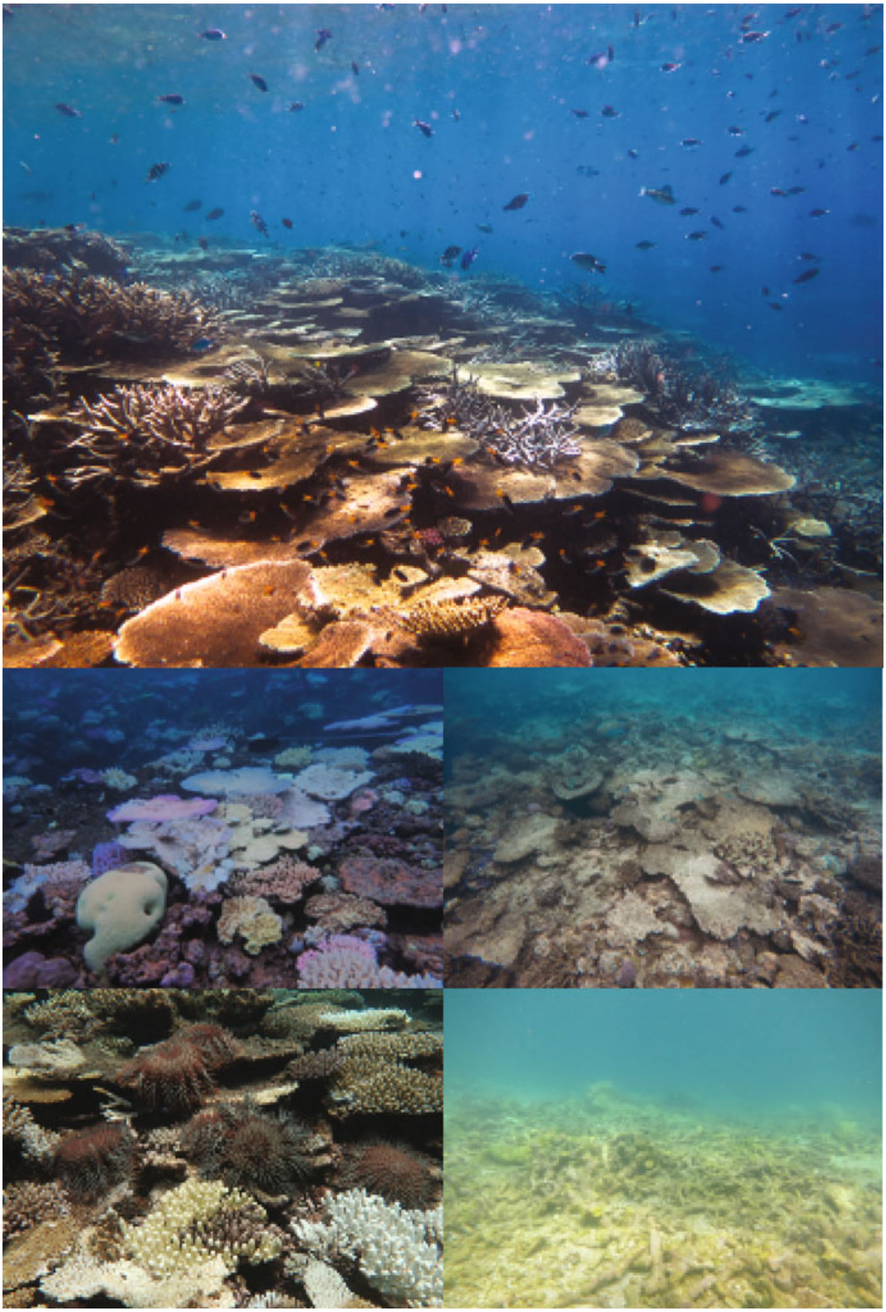


Fig. 10.2 Disturbances affecting coral assemblages on the Great Barrier Reef. From top left to bottom right: Characteristic shallow exposed reef habitat with very high coral cover, dominated by tabular *Acropora*; Recent (2020) bleaching in the central Great Barrier, with disproportionate effects on tabular *Acropora*; Dead coral in the aftermath of the 2016 bleaching, showing dead but intact colonies of *Acropora*; Crown-of-thorns starfish (*Acanthaster* cf. *solaris*) on the Great Barrier

the focus is on individual-, population-, community- or ecosystem responses. The ultimate impact of these disturbances depends on what proportion of corals actually die (Hughes et al. 2018b; Claar and Baum 2019; Leggat et al. 2019; Fig. 10.2), regardless of corresponding levels of coral bleaching. However, large-scale and necessary rapid surveys to assess the spatial extent of impacts during extreme temperature anomalies invariably rely on a single survey (Claar and Baum 2019) and tend to score the proportion of corals that exhibit some level bleaching (e.g., Hughes et al. 2017; Frade et al. 2018), ranging from partial bleaching or changes in overall colouration, where these corals may well survive (Bollati et al. 2020) to extreme *whitening* and early onset of tissue loss which invariably leads to whole colony mortality (Leggat et al. 2019). Given the increasing scale of mass-bleaching events it is not viable to assess the incidence or severity of bleaching from in-water surveys, thereby justifying rapid *ex situ* surveys (e.g., aerial surveys; Berkelmans and Oliver 1999), which have limited capacity to quantify coral cover or overall coral loss. To compare among different bleaching events (discrete years where mass coral bleaching was recorded) on the GBR, we compare the incidence (proportion of reefs considered) with severe levels (>30% of corals bleached) of coral bleaching (Fig. 10.3).

The five most significant (both in extent and severity) mass-bleaching episodes on the GBR (in 1998, 2002, 2016, 2017 and 2020), which correspond with the 5 hottest years on record, have very different footprints. In all five episodes, extensive aerial surveys have documented very widespread bleaching (Berkelmans et al. 2004; Hughes et al. 2019a, unpublished data). However, mass-bleaching in 1998 and 2002 was very moderate and spatially constrained, especially compared to the more recent episodes (Hughes et al. 2017). In 1998 and 2002, approximately 18.0% of reefs were severely bleached ($n = 654$ and 641, respectively). The proportion of reefs that were severely bleached in 2016 was nearly four times higher than in 1998 and 2002 and largely concentrated in the northern section of the GBR (Hughes et al. 2017). In-water surveys showed that resulting coral mortality on reefs that were severely bleached was 30–95% and increased in accordance with increasing bleaching severity and increasing heat intensity among reefs (Hughes et al. 2018b). There were also a substantial number of reefs where bleaching was extreme (>60% of coral bleached) and high levels of coral mortality across highly susceptible coral taxa (e.g., *Acropora* and *Seriatopora*) resulted in marked transformation in coral assemblages at these reefs (Hughes et al. 2018b). Severe bleaching was also recorded to depths of 40 m within the worst affected area, though bleaching severity diminished with increasing depth (Baird et al. 2018; Frade et al. 2018). Ecological impacts of the 2016 mass-bleaching were further compounded by mass-bleaching in the very next year (2017), representing the first recorded incidence of back-to-back mass-bleaching on the GBR (Hughes et al. 2019a). The impacts of this event were

Fig. 10.2 (continued) Reef feeding predominantly on *Acropora* corals; Shallow reef crest environment in the immediate aftermath of a cyclone in the northern Great Barrier Reef. All photographs: M. Pratchett

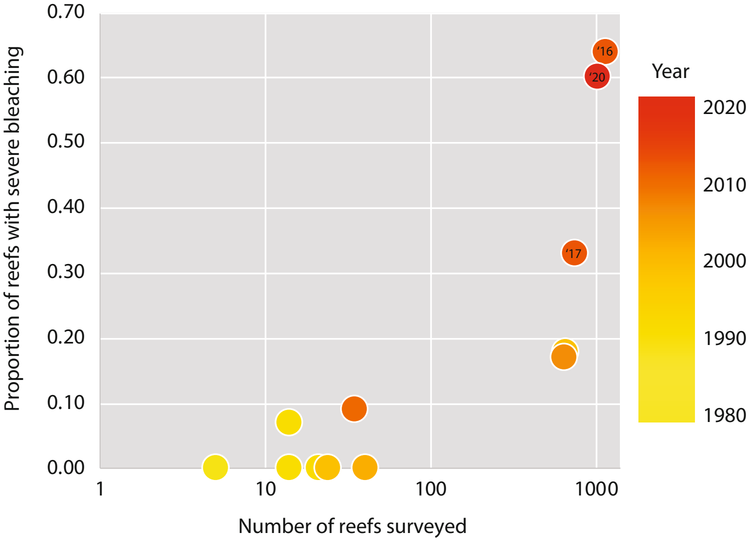


Fig. 10.3 Variation in the severity of mass-bleaching episodes recorded on Australia's Great Barrier Reef over the last four decades (1980–2020). The overall number of reefs surveyed was substantially higher in 1998, 2002, 2016, 2017 and 2020 when aerial surveys were undertaken, whereas the severity of other more localised bleaching episodes was documented with in-water surveys

less severe than in 2016, even though the heat stress was more intense, suggesting that bleaching responses of individual colonies may be moderated by recent exposure to elevated temperatures and/or the most susceptible colonies had already died (Hughes et al. 2019a). The footprint of 2017 bleaching event was similar, but slightly offset compared to 2016, thereby adding to the number of reefs subject to severe coral bleaching in recent years. There were also many reefs subject to severe bleaching in consecutive years.

Mass coral bleaching again occurred in 2020, representing the third major mass-bleaching episode in just 5 years. The footprint of this latest event was also very different to that of 2016 and 2017, and though the overall severity was slightly less than recorded in 2016, the 2020 mass-bleaching event was unprecedented in its spatial extent (Hughes et al. unpublished data). The full consequences of this latest (2020) bleaching event are not going to be known for some time, but it is now apparent that very few reefs have escaped severe coral bleaching in recent times. These events will have greatly conflated coral mortality and coral loss caused by other major disturbances, such as population irruptions of CoTS, which have not abated during this period (Westcott et al. 2020), and mortality from outbreaks of coral disease (Brodnicke et al. 2019). Consequently, average coral cover across the GBR will have further declined from already low levels (18.6%: 11.5–24.5%) recorded in 2017 (Mellin et al. 2019b). Perhaps even more importantly, extensive coral bleaching and coral mortality are associated with transformations in coral

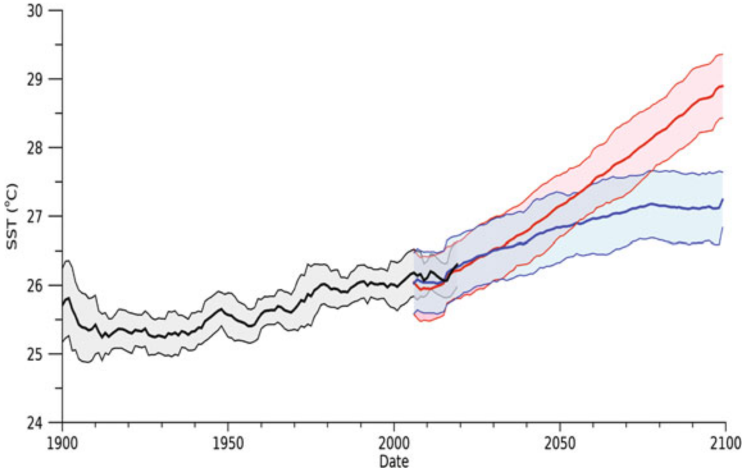


Fig. 10.4 Historical sea surface temperature in the Great Barrier Reef region (black line) has increased over the past century with continued warming projected through the twenty-first century, under representative concentration pathway (RCP) 4.5 (blue) and 8.5 (red). Values are presented as decadal means, with envelopes (±1 standard deviation) reflecting the spatial variability across pixels located within the GBR Marine Park (see figure) and, for future projections, also the variability in output from nine models (ACCESS1-0, ACCESS1-3, CanESM2, CSIRO-Mk-3-6-0, HadGEM2, MIROC5, MPI-ESM-LR, MPI-ESM-MR, MRI-CGCM3; acquired from https://esgf-node.llnl.gov/search/cmip5/)

assemblages (Hughes et al. 2018b) and declines in regional-scale capacity for recovery (Hughes et al. 2019b).

Future projections of environmental change paint a gloomy picture. Average surface water temperatures have increased 0.4–0.6 °C across the GBR since the early 1900s (Lough 2007; Hoegh-Guldberg 2019) and will continue to increase until at least 2050 (Fig. 10.4), owing to lags in climate forcing as well as the thermal inertia of the world's oceans (Mauritsen and Pincus 2017). Moreover, the annual maximum sea surface temperatures on the GBR, which occur in January to February and influence the incidence and severity of mass coral bleaching (Berkelmans and Oliver 1999; Heron et al. 2016), vary in direct accordance with changing average temperatures (Lough 2007). If global emissions continue to increase throughout this century, with continued increases in the burning of thermal coal, as represented by the representative concentration pathway (RCP) 8.5, there is strong agreement across climate models that there will be sustained increases in average sea surface temperatures reaching approximately 29 °C, or >3 °C above current reef-wide average sea surface temperatures (Fig. 10.4). Conversely, if emissions are rapidly reduced and total radiative forcing is stabilised before the end of the century (RCP 4.5), average sea surface temperatures across the GBR are expected to stabilise at approximately 27 °C, just 1 °C above current temperatures. These two different scenarios will have very different consequences for the intensity and frequency of

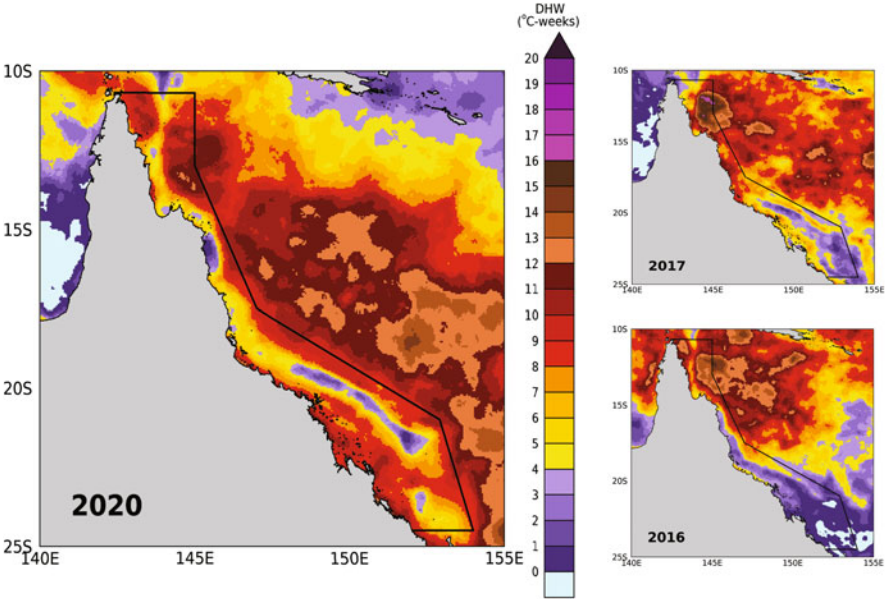


Fig. 10.5 Annual maximum thermal stress (Degree Heating Week, DHW) for the three most recent major bleaching events on the Great Barrier Reef: 2016, 2017 and 2020. The boundary of the GBR Marine Park is shown in each panel (black line). SST data from NOAA Coral Reef Watch (https://coralreefwatch.noaa.gov)

thermal stress events, linked to mass coral bleaching and mortality (Donner et al. 2005, 2018).

Spatiotemporal variation in the extent and severity of mass coral bleaching events on the GBR is tightly coupled with the distribution and intensity of sea surface temperature anomalies (e.g., Hughes et al. 2017). As expected, the bleaching severity at individual reefs, as well as corresponding levels of coral mortality, increases with increasing thermal stress (measured as Degree Heating Weeks, DHW; °C-weeks). In 2016, severe mass-bleaching (>30% of coral bleached) occurred where temperature anomalies were ≥4 °C-weeks, which was mainly in the northern third to half of the GBR (Fig. 10.5). Some reef also experienced much higher levels of heat exposure (8–10 °C-weeks), resulting extreme levels of coral bleaching and high rates of coral loss (Hughes et al. 2017, 2018a). In 2017, the spatial extent of intense heat exposure was much greater than in 2016, and reefs in the northern GBR where extreme bleaching was widespread were again subject to heat exposure ≥8 °C-weeks.

The extent and intensity of sea surface temperature anomalies recorded in 2020 was much greater than has been recorded on the GBR to date (Fig. 10.5). Virtually the entire geographical extent of GBR was exposed to heat exposure ≥4 °C-weeks, and large areas were exposed to ≥8 °C-weeks. Moreover, the cumulative footprint of the three most recent and most severe mass coral bleaching events (which have occurred within a 5 year period) encompasses the entire extent of the GBR. This broad-scale exposure to very intense temperatures is likely reflective of the future typology of mass-bleaching events, given projected increases in average and maximum temperatures of 1–3 °C. It is almost inevitable, therefore, that reefs around the world (including the GBR) will be subject to on-going degradation in coming decades (Veron et al. 2009). While individual reefs may have characteristics that proffer protection from heat stress in the short-term (West and Salm 2003; Hock et al. 2017; Beyer et al. 2018), longer-term consequences of continued warming and corresponding wide-ranging loss of ecological function across the entire reef systems will likely culminate in ecosystem collapse.

10.5 Is the Great Barrier Reef Collapsing?

Marked increases in the apparent incidence or impact of major disturbances on coral reefs often generate fatalist warnings of species extinctions or ecosystem collapse, which are later tempered by revelations of unexpected diversity in species responses, adaptive capacity and resilience (Grigg 1992; Hughes et al. 2003; Maynard et al. 2008; Pandolfi et al. 2011). However, ecological resilience is limited, and transgression of critical thresholds increases the likelihood of abrupt and irreversible changes (Rockström et al. 2009; Cumming and Peterson 2017; Turner et al. 2020). One of the challenges in interpreting existing data is that change is non-linear. Resilience thresholds can be difficult to recognise or quantify, even after they have been crossed (Rockström et al. 2009; Hughes et al. 2013), especially in marine systems where critical changes, such as species extinctions and functional losses, may go unnoticed (Roberts and Hawkins 1999; Burkepile and Thurber 2019). Even if coral reefs were seemingly resilient to past disturbances (but see Jackson et al. 2001), this provides limited assurances of on-going resilience to rapidly escalating effects of climate change (Heron et al. 2016; van Hooidonk et al. 2016; Hughes et al. 2018b). Ecosystem collapse may have already occurred on coral reefs in marginal environments, following population collapses of functionally important species (e.g., Riegl et al. 2018; Burt et al. 2019) and changing configurations of coral reef assemblages (McWilliam et al. 2020). For the GBR, there are some indicators that suggest collapse has occurred or is imminent (e.g., Hughes et al. 2019b), though the fundamental identity is as yet unchanged across large areas of the reef. Further degradation will not necessarily or inevitably result in ecosystem collapse (Mumby et al. 2011; Cumming and Peterson 2017), but on-going warming will increase the likelihood of collapse. One plausible scenario is that the combination of perennial disturbances and accelerating human pressures have pushed shallow reef systems to the boundary at which the capacity of stabilising feedbacks to maintain key components and interactions will be overcome, making them particularly vulnerable to future disturbances, as has already played in out more degraded systems (Hughes et al. 2013).

Changes in the absolute or relative abundance of individual species may have limited ecological consequence, owing to inherent processes (namely, functional redundancy and response diversity) that ensure the continuity of important ecosystem functions (e.g., Nash et al. 2016). However, the magnitude and extent of climate impacts, combined with pervasive and enduring effects of human exploitation and coastal development, is overwhelming inherent ecosystem resilience and restructuring coral reef ecosystems (Stuart-Smith et al. 2018; Williams and Graham 2019). In extreme instances, scleractinian corals have been replaced by macroalgae, soft corals or sponges as the dominant benthic biota (Norström et al. 2009; Graham et al. 2013), though it is more common to observe changes in predominance among different coral taxa (Pratchett et al. 2011). Shifts in coral composition are attributable to taxonomic differences in susceptibility to mass coral bleaching (Hughes et al. 2018b) and other major disturbances (Pratchett et al. 2014; Madin et al. 2018), but are reinforced or moderated by differential recovery capacity (Baker et al. 2008; Pratchett et al. 2020). Long-term shifts in coral composition generally follow one of two alternative pathways, attributable to differences in the frequency versus severity of disturbances (Pratchett et al. 2020); high frequency of moderate disturbances favours the predominance of robust and resistant coral species (e.g., massive *Porites*), whereas infrequent, but severe, disturbance favours corals capable of rapid growth and recolonisation (e.g., Acroporidae and Pocilloporidae). While the latter (predominance of corals that are highly susceptible to recurrent disturbances) would appear to be the least desirable condition, owing to dynamic instability in overall coral cover, these corals have disproportionate importance in reef accretion, topographic complexity, ecological integrity and habitat provisioning for reef-associated organisms (Pratchett et al. 2008; Johns et al. 2014; Alvarez-Filip et al. 2013; Ortiz et al. 2014). The loss of structurally complex corals, leading to declines in both coral cover and habitat complexity, will therefore have far-reaching consequences on reef-associated organisms and coral reef biodiversity (Wilson et al. 2006; Pratchett et al. 2008, 2018).

On the GBR, marked shifts in coral composition were documented across many reefs that experienced extreme levels of mass-bleaching in 2016 (Hughes et al. 2018b). Regional-scale shifts in coral composition reflected taxonomic differences in bleaching susceptibility (Loya et al. 2001), with disproportionate declines in Acroporidae and Pocilloporidae corals. These corals are theoretically capable of rapid recovery and have contributed to relatively rapid recovery recorded in the aftermath of other major disturbances on the GBR (Linares et al. 2011; Johns et al. 2014; Mellin et al. 2019b; McWilliam et al. 2020). Nonetheless, the minimum time required for recovery is 7–10 years (Johns et al. 2014), which exceeds the current and projected return times of mass-bleaching episodes (Veron et al. 2009). Moreover, the extent and magnitude of recent disturbances may have undermined the recovery capacity of these corals, as evident from system-wide declines in coral recruitment in the aftermath of back-to-back bleaching in 2016 and 2017 (Hughes et al. 2019b). This is attributed to overall declines in the size of the breeding population (Hughes et al. 2019b), but corals that survived the recent mass-bleaching are also likely have suppressed growth (Gold and Palumbi 2018; Anderson et al. 2019) and reproductive output (Howells et al. 2016). It is undeniable that the high prevalence and severity of recent mass-bleaching events have transformed coral assemblages on the GBR (Hughes et al. 2018b), and the likelihood of recovery and reassembly is very low, especially given accelerating changes in environmental conditions (Hoegh-Guldberg et al. 2007; Veron et al. 2009). Ultimately, the fate and future structure of the shallow reef environments across the GBR depends on actions that are taken now (or lack thereof) to redress global climate change.

With continued global warming, increasing frequency and severity of heatwaves will contribute to further declines in live coral cover on coral reefs worldwide with corresponding loss of ecosystem structure and function. At very low levels of coral cover (<10%) profound systemic changes may limit recovery and lead to lasting transformations in habitat structure (Wilson et al. 2006; Graham et al. 2015), with further consequences for biodiversity and productivity. It is unlikely that we will see comprehensive coral loss across the full extent of the GBR, but an increasing proportion of reefs will be characterised by non-coral habitats, with fundamentally different dynamics (Bellwood et al. 2018; Tebbett et al. 2020). In areas where corals do predominate, it is likely that there will be a very restricted suite of species (Pratchett et al. 2020), making these assemblages even more vulnerable to future disturbances, such that there will be large fluctuations in coral cover. Non-coral tropical reefs may provide some important goods and services (Graham et al. 2014), but will be very poor analogues of coral reef environments renowned for their high complexity, biodiversity and productivity (Veron et al. 2009).

10.6 Recasting Conservation Goals for Coral Reefs

The GBR marine park is arguably one of the best-managed marine protected areas in the world, supported by (1) ecosystem-based management that extends well beyond the park boundaries; (2) extensive research and monitoring; (3) effective collaboration and communication among management agencies and (4) strong public and industry support (Day and Dobbs 2013). There are, nonetheless, considerable challenges for managing contemporary and cumulative threats to the GBR, especially given the significant and increasing threat posed by global climate change (Hughes et al. 2017; Bellwood et al. 2019). Most critically, urgent action is required to reduce global greenhouse gas emissions to prevent long-term and more devastating impacts of climate change. This will require actions and actors that are well outside the traditional scale and scope of coral reef management (Hughes et al. 2017; Bellwood et al. 2019). However, climate change is undermining the integrity and value of this national asset and global icon (Heron et al. 2017) and effective responses must be commensurate with global scale and significance of this threat (Bellwood et al. 2019) requiring national and international action to immediately and drastically reduce carbon emissions. Meanwhile, coral reef managers must also limit all localised pressures and disturbances, especially those that undermine the resilience and natural adaptive capacity of coral reefs to cope with on-going environmental change (van Hooidonk et al. 2016; Hughes et al. 2017).

Beyond minimising and mitigating global climate change, there are a whole suite of management actions that need to be implemented and/or strengthened to conserve coral reefs, with the specific aim of conserving (and restoring where necessary) key habitats and species that are fundamental to the structure and function of these systems (Darling et al. 2019; Duarte et al. 2020). Priority must be given to addressing the specific disturbances and pressures that threaten these critical components of functioning coral reef ecosystems before trying to rebuild depleted populations or restore degraded habitats (Duarte et al. 2020). The magnitude and extent of ecosystem degradation also means that it is not possible or feasible to return coral reefs to their historical or pre-Anthropocene state (Graham et al. 2014; Bellwood et al. 2019; Duarte et al. 2020). It is also unrealistic to expect that biodiversity loss can now be prevented and prioritisation of conservation must consider the functional importance of individual species or groups (Bellwood et al. 2019). This will require inevitable compromises and revised expectations of intrinsic values associated with coral reefs (Anthony et al. 2020).

Management of the GBR is largely the responsibility of the Great Barrier Reef Marine Park Authority (GBRMPA), which itself has acknowledged the poor and declining condition of the GBR (GBRMPA 2019) and has committed to addressing climate change, as well as improving water quality. If effective, there is no doubt that these actions will go a long way towards improving the long-term outlook for the GBR (Ortiz et al. 2014, 2018). However, GBRMPA has relatively limited capacity to make necessary changes that are needed to reduce national emissions or reduce nutrients and pollutants entering the GBR. There are also significant governance constraints in effectively dealing with the threat of climate change and declining water quality on the GBR (Fidelman et al. 2013; Hughes et al. 2015). Moreover, current national decarbonisation policies are insufficient to meet internationally agreed emission reduction targets (den Elzen et al. 2019), necessary to stabilise temperatures in the next few decades. Given committed warming, there is a major focus on adaptation and restoration interventions aimed at increasing the capacity of corals to withstand and/or rapidly recover in the aftermath of climate impacts (e.g., Anthony et al. 2020). While this research is highlighting the key vulnerabilities of corals subject to rapidly changing environmental conditions (e.g., van Oppen et al. 2015; Quigley et al. 2019), the capacity to effectively intervene at meaningful scales is yet to be demonstrated (Boström-Einarsson et al. 2020). Meanwhile, it is dangerous to overstate the capacity to restore degraded systems or engineer solutions that detract from the need to cut emissions and effectively give license to unsustainable industries and activities to continue. Similarly, the increasing threat from climate change provides increased imperative to manage other causes of coral loss that are more amenable to direct intervention (Westcott et al. 2020). Improved management is necessary to increase the resilience of reef systems and organisms, but ecosystem collapse on Australia's GBR is inevitable if climate change continues unabated.

Acknowledgements The research summarised in this chapter was funded by the Australian Research Council (ARC) Centre of Excellence for Coral Reef Studies (CE140100020) and an ARC Discovery (DP180103199).

References

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proc R Soc B Biol Sci 276 (1669):3019–3025. https://doi.org/10.1098/rspb.2009.0339

Alvarez-Filip L, Carricart-Ganivet JP, Horta-Puga G, Iglesias-Prieto R (2013) Shifts in coral-assemblage composition do not ensure persistence of reef functionality. Sci Rep 3:3486. https://doi.org/10.1038/srep03486

Anderson KD, Cantin NE, Casey JM, Pratchett MS (2019) Independent effects of ocean warming versus acidification on the growth, survivorship and physiology of two *Acropora* corals. Coral Reefs 38(6):1225–1240. https://doi.org/10.1007/s00338-019-01864-y

Anthony KR, Helmstedt KJ, Bay LK, Fidelman P, Hussey KE, Lundgren P et al (2020) Interventions to help coral reefs under global change—A complex decision challenge. PLoS One 15(8):e0236399. https://doi.org/10.1371/journal.pone.0236399

Babcock RC, Plagányi ÉE, Condie SA, Westcott DA, Fletcher CS, Bonin MC et al (2020) Suppressing the next crown-of-thorns outbreak on the Great Barrier Reef. Coral Reefs 39:1233–1244. https://doi.org/10.1007/s00338-020-01978-8

Baird AH, Madin JS, Álvarez-Noriega M, Fontoura L, Kerry JT, Kuo CY et al (2018) A decline in bleaching suggests that depth can provide a refuge from global warming in most coral taxa. Mar Ecol Prog Ser 603:257–264. https://doi.org/10.3354/meps12732

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80 (4):435–471. https://doi.org/10.1016/j.ecss.2008.09.003

Beeden R, Maynard J, Puotinen M, Marshall P, Dryden J, Goldberg J, Williams G (2015) Impacts and recovery from severe tropical Cyclone Yasi on the Great Barrier Reef. PLoS One 10(4): e0121272. https://doi.org/10.1371/journal.pone.0121272

Bell JB, Ganachaud A, Gehrke PC, Griffiths SP, Hobday AJ, Hoegh-Guldberg O et al (2013) Mixed responses of tropical Pacific fisheries and aquaculture to climate change. Nat Clim Change 3:591–599. https://doi.org/10.1038/nlimate1838

Bellwood DR, Tebbett SB, Bellwood O, Mihalitsis M, Morais RA, Streit RP et al (2018) The role of the reef flat in coral reef trophodynamics: past, present, and future. Ecol Evol 8(8):4108–4119. https://doi.org/10.1002/ece3.3967

Bellwood DR, Pratchett MS, Morrison TH, Gurney GG, Hughes TP, Álvarez-Romero JG et al (2019) Coral reef conservation in the Anthropocene: Confronting spatial mismatches and prioritizing functions. Biol Conserv 236:604–615. https://doi.org/10.1016/j.biocon.2019.05.056

Bergstrom DM, Bricher PK, Raymond B, Terauds A, Doley D, McGeoch MA et al (2015) Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. J Appl Ecol 52 (3):774–783. https://doi.org/10.1111/1365-2664.12436

Berkelmans R, Oliver JK (1999) Large-scale bleaching of corals on the Great Barrier Reef. Coral Reefs 18(1):55–60. https://doi.org/10.1007/s003380050154

Berkelmans R, De'ath G, Kininmonth S, Skirving WJ (2004) A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. Coral Reefs 23(1):74–83. https://doi.org/10.1007/s00338-003-0353-y

Beyer HL, Kennedy EV, Beger M, Chen CA, Cinner JE, Darling ES et al (2018) Risk-sensitive planning for conserving coral reefs under rapid climate change. Conserv Lett 11(6):e12587. https://doi.org/10.1111/conl.12587

Bollati E, D'Angelo C, Alderdice R, Pratchett M, Ziegler M, Wiedenmann J (2020) Optical feedback loop involving dinoflagellate symbiont and scleractinian host drives colorful coral bleaching. Curr Biol 30(3):2433–2445. https://doi.org/10.1016/j.cub.2020.04.055

Boström-Einarsson L, Babcock RC, Bayraktarov E, Ceccarelli D, Cook N, Ferse SC et al (2020) Coral restoration–A systematic review of current methods, successes, failures and future directions. PLoS One 15(1):e0226631. https://doi.org/10.1371/journal.pone.0226631

Brodnicke OB, Bourne DG, Heron SF, Pears RJ, Stella JS, Smith HA et al (2019) Unravelling the links between heat stress, bleaching and disease: fate of tabular corals following a combined disease and bleaching event. Coral Reefs 38(4):591–603. https://doi.org/10.1007/s00338-019-01813-9

Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. PLoS One 2(8):e711. https://doi.org/10.1371/journal.pone.0000711

Burkepile DE, Thurber RV (2019) The long arm of species loss: How will defaunation disrupt ecosystems down to the microbial scale? BioScience 69(6):443–454. https://doi.org/10.1093/biosci/biz047

Burt JA, Paparella F, Al-Mansoori N, Al-Mansoori A, Al-Jailani H (2019) Causes and consequences of the 2017 coral bleaching event in the southern Persian/Arabian Gulf. Coral Reefs 38(4):567–589. https://doi.org/10.1007/s00338-019-01767-y

Cheal AJ, Wilson SK, Emslie MJ, Dolman AM, Sweatman H (2008) Responses of reef fish communities to coral declines on the Great Barrier Reef. Mar Ecol Prog Ser 372:211–223. https://doi.org/10.3354/meps07708

Cheal AJ, MacNeil MA, Emslie MJ, Sweatman H (2017) The threat to coral reefs from more intense cyclones under climate change. Glob Change Biol 23(4):1511–1524. https://doi.org/10.1111/gcb.13593

Claar DC, Baum JK (2019) Timing matters: survey timing during extended heat stress can influence perceptions of coral susceptibility to bleaching. Coral Reefs 38(4):559–565. https://doi.org/10.1007/s00338-018-01756-7

Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. Fish Fish 9:286–307. https://doi.org/10.1111/j.1467-2979.2008.00290.x

Cumming GS, Peterson GD (2017) Unifying research on social–ecological resilience and collapse. Trends Ecol Evol 32(9):695–713. https://doi.org/10.1016/j.tree.2017.06.014

Darling ES, McClanahan TR, Maina J, Gurney GG, Graham NA, Januchowski-Hartley F et al (2019) Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. Nat Ecol Evol 3(9):1341–1350. https://doi.org/10.1038/s41559-019-0953-8

Day JC, Dobbs K (2013) Effective governance of a large and complex cross-jurisdictional marine protected area: Australia's Great Barrier Reef. Mar Policy 41:14–24. https://doi.org/10.1016/j.marpol.2012.12.020

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27–year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci USA 109(44):17995–17999. https://doi.org/10.1073/pnas.1208909109

den Elzen M, Kuramochi T, Höhne N, Cantzler J, Esmeijer K, Fekete H et al (2019) Are the G20 economies making enough progress to meet their NDC targets? Energy Policy 126:238–250. https://doi.org/10.1016/j.enpol.2018.11.027

Dillon ME, Wang G, Huey RB (2010) Global metabolic impacts of recent climate warming. Nature 467(7316):704–706. https://doi.org/10.1038/nature09407

Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg OV (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. Glob Change Biol 11(12):2251–2265. https://doi.org/10.1111/j.1365-2486.2005.01073.x

Donner SD, Heron SF, Skirving WJ (2018) Future scenarios: a review of modelling efforts to predict the future of coral reefs in an era of climate change. In: van Oppen M, Lough J (eds) Coral bleaching. Springer, Cham, pp 325–341. https://doi.org/10.1007/978-3-319-75393-5_13

Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso JP et al (2020) Rebuilding marine life. Nature 580(7801):39–51. https://doi.org/10.1038/s41586-020-2146-7

Eakin CM, Morgan JA, Heron SF, Smith TB, Liu G, Alvarez-Filip L et al (2010) Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. PLoS One 5(11):e13969. https://doi.org/10.1371/journal.pone.0013969

Eakin CM, Sweatman HP, Brainard RE (2019) The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38(4):539–545. https://doi.org/10.1007/s00338-019-01844-2

Emslie MJ, Pratchett MS, Cheal AJ (2011) Effects of different disturbance types on butterflyfish communities of Australia's Great Barrier Reef. Coral Reefs 30(2):461–471. https://doi.org/10.1007/s00338-011-0730-x

Emslie MJ, Logan M, Williamson DH, Ayling AM, MacNeil MA, Ceccarelli D et al (2015) Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. Curr Biol 25(8):983–992. https://doi.org/10.1016/j.cub.2015.01.073

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ et al (2011) Trophic downgrading of planet Earth. Science 333(6040):301–306. https://doi.org/10.1126/science.1205106

Fidelman PI, Leitch AM, Nelson DR (2013) Unpacking multilevel adaptation to climate change in the Great Barrier Reef, Australia. Glob Environ Change 23(4):800–812. https://doi.org/10.1016/j.gloenvcha.2013.02.016

Frade PR, Bongaerts P, Englebert N, Rogers A, Gonzalez-Rivero M, Hoegh-Guldberg O (2018) Deep reefs of the Great Barrier Reef offer limited thermal refuge during mass coral bleaching. Nat Commun 9(1):1–8. https://doi.org/10.1038/s41467-018-05741-0

GBRMPA (2019) Great Barrier Reef Outlook Report 2019. Great Barrier Reef Marine Park Authority, Townsville

Glynn PW (1991) Coral reef bleaching in the 1980s and possible connections with global warming. Trends Ecol Evol 6(6):175–179. https://doi.org/10.1016/0169-5347(91)90208-F

Gold Z, Palumbi SR (2018) Long-term growth rates and effects of bleaching in *Acropora hyacinthus*. Coral Reefs 37(1):267–277. https://doi.org/10.1007/s00338-018-1656-3

Goreau TF, Goreau NI, Goreau TJ (1979) Corals and coral reefs. Sci Am 241(2):124–137. https://www.jstor.org/stable/10.2307/24965267

Graham NA, Wilson SK, Jennings S, Polunin NV, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. Proc Natl Acad Sci USA 103(22):8425–8429. https://doi.org/10.1073/pnas.0600693103

Graham NA, Bellwood DR, Cinner JE, Hughes TP, Norström AV, Nyström M (2013) Managing resilience to reverse phase shifts in coral reefs. Front Ecol Environ 11(10):541–548. https://doi.org/10.1890/120305

Graham NA, Cinner JE, Norström AV, Nyström M (2014) Coral reefs as novel ecosystems: embracing new futures. Curr Opin Environ Sustain 7:9–14. https://doi.org/10.1016/j.cosust.2013.11.023

Graham NA, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518(7537):94–97. https://doi.org/10.1038/nature14140

Grigg RW (1992) Coral reef environmental science: truth versus the Cassandra syndrome. Coral Reefs 11(4):183–186. https://doi.org/10.1007/BF00301990

Harrison HB, Álvarez-Noriega M, Baird AH, Heron SF, MacDonald C, Hughes TP (2018) Back-to-back coral bleaching events on isolated atolls in the Coral Sea. Coral Reefs 38:713–719. https://doi.org/10.1007/s00338-018-01749-6

Head CEI, Bayley DTI, Rowlands G, Roche RC, Tickler DM, Rogers AD et al (2019) Coral bleaching impacts from back-to-back 2015–2016 thermal anomalies in the remote central Indian Ocean. Coral Reefs 38:605–618. https://doi.org/10.1007/s00338-019-01821-9

Henson SA, Beaulieu C, Ilyina T, John JG, Long M, Séférian R et al (2017) Rapid emergence of climate change in environmental drivers of marine ecosystems. Nat Commun 8(1):14682. https://doi.org/10.1038/ncomms14682

Heron SF, Maynard J, van Hooidonk R, Eakin CM (2016) Warming trends and bleaching stress of the world's coral reefs 1985–2012. Sci Rep 6:38402. https://doi.org/10.1038/srep38402

Heron SF, Eakin CM, Douvere F, Anderson KL, Day JC, Geiger E et al (2017) Impacts of climate change on world heritage coral reefs: a first global scientific assessment. UNESCO World Heritage Centre, Paris

Hock K, Wolff NH, Ortiz JC, Condie SA, Anthony KR, Blackwell PG, Mumby PJ (2017) Connectivity and systemic resilience of the Great Barrier Reef. PLoS Biol 15(11):e2003355. https://doi.org/10.1371/journal.pbio.2003355

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50(8):839–866. https://doi.org/10.1071/MF99078

Hoegh-Guldberg O (2019) Coral reefs in a changing world. In: Hutchings P, Kingsford M, Hoegh-Guldbeer H (eds) The Great Barrier Reef: biology, environment and management. CRC, Boca Raton

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328(5985):1523–1528. https://doi.org/10.1126/science.1189930

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E et al (2007) Coral reefs under rapid climate change and ocean acidification. Science 318(5857):1737–1742. https://doi.org/10.1126/science.1152509

Hoogenboom MO, Frank GE, Chase TJ, Jurriaans S, Álvarez-Noriega M, Peterson K et al (2017) Environmental drivers of variation in bleaching severity of *Acropora* species during an extreme thermal anomaly. Front Mar Sci 4:376. https://doi.org/10.3389/fmars.2017.00376

Howells EJ, Ketchum RN, Bauman AG, Mustafa Y, Watkins KD, Burt JA (2016) Species-specific trends in the reproductive output of corals across environmental gradients and bleaching histories. Mar Pollut Bull 105(2):532–539. https://doi.org/10.1016/j.marpolbul-2015.11.034

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C et al (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301(5635):929–933. https://doi.org/10.1126/science.1085046

Hughes TP, Linares C, Dakos V, Van De Leemput IA, Van Nes EH (2013) Living dangerously on borrowed time during slow, unrecognized regime shifts. Trends Ecol Evol 28(3):149–155. https://doi.org/10.1016/j.tree.2012.08.022

Hughes TP, Day JC, Brodie J (2015) Securing the future of the Great Barrier Reef. Nat Clim Change 5(6):508–511. https://doi.org/10.1038/nclimate2604

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH et al (2017) Global warming and recurrent mass bleaching of corals. Nature 543(7645):373–377. https://doi.org/10.1038/nature21707

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM et al (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359(6371):80–83. https://doi.org/10.1126/science.aan8048

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM et al (2018b) Global warming transforms coral reef assemblages. Nature 556(7702):492–496. https://doi.org/10.1038/s41586-018-0041-2

Hughes TP, Kerry JT, Connolly SR, Baird AH, Eakin CM, Heron SF et al (2019a) Ecological memory modifies the cumulative impact of recurrent climate extremes. Nat Clim Change 9 (1):40–43. https://doi.org/10.1038/s41558-018-0351-2

Hughes TP, Kerry JT, Baird AH, Connolly SR, Chase TJ, Dietzel A et al (2019b) Global warming impairs stock–recruitment dynamics of corals. Nature 568(7752):387–390. https://doi.org/10.1038/s41586-019-1081-y

Idjadi JA, Edmunds PJ (2006) Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. Mar Ecol Prog Ser 319:117–127. https://doi.org/10.3354/meps319117

Iglesias-Prieto R, Matta JL, Robins WA, Trench RK (1992) Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. Proc Natl Acad Sci USA 89(21):10302–10305. https://doi.org/10.1073/pnas.89.21.10302

Iknayan KJ, Beissinger SR (2018) Collapse of a desert bird community over the past century driven by climate change. Proc Natl Acad Sci USA 115(34):8597–8602. https://doi.org/10.1073/pnas.1805123115

Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ et al (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530):629–637. https://doi.org/10.1126/science.1059199

Johns KA, Osborne KO, Logan M (2014) Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef. Coral Reefs 33(3):553–563. https://doi.org/10.1007/s00338-014-1148-z

Jokiel PL, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs 8(4):155–162

Keith DA, Rodríguez JP, Rodríguez-Clark KM, Nicholson E, Aapala K, Alonso A et al (2013) Scientific foundations for an IUCN Red List of Ecosystems. PLoS One 8(5):e62111. https://doi.org/10.1371/journal.pone.0062111

Leggat WP, Camp EF, Suggett DJ, Heron SF, Fordyce AJ, Gardner S et al (2019) Rapid coral decay is associated with marine heatwave mortality events on reefs. Curr Biol 29(16):2723–2730. https://doi.org/10.1016/j.cub.2019.06.077

Linares C, Pratchett MS, Coker DJ (2011) Recolonisation of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 438:97–104. https://doi.org/10.3354/meps09272

Lough J (2007) Climate and climate change on the Great Barrier Reef. In: Johnson JE, Marshall PA (eds) Climate change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, Van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4(2):122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

MacNeil MA, Mellin C, Matthews S, Wolff NH, McClanahan TR, Devlin M et al (2019) Water quality mediates resilience on the Great Barrier Reef. Nat Ecol Evol 3(4):620–627. https://doi.org/10.1038/s41559-019-0832-3

Madin JS, Baird AH, Bridge TC, Connolly SR, Zawada KJ, Dornelas M (2018) Cumulative effects of cyclones and bleaching on coral cover and species richness at Lizard Island. Mar Ecol Prog Ser 604:263–268. https://doi.org/10.3354/meps12735

Matthews SA, Mellin C, MacNeil A, Heron SF, Skirving W, Puotinen M et al (2019) High-resolution characterization of the abiotic environment and disturbance regimes on the Great Barrier Reef, 1985–2017. Ecology 100(2):e02574. https://doi.org/10.1002/ecy.2574

Mauritsen T, Pincus R (2017) Committed warming inferred from observations. Nat Clim Change 7 (9):652–625. https://doi.org/10.1038/nclimate3357

Maynard JA, Baird AH, Pratchett MS (2008) Revisiting the Cassandra syndrome; the changing climate of coral reef research. Coral Reefs 27(4):745–749. https://doi.org/10.1007/s00338-008-0432-1

McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D (2003) Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421 (6924):727–730. https://doi.org/10.1038/nature01361

McWilliam M, Pratchett MS, Hoogenboom MO, Hughes TP (2020) Deficits in functional trait diversity following recovery on coral reefs. Proc R Soc B Biol Sci 287(1918):20192628. https://doi.org/10.1098/rspb.2019.2628

Mellin C, Matthews S, Anthony KR, Brown SC, Caley MJ, Johns KA et al (2019a) Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. Glob Change Biol 25(7):2431–2445. https://doi.org/10.1111/gcb.14625

Mellin C, Thompson A, Jonker MJ, Emslie MJ (2019b) Cross-shelf variation in coral community response to disturbance on the Great Barrier Reef. Diversity 11(3):38. https://doi.org/10.3390/d11030038

Mellin C, Peterson EE, Puotinen M, Schaffelke B (2020) Representation and complementarity of the long-term coral monitoring on the Great Barrier Reef. Ecol Appl 30(6):e02122. https://doi.org/10.1002/eap.2122

Morris LA, Voolstra CR, Quigley KM, Bourne DG, Bay LK (2019) Nutrient availability and metabolism affect the stability of coral-symbiodiniaceae symbioses. Trends Microbiol 27 (8):678–689. https://doi.org/10.1016/j.tim.2019.03.004

Mullon C, Fréon P, Cury P (2005) The dynamics of collapse in world fisheries. Fish Fish 6 (2):111–120. https://doi.org/10.1111/j.1467-2979.2005.00181.x

Mumby PJ, Iglesias-Prieto R, Hooten AJ, Sale PF, Hoegh-Guldberg O, Edwards AJ et al (2011) Revisiting climate thresholds and ecosystem collapse. Front Ecol Environ 9(2):94–96. https://www.jstor.org/stable/41149695

Myers RA, Hutchings JA, Barrowman NJ (1997) Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecol Appl 7(1):91–106. https://doi.org/10.1890/1051-0761(1997)007[0091:WDFSCT]2.0.CO;2

Nagelkerken I, Munday PL (2016) Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. Glob Change Biol 22(3):974–989. https://doi.org/10.1111/gcb.13167

Nash KL, Graham NA, Jennings S, Wilson SK, Bellwood DR (2016) Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. J Appl Ecol 53 (3):646–655. https://doi.org/10.1111/1365-2664.12430

Newbold T (2018) Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. Proc R Soc B Biol Sci 285(1881):20180792. https://doi.org/10.1098/rspb.2018.0792

Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Mar Ecol Prog Ser 376:295–306. https://doi.org/10.3354/meps07815

Ortiz JC, Bozec YM, Wolff NH, Doropoulos C, Mumby PJ (2014) Global disparity in the ecological benefits of reducing carbon emissions for coral reefs. Nat Clim Change 4 (12):1090–1094. https://doi.org/10.1038/nclimate2439

Ortiz JC, Wolff NH, Anthony KR, Devlin M, Lewis S, Mumby PJ (2018) Impaired recovery of the Great Barrier Reef under cumulative stress. Sci Adv 4(7):eaar6127. https://doi.org/10.1126/sciadv.aar6127

Osborne K, Dolman AM, Burgess SC, Johns KA (2011) Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995–2009). PLoS One 6(3):e17516. https://doi.org/10.1371/journal.pone.0017516

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG et al (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301(5635):955–958. https://doi.org/10.1126/science.1085706

Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. Science 333(6041):418–422. https://doi.org/10.1126/science.1204794

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC et al (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355 (6332):eaai9214. https://doi.org/10.1126/science.aai9214

Perry CT, Morgan KM (2017) Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives reefs. Sci Rep 7:40581. https://doi.org/10.1038/srep40581

Perry CT, Murphy GN, Kench PS, Smithers SG, Edinger EN, Steneck RS et al (2013) Caribbean-wide decline in carbonate production threatens coral reef growth. Nat Commun 4:1402. https://doi.org/10.1038/ncomms2409

Pinsky ML, Jensen OP, Ricard D, Palumbi SR (2011) Unexpected patterns of fisheries collapse in the world's oceans. Proc Natl Acad Sci USA 108(20):8317–8322. https://doi.org/10.1073/pnas.1015313108

Pratchett MS (2010) Changes in coral assemblages during an outbreak of *Acanthaster planci* at Lizard Island, northern Great Barrier Reef (1995–1999). Coral Reefs 29(3):717–725. https://doi.org/10.1007/s00338-010-0602-9

Pratchett MS, Munday P, Wilson SK, Graham NA, Cinner JE, Bellwood DR et al (2008) Effects of climate-induced coral bleaching on coral-reef fishes—ecological and economic consequences. Oceanogr Mar Biol Annu Rev 46:251–296

Pratchett MS, Trapon M, Berumen ML, Chong-Seng K (2011) Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. Coral Reefs 30 (1):183–193. https://doi.org/10.1007/s00338-010-0678-2

Pratchett MS, McCowan D, Maynard JA, Heron SF (2013) Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. PLoS One 8(7):e70443. https://doi.org/10.1371/journal.pone.0070443

Pratchett MS, Caballes CF, Rivera-Posada JA, Sweatman HPA (2014) Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). Oceanogr Mar Biol Annu Rev 52:133–200

Pratchett MS, Thompson CA, Hoey AS, Cowman PF, Wilson SK (2018) Effects of coral bleaching and coral loss on the structure and function of reef fish assemblages. In: van Oppen M, Lough J (eds) Coral bleaching. Springer, Cham. https://doi.org/10.1007/978-3-319-75393-5_11

Pratchett MS, McWilliam MJ, Riegl B (2020) Contrasting shifts in coral assemblages with increasing disturbances. Coral Reefs 39:783–793. https://doi.org/10.1007/s00338-020-01936-4

Puotinen ML (2004) Tropical cyclones in the Great Barrier Reef, Australia, 1910–1999: a first step towards characterising the disturbance regime. Aust Geogr Stud 42(3):378–392. https://doi.org/10.1111/j.1467-8470.2004.00288.x

Puotinen M, Maynard JA, Beeden R, Radford B, Williams GJ (2016) A robust operational model for predicting where tropical cyclone waves damage coral reefs. Sci Rep 6:26009. https://doi.org/10.1038/srep26009

Puotinen M, Drost E, Lowe R, Depczynski M, Radford B, Heyward A, Gilmour J (2020) Towards modelling the future risk of cyclone wave damage to the world's coral reefs. Glob Change Biol. https://doi.org/10.1111/gcb.1513

Quigley KM, Bay LK, van Oppen MJ (2019) The active spread of adaptive variation for reef resilience. Ecol Evol 9(19):11122–11135. https://doi.org/10.1002/ece3.5616

Riegl B, Johnston M, Purkis S, Howells E, Burt J, Steiner SC, Sheppard CR, Bauman A (2018) Population collapse dynamics in *Acropora downingi*, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. Glob Change Biol 24(6):2447–2462. https://doi.org/10.1111/gcb.14114

Roberts CM, Hawkins JP (1999) Extinction risk in the sea. Trends Ecol Evol 14(6):241–246. https://doi.org/10.1016/S0169-5347(98)01584-5

Rockström J, Steffen W, Noone K, Persson Å, Chapin FS, Lambin EF et al (2009) A safe operating space for humanity. Nature 461(7263):472–475. https://doi.org/10.1038/461472a

Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. Curr Biol 24(9):1000–1005. https://doi.org/10.1016/j.cub.2014.03.026

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G et al (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 453(7193):353–357. https://doi.org/10.1038/nature06937

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM et al (2008) Baselines and degradation of coral reefs in the Northern Line Islands. PLoS One 3(2):e1548. https://doi.org/10.1371/journal.pone.0001548

Sharma S, Blagrave K, Magnuson JJ, O'Reilly CM, Oliver S et al (2019) Widespread loss of lake ice around the Northern Hemisphere in a warming world. Nat Clim Change 9(3):227–231. https://doi.org/10.1038/s41558-018-0393-5

Sheppard C (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. Nature 425:294–297. https://doi.org/10.1038/nature01987

Skirving WJ, Heron SF, Marsh BL, Liu G, De La Cour JL, Geiger EF et al (2019) The relentless march of mass coral bleaching: a global perspective of changing heat stress. Coral Reefs 38 (4):547–557. https://doi.org/10.1007/s00338-019-01799-4

Smale DA, Wernberg T, Oliver EC, Thomsen M, Harvey BP, Straub SC et al (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Change 9(4):306–312. https://doi.org/10.1038/s41558-019-0412-1

Smith KM, Payton TG, Sims RJ, Stroud CS, Jeanes RC, Hyatt TB et al (2019) Impacts of consecutive bleaching events and local algal abundance on transplanted coral colonies in the Florida Keys. Coral Reefs 38:851–861. https://doi.org/10.1007/s00338-019-01823-7

Stella JS, Pratchett MS, Hutchings PA, Jones GP (2011) Diversity, importance and vulnerability of coral-associated invertebrates. Oceanogr Mar Biol Annu Rev 49:43–116

Stuart-Smith RD, Brown CJ, Ceccarelli DM, Edgar GJ (2018) Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. Nature 560(7716):92–96. https://doi.org/10.1038/s41586-018-0359-9

Sully S, Burkepile DE, Donovan MK, Hodgson G, Van Woesik R (2019) A global analysis of coral bleaching over the past two decades. Nat Commun 10(1):1–5. https://doi.org/10.1038/s41467-019-09238-2

Sweatman H (2008) No-take reserves protect coral reefs from predatory starfish. Curr Biol 18(14): R598–R599. https://doi.org/10.1016/j.cub.2008.05.033

Sweatman H, Delean S, Syms C (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. Coral Reefs 30(2):521–531

Tebbett SB, Streit RP, Bellwood DR (2020) A 3D perspective on sediment accumulation in algal turfs: Implications of coral reef flattening. J Ecol 108(1):70–80. https://doi.org/10.1111/1365-2745.13235

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC et al (2004) Extinction risk from climate change. Nature 427:145–148. https://doi.org/10.1038/nature02121

Thomson JA, Burkholder DA, Heithaus MR, Fourqurean JW, Fraser MW, Statton J et al (2014) Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. Glob Change Biol 21(4):1463–1474. https://doi.org/10.1111/gcb.12694

Turner MG, Calder WJ, Cumming GS, Hughes TP, Jentsch A, LaDeau SL et al (2020) Climate change, ecosystems and abrupt change: science priorities. Philos Trans R Soc B 375 (1794):20190105. https://doi.org/10.1098/rstb.2019.0105

Vanhatalo J, Hosack GR, Sweatman H (2016) Spatiotemporal modelling of crown-of-thorns starfish outbreaks on the Great Barrier Reef to inform control strategies. J Appl Ecol 54 (1):188–197. https://doi.org/10.1111/1365-2664.12710

van Hooidonk R, Maynard J, Tamelander J, Gove J, Ahmadia G, Raymundo L et al (2016) Local-scale projections of coral reef futures and implications of the Paris Agreement. Sci Rep 6 (1):39666. https://doi.org/10.1038/srep39666

van Oppen MJ, Oliver JK, Putnam HM, Gates RD (2015) Building coral reef resilience through assisted evolution. Proceedings of the National Academy of Sciences. USA 112(8):2307–2313. https://doi.org/10.1073/pnas.1422301112

Vercelloni J, Liquet B, Kennedy EV, González-Rivero M, Caley MJ, Peterson EE et al (2020) Forecasting intensifying disturbance effects on coral reefs. Glob Change Biol 26(5):2785–2797. https://doi.org/10.1111/gcb.15059

Veron JE, Hoegh-Guldberg O, Lenton TM, Lough JM, Obura DO, Pearce-Kelly PA et al (2009) The coral reef crisis: The critical importance of <350 ppm CO_2. Mar Pollut Bull 58 (10):1428–1436. https://doi.org/10.1016/j.marpolbul.2009.09.009

Wakeford M, Done TJ, Johnson CR (2008) Decadal trends in a coral community and evidence of changed disturbance regime. Coral Reefs 27(1):1–3. https://doi.org/10.1007/s00338-007-0284-0

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ et al (2002) Ecological responses to recent climate change. Nature 416(6879):389–395. https://doi.org/10.1038/416389a

Wernberg T, Bennett S, Babcock RC, De Bettignies T, Cure K, Depczynski M et al (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353(6295):169–172. https://doi.org/10.1126/science.aad8745

West JM, Salm RV (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conserv Biol 17(4):956–967. https://doi.org/10.1046/j.1523-1739.2003.02055.x

Westcott DA, Fletcher CS, Kroon FJ, Babcock RC, Plagányi EE, Pratchett MS, Bonin MC (2020) Relative efficacy of three approaches to mitigate crown-of-thorns starfish outbreaks on Australia's Great Barrier Reef. Sci Rep 10(1):12594. https://doi.org/10.1038/s41598-020-69466-1

Wild C, Huettel M, Klueter A, Kremb SG, Rasheed MY, Jørgensen BB (2004) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. Nature 428 (6978):66–70. https://doi.org/10.1038/nature02344

Williams GJ, Graham NAJ (2019) Rethinking coral reef functional futures. Functional Ecology 33 (6):942–947. https://doi.org/10.1111/1365-2435.13374

Wilson SK, Graham NA, Pratchett MS, Jones GP, Polunin NV (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Glob Change Biol 12 (11):2220–2234. https://doi.org/10.1111/j.1365-2486.2006.01252.x

Wilson SK, Dolman AM, Cheal AJ, Emslie MJ, Pratchett MS, Sweatman HP (2009) Maintenance of fish diversity on disturbed coral reefs. Coral Reefs 28(1):3–14. https://doi.org/10.1007/s00338-008-043

Wooldridge SA, Done TJ (2009) Improved water quality can ameliorate effects of climate change on corals. Ecol Appl 19(6):1492–1499. https://doi.org/10.1890/08-0963.1

Sliding Toward the Collapse of Mediterranean Coastal Marine Rocky Ecosystems

11

Joaquim Garrabou, Jean-Baptiste Ledoux, Nathaniel Bensoussan, Daniel Gómez-Gras, and Cristina Linares

Abstract

Climate change is one of the biggest emerging threats to marine biodiversity in the Mediterranean Sea. In this chapter, we focus on the recurrent and large scale mass mortality events (MMEs) induced by marine heatwaves (MHWs), and their immediate and long-term impacts on structural octocorals from highly diverse coralligenous communities. By combining an accurate characterization of present and expected thermal stress conditions in coastal seawater from the surface down to 40 m depth with the state of the art on demography, population genetics, and

---

J. Garrabou (✉)
Institut de Ciències del Mar, CSIC, Barcelona, Spain

Aix-Marseille University, Mediterranean Institute of Oceanography (MIO), Université de Toulon, CNRS/IRD, Marseille, France
e-mail: garrabou@icm.csic.es

J.-B. Ledoux
Institut de Ciències del Mar, CSIC, Barcelona, Spain

CIIMAR/CIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental, Universidade do Porto, Porto, Portugal

N. Bensoussan
Institut de Ciències del Mar, CSIC, Barcelona, Spain

D. Gómez-Gras
Institut de Ciències del Mar, CSIC, Barcelona, Spain

Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Barcelona, Spain
e-mail: danielgomezgras@ucm.es

C. Linares
Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Barcelona, Spain
e-mail: cristinalinares@ub.edu

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_11

responses to thermal stress, we analyze the ongoing eco-evolutionary impacts and explore future trajectories of these emblematic Mediterranean communities.

Analysis of satellite-derived sea surface temperature (SST) trends over the three decades revealed a marked increase in MHW events in the Mediterranean Sea. The immediate impacts of MMEs on structural octocoral populations were dramatic decreases of their biomass (~60%). After 10–15 years since the occurrence of a NHW, there were no signs of population recovery, and in fact, a continued decrease was observed due to subsequent marine heatwaves.

The modeling of Mediterranean SST suggests longer and more severe marine heatwaves as the century progresses. In this thermal context, the eco-evolutionary dynamics of the structural octocorals will likely result in an abrupt collapse of impacted populations. Indeed, from the eco-evolutionary interaction, the demographic decline is expected to increase the strength of genetic drift due to the low recolonization capacity of the species. This may lead to an extinction vortex, in spite of the occurrence of potentially thermoresistant individuals suggesting some potential for adaptation to future conditions. The ongoing collapse of Mediterranean habitat-forming octocorals may drive to a functional void with severe consequences for coralligenous communities and services they provide.

The implementation of ambitious mitigation and adaptation policies compliant with the Paris agreement is urgently needed. In this context, we highlight the critical role of marine protected areas and the need for increasing their surface and improving their management.

11.1 Introduction

The Mediterranean Sea is a hot spot for marine biodiversity (Coll et al. 2010). Covering less than 1% of the world's oceans, it is home to about 10% of marine species with a high percentage (25–30%) of endemic species (Bianchi and Morri 2000; Boudouresque 2004). Mediterranean marine ecosystems support the development of coastal and national wide socioeconomic activities including food provision, coastal protection, and tourism. The Mediterranean region is one of the top tourist destinations in the world with more than 343 million annual visitors with an expected increase of at least 20% for the next 5 years (Fosse and Le Tellier 2017). At the same time, this region faces multiple pressures linked to human activities. Overfishing, pollution, non-indigenous species, and, in recent decades, impacts of climate change are all challenging the conservation of the rich Mediterranean biodiversity and the ecosystem services it provides (Cramer et al. 2018).

Climate change is already severely affecting the ocean functioning. An urgent call to action has risen to buffer and maintain the key roles that the ocean plays especially in the climate system (IPCC 2019; Hughes et al. 2017a, b). The impact of climate change on the Mediterranean Sea is particularly worrying. The region is considered a hot spot for impacts from climate change (Cramer et al. 2018). The Mediterranean is a midlatitude microtidal temperate warm sea (mean annual sea surface temperature of 19.7 ± 1.3 °C, Fig. 11.1) with a marked seasonality and important north-to-south and west-to-east environmental gradients (more than 6 °C difference in yearly mean sea surface temperature) (Fig. 11.1). The sea surface temperature of the Mediterranean has warmed by 1.48 °C on average for the entire basin over the 1982–2018 period (Pisano et al. 2020, Fig. 11.1). This corresponds to an increase of 0.41 °C per decade which is three to six times higher than the warming rate of oceans globally (Cramer et al. 2018). The warming trend is uneven within the Mediterranean (Skliris et al. 2012; Pastor et al. 2019), showing strong variability across ecoregions. For instance, higher total warming is reported from the Adriatic, Aegean, and Levantine ecoregions (1.6–1.9 °C average, locally >2 °C) compared to the Alboran and Western ecoregions (1.1–1.2 °C average, locally >1.5 °C) (Fig. 11.1). These warming trends are related to an increase in the occurrence of marine heatwaves "periods of extreme warm sea surface temperature that persist from day to month and can extend up to thousands of kilometers" (Frölicher et al. 2018; Oliver et al. 2018; Bensoussan et al. 2019a; Darmaraki et al. 2019a). Both, the increase in mean temperatures and thermal stress associated with the extreme thermal episodes, are the prominent drivers of the effects of climate change in the Mediterranean. This environmental change is a major concern for the conservation of Mediterranean marine biodiversity, as it is already affecting the structure and functioning of marine ecosystems and the related services they provide (Garrabou et al. 2009; Azzurro et al. 2019; Cramer et al. 2018).

Mediterranean marine ecosystems are subject to two main impacts associated with climate change: (1) the shift in species distribution (indigenous and nonindigenous; see Azzurro et al. 2019; Givan et al. 2018; Sala et al. 2011) and (2) the occurrence of unprecedented mass mortality events (MMEs) (Garrabou et al. 2019). In addition, less obvious effects were reported including species proliferations (e.g., mucilaginous blooms; Berdalet et al. 2017; Piazzi et al. 2018; Bensoussan et al. 2019a), changes in phenology (Díaz-Almela et al. 2007), and migration patterns (Sabatés et al. 2012). While it is difficult to predict the extent of climate change impacts on Mediterranean marine ecosystems and key species in the next decades, recent studies suggest the likely increased extinction risk for endemic fauna, a loss of habitat complexity, and changes in ecosystem structure and composition (Ben Rais Lasram and Mouillot 2009; Ben Rais Lasram et al. 2010; Sala et al. 2011; Verges et al. 2014; Azzurro et al. 2019; Montero-Serra et al. 2019).

Our main objective in this chapter is to discuss the immediate and long-term effects of climate change on Mediterranean marine biodiversity, focusing on marine heatwaves, that drive mass mortality events. Mass mortality events in the Mediterranean have been unprecedented in terms of their impacts on biodiversity and ecosystem structure. They have affected a large number of species (>90) from different phyla (e.g., Porifera, Cnidaria, Mollusca, Ascidiacea) over very large geographic areas, covering tens to thousands of kilometers of coastline. The impact at the population scale (i.e., mortality rates) was dramatic in some cases with up to 80% of individuals showing some degree of tissue necrosis (Cerrano et al. 2000; Garrabou et al. 2001, 2009, 2019). These events first have a direct impact on the populations of various species suffering high mortality rates, which cascades within

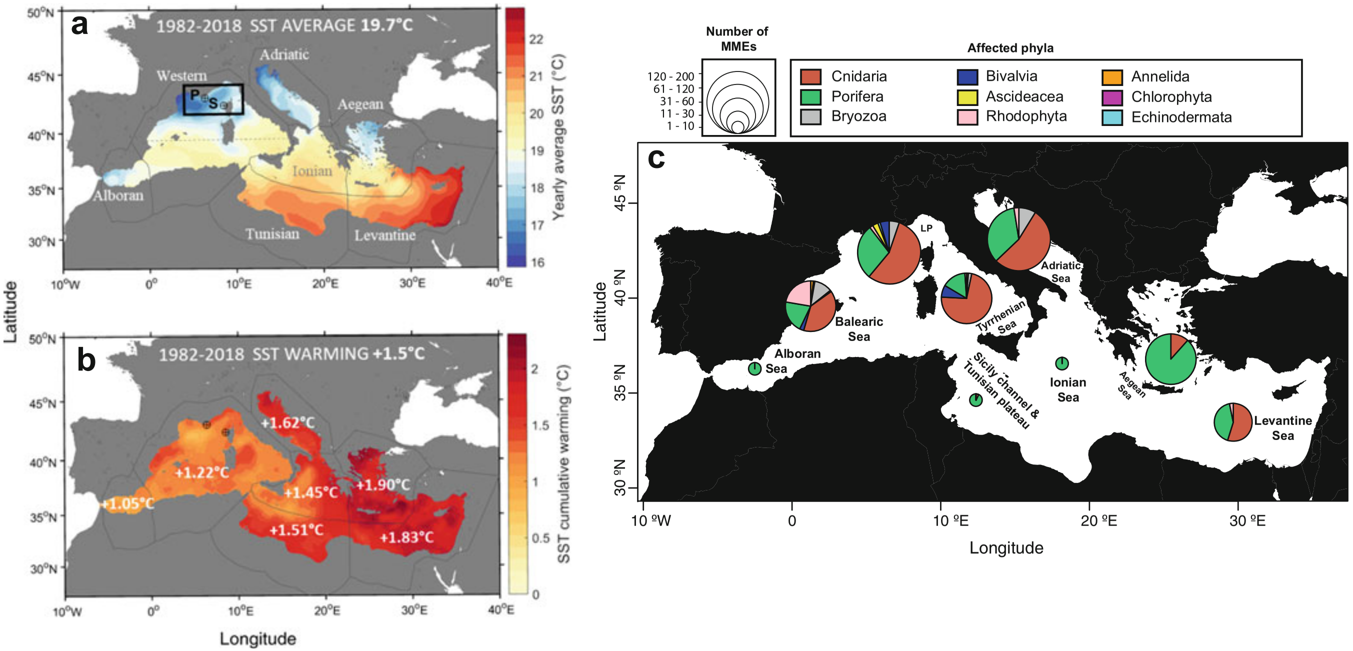


Fig. 11.1 Spatial maps of satellite-derived sea surface temperature and warming trends for the seven Mediterranean ecoregions: (**a**) yearly average sea surface temperature over the 1982–2018 period. The box includes two circles indicating the position of the Port-Cros MPA (P) and Scandola MPA (S). (**b**) Cumulative warming (in °C) over the period 1982–2018. The geographic position of the two locations considered in this chapter for detailed ecological analysis are shown as well as the southern limit considered for the NW Mediterranean Sea (39°N). Maps generated using EU Copernicus Marine Service Information. (**c**) Mass mortality events: geographic distribution and taxa affected over the period from 1979 to 2017 adapted from Garrabou et al. 2019

the communities and ecosystems, especially when affected species are foundation species (Linares et al. 2005; Garrabou et al. 2009; Rivetti et al. 2014; Marbà et al. 2015; Ponti et al. 2014; Verdura et al. 2019; Gómez-Gras et al. 2021).

Here we focus on the impacts of mass mortality events on coralligenous communities, some of the most diverse (>1600 sp.; Ballesteros 2006) and threatened communities in the Mediterranean (Ballesteros 2006; Garrabou et al. 2009, 2018). These communities present high habitat complexity resulting from the accumulation of encrusting coralline algae and the growth of a diverse array of long-lived macrobenthic species. Bearing in mind the increase in the frequency, duration, and intensity of summer marine heatwaves (Darmaraki et al. 2019b), the occurrence of mass mortality events is expected to increase in the coming decades. This scenario may likely drive coralligenous habitats toward collapse trajectories in many areas of the Mediterranean. Thereby, the impacts of mass mortality on coralligenous communities deserve urgent attention and the implementation of efficient management, conservation, and restoration measures.

In this chapter, we develop a multidisciplinary and integrated analysis to explore the responses to climate change focusing on structural octocoral species in coralligenous: the gorgonians. Some gorgonian species develop dense populations, playing a central ecological role, ensuring the benthic-pelagic coupling and increasing the structural complexity (tree-like colonies up to 1 m in height) (Gili and Coma 1998; Ballesteros 2006). Gorgonian populations dwelling from 10 m to 45 m depth have been strongly affected by mass mortalities. In this chapter, we focus on gorgonian species because (1) they are relatively well studied species for which we have abundant information, and, (2) due to their life history traits (e.g., longevity, low population dynamics) and their key structural role in coralligenous ecosystems, they are original and relevant models in conservation biology. We combined an accurate characterization of ongoing and expected thermal stress conditions in coastal seawater from surface down to 40 m with up-to-date knowledge on demography, population genetics, and responses to thermal stress to:

1. Characterize the sea surface marine heatwaves, their depth penetration, and their relationship with the observation of mass mortality events
2. Describe observed immediate lethal and sublethal effects of mortalities as well as recovery trajectories
3. Discuss future trajectories by:
   (a) Analyzing the future occurrence of marine heatwaves in the Mediterranean under three different climate change scenario (RCP2.6, RCP4.5, and RCP8.5)
   (b) Identifying the potential ecological-evolution and evolution-ecological interactions in these species to sketch their eco-evolutionary feedback loop
   (c) Scaling the feedback loop from a genetic to a community level
4. Provide an overview of the main management options to enhance climate change adaptation in Mediterranean coastal habitats

11.2 Marine Heatwaves and Mass Mortality Events in the Mediterranean

Mediterranean surface waters have warmed rapidly during the last decades as confirmed by satellite observation (Skliris et al. 2012; Von Schuckmann et al. 2017, 2018, 2019; Pastor et al. 2019; Pisano et al. 2020; Fig. 11.1). The Mediterranean sea surface temperature (SST) has warmed on average by 1.48 °C over the 1982–2018 period (Pisano et al. 2020). How fast and how deep this warming is occurring is the subject of much research, which is now taking advantage of the improved observational capabilities at high spatial-temporal resolution (e.g., satellite, moored platforms, and seabed stations). However, in contrast to continental studies, climatic series in the marine realm are scarce especially for the subsurface and coastal areas (Bates et al. 2018; Salat et al. 2019).

The study of coastal ocean dynamics is challenging because it is characterized by strong variability at high frequency and small spatial scales. These scales are relevant to understand ecological impacts, which require tracking changes in daily *T*° distribution and extreme *T*° events associated with the thermotolerance limits. In this chapter, we take advantage of two main and complementary high-resolution data sources: (1) reprocessed AVHRR satellite data from CMEMS back to 1982, which consist in daily gap-free maps of foundation SST at 4 km spatial horizontal resolution with improved accuracy and stability (Pisano et al. 2016), and (2) in situ temperature records by the T-MEDNet network (www.t-mednet.org) which provide high-resolution measurement (hourly at different depths) in the coastal zone at more than 70 sites around the Mediterranean (Garrabou et al. 2018; Bensoussan et al. 2019a). A previous analysis of coincident multi-year high-resolution satellite and in situ data has shown the applicability of this SST dataset for trend and marine heatwave analysis in the nearshore and coastal areas but also highlighted their limitations in hydrodynamic complex areas (Bensoussan et al. 2019a, b).

We analyzed the occurrence of marine heatwaves in the Western Mediterranean and Adriatic regions where most mass mortality events have been reported (Garrabou et al. 2019, Fig. 11.1). We also included analyses of MHW propagation across depth at local scales in the Western Mediterranean. We focus on heat stress episodes from June to November when MMEs took place. We applied two methods to quantify heat stress episodes: (1) the hierarchical characterization of marine heatwaves (MHW) proposed by Hobday et al. (2016, 2018), which is a quantification of the duration, intensity, and magnitude of extreme warm events (when *T*° remains > local daily threshold for at least 5 consecutive days) and (2) the occurrence of extreme hot days at the annual time scale (when SST > 99th percentile), as presented in Darmaraki et al. (2019b). In both cases, the 30-year period [1982–2011] SST was considered as a reference for climatology and statistics calculation. For in situ *T*° series, daily averages were calculated out of the hourly records, and the analysis was conducted considering the entire length of the available data set, ranging between 15 and 20 years depending on the considered site and depth.

11.2.1 Sea Surface Thermal Stress Signals in the Cold Northern Mediterranean Areas

Analysis of satellite-derived SST over recent decades has revealed a marked increase in *T*° extremes (SST99) and marine heatwave events at global scale, in the Mediterranean Sea, and within Mediterranean ecoregions (Oliver et al. 2018; Bensoussan et al. 2019a; Darmaraki 2019a; Smale et al. 2019, Fig. 11.2). In the NW Mediterranean Sea and Adriatic ecoregions, SST99 have increased by 1.3 °C and 2.4 °C, respectively, over the 1982–2018 period (linear trends, Fig. 11.2a). Meanwhile, extremely hot *T*° has become more frequent, with a total increase of 14 and 27 days, respectively (Fig. 11.2b). The long-term evolution of MHW showed common patterns in these two ecoregions, as shown by the cumulative number of MHW days during the period from June to November (Fig. 11.2c). In particular, a clear step change was shown following the summer 2003, which corresponded to a fourfold increase in MHW days on average for the two ecoregions (37 vs. 9 MHWs days/year, Fig. 11.2c).

In order to evaluate biological impacts, MHW metrics, in particular the total duration of MHW events, is considered a more relevant indicator of heat stress than other statistical descriptors (Smale et al. 2019). Here, we analyzed together the occurrence of surface MHWs and reported MMEs in the NW Mediterranean and in the Adriatic ecoregions until 2017 (Fig. 11.3). The results show a regime shift in the number of MMEs associated to MHWs in both ecoregions before and after year 2003. This corresponds to a shift in heat stress with on average fourfold higher MHWs day per year during the second period (i.e., 9 vs. 39 MHW days per year, Fig. 11.3). Although SST MHWs are reliable sign of increasing thermal stress in suprathermoclinal waters (above the seasonal thermocline, which develops in April–May and deepens till October–November) with potential harmful effects for shallow habitats, satellite-derived information is not optimal for detecting changes in deeper habitats (Bensoussan et al. 2019a). In particular, we note the high MHW days vs. low-impact MMEs in 2006 and 2014 and, conversely, low to no surface MHW days but high-impact MMEs in 1999 and 2009 in the NW Mediterranean Sea (Fig. 11.3). In fact, most MMEs during these years concerned subsurface macrobenthic populations dwelling at intermediate depth (e.g., 20–30 m depth). These observations have focused attention on characterizing heat stress conditions in intermediate waters from 5 m down to >40 m.

11.2.2 Subsurface Thermal Stress Signals in the Cold NW Mediterranean

Because of the complex thermal environment beneath the surface and the effect of seasonal stratification and winds on surface ocean, the link between SST and MMEs is not straightforward. Indeed, subsurface temperatures exhibit different variability modes compared to SST conditions, starting by the shift of the warm period from summer at the surface to autumn in deep habitats, when convective events deepen

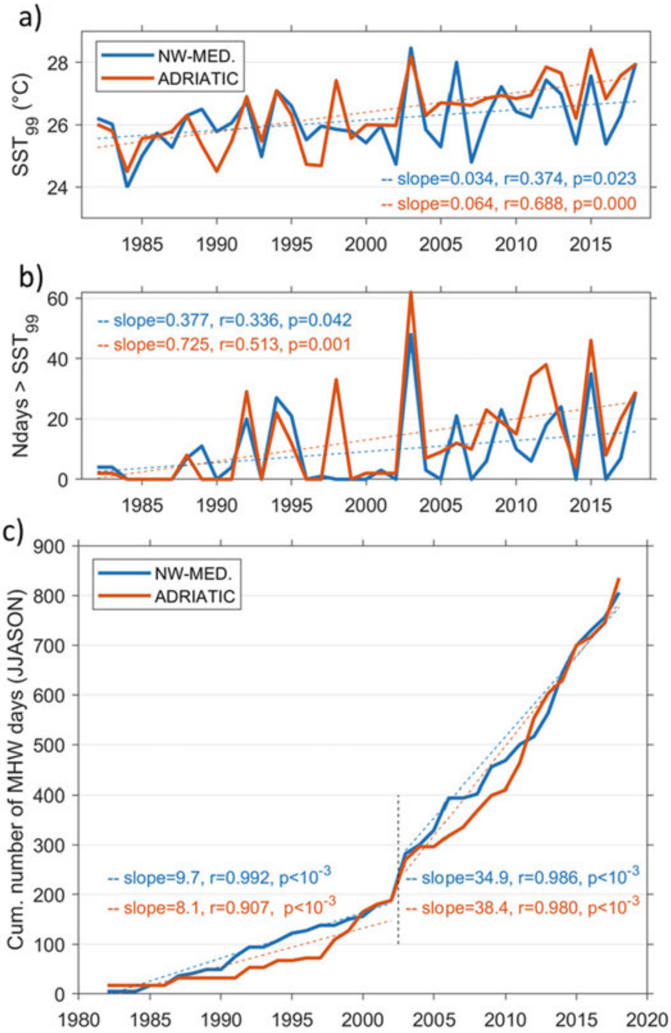


Fig. 11.2 (**a**) Evolution of SST 99th percentile (SST99) in the NW Mediterranean Sea and Adriatic Sea over the 1982–2017 period. (**b**) Yearly number of days above the 30 years average of SST99 (1982–2011) in these two ecoregions. (**c**) Cumulative number of marine heatwave days (MHW days) during the period from June to November for the NW Mediterranean Sea and Adriatic Sea over the 1982–2017 period. Generated using E.U. Copernicus Marine Service information. (CMEMS)

the seasonal thermocline (Fig. 11.4). Moreover, episodic wind-driven events such as upwelling and downwelling are known to cause abrupt changes in local stratification and strongly modulate the local impacts of regional heatwaves (Bensoussan et al. 2010; Pairaud et al. 2014). Overall, subsurface amplification of MHWs appears as a consistent feature under the influence of winds and seasonal stratifications.

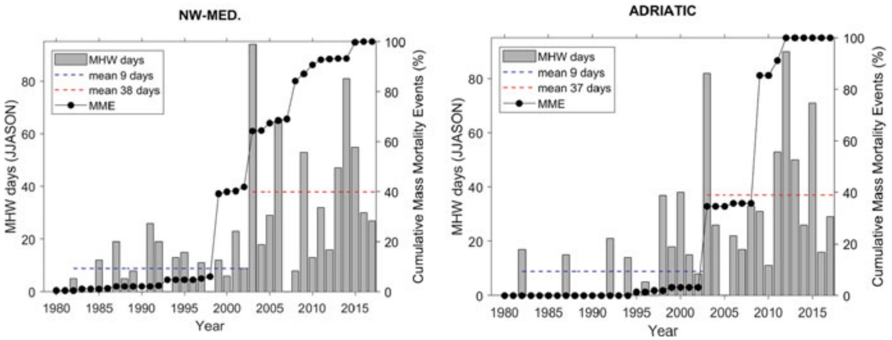


Fig. 11.3 Marine heatwave (MHW) days from June to November (histogram) and cumulative number of MMEs (line, in % of total reported from each region) for the NW Mediterranean Sea and Adriatic Sea from 1979 till 2017. MHWs were calculated from satellite-derived SST data obtained from CMEMS starting in 1982. Number of mass mortality events MMEs: 375 in the NW Mediterranean Sea and 159 in the Adriatic obtained from Garrabou et al. (2019)

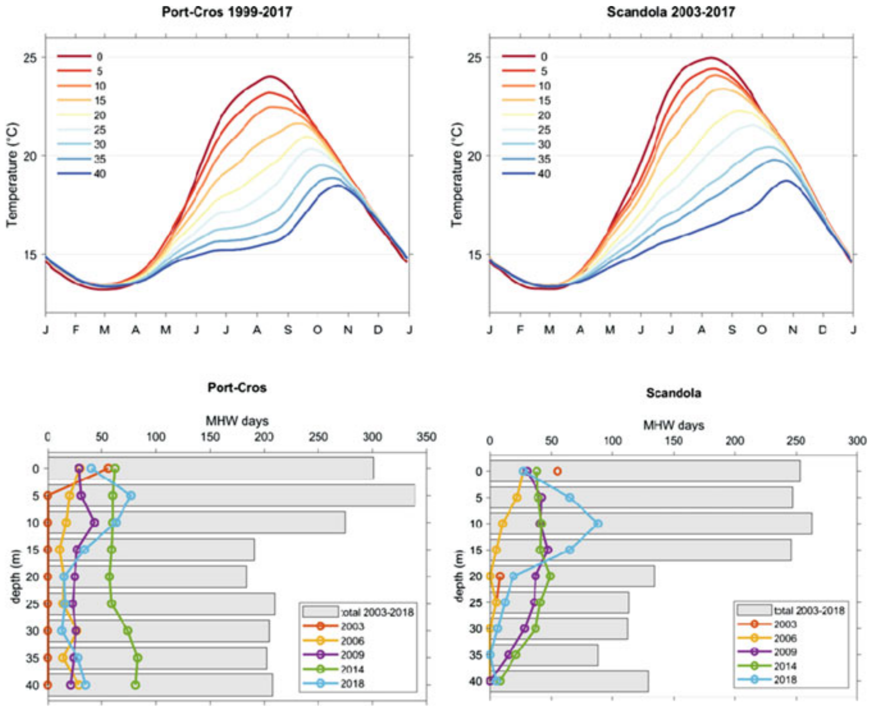


Fig. 11.4 Top: climatological mean temperature from surface to 40 m depth in two coastal areas obtained from joint analysis of satellite-derived SST data from CMEMS and in situ time series from T-MEDNet. Data series 1999–2017 for Port-Cros MPA and 2003–2017 for Scandola MPA. Bottom: total number of MHW days from surface to 40 m depth during the period from June to November for selected years for which MME were reported (lines) and over the entire observation period (histogram) in the coastal waters of Port-Cros MPA and Scandola MPA

We conducted local scale analysis combining satellite and in situ observations in order to yield better understanding of the occurrence of subsurface MHWs based on the long-term series from the T-MEDNet database (from 1999 or 2003 onward). Out of the 70 sites surveyed across the Mediterranean with the T-MEDNet network, we selected 2 marine protected areas (MPAs): Port-Cros MPA and Scandola MPA (Fig. 11.1). These two sites were selected based on the existence of long-term monitoring of both thermal conditions and the benthic biota, generally at the upper distribution limit of habitat-forming gorgonians. We analyzed the most conspicuous heat stress events using long-term observational data series available. In order to analyze the vertical distribution of MHWs, we calculated their duration (days), intensity ($T_{\max}$, $I_{\max}$ in °C), and overall magnitude (cumulated intensity in °C day, I_{cum}).

11.2.2.1 Subsurface MHWs Amplification

Episodic extreme warming events show strong spatial structuration and different modes along the depth gradient (Schaeffer and Roughan 2017; Bensoussan et al. 2019b; Darmaraki et al. 2019a). Over the past 15–20 years, numerous MHW days have been observed over the entire monitored depth range, from shallow to deep coastal habitats in the two selected MPAs (0–40 m, Fig. 11.4b). Importantly, the highest numbers of MHW days were observed at the depths of the shallow summer mixed layer, down to 10 and 15 m in Port-Cros MPA and Scandola MPA, respectively. At annual scale, different MHW vertical patterns were evidenced from the cumulative number of MHW days over the period from June to November (Fig. 11.4). Some patterns were restricted to the surface (e.g., 2003), amplified at shallow depth (e.g., 2018, see also Table 11.1) or propagated over the entire water column (e.g., 2009 and 2014) (Fig. 11.4). The timing of MHW, warm water advection, and variability in the stratification dynamics are likely to explain the strong differences observed between the surface MHW and the severity of impacts (Fig. 11.3).

The examination of the discrete MHW events showed differences in their timing along the depth, attesting strong subsurface amplification, as observed in the 1999 event in the NW Mediterranean Sea; the event was associated with an unprecedented MME outbreak (Cerrano et al. 2000; Perez et al. 2000; Crisci et al. 2011; Fig. 11.3). The 1999 MHW was characterized by moderate surface MHW in the NW Mediterranean Sea (Table 11.1, Hobday et al. 2018), while deep stratification anomaly with relative homothermy was evidenced along the coasts of Provence (e.g., Romano et al. 2000; Harmelin 2004). The analysis of 1999 data in Port-Cros MPA (Table 11.1) showed a MHW intensification at 25 m when compared to the surface with higher values for duration (37 vs. 11 days), maximum intensity (5.3 vs. 2.2 °C), and overall magnitude of the heat stress (I_{cum}, 140 vs. 20 °C day). The highest maximum intensity ($I_{\max}$) at 25 m depth was observed at the end of July 2017 (7.2 °C), i.e., more than a month after a strong regional surface MHW detected from satellite SST for that year (Table 11.1, Bensoussan et al. 2019b). Finally, the analysis of the summer 2003 MHW events is illustrative of inter-site variability. Indeed, the MHW was restricted to the surface in Port-Cros MPA, while in Scandola, our

Table 11.1 Characterization of some conspicuous MHW events at the surface and in situ (from 10 to 25 m depth) using different metrics for timing, duration, T_{max}, I_{max}, I_{cum}

Site	Depth	Start date	Duration (day)	T_{max} (°C)	I_{max} (°C)	I_{cum} (°C day)
Port-Cros NP	SST	18/09/1999	11	24.4	2.2	20
Port-Cros NP	25 m	22/08/1999	37	23.6	5.3	140
Port-Cros NP	SST	16/06/2017	9	24.2	3.2	21
Port-Cros NP	25 m	31/07/2017	10	25	7.2	48
Scandola MPA	SST	06/08/2003	28	28.5	3.5	88
Scandola MPA	20 m	26/08/2003[a]	8[a]	27.2[a]	5.1[a]	32[a]
Scandola MPA	SST	13/08/2018	12	28.6	3.6	35
Scandola MPA	10 m	03/07/2018	61	27.7	3.7	152

[a] Data available from this date

analysis showed the occurrence of extreme hot waters down to 20 m depth (>27 °C) with maximum intensity (I_{max}) > 5 °C (Fig. 11.4, Table 11.1).

11.3 Immediate Impacts, Sublethal Effects, and Recovery of Habitat-Forming Gorgonians from Mass Mortalities Events

11.3.1 Immediate Impacts and Sublethal Effects of Mass Mortality Events

Field surveys performed immediately or in the months/years after the observation of mass mortalities on gorgonian populations allow the estimation of both immediate and delayed demographic impacts of these events (see Garrabou et al. 2001, 2009; Linares et al. 2005, 2010). Two sampling approaches have been considered: (i) extensive surveys using random sampling within populations to provide rapid and static assessments of the health status of populations over large spatial scale and (ii) intensive surveys based on long-term monitoring of permanent plots, which allow obtaining accurate data on the impact and recovery of mortality and post mortality recruitment rates.

Extensive surveys are based on random sampling using quadrats (e.g., 50 × 50 cm) placed within the gorgonian populations. In each quadrat, density of colonies is determined, and for each colony, the height and the extent of tissue injury (differentiating from denuded axis and tissue overgrown by other organisms) are measured. The extent of tissue injury is estimated as the proportion of each colony's total surface that showed no tissue over the branches and/or was overgrowth by other organisms (Harmelin et al. 1999). In fact, the heat stress causes necrosis of the tissue (coenenchyma), resulting in denuded gorgonian skeletons that are then rapidly overgrown by other fast-growing organisms (e.g., filamentous algae and invertebrates) (Linares et al. 2005).

Intensive surveys map all colonies in permanent plots during the first visit, followed by surveys in which height, extent of injury differentiating from denuded axis, and tissue overgrown by other organisms were measured, as described above. Most permanent plots are monitored annually. Since all the colonies are mapped, total mortality is measured based on the colonies that disappear or show 100% tissue injury.

In both types of surveys, the colony biomass of the red gorgonian *Paramuricea clavata* is estimated with the following relationship: $B = 0.002 \times H^{2.61}$, where B is biomass in grams of dry mass and H is colony height in centimeters (Coma et al. 1998). Corrections for biomass loss caused by injuries are considered by subtracting the biomass equivalent to the percentage of the colony surface affected by injuries. Taking into account the obtained colonies biomass and density, the mean population biomass is then estimated.

Our analysis was focused on the MMEs reported for Port-Cros MPA and Scandola MPA, from which we generalize the results reported for other locations. In order to relate the observed impacts with heat stress, we conducted the analysis of high-resolution temperature series available using the MHWs approach but focusing on the depth levels in which affected populations dwell. In particular, for Port-Cros MPA and Scandola MPA, the affected populations dwell at 25 and 18 m depth, respectively.

11.3.1.1 Immediate Impacts

The immediate impacts of mass mortality events on gorgonian populations show an increase in the extent of colony injury (due to the partial or total necrosis of the coenenchyme of gorgonians) and a density decrease. In the two selected locations, Port-Cros MPA and Scandola MPA, an increase of partial mortality (injuries) in the populations of the red gorgonian *Paramuricea clavata* was observed (Fig. 11.5). Effectively, in 1999 and in 2003, Port-Cros MPA and Scandola MPA were affected by severe heat stress conditions, which were above the thermotolerance of this species (25 °C; e.g., Crisci et al. 2017; Kipson et al. 2012; Arizmendi-Mejía et al. 2015b) (Fig. 11.6).

This increase in partial mortality rates is a general pattern in most affected populations (e.g., Cerrano et al. 2000; Coma et al. 2006; Cupido et al. 2008; Huete-Stauffer et al. 2011). However, the density loss varies among populations because it largely depends on the percentage of total mortality. For instance, in Port-Cros, the density remained stable after the MME; meanwhile a steep decrease was observed in Scandola just after the event (Fig. 11.5).

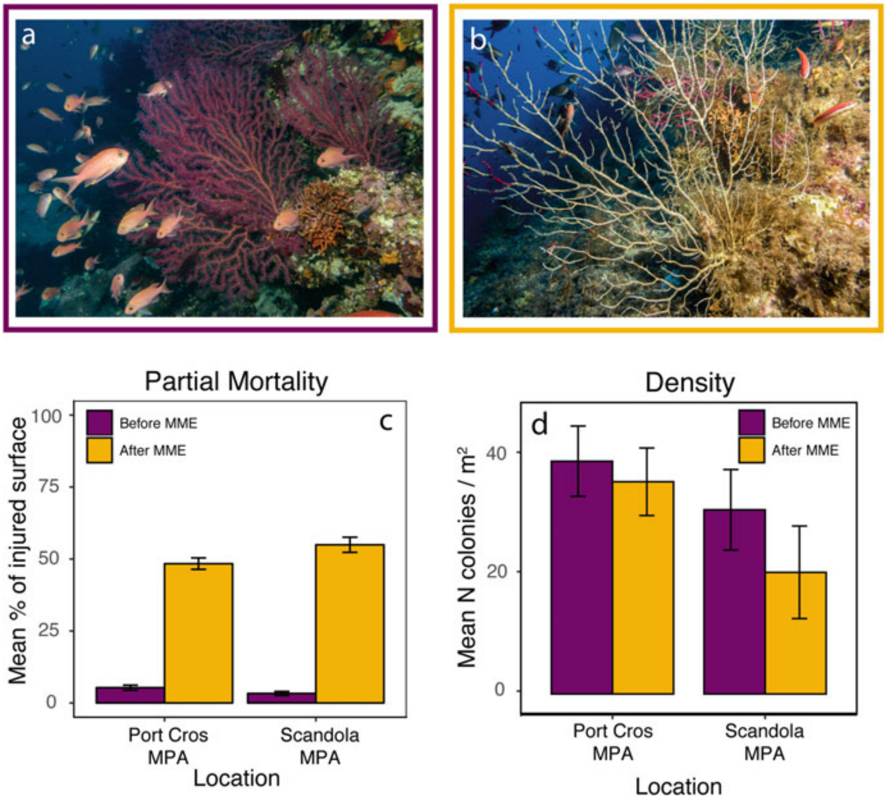


Fig. 11.5 Photographs (**a**) and (**b**) show respectively the non-disturbed state and the post-MME state of coralligenous assemblages impacted by marine heatwaves, respectively. Bottom plots show warming-driven changes in the partial mortality (mean % of injured tissue ± S.E) and density (mean number of *P. clavata* colonies ± S.E) after the marine heatwaves occurred in Port-Cros MPA in 1999 and Scandola MPA in 2003. Photos Photographs MedRecover research group ©

11.3.1.2 Sublethal Effects with Long-Term Consequences

Although the lethal effects of warming-induced mortalities on gorgonians has been widely studied over recent decades (e.g., population decline; see Perez et al. 2000; Cerrano et al. 2000; Linares et al. 2005; Coma et al. 2006; Cupido et al. 2008; Garrabou et al. 2009; Huete-Stauffer et al. 2011), subtle effects associated with thermal stress on the reproduction and early life stages of coralligenous species have been largely ignored. However, changes in fecundity, fertilization success, larval dispersal, and recruitment play a major role in promoting shifts in species' abundance and composition and should therefore be considered. Previous studies have shown severe effects of thermal stress on the reproduction of *P. clavata*. The greater reduction of fertility and number of gonads observed in female colonies compared to male colonies highlights that female colonies are more vulnerable to thermal stress (Linares et al. 2008a; Arizmendi-Mejía et al. 2015b). On the other hand, the apparent

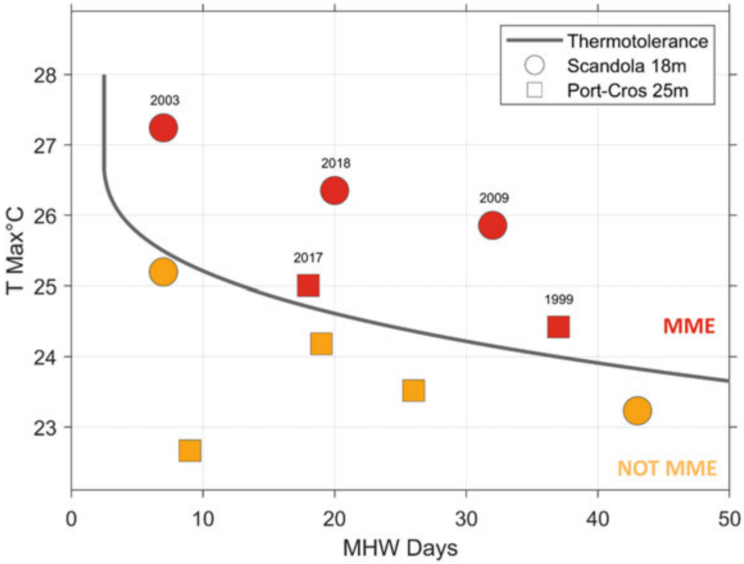


Fig. 11.6 Representation of heat stress at depth levels observed in situ according to the recorded maximum daily T° (T_{max} °C) and the total number of MHW days from June to November recorded in Scandola (18 m) (circles) and Port-Cros (25 m) (squares) marine protected areas. The curve indicates the thermotolerance response for the red gorgonian *Paramuricea clavata* obtained from the literature and author's results on thermotolerance experiments. The years for which MMEs were observed are indicated and the corresponding symbols are in red; the other years are indicated in orange (years with MHW T_{max}<22 °C are not shown)

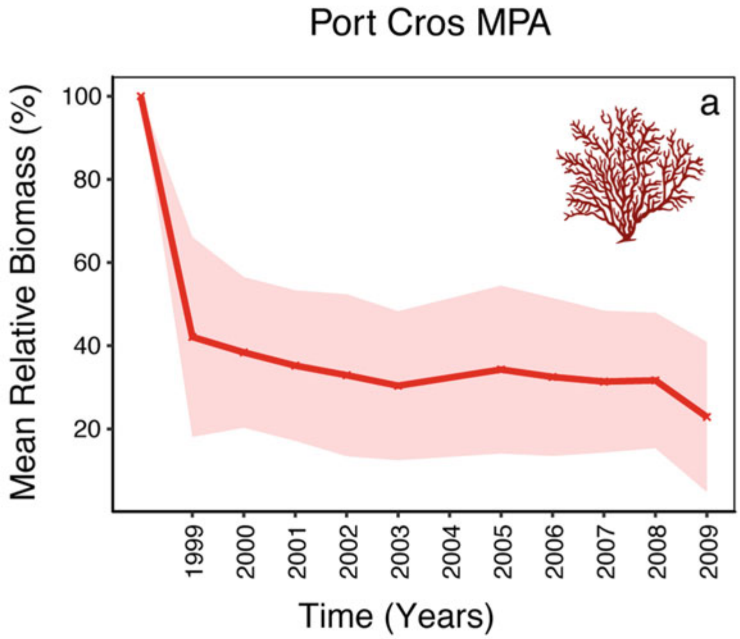
higher sensitivity of embryos suggests that thermal stress during embryonic development may be the most critical factor for the viability of *P. clavata* larvae (Kipson et al. 2012). The reproductive impairment has further implications for the recovery of affected populations in the long term. In the context of an ongoing warming trend and considering the importance of self-recruitment in *P. clavata* (Arizmendi-Mejía et al. 2015a), the reduced reproductive effort and viability of early life stages would jeopardize the persistence of affected populations and the species dispersal/recolonization capacities.

The impact of MMEs on intraspecific genetic diversity is still unknown and requires temporal surveys to be conducted. The genetic diversity parameters estimated during spatial genetic surveys in different gorgonian species (e.g., Ledoux et al. 2010a b; Mokhtar-Jamai et al. 2011; Costantini and Abbiati 2016; Masmoudi et al. 2016) are relevant baselines to characterize the temporal trends and the look for potential genetic diversity decline following MMEs. Such temporal surveys have been conducted in other marine (e.g., Reynolds et al. 2017; Momigliano et al. 2019) and terrestrial species (e.g., Segelbacher et al. 2008; Jansson et al. 2012). Nevertheless, these studies showed contrasted results from temporal stability to decrease of intraspecific genetic diversity (Millette et al. 2020; Leigh et al. 2019). Besides adequate sampling scheme, methodological refinements are needed to detect genetic imprints of ongoing global change (Millette et al. 2020).

11.3.2 Recovery Trajectories

The long-term monitoring of the red gorgonian *P. clavata* populations in the Port-Cros MPA and Scandola MPA allowed tracking the recovery trajectories after the impact of the 1999 and 2003 mass mortality events, respectively. In both locations, the immediate impact resulted in a decrease of about 60% of the initial biomass. Moreover, at the end of the monitoring period (10 and 14 years in Port-Cros and in Scandola, respectively), the biomass of colonies did not show any sign of recovery. On the contrary, in both cases, the biomass continued to decrease, reaching as much as 70% decline in initial biomass (Fig. 11.7). This lack of recovery may be explained by the impact of recurrent mortalities associated to other MHWs and the continuous loss of live biomass due to the breakage of highly affected surfaces (Fig. 11.6).

The described patterns of remarkable loss of biomass just after the event (up to 70%) and the lack of recovery in the two MPAs (see above) were also found in other populations affected by MMEs in the NW Mediterranean (Cerrano et al. 2000; Coma et al. 2006; Cupido et al. 2008; Linares et al. 2017; Verdura et al. 2019). Indeed, the slow growth rates and low recruitment exhibited by these species (Linares et al. 2007; Montero-Serra et al. 2018a, b) do not allow for a quick recovery of the biomass (Fig. 11.7). However, in some populations the exceptionally high recruitment, potentially due to different factors acting at microscale such as hydrodynamic conditions retaining larvae and low competition with other fast-growing organisms, was enough to recover density values similar to those before the MME (Cerrano et al. 2000; Cupido et al. 2008). A high genetic connectivity among populations in the Ligurian Sea may have facilitated their recovery from mass mortality events (Padron et al. 2018). Nonetheless, in general, recolonization from external sources is expected to be low (Mokhtar-Jamai et al. 2011 but see Aurelle et al. 2020). Most of the affected gorgonian species usually show significant spatial genetic structure at low spatial scale supporting a restricted connectivity. For instance, significant genetic differentiation is observed among populations separated by short distances ranging from tens of meters in the red coral (Ledoux et al. 2010a) to few kilometers in *Paramuricea clavata* (Arizmendi-Mejía et al. 2015a). Accordingly, overall the recovery of impacted populations is expected to be a long-term and mostly local process. Overall, two trajectories after MME have been described in affected populations (Fig. 11.8). One is a decline of the mean size of colonies attributable to the loss by breakage of injured parts and entire injured/dead colonies but a stabilization of the density values due to the incorporation of new colonies. The other is that MMEs drive communities toward a stable mean size of colonies and population structure because injuries and subsequent loss of colonies affect all colony sizes; however, in this trajectory populations show a significant loss of density given the low recruitment rate and loss of entire colonies. Both trajectories cause significant loss of biomass resulting in a dramatic decrease of structural



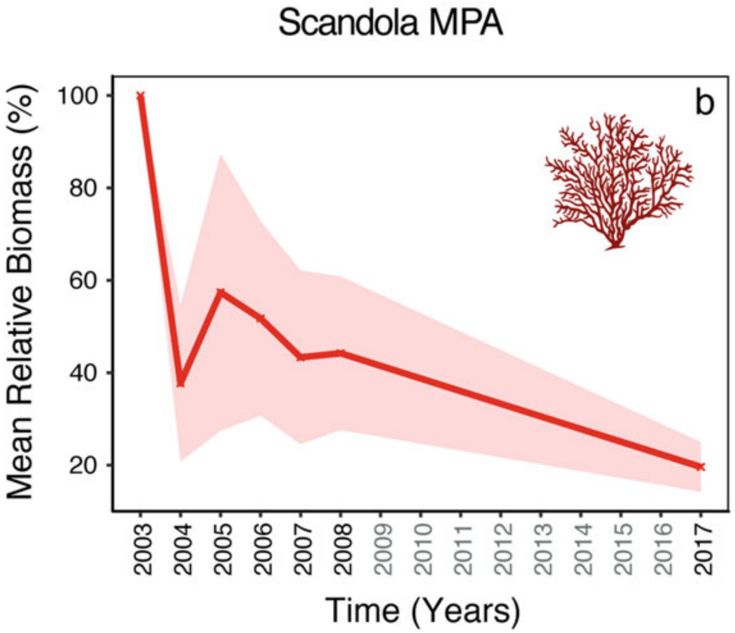


Fig. 11.7 Long-term mean trajectories of relative biomass (±S.E) from different *P. clavata* populations affected by warming-induced MMEs occurred in Port-Cros MPA and Scandola MPA in 1999 and 2003, respectively. Years shown in black are those in which information has been obtained in situ from transects, while years in grey have been extrapolated

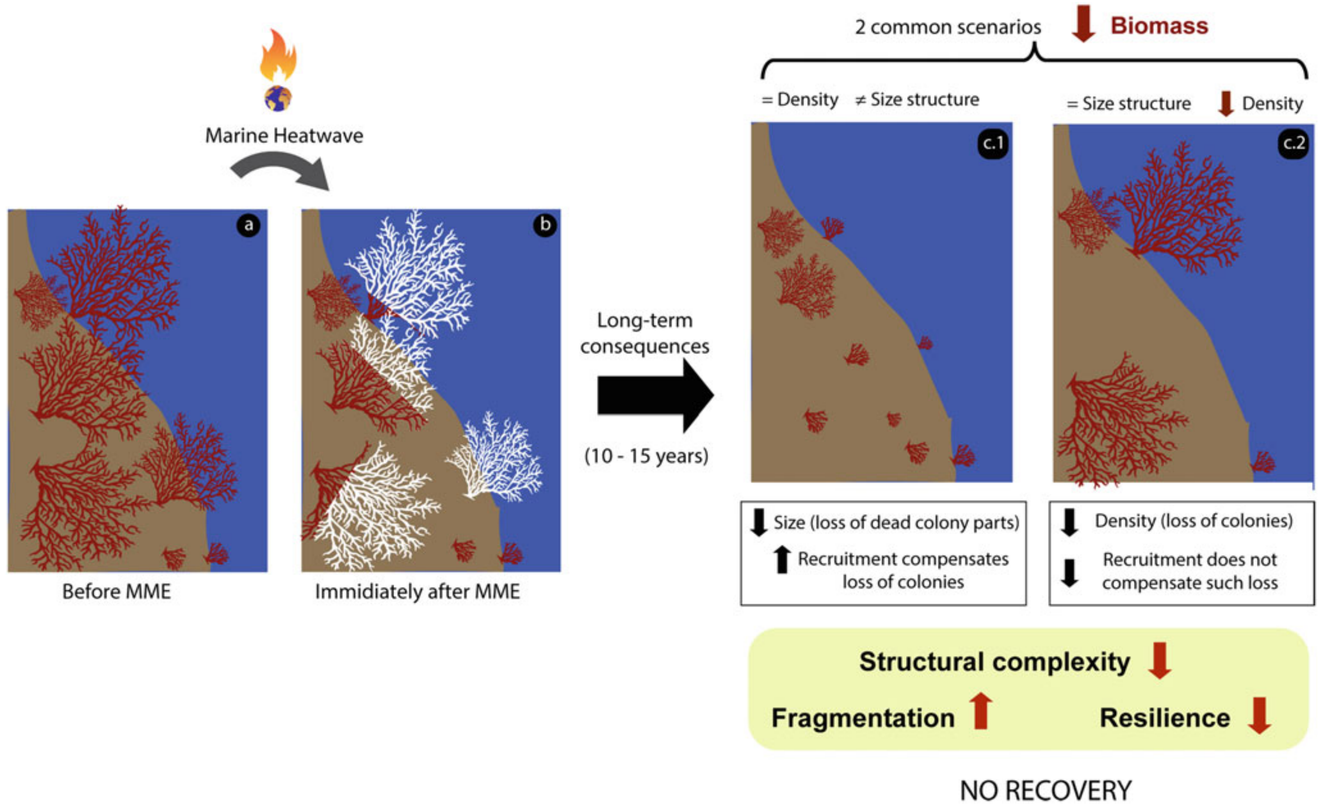


Fig. 11.8 Schematic representation of some of the most common observed long-term consequences of warming-induced MMEs for gorgonian populations. (**a**) Baseline state of coralligenous assemblages in absence of disturbance. (**b**) The same community after a MME, where partial and total tissue necrosis (in white),

complexity and high fragmentation of populations, increasing the genetic isolation of affected populations and their reproductive impairment (Ledoux et al. 2020; see section above).

Box 11.1 Description of Demographic and Genetic Features of Octocorals

The demography and population dynamics of structural octocorals from the coralligenous communities has been mainly characterized in four different species: the red coral, *Corallium rubrum*; the red gorgonian, *Paramuricea clavata* (Gori et al. 2007; Kipson et al. 2015; Linares et al. 2008a, b); the yellow gorgonian, *Eunicella cavolini* (Sini et al. 2015); and the white gorgonian, *Eunicella singularis* (Gori et al. 2007, 2011; Linares et al. 2008b). From these studies, structural octocorals are usually long-lived species (hundreds of years; e.g., Montero-Serra et al. 2018a, b) showing recruitment by pulse (e.g., Garrabou and Harmelin 2002; Montero-Serra et al. 2015), low growth rates (mm per year; e.g., Marschal et al. 2004; Torrents et al. 2005), and late sexual maturity (> 10 years old) (e.g., Torrents et al. 2005; Linares et al. 2007). Those octocorals are thus characterized by slow population dynamics, which contrasts with the recurrence rate of the mass mortality events.

The spatial patterns of neutral genetic structure has been characterized in the four species at various geographic scales covering different portions of their distribution ranges (e.g., Arizmendi-Mejía et al. 2015a; Aurelle et al. 2011; Costantini et al. 2007a, b, Costantini and Abbiati 2016; Cánovas-Molina et al. 2018; Ledoux et al. 2010a, b; Masmoudi et al. 2016; Mokhtar-Jamai et al. 2011, 2013). Levels of genetic diversity were moderate to high in the four species. With the exception of *Eunicella singularis* (Costantini and Abbiati 2016), significant genetic structure was observed in all the species among populations separated by tens of meters (e.g., *Corallium rubrum*, Ledoux et al. 2010a) to kms (e.g., *E. cavolini*, Masmoudi et al. 2016). At large geographic scale, spatial patterns of genetic structure usually combined regional genetic cluster and isolation by distance (e.g., Masmoudi et al. 2016). Gene flow in these species is relatively low, occurs mainly among close by populations, and decreases function of the geographic distance among populations. While only few studies focused on contemporary connectivity, the available results

(continued)

Fig. 11.8 (continued) can be observed in different colonies. (**c**) and (**d**) represent two different common situations observed after more than a decade in impacted coralligenous assemblages, where regardless of density or size structure patterns, biomass has been deeply reduced making population far from recovery. If more years pass without any other major disturbances, populations may ultimately return to their original state in terms of biomass, density, and size structure. However, new disturbances affecting these impacted assemblages could lead to a total collapse of the populations that would become ecologically extinct/population extirpation (not shown in the image)

Box 11.1 (continued)

confirmed the restricted dispersal capacities with low numbers of migrants shared among populations (e.g., Arizmendi-Mejía et al. 2015a; Aurelle et al. 2020, but see Padron et al. 2018). Overall, Mediterranean octocoral populations seems to be mainly closed systems relying mostly on self-recruitment. The short-term recolonization of populations impacted by MMEs is likely to occur mainly from local surviving individuals with a low contribution of external sources. Further studies are needed to characterize the temporal dynamics of the recolonization in these species and to assess whether or not active restoration through transplantation of resistant individuals (i.e., assisted gene flow) remains the only way to hamper the collapse of these populations.

11.4 Expected Future Trajectories in the Coralligenous Communities

11.4.1 Analyzing the Occurrence of Marine Heatwaves in the Mediterranean under Twenty-First Century Climate Change Scenario

The future evolution of Mediterranean sea surface temperature was evaluated using a dedicated ensemble of fully coupled regional climate system models from the Med-CORDEX initiative and a multi-scenario approach (Darmaraki et al. 2019b). The mean ensemble response to an extreme climate scenario (RCP8.5) indicates an average increase of Mediterranean SST of 3 °C and temperature extremes of 4 °C by the end of the century. Furthermore, it was found that long periods of extreme hot temperatures (>SST99) are expected to occur every year between June and October, to be about four times more intense (anomaly) and to last up to 3 months longer than under present conditions. Mitigation effects in reducing the greenhouse gas forcing (e.g., RCP4.5) were reflected mostly toward the 2070–2100 period, while model uncertainty dominated future climate evolution by 2050 (Darmaraki et al. 2019b, Fig. 11.9a).

We further analyze the future evolution of SST and marine heatwaves for the NW Mediterranean and Adriatic ecoregions (Fig. 11.1) by using two models representative of some high and low response to global warming and different emission scenarios as available (Fig. 11.9). The simulations were obtained from Centre National de Recherches Météorologique (CNRM for RCPs 8.5, 4.5, and 2.6) and Euro-Mediterranean Center on Climate Change (CMCC for RCP8.5). These simulations considered both high-resolution spatial (10–20 km) and temporal (daily) scales.

In Fig. 11.9a we showed the 1951–2100 evolution of average yearly SST obtained for the NW Mediterranean Sea by combining historical run (years 1950–2005) and twenty-first century scenarios (years 2006–2100) together with observations (satellite-derived SST from 1982 to 2018). The model data fit well to observations although showing lower warming trends, in particular for CNRM simulation. Significant differences occur between the two models and the three emission scenarios mostly after 2050, leading to contrasting trajectories by the end of the century when SST warming is projected to reach 3.3–4.4 °C (RCP8.5), 1.8 °C (RCP4.5) and 1 °C (RCP2.6) (Fig. 11.9a). Projections of future SST warming were very similar for the Adriatic with less than 10% differences when compared to the NW Mediterranean Sea (Table 11.2).

Future evolution of MHW was evaluated considering, as above, the period from June to November (results are expressed in relative frequency %). In Fig. 11.9b, we show the modeled evolution of MHW days for the NW Mediterranean ecoregion (11 years running average) together with results from observations. Our analysis indicates sustained increase in the occurrence frequency of MHW days over the next decade to levels far above those observed during the exceptional year 2003, regardless of the emission scenario considered. By 2050, and under carbon emission scenario RCPs 2.6 and 4.5, MHWs are expected to last for ca. 60% of the period (3.5 months) vs. 73–85% (4.5–5 months) under the extreme emission scenario RCP8.5. Marine heatwave frequency is projected to continue to rise during the second half of the century, up to 80–100% of the June to November period, except under RCP2.6 where a decreasing trend is evidenced after 2070. Our analysis indicated not only longer but also more severe MHWs, with a two to threefold increase in maximum intensity (anomaly) during the second half of the twenty-first century, depending on scenarios. Similar patterns of MHW increasing frequency and intensification are also evidenced for the Adriatic (Table 11.2).

Overall, future SST and MHW trends over the Mediterranean Sea and northern cold ecoregions can be considered reliable signs of increasing harmful conditions affecting marine ecosystems such as the coralligenous communities targeted in this chapter.

11.4.2 Exploring Future Trajectories for Coralligenous Communities

As shown in the previous sections, in the last decade, extensive field surveys following the MMEs (e.g., Coma et al. 2006; Garrabou et al. 2001, 2009; Linares et al. 2005) combined to in-depth analyses of the thermal regimes (e.g., Bensoussan et al. 2010; Crisci et al. 2011) and experimental studies in the field or in controlled conditions (e.g., Ledoux et al. 2015; Crisci et al. 2017; Torrents et al. 2008) were conducted to improve our understanding of the interaction among octocoral populations and their local thermal environments.

Besides an immediate and dramatic decrease in population abundance (density and biomass; Fig. 11.8), continuous population density decreases were observed even 4 years after the observation of the initial mass mortality event, emphasizing the

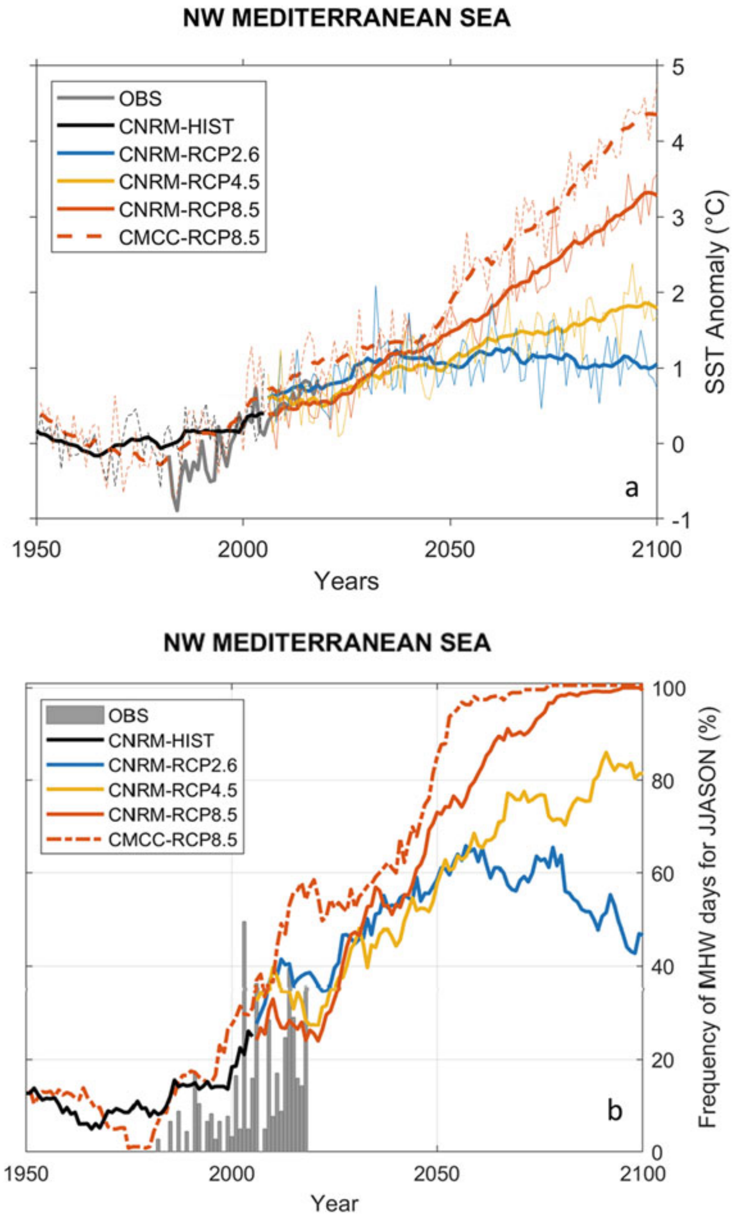


Fig. 11.9 (**a**) Past and future evolution of NW Mediterranean SST Anomaly from two models representative of some low (CNRM) and high (CMCC) response to global warming. Results show the combination of historical run (1950–2005, HIST) and different emission scenario when available (2006–2100, RCP2.6, RCP4.5, and RCP8.5). The model data were obtained from the Med-CORDEX initiative. The 1982–2018 SST satellite observations (OBS) obtained from CMEMS are also shown. (**b**) Same as above for the evolution of marine heatwave days during the June to November period of each year (results shown indicate the relative frequency in %)

Table 11.2 Future evolution of SST Anomaly (SSTA, in °C), marine heatwave days (MHW days), and maximum intensity (MHW-IMAX, in °C) under different models (CNRM, CMCC) and emission scenario (RCP2.6, RCP4.5 and RCP8.5) for the NW Mediterranean (NWM) and Adriatic (ADR) ecoregions. Results indicate decadal average values for mid (2040–2050) and end (2090–2100) of the twenty-first century. Model data obtained from the Med-CORDEX initiative

		Ecoregion	CNRM RCP2.6	CNRM RCP4.5	CNRM RCP8.5	CMCC RCP8 0.5
2040–2050	SSTA (°C)	NWM	1.1	1.0	1.3	1.4
		ADR	1.1	1.1	1.4	1.5
	MHW days	NWM	105	94	110	125
		ADR	98	97	124	126
	MHW-IMAX (°C)	NWM	2.5	2.6	2.5	2.4
		ADR	2.7	2.7	2.7	2.2
2090–2100	SSTA (°C)	NWM	1.0	1.8	3.2	4.3
		ADR	1.1	2.0	3.3	4.1
	MHW days	NWM	83	151	182	183
		ADR	80	152	181	183
	MHW-IMAX (°C)	NWM	2.3	3.0	5.5	6.0
		ADR	2.4	2.7	5.1	5.6

delayed impacts of the events (e.g., Linares et al. 2005, data not shown). These results question the maintenance of central processes (e.g., reproduction) for the long-term dynamics of impacted populations. Indeed, the reproductive impairment is identified as one of the main sublethal effects observed in these populations (Kipson et al. 2012; Arizmendi-Mejía et al. 2015a).

Differential impacts at all biological levels (i.e., among species, populations, individuals and even within colonies) are one of the main characteristics of the MMEs. For instance, after the 1999 event, the percentage of dead colonies in red coral populations from the southeastern coast of France varied from less than 2% to more than 40% (Garrabou et al. 2001). After the 2003 event, populations of *P. clavata* from the same area showed percentage of colonies affected by necrosis ranged from 2 to 80% (Garrabou et al. 2009). Interestingly, this suggests the occurrence of warming-resistant individuals.

In the following sections, we discuss how these decreases in population abundance may impact the dynamics and evolution of the populations and in turn, whether adaptation to changing environmental conditions may have occurred.

From ecology to evolution: How will these ecological declines impact the evolution of gorgonian populations? Elements of response can be obtained by focusing on different issues, for instance, by understanding the interaction between density and reproduction in these species. Understanding how the density and/or biomass decline will affect reproduction and, accordingly, the balance among evolutionary forces interacting with the population dynamics is a topic that has just begun to be addressed (Ledoux et al. 2020). The working hypothesis is that the decrease of reproductive individuals will disrupt the reproductive patterns and, accordingly, will lead to a significant increase of inbreeding and genetic drift. In contrast, we can expect an increase of gamete dispersal, which may buffer to some extent the decrease of adult density, counterbalancing the expected drift effect. The impact of local extinctions on the connectivity among populations and by consequence on their evolution should also require further consideration. To date, the contemporary connectivity (i.e., over short time scale) of structural octocorals seems to be restricted and occurring mainly among neighboring populations (few kms; see Arizmendi-Mejía et al. 2015a but see Padron et al. 2018). The resulting pattern of gene flow usually follows a model of isolation by distance. Disruption of those patterns would increase the genetic isolation of the populations, strengthening the detrimental impact of genetic drift, and inbreeding in the whole system. Further work is needed to refine the impact of ecology on the evolution of the species. Characterizing the temporal dynamics and reproductive patterns of demographically depleted populations would allow better estimating their recovery potential and trajectories. Looking for putative processes that may counterbalance the expected impact of genetic drift resulting from density decreases of reproductive individuals should also be considered as a high priority for research. The role of genetic drift during adaptation process in these species (Alleaume-Benharira et al. 2006; Crisci et al. 2017) also needs be characterized to refine our ability to predict the population trajectory in the warming environment.

From evolution to ecology: Most of the impacted gorgonian species (e.g., for *Paramuricea clavata*; see Boavida et al. 2016) are characterized by wide geographic and bathymetric distributions, which span highly contrasted environments with different thermal regimes. This supports the idea that efficient thermal adaptation has occurred in the past. Moreover, the hard selection experiment currently at stake with the MMEs shows that some individuals or populations may have the capacity to deal with some degrees of warming. The occurrence of resistant phenotypes was confirmed experimentally (e.g., Ledoux et al. 2015; Arizmendi-Mejía et al. 2015a; Crisci et al. 2017). Whether those potentially resistant phenotypes are due to gene expression plasticity (frontloading vs. differential capacity for gene expression plasticity; see Kenkel and Matz 2016) or resistant genetic variants remains to be explored. In this context, genetic rescue, the recolonization of depleted populations by existing alleles coding for thermo-resistance phenotypes via migration, should be considered as a way to achieve adaptation to the changing thermal regime. In addition to the identification of potential genetic factors involved in the response to thermal stress, further characterization of the dispersal patterns in impacted species is needed to formally test the relevance of the genetic rescue scenario. Genetic rescue may be enhanced by the development of assisted gene flow based on transplantation of thermoresistant individuals. Moreover, whether or not the physiological variation(s) allowing to deal with thermal stress will have a cost impacting the population dynamics (e.g., lower reproductive outputs or growth rates of resistant individuals) is an open question. Linking trait variations such as resistance to thermal stress to population dynamics will be highly challenging. A characterization of the demographic parameters (e.g., growth, fecundity) of resistant individuals may give first elements of response.

This quick sketch of the eco-evolutionary dynamics drawn here highlights the massive challenge represented by the expected thermal stress for structural octocorals. It suggests that an abrupt collapse of impacted populations is a likely hypothesis. From an ecological-evolutionary interaction point of view, we can expect a positive feedback of the population demographic decline on the genetic drift leading to an extinction vortex. Nevertheless, there is still hope, particularly considering the occurrence of potentially thermoresistant individuals. Whether or not the evo-eco interaction, through the spread and recolonization of thermoresistant individuals (e.g., Matz et al. 2020), will be strong enough for the system to reach a new equilibrium deserves further attention from the scientific community.

11.4.3 Future Configurations of Coralligenous Assemblages: From Population to Ecosystem Impacts

Given that most affected species during the mass mortality events, such as gorgonian species, play a crucial role in providing habitat complexity, what is the impact of the current decline of these species on the whole coralligenous assemblages? It has been suggested that the occurrence of the red gorgonian *Paramuricea clavata* improves bioconstruction process and supports high species diversity in the coralligenous. The red gorgonian may play a role in stabilizing the community, buffering the negative impact of invasive species and other disturbances (e.g., mucilaginous aggregates) (Ponti et al. 2018). Other central ecological processes for the dynamics of associated species, such as recruitment, may be facilitated by the presence of *P. clavata* (Ponti et al. 2014). In this context, the demographic decline of *P. clavata* induced by mortality events may have dramatic consequences with cascading effects at the ecosystem level that might jeopardize the maintenance of the structure and functioning of coralligenous assemblages.

Under non-disturbed conditions, coralligenous assemblages are characterized by their prominent stability, with structure and composition being commonly maintained over decades to centuries (Teixidó et al. 2011; Bertolino et al. 2014, 2016, 2017; Casas-Güell et al. 2015). However, as already reported in tropical coral reefs impacted by marine heatwaves (Hughes et al. 2018), this long-term stability could be threatened due to recurrent thermal stress events. A recent study performed in Cabrera National Park (Spain) after an intense marine heatwave linked the loss of gorgonian biomass and density to the progressive loss in overall taxonomic biodiversity (Verdura et al. 2019). Therefore, deciphering how such compositional changes may affect the functioning of coralligenous assemblages is a major concern for conservation ecologists in the Mediterranean.

Theoretical ecology predicts that the functioning of assemblages impacted by climate change may be stabilized through compensatory dynamics among functionally redundant species, if there is response diversity (i.e., difference among species' responses to environmental fluctuations as proposed in the insurance hypothesis) (Yachi and Loreau 1999). Such compensatory dynamics were already observed in the field. For instance, the massive die-off of the sensitive staghorn coral *Acropora* *cervicornis* that occurred in Belizean reefs during the 1980s due to disease and high seawater temperature was compensated by an increase of the previously uncommon and more resistant lettuce coral *Agaricia tenuifolia*, which became the main reef builder (Nyström 2006). In the coralligenous assemblages, a great diversity of responses to warming has been observed among co-occurring species (Garrabou et al. 2009; Pagès-Escolà et al. 2018; Gómez-Gras et al. 2019). This response diversity could facilitate the maintenance of assemblage functioning. However, as in the above described case, response diversity also requires the presence of functional redundancy to produce a stabilizing effect (Walker 1995; Nyström 2006). Unfortunately, the preliminary results of long-term functional trait-based studies conducted in these communities suggest a lack of functional redundancy in sensitive key functional groups, such as the habitat-forming octocorals. As a consequence, we expect that the impact of repeated MMEs may trigger drastic functional shifts in these communities in response to the expected warming context (Gómez-Gras et al. 2021). Overall, the ongoing collapse of Mediterranean habitat-forming octocorals may drive to a functional void. The most straightforward way this might happens is that the habitat provided by the gorgonians (erect stratum) can ultimately affect the integrity of coralligenous assemblages and their associated biodiversity. We are still far from fully understanding how coralligenous assemblages functioning will evolve in a warmer Mediterranean Sea. Notwithstanding, the simplification of the habitat is already evident in many impacted locations and may result in severe consequences for coralligenous communities and services they provide.

11.5 Management Options for the Coralligenous Assemblages in the Anthropocene Era

As this chapter suggests, coralligenous assemblages in the Mediterranean have entered a dangerous collapse trajectory with severe and unexpected consequences for some key ecosystems and the goods and services they provide (Fig. 11.10). Ambitious mitigation and adaptation measures are urgently needed to limit surface warming well below 2 °C above pre-industrial levels. To tackle this challenge, the role of ocean-based solutions has been recently highlighted (Gattuso et al. 2019). Among them, the establishment of marine protected areas networks (MPAs) is one of the key measures for its technical readiness and potential effectiveness (Gattuso et al. 2019; Hoegh-Guldberg et al. 2019). In fact, effective protection, especially in full protected MPAs where the impacts other human activities are absent, can address both mitigation and adaptation measures (Roberts et al. 2017). In this sense, MPAs contribute to the protection of habitats, such as coralligenous assemblages, and seagrass meadows that play a role in preserving and enhancing carbon sinks as well as ensuring the functioning of food webs that drive the storage and transport of biomass from shallow to deep environments. Regarding adaptation, MPAs can play multiple roles. On one hand, protection can enhance the ecological resilience through the reduction and/or complete removal of local stressors and enhancing the overall conservation status of populations, species, and habitats,

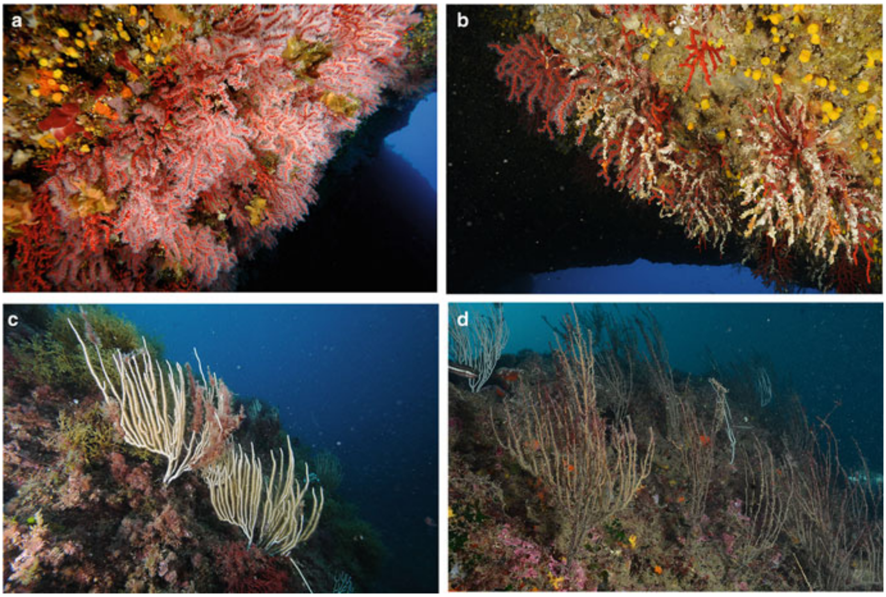


Fig. 11.10 State of non-disturbed (**a**, **b**) and the post-MME impacted (**d**, **c**) by marine heatwaves of coralligenous assemblages dominated by the white gorgonian *Eunicella singularis* and the red coral *Corallium rubrum*, respectively. Photos MedRecover research group ©

therefore increasing ecosystem resilience (Micheli et al. 2012; Hixon et al. 2014; Simard et al. 2016; Roberts et al. 2017). However, recent studies, reporting the impacts of severe marine heatwaves, as well as the warming scenarios, questioned the effectiveness of protection to counteract the effects of climate change (Côté and Darling 2010; Bruno et al. 2018; Hughes et al. 2018; Montero-Serra et al. 2019). In fact, our results on population monitoring performed within MPAs also challenge the effectiveness of MPAs, although we do not have information from outside the MPAs to compare the benefits from protection. In this sense, long-term monitoring programs in MPAs including different levels of protection are crucial to fully understand the lethal and sublethal impacts of global warming in marine ecosystems and to assess potential mechanisms of the species and populations to respond to environmental changes (Micheli et al. 2012; Kersting and Linares 2019). This point highlights the essential role of MPAs in building a network of sentinel observatories on climate change (Otero et al. 2013).

Beyond their ecological role, MPAs are privileged areas to promote the engagement of key stakeholders to develop joint adaptation measures to face to climate change impacts. Likewise, these areas, especially in the Mediterranean region, play a major role for outreach, education, and communication to the general public on climate change issues, which can engage society to reduce greenhouse gases emissions (Simard et al. 2016).

In order to promote the role of MPAs as ocean-based solutions in the Mediterranean, we first need to conduct further studies on key processes to effectively enhance the ecological mitigation and adaptation roles of MPAs. Secondly, we need to reach the conservation target of 10% by 2020 agreed by the Parties of the Convention on Biological Diversity (Aichi Target 11); current MPAs is around 6% (Claudet et al. 2020). This goal should focus for a significant increase the proportion of no take areas which are the most effective to tackle climate change impacts. Unfortunately, these fully protected areas are currently below the 1% in the Mediterranean (Claudet et al. 2020). Thirdly, we need to ensure that MPAs are effectively and well managed. At present, a great proportion of Mediterranean MPAs are considered "paper parks" since many lack management plans; even fewer include measures to adapt to climate change (Rilov et al. 2019; Garrabou et al. 2019; Claudet et al. 2020). In conclusion, despite clear limitations to prevent climate impacts from scenarios with more intense and frequent marine heatwaves, MPAs are excellent "laboratories" for scientific research, testing adaptation, and mitigation strategies and enhance management strategies for conservation. The information and lessons learnt may be then transferred to non-protected areas to sustain the resilience of marine ecosystems.

Acknowledgments This study has been partially supported by the Interreg Med Programme (Project MPA-Adapt -Grant number 1197 | 1MED15_3.2_M2_337 and Project MPA-ENGAGE-grant number: 5216 | 5MED18_3.2_M23_007), by the European Union's Horizon 2020 Research and Innovation Programme under grant agreement no 689518 (MERCES), by the Spanish Government (Smart project (CGL2012-32194) and Heatmed research project (RTI2018-095346-B-I00, *MCIU/AEI/FEDER*, *UE*), and by FCT – Foundation for Science and Technology (UIDB/04423/2020 and UIDP/04423/2020). CL was funded by an ICREA Academia from the Catalan Institution for *Research* and *Advanced* Studies. DG-G was supported by an FPU grant (FPU15/05457) from the Spanish Ministry of Education.

We thank Samuel Somot from CNRM, Piero Lionello, and Enrico Scoccimarro from CMCC for facilitating access to the RCSMs simulations performed as part of the Med-CORDEX experiment. We also thank Jean-Marie Dominici from Parc Naturel Regional de Corse and Marion Peirache from Port-Cros National Park for the facilities and support to conduct field work in Scandola and Port-Cros MPAs. Finally, we want to thank our colleagues, technicians, and students that have been participating and contributing to field work and data analysis of temperature and demographic long-term data series; without them this work would not have been possible.

References

Alleaume-Benharira M, Pen I, Ronce O (2006) Patterns of adaptation within a species range: interactions between drift and gene flow. J Evol Biol 19:203–215

Arizmendi-Mejía R, Linares C, Garrabou J, Antunes A et al (2015a) Combining genetic and demographic data for the conservation of a Mediterranean marine habitat-forming species. PLoS One 10(3):e0119585. https://doi.org/10.1371/journal.pone.0119585

Arizmendi-Mejía R, Ledoux JB, Antunes A, Thanopoulou Z et al (2015b) Demographic responses to warming: reproductive maturity and sex influence vulnerability in an octocoral. Coral Reefs 34:1207–1216. https://doi.org/10.1007/s00338-015-1332-9h

Aurelle D, Ledoux JB, Rocher C, Borsa P et al (2011) Phylogeography of the red coral (*Corallium rubrum*): inferences on the evolutionary history of a temperate gorgonian. Genetica 139:855–869

Aurelle D, Tariel J, Zuberer F, Haguenaguer A, Ribout C et al (2020) Genetic insights into recolonization processes of Mediterranean octocorals. Mar Biol 167:73. https://doi.org/10.1007/s00227-020-03684-z

Azzurro E, Sbragaglia V, Cerri J, Bariche L et al (2019) Climate change, biological invasions, and the shifting distribution of Mediterranean fishes: a large-scale survey based on local ecological knowledge. Glob Change Biol 201900:1–14. https://doi.org/10.1111/gcb.14670

Ballesteros E (2006) Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanogr Mar Biol 44:123–195

Bates AE, Helmuth B, Burrows MT, Duncan MI et al (2018) Biologists ignore ocean weather at their peril. Nature 560:299–301

Ben Rais Lasram FBR, Mouillot D (2009) Increasing southern invasion enhances congruence between endemic and exotic Mediterranean fish fauna. Biol Invasions 11:697–711. https://doi.org/10.1007/s10530-008-9284-4

Ben Rais Lasram F, Guilhaumon F, Albouy C, Somotz S et al (2010) The Mediterranean Sea as a ‘cul-de-sac’ for endemic fishes facing climate change. Glob Chang Biol 16:3233–3245

Bensoussan N, Romano JC, Harmelin JG, Garrabou J (2010) High resolution characterization of Northwest Mediterranean coastal waters thermal regimes: to better understand responses of benthic communities to climate change. Estuarine Coastal and Shelf Sci 87:431–441. https://doi.org/10.1016/j.ecss.2010.01.008

Bensoussan N, Cebrian E, Dominici JM, Kersting DK, et al. (2019a) Using CMEMS and the Mediterranean marine protected area sentinel network to track ocean warming effects in coastal areas. In: Copernicus marine Service Ocean state report, issue 3, Journal of Operational Oceanography

Bensoussan N, Chiggiato J, Buongiorno Nardelli B, et al. (2019b) Insights on 2017 marine heat waves in the Mediterranean Sea. Copernicus marine Service Ocean state report #3 Journal of Operational Oceanography

Berdalet E, Tester PA, Chinain M, Fraga S et al (2017) Harmful algal blooms in benthic systems: recent progress and future research. Oceanography 30(1):36–45. https://doi.org/10.5670/oceanog.2017.108

Bertolino M, Calcinai B, Cattaneo-Vietti R, Cerrano C et al (2014) Stability of the sponge assemblage of Mediterranean coralligenous concretions along a millennial time span. Mar Ecol 35:149–158. https://doi.org/10.1111/maec.2014.35.issue-2

Bertolino M, Betti F, Bo M, Cattaneo-Vietti R et al (2016) Changes and stability of a Mediterranean hard bottom community over 25 years. J Mar Biol Asscn UK 96:341–350. https://doi.org/10.1017/S0025315415001186

Bertolino M, Costa G, Carella M, Cattaneo-Vietti R (2017) The dynamics of a Mediterranean coralligenous sponge assemblage at decennial and millennial temporal scales. PLoS One 12: e0177945. https://doi.org/10.1371/journal.pone.0177945

Bianchi CN, Morri C (2000) Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. Mar Pollut Bull 40(5):367–376. https://doi.org/10.1016/S0025-326X(00)00027-8

Boavida J, Silva I, Assis J, Serrão EA (2016) Overlooked habitat of a vulnerable gorgonian revealed in the Atlantic and Mediterranean by niche modelling. Sci Rep 6:36460. https://doi.org/10.1038/srep36460

Boudouresque CF (2004) Marine biodiversity in the Mediterranean: status of species, populations and communities. Sci Rep Port-Cros National Park, France 20:97–146

Bruno JF, Bates AE, Cacciapaglia C, Pike EP et al (2018) Climate change threatens the world’s marine protected areas. Nat Clim Chang 8:499–503. https://doi.org/10.1038/s41558-018-0149-2

Cánovas-Molina A, Montefalcone M, Bavestrello G, Masmoudi MB et al (2018) From depth to regional spatial genetic differentiation of Eunicella cavolini in the NW Mediterranean. Comptes Rendus Biologies, Elsevier Masson 341(9–10):421–432. https://doi.org/10.1016/j.crvi.2018.09.002

Casas-Güell E, Teixidó N, Garrabou J, Cebrian E (2015) Structure and biodiversity of coralligenous assemblages over broad spatial and temporal scales. Mar Biol 162:901–912. https://doi.org/10.1007/s00227-015-2635-7

Cerrano C, Bavestrello G, Bianchi CN, Cattaneo-vietti R et al (2000) A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (northwestern Mediterranean), summer 1999. Ecol Letters 3:284–293. https://doi.org/10.1046/j.1461-0248.2000.00152.x

Claudet J, Loiseau C, Sostres M, Zupan M (2020) Underprotected marine protected areas in a global biodiversity hotspot. One Earth 2:380–384

Coll M, Piroddi C, Steenbeek J, Kaschner K et al (2010) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PLoS One 5(8):e11842. https://doi.org/10.1371/journal.pone.0011842

Coma R, Ribes M, Zabala M, Gili JM (1998) Growth in a modular colonial marine invertebrate. Estuarine Coastal Shelf Science 47:459–470. https://doi.org/10.1006/ecss.1998.0375

Coma R, Linares C, Ribes M, Diaz D et al (2006) Consequences of a mass mortality event on the populations of the gorgonian *Eunicella singularis* (Cnidaria: Octocorallia) in Menorca (Balearic Islands, NW Mediterranean). Mar Ecol Prog Ser 327:51–60

Costantini F, Abbiati M (2016) Into the depth of population genetics: pattern of structuring in mesophotic red coral populations. Coral Reefs 35:39–52

Costantini F, Fauvelot C, Abbiati M (2007a) Fine-scale genetic structuring in *Corallium rubrum*: evidence of inbreeding and limited effective larval dispersal. Mar Ecol Prog Ser 340:109–119

Costantini F, Fauvelot C, Abbiati M (2007b) Genetic structuring of the temperate gorgonian coral (*Corallium rubrum*) across the western Mediterranean Sea revealed by microsatellites and nuclear sequences. Mol Ecol 16:5168–5182

Côté IM, Darling ES (2010) Rethinking ecosystem resilience in the face of climate change. PLoS Biol 8:e1000438

Cramer W, Guiot J, Fader M, Garrabou J et al (2018) Climate change and interconnected risks to sustainable development in the Mediterranean. Nat Clim Chang 8:972–980. https://doi.org/10.1038/s41558-018-0299-292

Crisci C, Bensoussan N, Romano JC, Garrabou J (2011) Temperature anomalies and mortality events in marine communities: insights on factors behind differential mortality impacts in the NW Mediterranean. PLoS One 6:e23814. https://doi.org/10.1371/journal.pone.0023814

Crisci C, Ledoux JB, Mokhtar-Jamaï K, Bally M et al (2017) Regional and local environmental conditions do not shape the response to warming of a marine habitat-forming species. Sci Rep 7:50–69. https://doi.org/10.1038/s41598-017-05220-4

Cupido R, Cocito S, Sgorbini S, Bordone A, Santangelo G (2008) Response of a gorgonian (*Paramuricea clavata*) population to mortality events: recovery or loss? Aquat Conserv: Mar Freshw Ecosyst 18(6):984–992

Darmaraki S, Somot S, Sevault F, Nabat P (2019a) Past variability of Mediterranean Sea marine heatwaves. Geophys Res Lett 46:9813–9823. https://doi.org/10.1029/2019GL082933

Darmaraki S, Somot S, Sevault F, Nabat P et al (2019b) Future evolution of marine heatwaves in the Mediterranean Sea. Clim Dynam 53:1371–1392. https://doi.org/10.1007/s00382-019-04661-z

Diaz-Almela E, Marba N, Duarte CM (2007) Consequences of Mediterranean warming events in seagrass (*Posidonia oceanica*) flowering records. Glob Chang Biol 13:224–235. https://doi.org/10.1111/j.1365-2486.2006.01260.x

Fosse J, Le Tellier J (2017) Sustainable tourism in the Mediterranean: state of play and strategic directions. Plan bleu. Valbonne. (plan bleu paper, 17)

Frölicher TL, Fischer EM, Gruber N (2018) Marine heatwaves under global warming. Nature 560 (7718):360. https://doi.org/10.1038/s41586-018-0383-9

Garrabou J, Harmelin JG (2002) A 20-year study on life-history traits of a harvested long- lived temperate coral in the NW Mediterranean: insights into conservation and management needs. J Anim Ecol 71:966–978

Garrabou J, Perez T, Sartoretto S, Harmelin JG (2001) Mass mortality event in red coral (*Corallium rubrum*, Cnidaria, Anthozoa, Octocorallia) populations in Provence region (France, NW Mediterranean). Mar Ecol Prog Ser 217:263–272. https://doi.org/10.3354/meps217263

Garrabou J, Coma R, Bensoussan N, Bally M et al (2009) Mass mortality in northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Glob Chang Biol 15:1090–1103. https://doi.org/10.1111/j.1365-2486.2008.01823.x

Garrabou J, Bazairi H, Espinos F, Ramdani M, et al. (2018) MME-T-MEDNet: mass mortality events in mediterranean marine coastal ecosystems. http://hdl.handle.net/10261/171445

Garrabou J, Gómez-Gras D, Ledoux J-B, Linares C et al (2019) Collaborative database to track mass mortality events in the Mediterranean Sea. Front Mar Sci 6:707. https://doi.org/10.3389/fmars.2019.00707

Gattuso JP, Magnan AK, Gallo ND, Her D, et al. (2019) Opportunities for increasing ocean action in climate strategies. IDDRI, Policy Brief N°02/19

Gili JM, Coma R (1998) Benthic suspension feeders: their Para- mount role in littoral marine food webs. Trends Ecol Evol 13:316–332

Givan O, Edelist D, Sonin O, Belmaker J (2018) Thermal affinity as the dominant factor changing Mediterranean fish abundances. Glob Chang Biol 24(1):80–89. https://doi.org/10.1111/gcb.13835

Gómez-Gras D, Linares C, de Caralt S, Cebrian E et al (2019) Response diversity in Mediterranean coralligenous assemblages facing climate change: insights from a multi-specific thermotolerance experiment. Ecol Evol 9(7):4168–4180. https://doi.org/10.1002/ece3.5045

Gómez-Gras D, Linares C, Dornelas M, Madin JS, Brambilla V, Ledoux J-B, López-Sendino P, Bensoussan N, Garrabou J (2021) Climate change transforms the functional identity of Mediterranean coralligenous assemblages. Ecol Lett. https://doi.org/10.1111/ele.13718

Gori A, Linares C, Rossi S, Coma R, Gili JM (2007) Spatial variability in reproductive cycle of the gorgonians *Paramuricea clavata* and *Eunicella singularis* (Anthozoa, Octocorallia) in the Western Mediterranean Sea. Mar Biol 151:1571–1584

Gori A, Rossi S, Berganzo E, Pretus JL et al (2011) Spatial distribution patterns of the gorgonians *Eunicella singularis, Paramuricea clavata* and *Leptogorgia sarmentosa* (cape of Creus, northwestern Mediterranean Sea). Mar Biol 158:143–158

Harmelin JG (2004) Environnement thermique du benthos côtier de l'île de port-Cros (parc national, France, Méditerranée Nord-occidentale) et implications biogéographiques. Sci Rep Port-Cros Nat Park Fr 20:173–194

Harmelin JG, Sartoretto S, Francour P(1999) Mise en place d'une stratégie de suivide l'ichtyofaune et des peuplements deGorgonaires de l'archipel de Riou. ContratVille de Marseille, Direction de l'environne-ment et des Déchets & Centre d'Océanologiede Marseille. COM, Marseille, pp 1–110

Hixon MA, Johnson DW, Sogard SM (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES J Mar Sci 71:2171–2185

Hobday AJ, Alexander LV, Perkins SE, Smale DA et al (2016) A hierarchical approach to defining marine heatwaves. Prog Ocean 141:227–238. https://doi.org/10.1016/j.pocean.2015.12.014

Hobday AJ, Spillman CM, Eveson JP, Hartog JR et al (2018) A framework for combining seasonal forecasts and climate projections to aid risk management for fisheries and aquaculture. Front Mar Sci 5:137. https://doi.org/10.3389/fmars.2018.00137

Hoegh-Guldberg O, Jacob D, Taylor M, Guillen-Bolaños T et al (2019) The human imperative of stabilizing global climate change at 1.5°C. Science 365(6459):eaaw6974. https://doi.org/10.1126/science.aaw6974

Huete-Stauffer C, Vielmini I, Palma M, Navone A et al (2011) *Paramuricea clavata* (Anthozoa, Octoralia) loss in the marine protected area of Tavolara (Sardinia, Italy) due to a mass mortality event. Mar Ecol 32(Suppl. 1):107–116

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG et al (2017a) Global warming and recurrent mass bleaching of corals. Nature 543:373–377. https://doi.org/10.1038/nature21707

Hughes TP, Barnes ML, Bellwood DR, Cinner JE et al (2017b) Coral reefs in the Anthropocene. Nature 546:82–90. https://doi.org/10.1038/nature22901

Hughes TP, Kerry JT, Baird AH, Connolly SR et al (2018) Global warming transforms coral reefs assemblages. Nature 556:492–496. https://doi.org/10.1038/s41586-018-0041-2

IPCC (2019) IPCC special report on the ocean and cryosphere in a changing climate. In: Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Alegría A, Nicolai M, Okem A, Petzold J, Rama B, Weyer NM (eds). In press

Jansson E, Ruokonen M, Kojola I, Aspi J (2012) Rise and fall of a wolf population: genetic diversity and structure during recovery, rapid expansion and drastic decline. Mol Ecol 21:5178–5519. https://doi.org/10.1111/mec.1200

Kenkel CD, Matz MV (2016) Gene expression plasticity as a mechanism of coral adaptation to a variable environment. Nat Ecol Evol 7;1(1):14. https://doi.org/10.1038/s41559-016-0014. PMID: 28812568.

Kersting DK, Linares C (2019) Living evidence of a fossil survival strategy raises hope for warming-affected corals. Sci Adv 5(10):eaax2950. https://doi.org/10.1126/sciadv.aax2950

Kipson S, Linares C, Teixidó N, Bakran-Petricioli T, Garrabou J (2012) Effects of thermal stress on early developmental stages of a gorgonian coral. Mar Ecol Prog Ser 470:69–78

Kipson S, Linares C, Čižmek H et al (2015) Population structure and conservation status of the red gorgonian *Paramuricea clavata* (Risso, 1826) in the eastern Adriatic Sea. Mar Ecol 36:982–993. https://doi.org/10.1111/maec.12195

Ledoux JB, Mokthar-Jamai K, Roby C, Feral JP et al (2010a) Genetic survey of shallow populations of the Mediterranean red coral [*Corallium rubrum* Linnaeus, 1758]: new insights into evolutionary processes shaping nuclear diversity and implications for conservation. Mol Ecol 19:675–690

Ledoux JB, Garrabou J, Bianchimani O, Drap P et al (2010b) Fine-scale genetic structure and inferences on population biology in the threatened Mediterranean red coral, *Corallium rubrum*. Mol. Ecol 19:4204–4216

Ledoux JB, Aurelle D, Bensoussan N, Marschal C et al (2015) Potential for adaptive evolution at species range margins: contrasting interactions between red coral populations and their environment in a changing ocean. Ecol Evol 5:1178–1192. https://doi.org/10.1002/ece3.1324

Ledoux JB, Frías-Vidal S, Montero-Serra I, Antunes A, Casado-Bueno C (2020) Assessing the impact of population decline on mating system in the overexploited Mediterranean red coral. Aquat Conserv. https://doi.org/10.1002/aqc.3327

Leigh DM, Hendry AP, Vázquez-Domínguez E, Friesen VL (2019) Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. Evol Appl 12:1505–1512. https://doi.org/10.1111/eva.12810

Linares C, Coma R, Diaz D, Zabala M et al (2005) Immediate and delayed effects of a mass mortality event on gorgonian population dynamics and benthic community structure in the NW Mediterranean Sea. Mar Ecol Prog Ser 305:127–137. https://doi.org/10.3354/meps305127

Linares C, Doak D, Coma R, Diaz D, Zabala M (2007) Life history and population viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. Ecology 88:918–928. https://doi.org/10.1890/05-1931

Linares C, Coma R, Mariani S, Díaz D et al (2008a) Early life history of the Mediterranean gorgonian *Paramuricea clavata*: implications for population dynamics. Invertebr Biol 127:1–11. https://doi.org/10.1111/j.1744-7410.2007.00109.x

Linares C, Coma R, Garrabou J, Díaz D, Zabala M (2008b) Size distribution, density and disturbance in two mediterranean gorgonians *Paramuricea clavata* and *Eunicella singularis*. J Appl Ecol 45:688–699. https://doi.org/10.1111/j.1365-2664.2007.01419.x

Linares C, Zabala M, Garrabou J, Coma R, Díaz D, Hereu B, Dantart L (2010) Assessing the impact of diving in coralligenous communities. The usefulness of demographic studies of red gorgonian populations Travaux scientifques de Parc National de Port-Cros (France) 24:161–184

Linares C, Ballesteros E, Verdura J, Aspillaga E, et al (2017) Efectos del cambio climático sobre la gorgonia Paramuricea clavata y el coralígeno asociado en el Parque Nacional Marítimo-

Terrestre del archipiélago de Cabrera. In: Amengual P (ed) Proyectos de investigación en Parques nacionales: convocatoria 2012–2015. OA de PN, pp 45–67

Marbà N, Jordà G, Agusti S, Girard C, Duarte C, M. (2015) Footprints of climate change on Mediterranean Sea biota. Front Mar Sci 2:00056. https://doi.org/10.3389/fmars.2015.00056

Marschal C, Garrabou J, Harmelin JG, Pichon M (2004) A new method for measuring growth and age in the precious red coral *Corallium rubrum* (L.). Coral Reefs 23:423–432. https://doi.org/10.1007/s00338-004-0398-6

Masmoudi MB, Chaoui L, Topçu NE, Hammami P et al (2016) Contrasted levels of genetic diversity in a benthic Mediterranean octocoral: consequences of different demographic histories? Ecol Evol 6(24):8665–8678. https://doi.org/10.1002/ece3.2490

Matz MV, Treml EA, Haller BC (2020) Estimating the potential for coral adaptation to global warming across the indo-West Pacific. Glob Change Biol. 26:3473–3481. https://doi.org/10.1111/gcb.15060

Micheli F, Saenz-Arroyo A, Greenley A, Vazquez L et al (2012) Evidence that marine reserves enhance resilience to climatic impacts. PLoS One 7:e40832

Millette KL, Fugère V, Debyser C, Greiner A et al (2020) No consistent effects of humans on animal genetic diversity worldwide. Ecol Lett 23(1):55–67. https://doi.org/10.1111/ele.13394

Mokhtar-Jamai K, Pascual M, Ledoux JB, Coma R et al (2011) From global to local genetic structuring in the red gorgonian *Paramuricea clavata*: the interplay between oceano- graphic conditions and limited larval dispersal. Mol Ecol Wiley 20:3291–3305. https://doi.org/10.1111/j.1365-294X.2011.05176.x. hal-00847206

Mokhtar-Jamai K, Coma R, Wang J, Zuberer F et al (2013) Role of evolutionary and ecological factors in the reproductive success and the spatial genetic structure of the temperate gorgonian *Paramuricea clavata*. Ecol Evol 3(6):1765–1779

Momigliano P, Jokinen H, Calboli F, Aro E, Merilä J (2019) Cryptic temporal changes in stock composition explain the decline of a flounder (Platichthys spp.) assemblage. Evol Appl 12:549–559. https://doi.org/10.1111/eva.12738

Montero-Serra I, Linares C, Garcia M, Pancaldi F et al (2015) Harvesting effect, recovery patterns and management strategies for a long-lived and structural precious coral. PLoS One 10(2): e0117250. https://doi.org/10.1371/journal.pone.0117250

Montero-Serra I, Garrabou J, Doak DF, Figuerola L et al (2018a) Accounting for life-history strategies and timescales in marine restoration. Conserv Lett 11(1):1–9. https://doi.org/10.1111/conl.12341

Montero-Serra I, Linares C, Doak DF, Ledoux JB, Garrabou J (2018b) Strong linkages between depth, longevity and demographic stability across marine sessile species. Proc R Soc B 285 (1873):20172688. https://doi.org/10.1098/rspb.2017.2688

Montero-Serra I, Garrabou J, Doak DF, Ledoux DF, Linares C (2019) Marine protected areas enhance structural complexity but do not buffer the consequences of ocean warming for an overexploited precious coral. J Appl Ecol 56:1063–1074. https://doi.org/10.1111/1365-2664.13321

Nyström M (2006) Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. Ambio 35:30–35. https://doi.org/10.1579/0044-7447-35.1.30

Oliver ECJ, Donat MG, Burrows MT, Moore PJ et al (2018) Longer and more frequent marine heatwaves over the past century. Nat Commun 9:1324. https://doi.org/10.1038/s41467-018-03732-9

Otero M, Cebrian E, Francour P, Galil B, Savini D (2013) Monitoring marine invasive species in Mediterranean marine protected areas (MPAs): a strategy and practical guide for managers. IUCN, Malaga, p 136

Padron M, Costantini F, Bramanti L, Guizien K, Abbiati M (2018) Genetic connectivity supports recovery of gorgonian populations impacted by climate change. Aquatic Conserv*:* Mar Freshw Ecosyst:1–12

Pagès-Escolà M, Hereu B, Garrabou J, Montero-Serra I et al (2018) Divergent responses to warming of two common co-occurring Mediterranean bryozoans. Sci Rep 8:174555. https://doi.org/10.1038/s41598-018-36094-9

Pairaud IL, Bensoussan N, Garreau P, Faure V, Garrabou J (2014) Impacts of climate change on coastal benthic ecosystems: assessing the current risk of mortality outbreaks associated with thermal stress in NW Mediterranean coastal areas. *Topical Collection on the 16th biennial workshop of the Joint Numerical Sea Modelli*. Ocean Dyn 64:103–115. https://doi.org/10.1007/s10236-013-0661-x

Pastor F, Valiente JA, Palau JL (2019) Sea surface temperature in the mediterranean: Trends and spatial patterns (1982–2016). Pure Appl Geophys 175:4017. https://doi.org/10.1007/s00024-017-1739-z

Perez T, Garrabou J, Sartoretto S, Harmelin JG et al (2000) Mortalité massive d'invertébrés marins: un événemnt sans précédent en Méditerranée nord-occidentale. Comptes Rendus de l'Académie des Sciencies Series III Life Sciences 323:853–865. https://doi.org/10.1016/S0764-4469(00)01237-3

Piazzi L, Atzori F, Cadoni N, Cinti MF, Frau F, Ceccherelli G (2018) Benthic mucilage blooms threaten coralligenous reefs. Mar Environ Res 140:145–151. https://doi.org/10.1016/j.marenvres.2018.06.011

Pisano A, Buongiorno Nardelli B, Tronconi C, Santoleri R (2016) The new Mediterranean optimally interpolated pathfinder AVHRR SST dataset (1982–2012). Remote Sensing Environ 176:107–116. https://doi.org/10.1016/j.rse.2016.01.019

Pisano A, Marullo S, Artale V, Falcini F, Yang C, Leonelli FE, Santoleri R, Buongiorno Nardelli B (2020) New evidence of Mediterranean climate change and variability from sea surface temperature observations. Remote Sens 2020(12):132. https://doi.org/10.3390/rs12010132

Ponti M, Parlini RA, Ventra V, Greco D et al (2014) Ecological shifts in Mediterranean coralligenous assemblages related to gorgonian forest loss. PLoS One 9(7):e102782. https://doi.org/10.1371/journal.pone.0102782

Ponti M, Turicchia E, Ferro F, Cerrano C, Abbiati M (2018) The understorey of gorgonian forests in mesophotic temperate reefs. Aquat Conserv Marine Fresh Water Ecosystems 28(5):1153–1166. https://doi.org/10.1002/aqc.2928

Reynolds L, Stachowicz J, Hughes A et al (2017) Temporal stability in patterns of genetic diversity and structure of a marine foundation species (*Zostera marina*). Heredity 118:404–412. https://doi.org/10.1038/hdy.2016.114

Rilov G, Mazaris AD, Stelzenmüller V, Helmuth B, Wahl M et al (2019) Adaptive marine conservation planning in the face of climate change: what can we learn from physiological, ecological and genetic studies? Global Ecol Conserv 17:e00566. https://doi.org/10.1016/j.gecco.2019.e00566

Rivetti I, Fraschetti S, Lionello P, Zambianchi E, Boero F (2014) Global warming and mass mortalities of benthic invertebrates in the Mediterranean Sea. PLoS One 9(12):e115655. https://doi.org/10.1371/journal.pone.0115655

Roberts CM, O'Leary BC, McCauley DJ, Cury PM et al (2017) Marine reserves can mitigate and promote adaptation to climate change. Proc Natl Acad Sci 114:6167–6175. https://doi.org/10.1073/pnas.1701262114

Romano JC, Bensoussan N, Younes WAN, Arlhac D (2000) Anomalie thermique dans les eaux du golfe de Marseille durand l'été 1999. Une explication partielle de la mortalité d'invertébrés fixés? C R Acad Sci III Sci Vie 323:415

Sabates A, Martın P, Raya V (2012) Changes in life-history traits in relation to climate change: bluefish (*Pomatomus saltatrix*) in the northwestern Mediterranean. ICES J Mar Sci 69(6):1000–1009. https://doi.org/10.1093/icesjms/fss053

Sala E, Kizilkaya Z, Yildirim D, Ballesteros E (2011) Alien marine fishes deplete algal biomass in the eastern Mediterranean. PLoS One 6(2):e17356. https://doi.org/10.1371/journal.pone.0017356

Salat J, Pascual J, Flexas M et al (2019) Ocean Dyn 69:1067. https://doi.org/10.1007/s10236-019-01285-z

Schaeffer A, Roughan M (2017) Subsurface intensification of marine heatwaves off southeastern Australia: The role of stratification and local winds. Geophys Res Lett 44:5025–5033. https://doi.org/10.1002/2017GL073714.

Segelbacher G, Manel S, Tomiuk J (2008) Temporal and spatial analyses disclose consequences of habitat fragmentation on the genetic diversity in capercaillie (Tetrao urogallus). Mol Ecol 17:2356–2367. https://doi.org/10.1111/j.1365-294X.2008.03767.x

Simard F, Laffoley D, Baxter JM (2016) Marine protected areas and climate change: adaptation and mitigation. Synergies, opportunities and challenges. IUCN, Gland, Switzerland, p 52

Sini M, Kipson S, Linares C, Koutsoubas D, Garrabou J (2015) The yellow gorgonian *Eunicella cavolini*: demography and disturbance levels across the Mediterranean Sea. PLoS One 10(5): e0126253. https://doi.org/10.1371/journal.pone.0126253

Skliris N, Sofianos S, Gkanasos A, Mantziafou A et al (2012) Decadal scale variability of sea surface temperature in the Mediterranean Sea in relation to atmospheric variability. Ocean Dynam 62(1):13–30. https://doi.org/10.1007/s10236-011-0493-5

Smale DA, Wernberg T, Oliver ECJ, Thomsen M et al (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Chang 9:306–312. https://doi.org/10.1038/s41558-019-0412-1

Teixidó N, Garrabou J, Harmelin JG (2011) Low dynamics, high longevity and persistence of sessile structural species dwelling on Mediterranean coralligenous outcrops. PLoS One 6(8): e23744. https://doi.org/10.1371/journal.pone.0023744

Torrents O, Garrabou J, Marschal C, Harmelin JG (2005) Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) (Octocorallia, Gorgonacea) in the Marseilles area (France, NW Mediterranean). Biol Conserv 121:391–397

Torrents O, Tambuté E, Caminiti N, Garrabou J (2008) Upper thermal thresholds of shallow vs. deep populations of the precious Mediterranean red coral *Corallium rubrum*: assessing the potential effects of warming in the NW Mediterranean. J Exp Mar Biol Ecol 357:7–19. https://doi.org/10.1016/j.jembe.2007.12.006

Verdura J, Linares C, Ballesteros E, Coma R et al (2019) Biodiversity loss in a Mediterranean ecosystem due to an extreme warming event unveils the role of an engineering gorgonian species. Sci Rep 9:5911. https://doi.org/10.1038/s41598-019-41929-0

Verges A et al (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B 281:20140846. https://doi.org/10.1098/rspb.2014.0846

Von Schuckmann K, Le Traon PY, Smith N, Pascual A, Brasseur P, Fennel K et al (2017) The copernicus marine environment monitoring service ocean state report. J Oper Oceanogr 9:235–320. https://doi.org/10.1080/1755876X.2016.1273446

Von Schuckmann, Le Traon VY, Smith N, Pascual A, Brasseur P, Fennel K, Djavidnia S et al (2018) Copernicus marine service ocean state report. J. Oper. Oceanogr 11:1–142. https://doi.org/10.1080/1755876X.2018.1489208

Von Schuckmann, Le Traon VY, Smith N, Pascual A, Brasseur P, Fennel K, Djavidnia S et al (2019) Copernicus marine service ocean state report, issue 3. J Oper Oceanogr 12:1–123. https://doi.org/10.1080/1755876X.2019.1633075

Walker B (1995) Conserving biological diversity through ecosys-tem resilience. Conserv Biol 9:747–752. https://doi.org/10.1046/j.1523-1739.1995.09040747.x

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc Nat Acad Sci USA 96:1463–1468. https://doi.org/10.1073/pnas.96.4.1463

Marine Heatwave Drives Collapse of Kelp Forests in Western Australia

12

Thomas Wernberg

Abstract

Marine heatwaves (MHWs) are discrete, unusually warm-water events which can have devastating ecological impacts. In 2011, Western Australia experienced an extreme MHW, affecting >2000 km of coastline for >10 weeks. During the MHW temperatures exceeded the physiological threshold for net growth (~23 °C) for kelp (*Ecklonia radiata*) along large tracts of coastline. Kelp went locally extinct across 100 km of its northern (warm) distribution. In total, an estimated 43% of the kelp along the west coast perished, and widespread shifts in species distributions were seen across seaweeds, invertebrates and fish. With the loss of kelp, turf algae expanded rapidly and now cover many reefs previously dominated by kelp. The changes in ecosystem structure led to blocking of kelp recruitment by expansive turfs and elevated herbivory from increased populations of warm-water fishes—feedback processes that prevent the recovery of kelp forests. Water temperature has long returned to pre-MHW levels, yet today, 8 years after the event, the kelp forests have not recovered. This supports initial concerns that the transformation to turf reefs represents a persistent change to a turf-dominated state. MHWs are a manifestation of ocean warming; they are being recorded with increasing frequency in all oceans, and these extreme events are set to shape our future marine ecosystems.

T. Wernberg (✉)
UWA Oceans Institute, The University of Western Australia, Perth, WA, Australia

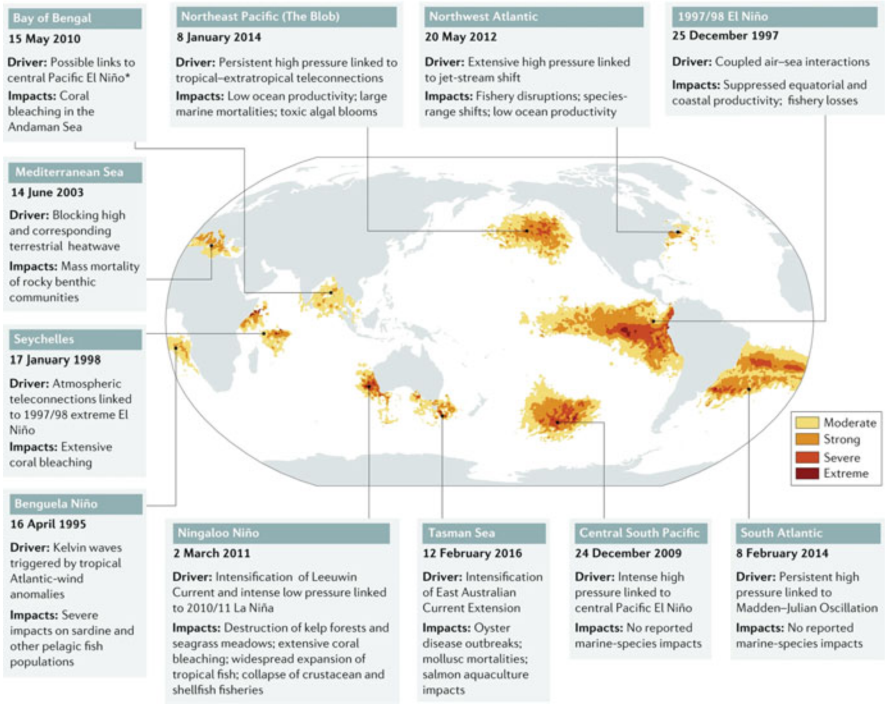
School of Biological Sciences, The University of Western Australia, Perth, WA, Australia
e-mail: Thomas.wernberg@uwa.edu.au

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_12

12.1 Marine Heatwaves and Global Kelp Forests

Discrete periods of unusually warm conditions occur in the ocean as well as on land (Hobday et al. 2016; Perkins and Alexander 2012). The occurrence of these ‘marine heatwaves’ (MHWs) has not been widely appreciated until recently, when several prominent events made headlines globally (Frölicher and Laufkötter 2018; Hobday et al. 2018). For example, the largest marine heatwave recorded in the past ~40 years of satellite-derived global sea surface temperatures occurred in 2015/16 in the northeast Pacific, where it became widely known as ‘The Blob’ (Fig. 12.1). At its peak extent on 15 February 2015 The Blob covered 11.8 Mkm^2, reaching a maximum intensity of 6.7 °C above the long-term mean on 28 June 2015 (Holbrook et al. 2019). While The Blob was the largest and longest marine heatwave recorded so far, it was not the most intense. Many smaller and shorter events have reached higher maximum intensities, with the 2012 marine heatwave in the northeast Atlantic reaching a whopping 10.3 °C above the long-term mean on 23 March 2012 (Holbrook et al. 2019). It is, however, not the absolute extent, duration or intensity which determines how anomalous or severe a marine heatwave is, but instead the relative deviation from the temperature variation normally experienced at a location (Hobday et al. 2018).



Bay of Bengal
15 May 2010
Driver: Possible links to central Pacific El Niño*
Impacts: Coral bleaching in the Andaman Sea

Northeast Pacific (The Blob)
8 January 2014
Driver: Persistent high pressure linked to tropical–extratropical teleconnections
Impacts: Low ocean productivity; large marine mortalities; toxic algal blooms

Northwest Atlantic
20 May 2012
Driver: Extensive high pressure linked to jet-stream shift
Impacts: Fishery disruptions; species-range shifts; low ocean productivity

1997/98 El Niño
25 December 1997
Driver: Coupled air–sea interactions
Impacts: Suppressed equatorial and coastal productivity; fishery losses

Mediterranean Sea
14 June 2003
Driver: Blocking high and corresponding terrestrial heatwave
Impacts: Mass mortality of rocky benthic communities

Seychelles
17 January 1998
Driver: Atmospheric teleconnections linked to 1997/98 extreme El Niño
Impacts: Extensive coral bleaching

Benguela Niño
16 April 1995
Driver: Kelvin waves triggered by tropical Atlantic-wind anomalies
Impacts: Severe impacts on sardine and other pelagic fish populations

Ningaloo Niño
2 March 2011
Driver: Intensification of Leeuwin Current and intense low pressure linked to 2010/11 La Niña
Impacts: Destruction of kelp forests and seagrass meadows; extensive coral bleaching; widespread expansion of tropical fish; collapse of crustacean and shellfish fisheries

Tasman Sea
12 February 2016
Driver: Intensification of East Australian Current Extension
Impacts: Oyster disease outbreaks; mollusc mortalities; salmon aquaculture impacts

Central South Pacific
24 December 2009
Driver: Intense high pressure linked to central Pacific El Niño
Impacts: No reported marine-species impacts

South Atlantic
8 February 2014
Driver: Persistent high pressure linked to Madden–Julian Oscillation
Impacts: No reported marine-species impacts

Fig. 12.1 Prominent marine heatwaves globally. The largest marine heatwave ever recorded was ‘The Blob’, which covered large parts of the Pacific Ocean in 2015/16 (from Holbrook et al. 2020)

Marine heatwaves originate from the interactions between a very broad range of atmospheric and oceanographic processes that cause variation in ocean temperature, at scales up to thousands of kilometers over weeks to decades and centuries (Holbrook et al. 2019). While they are natural phenomena, their increasing frequency, duration and intensity are a consequence of increasing ocean temperatures due to ongoing anthropogenic climate change (Frölicher et al. 2018; Oliver et al. 2017, 2018, 2019). Critically, in less than a decade, marine heatwaves have emerged as one of the most pervasive and acute changes to the global ocean (Hobday et al. 2018; Holbrook et al. 2019; Oliver et al. 2018). Over the first 30 years of satellite recorded sea surface temperatures there was a 95% increase in coasts experiencing 'extremely hot' conditions globally (Lima and Wethey 2012) and on average the number of days with marine heatwave conditions in the global ocean has increased by >50% over the last century, with an accelerating frequency since ~1980 (Oliver et al. 2018). This implies that, on average, a location which at the beginning of the previous century experienced 30 marine heatwave days per year now experiences 45 days of unusually warm conditions. This represents a substantial increase in the thermal pressure on marine species. Alarmingly, this thermal forcing has been unequivocally linked to widespread, often catastrophic, impacts on marine ecosystems and the broad range of ecosystem services humans derive from the oceans, including fisheries and aquaculture, recreational activities and biodiversity conservation (Smale et al. 2019). For example, the 2003 Mediterranean MHW caused mass mortality of at least 25 invertebrate species across thousands of kilometres (Garrabou et al. 2009) and The Blob resulted in low open ocean productivity, deaths of thousands of sea lions and sea birds and an unprecedented toxic algal bloom which impacted the shellfish industry (Gentemann et al. 2017).

Kelp forests are highly productive marine ecosystems dominated by large seaweeds. They occur at all latitudes but are particularly prominent in temperate to polar environments where they support vast biodiversity and valuable ecological services such as important recreational and commercial fisheries (Wernberg et al. 2019b). Kelp forests have been in decline globally over the past 50 years (Krumhansl et al. 2016; Wernberg et al. 2019b) linked in many cases to warming and marine heatwaves (Filbee-Dexter and Wernberg 2018). In Australia, kelp forests (*Ecklonia radiata*) are found throughout the Great Southern Reef across the southern coastline of the continent (Bennett et al. 2016). In recent decades, kelp forests have shown local to regional declines in almost every part of this unique large-scale ecosystem due to a range of processes including eutrophication, over grazing, warming and marine heatwaves (Wernberg et al. 2019a). One of the most conspicuous cases occurred in the Austral summer of 2010/11 when the west coast of Australia was hit by an extreme marine heatwave. This chapter synthesises the effects of the 2011 marine heatwave on kelp forests and temperate reefs in Western Australia, and discusses the outlook for these important ecosystems under future climate change. Management strategies to address habitat collapse and recovery are also discussed.

12.2 The 2011 Western Australian Marine Heatwave

In late 2010 and early 2011 (austral summer), a severe warming event developed along the west coast of Australia (Fig. 12.2). The event, which became known as the 'Ningaloo Niño' (Feng et al. 2013), developed into a category IV extreme marine heatwave which, at its peak, covered an area of 950,000 km^2 and had a maximum intensity of 6.8 °C above the long-term climatological mean (Holbrook et al. 2019). The intensity of the event substantially exceeded all previous temperature records seen in 140 years of measurements from the Hadley Centre and 215 years of local coral cores (Wernberg et al. 2013, 2016a; Zinke et al. 2014). The MHW lasted 66 days, and with 24% of the time as a category III (severe) or IV (extreme) event, it has been one of the worst marine heatwaves recorded globally (Hobday et al. 2018). The subsequent two summers were also exceptionally warm, with maximum intensities of 5.1 °C and 4.0 °C above the climatological mean, respectively (Holbrook et al. 2019).

The marine heatwave was driven by a combination of oceanographic and atmospheric conditions superimposed onto a trend of increasing ocean temperatures over the past four decades (Fig. 12.3). Unusually strong La Niña conditions caused an

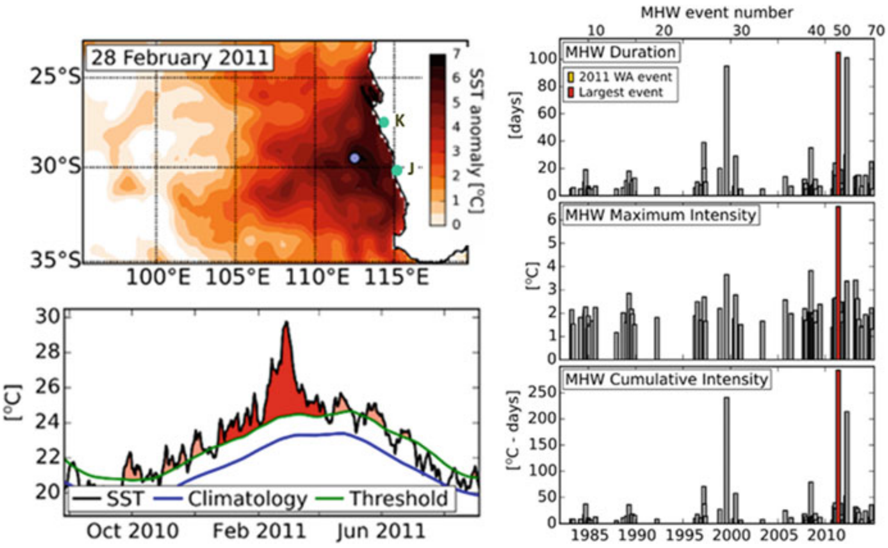


Fig. 12.2 The Western Australian 2011 Marine Heatwave. Sea surface temperature (SST) anomaly on the peak day of the marine heatwave (MHW). The blue dot shows the location from which 1/4° resolution time series of SST were extracted from NOAA OISST for the detection of MHWs. The green dots show Kalbarri (K) and Jurien Bay (J) where biolocal impacts were observed. SST climatology (blue), 90th percentile MHW threshold (green) and SST time series (black) for the MHW, where the red filled area indicates the period associated with the main MHW, while shaded orange indicates other MHWs identified over the year. The duration (D), maximum intensity (Imax) and cumulative intensity (Icum) of each MHW detected in the time series (1982–2013), with every tenth event identified on the upper *x*-axis (from Hobday et al. 2016)

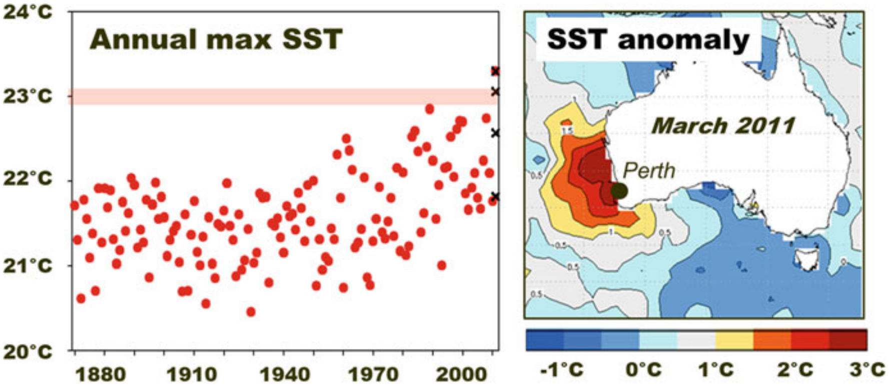


Fig. 12.3 Sea surface temperatures (SST) off Perth from 1970 to 2011 (left) and SST anomalies around Australia in March 2011 where the marine heatwave peaked (right). The red band indicates the temperature threshold above which kelp (*Ecklonia radiata*) is unable to maintain net growth (Wernberg et al. 2019a). Black X's show monthly maximum temperatures during the 4 months covering the MHW (Dec 2010, Jan, Feb, Mar 2011). Temperatures are HadISST1 data (see Wernberg et al. 2013 for further detail)

increased flow of the Leeuwin Current, pushing warm tropical water farther south along the west coast than normal. At the same time calm winds facilitated an anomalously high transfer of heat from the air to the sea (Feng et al. 2013; Holbrook et al. 2019). The extreme temperatures engulfed the entire southwestern corner of the continent (Fig. 12.3), where terrestrial ecosystems also experienced heatwave conditions that had detrimental effects on key biota such as eucalypt trees (*Eucalyptus marginata*) and threatened black cockatoos (*Calyptorhynchus latirostris*) (Ruthrof et al. 2018). While there have been no formal assessments of the economic consequences of this linked terrestrial-marine extreme event, the socio-economic costs must have been severe across the region considering the impacts on biodiversity, forests, crops and fisheries. For example, several valuable west coast fisheries collapsed, including the reef-associated fisheries for Roe's abalone (*Haliotis roei*) and western rock lobster (*Panulirus Cygnus*) in Kalbarri north of Perth, neither of which have shown signs of recovery (Caputi et al. 2019).

12.3 Kelp Forests: The Biological Engine of the Great Southern Reef

The coastal epicentre of the MHW coincided with the northwestern distribution limit of Australia's Great Southern Reef, an interconnected system of temperate rocky reefs dominated by kelp forests (Bennett et al. 2016)—an ecosystem typically associated with cool temperate and polar latitudes (Wernberg et al. 2019b). Up to 16 times more productive than Australia's most productive wheat fields (Bennett et al. 2016) these kelp forests are the biological engine of the Great Southern Reef, one of the most unique temperate marine ecosystems in the world: across at least 7 major phyla of seaweeds, invertebrates and reef fishes, between 30 and 80% of species are endemic to Australia (Bennett et al. 2016, Fig. 12.4).

Before the MHW, common kelp (*Ecklonia radiata*, Wernberg et al. 2019a) and habitat-forming fucoids such as strapweed (*Scytothalia dorycarpa*, Coleman and Wernberg 2017) were abundant on most rocky reefs between 0 and 40 m depth along ~800 km coastline from The Capes (34°S) to Kalbarri (28°S) (Marzinelli et al. 2015; Wernberg et al. 2011b). In fact, these cool-water kelp forests covered 70–90% of most reefs irrespective of latitude (Wernberg et al. 2011b; Figs. 12.5 and 12.6, Wernberg et al. 2010) and reef communities from the Capes to Kalbarri were almost identical, as they were dominated by the same cool-water species (Wernberg et al. 2016a).

The unique marine ecosystems along the west coast responded immediately to the marine heatwave. Warm-water charismatic megafauna such as tiger and whale sharks were observed hundreds of kilometres farther south than normal, there were fish kills, starving sea birds, mass mortality of abalone, unprecedented coral bleaching, and fouling and mortality of seagrasses and seaweeds (Pearce et al. 2011). While many of these initial observations were qualitative anecdotes, their collective represents a strong testimony of how all levels of the ecosystem were affected, from macrophyte primary producers to vertebrate apex predators.

12.4 Kelp Forests Transformed to Turf Reefs

The most extensive and conspicuous impact of the MHW was the loss of kelp forests across extensive tracts of rocky reef and their replacement by algal turfs, small filamentous and foliose seaweeds tightly packed with sediments (Figs. 12.5 and 12.6). The impacts were greatest at the warm distribution limit of temperate reefs, where there was a ~100 km range contraction of both common kelp (Wernberg et al. 2016a) and strapweed (Smale and Wernberg 2013) from their northern distribution limits in Kalbarri and Jurien Bay, respectively. Overall, an estimated 43% of common kelp forests between the Capes and Kalbarri were lost as a consequence of the 2011 MHW (Wernberg et al. 2016a).

At the same time, there was a decline in cool-water species and expansion of warm-water species including seaweeds, invertebrates and many reef fishes, resulting in an overall ‘tropicalisation’ of the reef communities (Bennett et al. 2015; Lenanton et al. 2017; Richards et al. 2016; Smale et al. 2017; Wernberg et al. 2013, 2016a). Specifically, at many sites kelp, turban snails (*Lunella torquata*) and purple urchins (*Heliocidaris erythrogramma*), which are characteristic of cooler waters, declined or disappeared while warm-water seaweeds including *Sargassum*, *Lobophora* and *Padina* increased substantially in cover and biomass (Smale and Wernberg 2013; Wernberg et al. 2016a). A 2–3-fold increase in the occurrence of small (juvenile) coral colonies was also observed (Tuckett et al. 2017; Wernberg et al. 2016a) along with an increase in western long-spined urchins (*Centrostephanus tenuispinus*) (Smale et al. 2017) and range-extensions of many

Fig. 12.4 Unique fauna and flora of the Great Southern Reef. From top left to bottom right: Australian sea lion (*Neophoca cinerea*), harlequin fish (*Othos dentex*), weedy seadragon (*Phyllopteryx taeniolatus*), biscuit star (*Pentagonaster duebeni*), western long-spined urchin (*Centrostephanus tenuispinus*), Jourdan's turban (*Turbo jourdani*), western rock lobster (*Panulirus cygnus*), strapweed (*Scytothalia dorycarpa*), Neptunes' shield (*Rhodopeltis borealis*), red sausage weed (*Gloiosaccion brownii*) and green scalpel weed (*Caulerpa scalpelliformis*) (all photos T. Wernberg)

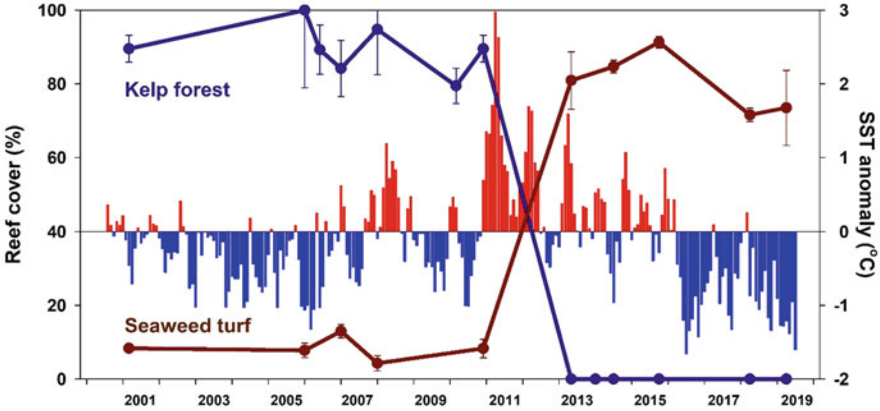


Fig. 12.5 Collapse of kelp forests and the rise of turfs in Kalbarri, Western Australia. Prior to the 2011 marine heatwave (big red spike) kelp forests (dark blue line) covered 80–100% of reef surfaces (Fig. 12.6, left). After the MHW kelp forests were completely gone and the reefs were quickly covered in 70–90% turf algae (dark red line) (Fig. 12.6, right). The blue and red bars show satellite-derived (OISST) monthly mean sea surface temperature anomalies relative to the long-term climatological baseline (1982–2018) (Wernberg et al. 2016a)

other invertebrates including sponges, crustaceans and echinoderms (Richards et al. 2016).

Reef fishes showed particularly conspicuous changes after the MHW (Bennett et al. 2015; Parker et al. 2019; Richards et al. 2016). At the northern end of temperate reefs around Port Gregory and Kalbarri, cool-water species such as herring cale (*Olisthops cyanomelas*), and dusky morwong (*Dactylophora nigricans*) declined and warm-water species increased (Bennett et al. 2015). Overall, more new species of reef fishes were observed than existing species disappeared, resulting in an overall increase in species richness. Increases were seen across most functional groups of reef fishes. More specifically, the influx of new fish species resulted in higher abundances of herbivorous fish, higher grazing activity and an increase in the functional diversity of these fish (Bennett et al. 2015): before the MHW there were relatively few herbivorous fishes and they were dominated by 'browsers' (fish that bite at the top of the seaweeds, such as sea chubs [*Kyphosus* spp.]). After the MHW 'grazers' (fish that bite small algae and mixed turf and sediments at the bottom, such as parrot fish [*Scarus* spp.]) became very abundant. The region experienced a 400% increase in abundance of fish herbivores with consumption rates comparable to those seen in healthy coral reefs (Bennett et al. 2015). At the same time, Rottnest Island 20 km off the coast of Perth experienced record levels of recruitment of tropical fish (Pearce et al. 2011).

Before the MHW, rabbitfish (*Siganus fuscescens*), a common fish in subtropical and tropical reefs that both browses and grazes, was rarely seen south of Kalbarri and had not been recorded in fish transects from Perth (Zarco-Perello et al. 2017). However, after the MHW, rabbitfish established persistent populations at many reefs as far south as Perth (~32°S) (Lenanton et al. 2017; Zarco-Perello et al.

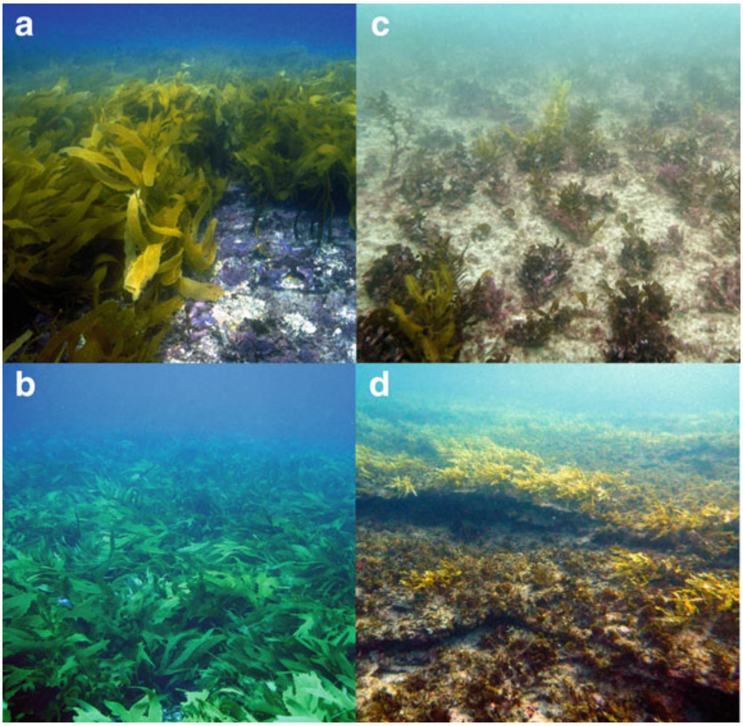


Fig. 12.6 Before the 2011 MHW reefs in Kalbarri (**a**: 2005) were covered by a dense canopy of kelp (*Ecklonia radiata*) with an understorey comprised of pink crusts of coralline algae and small shade tolerant foliose red algae typical of cool water (e.g. *Rhodopeltis*, *Rhodymenia* and *Pterocladia*). On most reefs, the cover was extensive, and indistinguishable from other locations (Wernberg et al. 2010) (**b**: Hamelin Bay, ca. 800km to the south). After the MHW kelps were gone and the reef surface was covered by sediment-packed turf algae and small foliose brown algae typical of warmer environments (e.g. *Lobophora*, *Padina* and *Sargassum*; **c**: 2013, **d**: 2017) (photos: T. Wernberg)

2017), where they today are the most abundant herbivores with negative impact on kelp (Fig. 12.7, Zarco-Perello et al. 2017). A small commercial fishery for rabbitfish, which is still in existence, even opened in Cockburn Sound (Perth) (Lenanton et al. 2017). Rabbitfish has also expanded down the east coast of Australia, where their grazing over a 10-year period contributed to the disappearance of kelp forests at sites around the Solitary Islands (~30°S) (Vergés et al. 2016).

Although the extreme water temperatures of the MHW have subsided, the turf reefs between Port Gregory and Kalbarri have persisted since the extreme event (Fig. 12.5). The few kelp individuals that have been observed have had very poor survivorship and >9 yeras after the MHW there are no signs of recovery at the reefs observed for almost 20 years (cf. Fig. 12.5) at the northern extent of the historical distribution of kelp forests (T. Wernberg, personal observation, 2020). It is likely that turf algae blocking kelp recruits and the increase in grazing rates by herbivorous

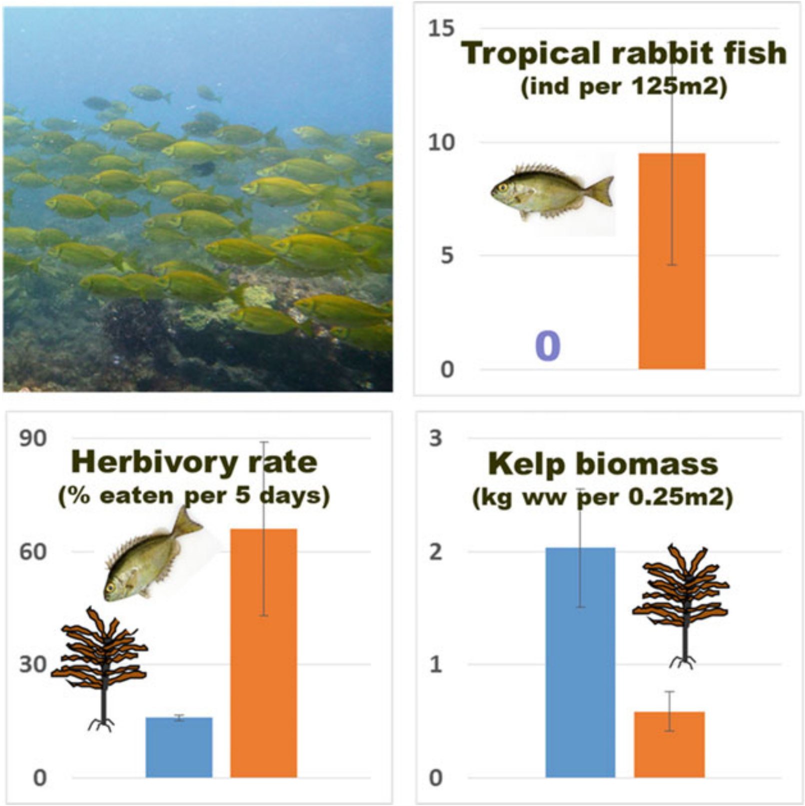


Fig. 12.7 Before the MHW rabbitfish (top left, photo: T. Wernberg) were only rarely seen south of Kalbarri. After the MHW they became common, even dominant, at many reefs as far south as Perth (bar graphs, blue before, orange after the MHW, error bars: standard error), where they continue to persist and negatively affect local kelp forests (data from Zarco-Perello et al. 2017)

fishes together present major inhibitory feedback mechanisms that now prevent the recovery of kelp forests, and instead promote and maintain domination by turfs (Fig. 12.8, Bennett et al. 2015; Filbee-Dexter and Wernberg 2018; Zarco-Perello et al. 2017).

12.5 Thresholds of Kelp Forest Collapse

Kelps are generally considered cool-water species (Wernberg et al. 2019b). This is also true for *Ecklonia radiata* even if it is one of the most warm-tolerant laminarian kelp species (Wernberg et al. 2019a). Physiological studies have shown that net photosynthesis of *E. radiata* increases with temperature until ~24 °C after which it drops rapidly, as a consequence of collapsing photosynthesis and increasing

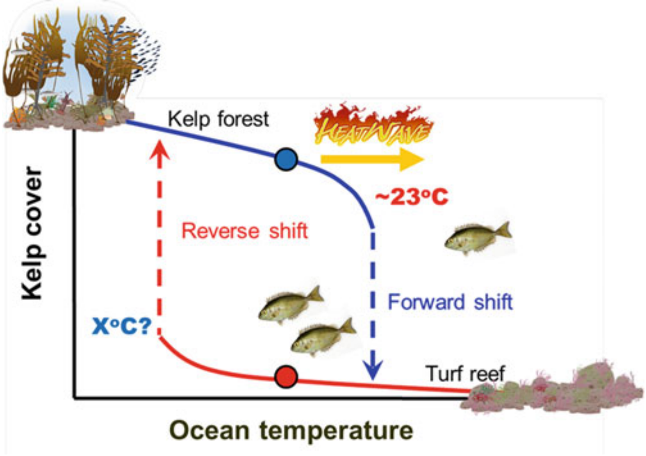


Fig. 12.8 Schematic summarising the heatwave driven regime shift from kelp forests to turf reefs. The heatwave pushed kelps beyond their temperature tolerance, causing their collapse and allowing the expansion of turf algae (forward shift, blue). At the same time there was an influx of warm-water fish herbivores. Subsequently, even after temperatures returned to pre-heatwave conditions or cooler, the kelp forest has not recovered, indicating hysteresis in the system. It is unknown how much cooler it needs to be, or what other perturbations might be required, before the system can revert back to kelp (reverse shift, red)

respiration at higher temperatures °C (Smale and Wernberg 2013; Stæhr and Wernberg 2009; Wernberg et al. 2016b).

Extensive measurements of growth and erosion have shown a threshold of ~23 °C above which *E. radiata* is no longer able to maintain positive net growth (i.e. above 23 °C it erodes and disintegrates faster than it grows) (Wernberg et al. 2019a). This threshold for persistence corresponds to the physiological threshold for maximum net photosynthesis, and observations of reduced growth and survivorship at the Houtman Abrolhos Islands (~28°S) near the warm range limit of kelp on the west coast (Hatcher et al. 1987), where temperatures often reach 24 °C. It is further consistent with the observed negative relationship between growth and summer temperatures >21 °C in Perth (~32 °S) (Bearham et al. 2013). Importantly, ocean temperatures exceeded the ~23 °C threshold for at least 2 of the 4 months the MHW lasted (Fig. 12.3, Wernberg et al. 2018).

The ultimate cause of the decline and local extirpation of habitat-forming kelps was likely prolonged extreme temperatures. However, the effect was likely exacerbated by the underlying patterns of genetic diversity along the coastline. Specifically, the southern (cool) kelp forests have higher levels of genetic diversity than the northern (warm) kelp forests (Wernberg et al. 2018). Indeed, canopy clearing experiments at different latitudes prior to the MHW suggested that northern (warm) locations had lower resilience to disturbance than southern (warm) locations (Wernberg et al. 2010).

The MHW affected the entire reef community and likely contributed to all species responses. However, warming per se might not have been the only contributing factor for many species. For example, the MHW was in part caused by an exceptionally strong poleward flow of the warm Leeuwin Current (Feng et al. 2013), increasing the delivery of warm-water fish recruits to temperate latitudes (Hutchins and Pearce 1994; Pearce et al. 2011). Moreover, many tropical fish (Beck et al. 2017) and coral (Tuckett et al. 2017) require open reef patches to recruit, and might have been restricted more by the dense kelp canopy prior to the MHW than low temperature per se. Their expansion after the MHW could therefore, at least partly, have been driven by competitive release with the disappearance of the canopy, rather than temporarily elevated temperatures.

In summary, the cumulative evidence strongly suggests that, the ultimate cause of the collapse of kelp forests, and regime shift to turf reefs, was extreme temperatures exceeding the physiological threshold for net growth (~23 °C) of the main habitat-forming kelps for a prolonged period (8–10 weeks) (Fig. 12.8). Where the kelp disappeared, competitive release allowed turf algae to expand. At the same time an unusually high influx of warm-water herbivores such as rabbitfish (*Siganus fuscescens*), sea chub (*Kyphosus* spp.) and parrot fish (*Scarus* spp.) caused a substantial increase in grazing pressure. The expansive turf and increased grazing now effectively counteract any potential recruitment and recovery of the kelp forest. Temperatures have long returned to pre-heatwave conditions (Fig. 12.5), indeed the past couple of winters have been some of the coldest on record (e.g. Tuckett and Wernberg 2018), yet the system has shown considerable hysteresis and has not yet returned to kelp forests. It is unknown how much cooler it needs to be, or what other perturbations to the fish or turf communities might be required, before the system can revert back to kelp.

12.6 The Future of Kelp Forests in Western Australia

Current projections for global warming indicate that even if carbon emissions were to cease altogether, the planet is locked into at least another +0.5 °C increase in mean temperature in addition to the +1 °C above pre-industrial levels already recorded (Mauritsen and Pincus 2017). Realistically, however, the increase will be much greater over the coming decades as carbon emissions have been tracking scenarios projecting as much as +2.7 °C or more from today by 2100 (Peters et al. 2012). The +1 °C already recorded has been associated with a 50% increase in global marine heatwaves (Oliver et al. 2018). While marine heatwaves are also natural phenomena, modelling studies have shown anthropogenic climate change to cause a substantial increase in their severity and likelihood of occurrence (Frölicher et al. 2018; Oliver et al. 2017). Consequently, projections predict severe increases in both the intensity and duration of marine heatwaves as the global oceans continue to warm (Oliver et al. 2019). Marine heatwaves are, therefore, now recognised as a major force that will impact marine ecosystems and associated ecosystem services into the future (Frölicher et al. 2018; Smale et al. 2019). If climate change keeps tracking the pessimistic trajectory of warming, the west coast of Western Australia could reach permanent MHW conditions relative to current baselines sometime between 2040 and 2060 (Oliver et al. 2019). Like the 2011 event, future MHWs in southwestern Australia will likely be associated with variations in the southward flow of the Leeuwin Current, which in turn is strongly influenced by the ENSO cycle and La Niña conditions in particular (Feng et al. 2013). Given projections of a doubling in the frequency of extreme La Niña events in the coming decades (Cai et al. 2015) a near future of more severe MHWs seems inescapable for the southwest.

Species distribution models for kelp and other large seaweed in Australia project substantial range contractions by the year 2100 (Martínez et al. 2018). Even under the most aggressive, likely unrealistic carbon mitigation scenario (RCP2.6, van Vuuren et al. 2011), most of the modelled species were projected to lose 50–80% of their current distribution (Martínez et al. 2018). More specifically, in Western Australia, currently dominant species like strapweed (*Scytothalia dorycarpa*) and kelp (*Ecklonia radiata*) are projected to disappear from the west coast to be confined to small pockets on the south coast (Martínez et al. 2018). Importantly, these projections are based on gradual increases in mean ocean temperatures and are therefore likely to be highly conservative estimates because they do not incorporate the compounding impacts of extreme evens such as MHWs, biological species interactions such as changes in herbivory or additional stressors from non-climate related processes including eutrophication, pollution and fishing (Connell et al. 2008; Ling et al. 2009; Vergés et al. 2014; Wernberg et al. 2011a). Projections and recent case-studies for kelp forests in New Zealand (Thomsen et al. 2019), Japan (Takao et al. 2015; Tanaka et al. 2012), Europe (Assis et al. 2017; Filbee-Dexter et al. 2020) and North America (Wilson et al. 2019) paint a similarly bleak future for many kelp forests globally.

To date there have been few signs that the northern kelp forests in Western Australia are recovering from the impacts of the 2011 MHW and the shift to turf and other seaweeds could be long-term persistent or even irreversible. The decline in kelp and transitions to turf seen in Western Australia and across Australia (Coleman and Wernberg 2017; Wernberg et al. 2019a) are part of a broader picture of declining kelp forests and expanding turf reefs globally (Filbee-Dexter and Wernberg 2018; Krumhansl et al. 2016; Wernberg et al. 2019b). Worryingly, up to 61% of the world's kelp forests have been in decline over the past five decades (Krumhansl et al. 2016; Wernberg et al. 2019b), and many regionally different direct and indirect processes are causing these declines, including harvesting, fishing, herbivory, eutrophication, warming and heatwaves (Filbee-Dexter and Wernberg 2018; Krumhansl et al. 2016). While it is clear that many different drivers can lead to the same outcome—loss of kelp forests—the emerging picture is, that warming and marine heatwaves have been implicated, in one way or another, in most cases although baseline data rarely are sufficiently robust to tease apart their relative contribution (Filbee-Dexter and Wernberg 2018). However, where reefs have transitioned from kelp forests to turf reefs, there have been no reports of turf reefs recovering back to past kelp forests (Filbee-Dexter and Wernberg 2018). In light of this, and the overwhelmingly consistent projections of environmental changes that will be increasingly challenging to kelp forests, it is difficult to be optimistic for the long-term future of kelp forests in Western Australia.

12.7 Help the Kelp: Something Can Be Done

It is easy to get mesmerised and paralysed by the magnitude and complexity of the problems associated with climate change and increasing MHWs. However, several things can and should be done to mitigate and minimise the ecological and socio-economic consequences of marine heatwaves and changing ecosystems (e.g. Vergés et al. 2019).

First, treat the root cause: ocean warming caused by anthropogenic emissions of greenhouse gasses. It is critical to curb carbon emissions as this is the only safe way to limit future warming (Peters et al. 2012). This will be an important investment for future generations, as lag effects from CO_2 already emitted will result in significant warming over the coming century regardless of present-day actions (Mauritsen and Pincus 2017).

Second, because the oceans will continue to warm over the coming century, it will be necessary to invest in boosting the resilience of kelp forests and other marine ecosystems (Wernberg et al. 2019b; Coleman et al. 2020). This implies a shift in research focus from cataloguing calamities to providing solutions based around a range of options. Passive approaches include catchment management, marine protected areas and fishing restrictions all of which aim to increase the resistance of marine ecosystems through limiting their exposure to multiple stressors (e.g. eutrophication and pollution), that compound the impacts of warming (Strain et al. 2014; Wernberg et al. 2011a), or protects natural ecological processes (e.g. predation, herbivory) that confer ecosystem resistance to change (Bates et al. 2014; Ghedini et al. 2015). However, passive approaches can be slow or inefficient (e.g. Bruno et al. 2019), and where changes have gone too far or are happening too fast, active intervention could be required. Active interventions seek to maintain or re-establish ecosystems (or key ecosystem services) through direct manipulation ranging from habitat rehabilitation and restoration through translocation (assisted migration), species replacements (functional redundancy) and assisted evolution of strong genotypes to gene editing and fully synthetic biology (reviewed in Coleman and Goold 2019; Layton et al. 2019; Vergés et al. 2019; Wernberg et al. 2019b; Coleman et al. 2020). While several of these options currently are ethically contentious (e.g. gene editing), it is nevertheless important to do the science and have the initial conversations that will ultimately assist the best decisions if and when these more extreme measures become the only option to ensure long-term survival of kelp forests (Filbee-Dexter and Smajdor 2019). On the more practical side of things, both new technology and old-fashioned enginuity can be used to improve the success of local interventions. For example, managers could use shape-recognising underwater robots to seek out and kill kelp eating sea urchins (Layton et al. 2019) or the simple yet efficient idea of seeding kelp onto gravel, which can then be scattered across large areas dominated by turf, at low cost (Fredriksen et al. 2020).

Third, acknowledging that some changes are inevitable and focusing attention on understanding what future marine ecosystems might look like can help identify and take advantage of new opportunities might arise. More specifically, in many cases it will not be possible (or feasible) to halt or revert ecosystem change (Johnson et al. 2017). In this context, ocean warming and marine heatwaves will have ecological winners as well as losers, and new ecosystem services will grow where current ones are lost (Vergés et al. 2019). For example, while the 2011 MHW led to declines and collapses in several west coast fisheries (Caputi et al. 2019) it also opened the opportunity for a small new fishery for rabbitfish (Lenanton et al. 2017).

Climate change, and with it the exposure to extreme events including marine heatwaves, will only go in one direction for the foreseeable future. Indeed, one of the few certainties at the moment is that the reefs of tomorrow will be substantially different from the reefs of today, and that marine heatwaves will play a key role in shaping the structure and function of our future coastal ecosystems.

Acknowledgements The research summarised in this book chapter was undertaken with support from the Australian Research Council (DP0555929, FT110100174, DP160100114, DP170100023) and the Hermon Slade Foundation (HSF13/13). I am grateful to the marine heatwaves working group (http://www.marineheatwaves.org/) for inspiration and discussions and Mads Thomsen, Karen Filbee-Dexter, Pep Canadell and Rob Jackson for comments on various versions of this manuscript.

References

Assis J, Berecibar E, Claro B, Alberto F, Reed D, Raimondi P, Serrão EA (2017) Major shifts at the range edge of marine forests: the combined effects of climate changes and limited dispersal. Sci Rep 7:44348. https://doi.org/10.1038/srep44348

Bates AE, Barrett NS, Stuart-Smith RD, Holbrook NJ, Thompson PA, Edgar GJ (2014) Resilience and signatures of tropicalization in protected reef fish communities. Nat Clim Change 4:62–67. https://doi.org/10.1038/nclimate2062

Bearham D, Vanderklift M, Gunson J (2013) Temperature and light explain spatial variation in growth and productivity of the kelp Ecklonia radiata. Mar Ecol Prog Ser 476:59–70. https://doi.org/10.3354/meps10148

Beck HJ, Feary DA, Nakamura Y, Booth DJ (2017) Temperate macroalgae impacts tropical fish recruitment at forefronts of range expansion. Coral Reefs 36(2):639–651

Bennett S, Wernberg T, Harvey ES, Santana-Garcon J, Saunders B (2015) Tropical herbivores provide resilience to a climate mediated phase-shift on temperate reefs. Ecol Lett 18:714–723. https://doi.org/10.1111/ele.12450

Bennett S, Wernberg T, Connell SD, Hobday AJ, Johnson CR, Poloczanska ES (2016) The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. Mar Freshw Res 67(1):47–56. https://doi.org/10.1071/MF15232

Bruno JF, Côté IM, Toth LT (2019) Climate change, coral loss, and the curious case of the parrotfish paradigm: why don't marine protected areas improve reef resilience? Ann Rev Mar Sci 11(1):307–334. https://doi.org/10.1146/annurev-marine-010318-095300

Cai W, Wang G, Santoso A, McPhaden MJ, Wu L, Jin F-F et al (2015) Increased frequency of extreme La Nina events under greenhouse warming. Nat Clim Change 5:132–137. https://doi.org/10.1038/nclimate2492

Caputi N, Kangas M, Chandrapavan A, Hart A, Feng M, Marin M, Lestang Sd (2019) Factors affecting the recovery of invertebrate stocks from the 2011 Western Australian extreme marine heatwave. Front Mar Sci 6(484). https://doi.org/10.3389/fmars.2019.00484

Coleman MA, Goold HD (2019) Harnessing synthetic biology for kelp forest conservation. J Phycol 55:745–751. https://doi.org/10.1111/jpy.12888

Coleman MA, Wernberg T (2017) Forgotten underwater forests: the key role of fucoids on Australian temperate reefs. Ecol Evol 7(20):8406–8418. https://doi.org/10.1002/ece3.3279

Coleman, M. A., G. Wood, K. Filbee-Dexter, A. J. P. Minne, H. D. Goold, A. Vergés, E. M. Marzinelli, P. D. Steinberg, and T. Wernberg. 2020. Restore or Redefine: Future Trajectories for Restoration. Frontiers in Marine Science 7.

Connell SD, Russell BD, Turner DJ, Shepherd SA, Kildea T, Miller D et al (2008) Recovering a lost baseline: missing kelp forests from a metropolitan coast. Mar Ecol Prog Ser 360:63–72

Feng M, McPhaden MJ, Xie S-P, Hafner J (2013) La Niña forces unprecedented Leeuwin Current warming in 2011. Sci Rep 3:1277. https://doi.org/10.1038/srep01277

Filbee-Dexter K, Smajdor A (2019) Ethics of assisted evolution in marine conservation. Front Mar Sci 6(20). https://doi.org/10.3389/fmars.2019.00020

Filbee-Dexter K, Wernberg T (2018) Rise of turfs: a new battlefront for globally declining kelp forests. BioScience 68(2):64–76. https://doi.org/10.1093/biosci/bix147

Filbee-Dexter K, Wernberg T, Grace SP, Thormar J, Fredriksen S, Narvaez CN et al (2020) Marine heatwaves and the collapse of marginal North Atlantic kelp forests. Sci Rep. https://doi.org/10.1038/s41598-020-70273-x

Fredriksen S, Filbee-Dexter K, Norderhaug KM, Steen H, Bodvin T, Coleman MA et al (2020) Green gravel: a novel restoration tool to combat kelp forests decline. Sci Rep 10:3983. https://doi.org/10.1038/s41598-020-60553-x

Frölicher TL, Laufkötter C (2018) Emerging risks from marine heat waves. Nat Commun 9(1):650. https://doi.org/10.1038/s41467-018-03163-6

Frölicher TL, Fischer EM, Gruber N (2018) Marine heatwaves under global warming. Nature 560 (7718):360–364. https://doi.org/10.1038/s41586-018-0383-9

Garrabou J, Coma R, Bensoussan N, Bally M, ChevaldonnÉ P, Cigliano M et al (2009) Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Glob Chang Biol 15(5):1090–1103. https://doi.org/10.1111/j.1365-2486.2008.01823.x

Gentemann CL, Fewings MR, García-Reyes M (2017) Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. Geophys Res Lett 44(1):312–319. https://doi.org/10.1002/2016gl071039

Ghedini G, Russell BD, Connell SD (2015) Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. Ecol Lett 18(2):182–187. https://doi.org/10.1111/ele.12405

Hatcher BG, Kirkman H, Wood WF (1987) Growth of the kelp *Ecklonia radiata* near the northern limit of its range in Western Australia. Mar Biol 95(1):63–72

Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver ECJ et al (2016) A hierarchical approach to defining marine heatwaves. Prog Oceanogr 141:227–238. https://doi.org/10.1016/j.pocean.2015.12.014

Hobday AJ, Oliver ECJ, Sen Gupta A, Benthuysen JA, Burrows MT, Donat MG et al (2018) Categorizing and naming marine heatwaves. Oceanography 31(2):62–173. https://doi.org/10.5670/oceanog.2018.205

Holbrook NJ, Scannell HA, Sen Gupta A, Benthuysen JA, Feng M, Oliver ECJ et al (2019) A global assessment of marine heatwaves and their drivers. Nat Commun 10(1):2624. https://doi.org/10.1038/s41467-019-10206-z

Holbrook NJ, Sen Gupta A, Oliver ECJ, Hobday AJ, Benthuysen JA, Scannell HA et al (2020) Keeping pace with marine heatwaves. Nat Rev Earth Environ 1(9):482–493. https://doi.org/10.1038/s43017-020-0068-4

Hutchins JB, Pearce AF (1994) Influence of the Leeuwin current on recruitment of tropical Reef fishes at Rottnest Island, Western Australia. Bull Mar Sci 54(1):245–255

Johnson CR, Chabot RH, Marzloff MP, Wotherspoon S (2017) Knowing when (not) to attempt ecological restoration. Restor Ecol 25(1):140–147. https://doi.org/10.1111/rec.12413

Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC et al (2016) Global patterns of kelp forest change over the past half-century. Proc Natl Acad Sci USA 113 (48):13785–13790. https://doi.org/10.1073/pnas.1606102113

Layton C, Coleman M, Marzinelli E, Steinberg P, Swearer S, Vergés A, et al (2019) Restoring kelp habitat in Australia. In: McLeod IM, Boström-Einarsson L, Johnson CR, Kendrick G, Layton C, Rogers AA, Statton J (eds) The role of restoration in conserving matters of national environmental significance. Report to the National Environmental Science Programme, Marine Biodiversity Hub

Lenanton RCJ, Dowling CE, Smith KA, Fairclough DV, Jackson G (2017) Potential influence of a marine heatwave on range extensions of tropical fishes in the eastern Indian Ocean—Invaluable contributions from amateur observers. Reg Stud Mar Sci 13:19–31. https://doi.org/10.1016/j.rsma.2017.03.005

Lima FP, Wethey DS (2012) Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nat Commun 3:704. https://doi.org/10.1038/ncomms1713

Ling SD, Johnson CR, Frusher SD, Ridgway KR (2009) Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc Natl Acad Sci U S A 106:22341–22345

Martínez B, Radford B, Thomsen MS, Connell SD, Carreño F, Bradshaw CJA et al (2018) Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. Divers Distrib 24(10):1350–1366. https://doi.org/10.1111/ddi.12767

Marzinelli EM, Williams SB, Babcock RC, Barrett NS, Johnson CR, Jordan A et al (2015) Large-scale geographic variation in distribution and abundance of Australian Deep-Water Kelp Forests. PLoS One 10(2):e0118390. https://doi.org/10.1371/journal.pone.0118390

Mauritsen T, Pincus R (2017) Committed warming inferred from observations. Nat Clim Change 7:652. https://doi.org/10.1038/nclimate3357

Oliver ECJ, Benthuysen JA, Bindoff NL, Hobday AJ, Holbrook NJ, Mundy CN, Perkins-Kirkpatrick SE (2017) The unprecedented 2015/16 Tasman Sea marine heatwave. Nat Commun 8:16101. https://doi.org/10.1038/ncomms16101

Oliver ECJ, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV et al (2018) Longer and more frequent marine heatwaves over the past century. Nat Commun 9(1):1324. https://doi.org/10.1038/s41467-018-03732-9

Oliver ECJ, Burrows MT, Donat MG, Gupta AS, Alexander LV, Perkins-Kirkpatrick SE et al (2019) Projected marine heatwaves in the 21st century and the potential for ecological impact. Front Mar Sci. https://doi.org/10.3389/fmars.2019.00734

Parker JRC, Saunders BJ, Bennett S, DiBattista JD, Shalders TC, Harvey ES (2019) Shifts in Labridae geographical distribution along a unique and dynamic coastline. Divers Distrib 25 (11):1787–1799. https://doi.org/10.1111/ddi.12980

Pearce A, Lenanton R, Jackson G, Moore J, Feng M, Gaughan D (2011) The “marine heat wave” off Western Australia during the summer of 2010/11. Fisheries Research Report No. 222. Department of Fisheries, Western Australia. 40pp

Perkins SE, Alexander LV (2012) On the measurement of heat waves. J Clim 26(13):4500–4517. https://doi.org/10.1175/JCLI-D-12-00383.1

Peters GP, Andrew RM, Boden T, Canadell JG, Ciais P, Le Quéré C et al (2012) The challenge to keep global warming below 2 °C. Nat Clim Change 3:4–6. https://doi.org/10.1038/nclimate1783

Richards Z, Kirkendale L, Moore G, Hosie A, Huisman J, Bryce M et al (2016) Marine biodiversity in temperate Western Australia: multi-taxon surveys of minden and roe reefs. Diversity 8(7). https://doi.org/10.3390/d8020007

Ruthrof KX, Breshears DD, Fontaine JB, Froend RH, Matusick G, Kala J et al (2018) Subcontinental heat wave triggers terrestrial and marine, multi-taxa responses. Sci Rep 8(1):13094. https://doi.org/10.1038/s41598-018-31236-5

Smale D, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species. Proc R Soc B 280:20122829

Smale DA, Wernberg T, Vanderklift MA (2017) Regional-scale variability in the response of benthic macroinvertebrate assemblages to a marine heatwave. Mar Ecol Prog Ser 568:17–30. https://doi.org/10.3354/meps12080

Smale DA, Wernberg T, Oliver EJJ, Thomsen MS, Harvey BP, Straub SC et al (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Change 9:306–312. https://doi.org/10.1038/s41558-019-0412-1

Stæhr PA, Wernberg T (2009) Physiological responses of *Ecklonia radiata* (Laminariales) to a latitudinal gradient in ocean temperature. J Phycol 45(1):91–99. https://doi.org/10.1111/j.1529-8817.2008.00635.x

Strain EMA, Thomson RJ, Micheli F, Mancuso FP, Airoldi L (2014) Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. Glob Chang Biol 20(11):3300–3312. https://doi.org/10.1111/gcb.12619

Takao S, Kumagai NH, Yamano H, Fujii M, Yamanaka Y (2015) Projecting the impacts of rising seawater temperatures on the distribution of seaweeds around Japan under multiple climate change scenarios. Ecol Evol 5(1):213–223. https://doi.org/10.1002/ece3.1358

Tanaka K, Taino S, Haraguchi H, Prendergast G, Hiraoka M (2012) Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. Ecol Evol 2 (11):2854–2865. https://doi.org/10.1002/ece3.391

Thomsen MS, Mondardini L, Alestra T, Gerrity S, Tait L, South PM et al (2019) Local extinction of bull kelp (Durvillaea spp.) due to a marine heatwave. Front Mar Sci 6(84). https://doi.org/10.3389/fmars.2019.00084

Tuckett CA, Wernberg T (2018) High-latitude corals tolerate severe cold spell. Front Mar Sci 5(14). https://doi.org/10.3389/fmars.2018.00014

Tuckett CA, de Bettignies T, Fromont J, Wernberg T (2017) Expansion of corals on temperate reefs: direct and indirect effects of marine heatwaves. Coral Reefs 36(3):947–956. https://doi.org/10.1007/s00338-017-1586-5

van Vuuren DP, Edmonds J, Kainuma M, Riahi K, Thomson A, Hibbard K et al (2011) The representative concentration pathways: an overview. Clim Change 109(1):5–31. https://doi.org/10.1007/s10584-011-0148-z

Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E et al (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc Roy Soc B Biol Sci 281(1789):20140846. https://doi.org/10.1098/rspb.2014.0846

Vergés A, Doropoulos C, Malcolm HA, Skye M, Garcia-Pizá M, Marzinelli EM et al (2016) Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. Proc Natl Acad Sci USA 113(48):13791–13796. https://doi.org/10.1073/pnas.1610725113

Vergés A, McCosker E, Mayer-Pinto M, Coleman MA, Wernberg T, Ainsworth T, Steinberg PD (2019) Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. Funct Ecol 33:1000–1013. https://doi.org/10.1111/1365-2435.13310

Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecol Lett 13:685–694

Wernberg T, Russell BD, Moore PJ, Ling SD, Smale DA, Campbell A et al (2011a) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. J Exp Mar Biol Ecol 400(1-2):7–16. https://doi.org/10.1016/j.jembe.2011.02.021

Wernberg T, Thomsen MS, Tuya F, Kendrick GA (2011b) Biogenic habitat structure of seaweeds change along a latitudinal gradient in ocean temperature. J Exp Mar Biol Ecol 400 (1–2):264–271. https://doi.org/10.1016/j.jembe.2011.02.017

Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T et al (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Change 3:78–82. https://doi.org/10.1038/NCLIMATE1627

Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M et al (2016a) Climate-driven regime shift of a temperate marine ecosystem. Science 353(6295):169–172. https://doi.org/10.1126/science.aad8745

Wernberg T, de Bettignies T, Bijo AJ, Finnegan P (2016b) Physiological responses of habitat-forming seaweeds to increasing temperatures. Limnol Oceanogr 61:2180–2190

Wernberg T, Coleman MA, Bennett S, Thomsen MS, Tuya F, Kelaher BP (2018) Genetic diversity and kelp forest vulnerability to climatic stress. Sci Rep 8(1):1851. https://doi.org/10.1038/s41598-018-20009-9

Wernberg T, Coleman M, Babcock R, Bell S, Bolton J, Connell S et al (2019a) Biology and ecology of the globally significant kelp *Ecklonia radiata*. Oceanogr Mar Biol Annu Rev 57:265–324

Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen M (2019b) Status and trends for the world's kelp forests. In: Sheppard C (ed) World seas: an environmental evaluation, 2nd ed, Vol. III: Ecological issues and environmental impacts. Elsevier, London, pp 57–78

Wilson KL, Skinner MA, Lotze HK (2019) Projected 21st-century distribution of canopy-forming seaweeds in the Northwest Atlantic with climate change. Divers Distrib 25(4):582–602. https://doi.org/10.1111/ddi.12897

Zarco-Perello S, Wernberg T, Langlois TJ, Vanderklift MA (2017) Tropicalization strengthens consumer pressure on habitat-forming seaweeds. Sci Rep 7(1):820. https://doi.org/10.1038/s41598-017-00991-2

Zinke J, Rountrey A, Feng M, Xie S-P, Dissard D, Rankenburg K et al (2014) Corals record long-term Leeuwin current variability including Ningaloo Nino/Nina since 1795. Nat Commun 5:3607. https://doi.org/10.1038/ncomms4607

Impact of Marine Heatwaves on Seagrass Ecosystems

13

Oscar Serrano, Ariane Arias-Ortiz, Carlos M. Duarte, Gary A. Kendrick, and Paul S. Lavery

Abstract

Seagrass meadows deliver important ecosystem services such as nutrient cycling, enhanced biodiversity, and contribution to climate change mitigation and adaptation through carbon sequestration and coastal protection. Seagrasses, however, are facing the impacts of ocean warming and marine heatwaves, which are

---

O. Serrano (✉)
School of Science & Centre for Marine Ecosystems Research, Edith Cowan University, Joondalup, WA, Australia

Centro de Estudios Avanzados de Blanes, Consejo Superior de Investigaciones Científicas, Blanes, Spain
e-mail: o.serranogras@ecu.edu.au

A. Arias-Ortiz
Ecosystem Science Division, Department of Environmental Science, Policy and Management, University of California at Berkeley, Berkeley, CA, USA

Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA, USA
e-mail: aariasortiz@berkeley.edu

C. M. Duarte
King Abdullah University of Science and Technology (KAUST), Red Sea Research Center (RSRC), Thuwal, Saudi Arabia
e-mail: carlos.duarte@kaust.edu.sa

G. A. Kendrick
School of Biological Sciences, The University of Western Australia, Crawley, Australia

UWA Oceans Institute, The University of Western Australia, Crawley, Australia
e-mail: gary.kendrick@uwa.edu.au

P. S. Lavery
School of Science & Centre for Marine Ecosystems Research, Edith Cowan University, Joondalup, WA, Australia
e-mail: p.lavery@ecu.edu.au

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_13

altering their ecological structure and function. Shifts in species composition, mass mortality events, and loss of ecosystem complexity after sudden extreme climate events are increasingly common, weakening the ecosystem services they provide. In the west coast of Australia, Shark Bay holds between 0.7 and 2.4% of global seagrass extent (>4300 km^2), but in the austral summer of 2010/2011, the Ningaloo El Niño marine heatwave resulted in the collapse of ~1300 km^2 of seagrass ecosystem extent. The loss of the seagrass canopy resulted in the erosion and the likely remineralization of ancient carbon stocks into 2–4 Tg $CO_{2\text{-eq}}$ over 6 years following seagrass loss, increasing emissions from land-use change in Australia by 4–8% per annum. Seagrass collapse at Shark Bay also impacted marine food webs, including dugongs, dolphins, cormorants, fish communities, and invertebrates. With increasing recurrence and intensity of marine heatwaves, seagrass resilience is being compromised, underlining the need to implement conservation strategies. Such strategies must precede irreversible climate change-driven tipping points in ecosystem functioning and collapse and result from synchronized efforts involving science, policy, and stakeholders. Management should aim to maintain or enhance the resilience of seagrasses, and using propagation material from heatwave-resistant meadows to restore impacted regions arises as a challenging but promising solution against climate change threats. Although scientific evidence points to severe impacts of extreme climate events on seagrass ecosystems, the occurrence of seagrass assemblages across the planet and the capacity of humans to modify the environment sheds some light on the capability of seagrasses to adapt to changing ecological niches.

13.1 Introduction

A pressing question in ecology and evolutionary research is “How can we decipher the consequences of anthropogenic climate change on the structure and function of ecosystems?” This is crucial for the conservation of biodiversity and human well-being. Marine ecosystems play a key role in the Earth’s ecology, but there is much we do not understand about how climate change is impacting them (Pecl et al. 2017). Recent studies show that sharp increases in greenhouse gas emissions resulting in ocean warming are driving widespread changes in marine ecosystems not seen for millions of years, including ecosystem collapses with possibly irreversible transformations (Hoegh-Guldberg and Bruno 2010; Poloczanska et al. 2013). Plausible ecological consequences of anthropogenic climate change include shifts in the distribution of species, mass mortality of habitat-forming species, alterations in food web structure, and reduced ocean productivity (Kelleway et al. 2016; Duke et al. 2017; Hughes et al. 2018). Shifts in the condition of marine ecosystems occur in response to gradual climate change processes or sudden nonlinear transformations (e.g., state changes or ecosystem collapse) linked to extreme climate events (Henson et al. 2017). Owing to the importance of the oceans in driving life in our planet, supporting biodiversity, regulating climate, and contributing to food security, there is a pressing need to reduce greenhouse gas emissions worldwide to reverse or slow-down anthropogenic climate change feedbacks and the associated risks involved.

Oscillations in the ocean climate system occur naturally at seasonal to decadal timescales, such as the El Niño-Southern Oscillation (ENSO) that brings periodic warming in sea surface temperatures across the central Pacific (Alheit and Bakun 2010). However, an increasing number of studies show that the magnitude, duration, and recurrence of extreme climate conditions are increasing as a result of anthropogenic climate change (Frölicher et al. 2018). Changes in ocean currents and climate can strongly impact the ecology of marine ecosystems, as shown by recent impacts of ENSO variability on foundation species such as mangroves (Feller et al. 2017), seagrasses (Unsworth et al. 2018), kelp forests (Krumhansl et al. 2016), and coral reefs (Hughes et al. 2017). Some of the most remarkable impacts of anthropogenic climate change that resulted in the collapse of marine ecosystems have been reported in subtropical and tropical Australia, where climate anomalies resulted in mass mortality events of marine ecosystems. A record-breaking marine heatwave hit the Great Barrier Reef in 2016, which entailed massive coral die-off and impacted the three-dimensionality and ecological functioning of one third of the world's largest coral reef ecosystem (Hughes et al. 2018). Similarly, sudden and widespread dieback of mangrove forests was reported along 1000 km of coastline in the Gulf of Carpentaria in 2016, as a result of temporary extreme climate conditions leading to high seawater temperatures, drought conditions, and a decrease in sea level (Duke et al. 2017). An unprecedented marine heatwave established along the west coast of Australia in 2011 resulting in a shift from kelp forests to seaweed turfs and the death of more than 1300 km^2 of seagrass along Shark Bay in Western Australia as a result of heat stress (Wernberg et al. 2016; Arias-Ortiz et al. 2018; Strydom et al. 2020). Large-scale seagrass dieback events linked to marine heatwaves have been reported to occur since 1990s (Seddon et al. 2000) and will continue to occur based on present and future climate change scenarios. Because extreme climate events cause shocking impacts on marine ecosystems and the ecosystem services they provide, understanding their effects is critical to improving the capacity of scientists and environmental managers to understand, predict, determine, and best manage future ecological change.

In this chapter we review the impacts of climate change and marine heatwaves on the ecological structure and function of seagrass ecosystems. Seagrasses are a polyphyletic group (i.e., formed by separate ancestors) of 72 species from 4 families of the Alistamatales that colonized the ocean multiple times over a 35 million-year period (Short et al. 2011). The ability of seagrasses to resist and recover from marine heatwaves remains poorly understood, and here we describe seagrass ecosystem processes and trajectories under anthropogenic climate change. Specific focus is given on the impacts of seagrass ecosystem collapse at Shark Bay due to the 2010/2011 marine heatwave. We review the impact of marine heatwaves on seagrass ecosystem services and, in particular, estimate the likely CO_2 emissions resulting from the remineralization of soil carbon stocks accumulated over millennia underneath the meadows at Shark Bay. We describe inherent mechanisms by seagrasses to cope with transient warming, aiming to understand future trajectories and highlight management strategies that can enhance the capacity of seagrasses to adapt and survive anthropogenic climate change.

13.2 Response of Seagrass Ecosystems Under Climate Change Threats

Seagrasses have thrived on Earth for more than 60 million years, persisting over evolutionary and ecological timescales including periods with climate characteristics comparable in magnitude to plausible future climate change scenarios. As a result, they are inherently dynamic and have mechanisms to cope with transient warming, namely, genetic adaptations and physiological acclimation that may facilitate the resilience of seagrasses to warming and marine heatwaves. For example, the rapid activation of photo-protective mechanisms including heat-responsive genes can result in higher photosynthetic stability, respiratory acclimation activation, and, thereby, enhanced resistance to heat stress (Marín-Guirao et al. 2016, 2017; Beca-Carretero et al. 2018). However, warming and marine heatwaves could result in photosynthetic injury, impaired carbon balance, climate-mediated changes in herbivory and diseases (Vergés et al. 2014; Marín-Guirao et al. 2016; Sullivan et al. 2018) that can ultimately lead to mass mortality events and the collapse of seagrass ecosystems (Short et al. 2011). The complexity of processes involved in the response of seagrass to temperature stress, together with the unprecedented velocity of climate change and its magnitude (Loarie et al. 2009), raises the question of whether seagrasses will be able to adapt and survive anthropogenic climate change.

The ability of seagrasses to resist disturbance and recover from marine heatwaves remains poorly understood but will vary across species and possibly among populations of the same species within regions as a function of their thermal tolerances (Short et al. 2011). It will largely depend on the spatial scale of meadow affected, favorable environmental conditions prevailing at the site after disturbance, genotypic diversity, the recurrence of climate disturbances, and the life history strategy of seagrasses (Hughes and Stachowicz 2004; Montefalcone et al. 2015; O'Brien et al. 2018). Overall, meadows formed by slow-growing and long-living species typical of temperate climates (e.g., *Posidonia*, *Amphibolis*, and *Zostera*) are highly vulnerable to climate change disturbances, while smaller colonizing species typical of tropical regions (e.g., *Halodule*, *Halophila*, and *Syringodium*) are more resilient to warming and marine heatwaves (O'Brien et al. 2018). Large persistent seagrass species have higher resistance capacity to disturbance but recover more slowly compared to smaller seagrass that decline and recover more quickly (Kilminster et al. 2015). Seagrass die-off events have been reported mainly for temperate, large, and long-living seagrass, resulting in a shift from a foundation seagrass meadow habitat to a bare sandy substrate and entailing losses in habitat structure and complexity. If favorable conditions return following seagrass ecosystem collapse, pioneering, fast-growing, and/or low biomass species can colonize bare sands, and in the long term, the slow-growing, long-living, and large seagrass species can re-establish climax seagrass ecosystems (Kendrick et al. 2019).

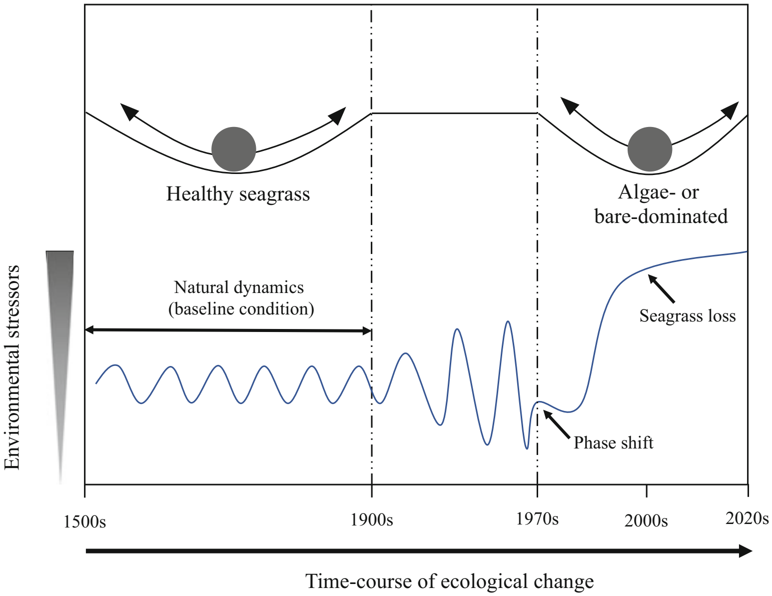


Fig. 13.1 Shifts in the condition of seagrass ecosystems in response to anthropogenic stressors such as eutrophication and climate change. Disturbances resulting in a shift from a foundation seagrass meadow habitat to a bare sandy substrate, entailing losses in habitat structure and complexity weakening the ecosystem services they provide

Since the beginning of the twentieth century, widespread die-off of seagrass meadows has been estimated at 0.9% year^{-1}, linked to a variety of factors including coastal development and associated eutrophication and sediment discharges (Waycott et al. 2009; Fig. 13.1). More recently, conservation and management actions have resulted in the deceleration and reversal of declining trends in some locations (de los Santos et al. 2019). However, while actions to mitigate impacts may be beneficial at the local scale, models linking seagrass population ecology and climate change scenarios predict severe future impacts, with marine heatwaves a major concern (Jordà et al. 2012). The widespread losses of *Amphibolis*, *Zostera*, and *Posidonia* species in the Atlantic and Indian Oceans and the Mediterranean Sea have been linked to marine heatwaves (Seddon et al. 2000; Marbà and Duarte 2010; Nowicki et al. 2017; Shields et al. 2019). Such losses highlight that temperate seagrass meadows are highly vulnerable to warming, which can induce mass mortality events and phase shifts posing an important threat to this key ecosystem (Fig. 13.2). Mortality rates can increase over short-term summertime heat stress events. For example, a 3 °C increase in average summer seawater temperatures resulted in up to a threefold increase in mortality of *P. oceanica* in the Mediterranean Sea (Marbà and Duarte 2010), and modelling predicted the functional extinction of seagrass *P. oceanica* meadows within the Mediterranean Sea by 2050 under a moderately optimistic scenario of greenhouse gas emissions (Jordà et al. 2012).

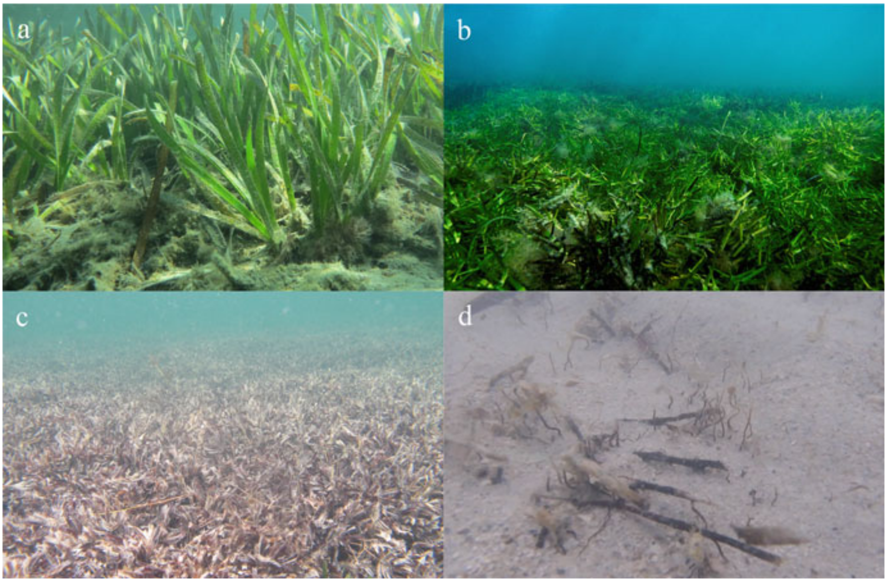


Fig. 13.2 Pictures of seagrass meadows (*Posidonia* spp. and *Amphibolis* spp.) prior (**a**, **b**) and after (**c**, **d**) the 2010/11 marine heatwave at Shark Bay (Western Australia)

However, predictive models have yet to be tested for other seagrass species to further understand the future trajectories of the meadows under climate change threat. Leaving aside the uncertainties linked to modelling future seagrass ecosystem dynamics, increasing scientific evidence points to accelerating "tropicalization" and transformation of temperate and subtropical seagrass meadows mainly driven by rising sea temperatures, marine heatwaves, and poleward shifts in the distribution of tropical herbivores (Hyndes et al. 2017). The tropicalization of ecosystems entails widespread losses of extremely productive ecosystems such as macroalgal forests and temperate seagrass meadows and has been defined as an increase in the ratio of tropical to temperate taxa or drastic shifts in species composition, abundances, and interactions driven by climate change (Wernberg et al. 2013; Vergés et al. 2014).

13.3 Impact of Marine Heatwaves on Seagrass Ecosystem Services

Seagrass meadows rank among the most valuable ecosystems on Earth owing to the delivery of important ecosystem services such as nutrient cycling, enhanced biodiversity, and contribution to climate change mitigation and adaption through carbon sequestration and coastal protection (Duarte et al. 2013; Cullen-Unsworth et al. 2014). Altered structure and function of seagrass ecosystems in response to climate change are, therefore, expected to have ecological, social, and economic consequences. Shifts in species composition and mass mortality events result in a loss of ecosystem complexity, weakening the ecosystem services they provide, including consumer populations such as turtles and dugongs, with implications for species dynamics, food web structure, fisheries, and carbon sequestration (Kendrick et al. 2019). Among all the ecosystem services seagrass meadows provide, their capacity to sequester CO_2 has recently generated interest for its potential role in mitigating climate change (Duarte et al. 2013). The organic-rich deposits beneath seagrass meadows can reach several meters in thickness and 6000 years of age and store about twice the carbon per hectare as terrestrial soils (Mateo et al. 1997; Fourqurean et al. 2012). However, loss of the seagrass canopy due to disturbances such as marine heatwaves can expose the soil organic carbon stocks to hydrodynamic forces, which in turn result in the rapid erosion and remineralization of ancient stocks into CO_2, contributing to climate change. CO_2 emissions from loss of seagrass ecosystems globally have been estimated at 0.15–1 Pg CO_2 per year (Pendleton et al. 2012; Fourqurean et al. 2012), which are equivalent to ~3% of those from deforestation globally (van der Werf et al. 2009).

13.3.1 Shark Bay: A World Heritage Site Threatened by Climate Change

At the most westerly end of the Australian continent, Shark Bay has exceptional natural features, including one of the largest and most diverse seagrass meadows in the world, the most diverse and abundant living stromatolite forms, and rich marine life (Dowling 1991). Owing to these and other exceptional natural values, Shark Bay, covering an area of 23,000 km^2, was declared a World Heritage Site in 1991. Despite the relative remoteness, pristineness, and low human impacts in Shark Bay, over the past decades its marine ecosystems did not escape the effects of climate change (Fig. 13.3). Shark Bay is located at the interface between temperate and tropical climates, and, therefore, the effects of climate change are anticipated to be greatest in this region (Hyndes et al. 2017).

The coast of Western Australia is influenced by poleward shifts in the Leeuwin Current that brings warm waters from the tropical Indian Ocean southward along the continental platform. The Leeuwin Current is largely influenced by the El Niño-Southern Oscillation (ENSO), the Earth's most prominent source of interannual climate variability (Cai et al. 2015). ENSO switches irregularly between the El Niño warm phase and the La Niña cold phase, entailing global shifts in weather conditions and ecosystem dynamics (McPhaden et al. 2006). In the coast off Western Australia, however, La Niña can result in an intensification of the Leeuwin Current and marine heatwaves, while El Niño weakens the Leeuwin Current resulting in colder water temperatures (Feng et al. 2008). During La Niña events, northerly winds combined with strong Leeuwin Current during summer increase summer maximum ocean temperatures by up to 2–4 °C in Shark Bay, placing its ecosystems at major risk owing to its shallow and enclosed geomorphology (Kendrick et al. 2019). Although climate models based on future greenhouse gas emission scenarios show high uncertainty on the frequency of ENSO phases, they are consistent in

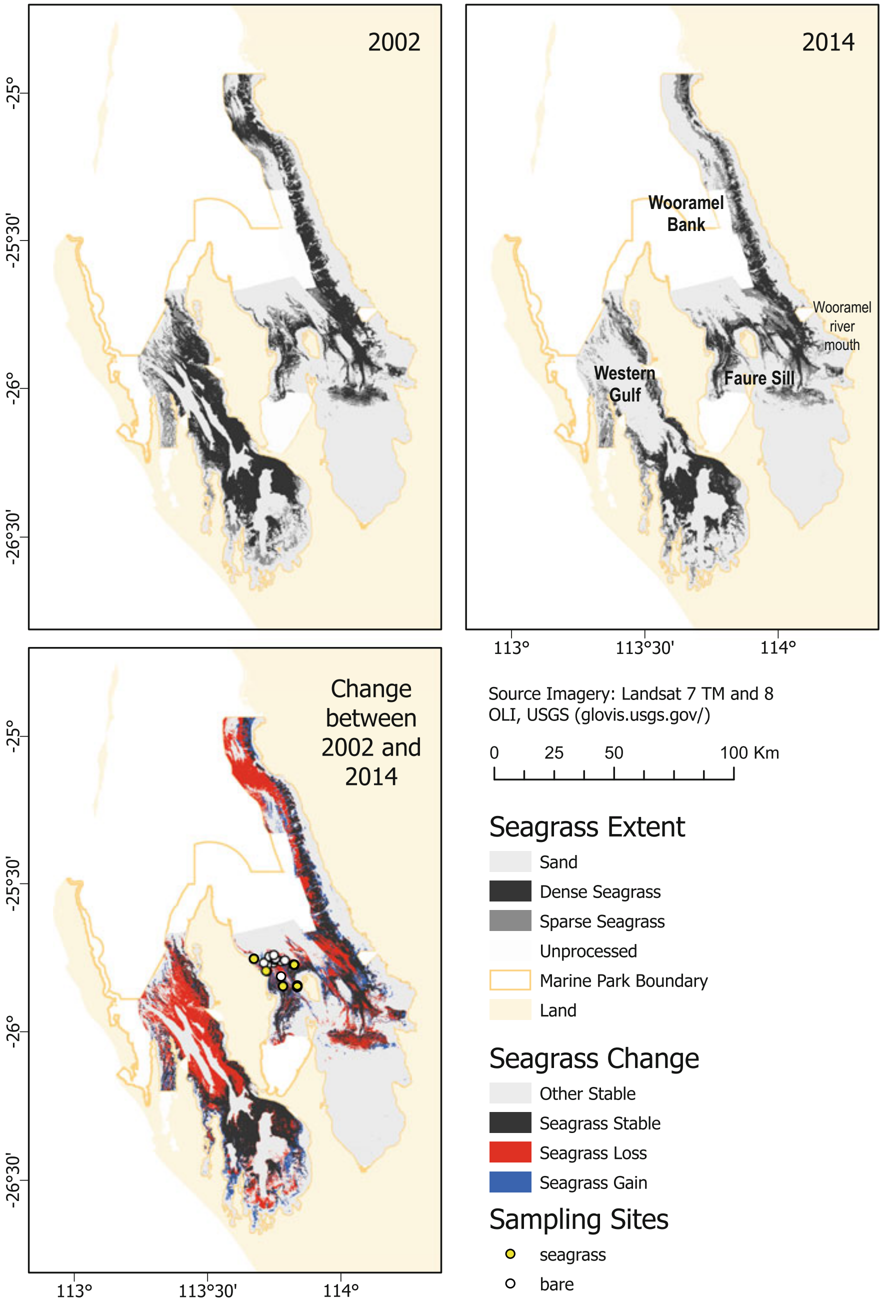


Fig. 13.3 Change in seagrass extent within Shark Bay World Heritage Site before (2002) and after (2014) the 2010/2011 marine heatwave. Black shaded areas show dense regions with seagrass cover >40%; grey shaded areas indicate sparse seagrass cover (<40%); red shaded areas indicate seagrass loss, while dark blue areas show seagrass gains; light grey shaded areas indicate sandy bottoms, and areas with no data are shown in white. The gold contour indicates the Shark Bay Marine Park boundary. Study sites within the studied region between Monkey Mia and Faure Island are

predicting increased intensity of both El Niño and La Niña ENSO climate anomalies (Cai et al. 2015), including the subtropical and temperate coastlines of Western Australia phenomena (Feng et al. 2013; Wernberg et al. 2016). In particular, in the austral summer of 2010/2011, the Ningaloo La Niña marine heatwave occurred for more than 8 weeks along ~1000 km of the west Australian coastline. It transferred tropical waters of up to 4 °C warmer than prevailing summer temperatures that decimated seagrass ecosystems formed by long-living and persistent species over millennia (Pearce et al. 2011; Kendrick et al. 2019). Since then, climate change has emerged as an additional threat to the World Heritage values. Underlying the increased intensity and frequency of climate anomalies, there is a gradually rising water temperature trend associated with global warming, and the waters immediately offshore of Western Australia are warming more rapidly than the average over the Indian Ocean (Caputi et al. 2009; Pearce and Feng 2007). This phenomenon further compromises the capacity of ecosystems to recover from disturbances and is resulting in alterations to the ecological niches of species.

Shark Bay holds >4300 km^2 of one of the most diverse assemblage of seagrasses worldwide, occupying between 0.7 and 2.4% of global seagrass extent (Arias-Ortiz et al. 2018; Strydom et al. 2020). Although seagrasses have thrived over millennia in Shark Bay, playing a major role in shaping its stratigraphic architecture through the formation of banks and channels (Bufarale and Collins 2015), unprecedented widespread seagrass losses occurred due to the 2010/11 marine heatwave (Arias-Ortiz et al. 2018). The transfer of tropical warm waters down the coast of Western Australia resulted in the collapse of the climax seagrass species *Amphibolis antarctica* and *Posidonia australis* as a result of thermal stress, with more than 1300 km^2 losses of seagrass habitat extent between 2010 and 2014 (Strydom et al. 2020). Following the marine heatwave, extensive defoliation of mainly *A. antarctica* was observed, and the subsequent death of shoots occurred 1–2 years after in 60–80% of the meadows at Shark Bay (Kendrick et al. 2019). The bare areas generated allowed the colonization of small fast-growing tropical species (e.g., *Halodule uninervis*) in some areas (not quantified), which have opportunistic and ephemeral dynamics and typically precede the establishment of slow-growing and large seagrass species such as *Amphibolis* and *Posidonia* (Strydom et al. 2020). The succession of species emphasizes the dynamic nature of seagrass ecosystems, which may result in the return of the *Amphibolis* and *Posidonia* climax ecosystems. However, the loss of ~1300 km^2 of climax seagrass ecosystems has persisted until present, with the exception of 125 km^2 recovered between 2014 and 2016 in a particular area in the Western Gulf of Shark Bay (Strydom et al. 2020). When slow-growing seagrass species forming climax ecosystems are disturbed, they can take decades to recover (O'Brien et al. 2018). Indeed, the ongoing ocean warming and the recurrence of marine heatwaves, together with additional environmental pressures

Fig. 13.3 (continued) represented as solid dots (vegetated sites) and open circles (bare sites). Figure modified from Arias-Ortiz et al. (2018)

such as sea bed destabilization and increased turbidity and nutrients, can jeopardize the recovery process (Nowicki et al. 2017).

Ocean warming is altering the ecological structure and function of marine ecosystems, with marine introductions driven by the tropicalization of Shark Bay's waters threatening the uniqueness and diversity of native assemblages (Wyatt et al. 2005), and marine heatwaves increasingly impacting the resilience of foundation seagrass ecosystems (Kendrick et al. 2019). Marine heatwave effects on seagrass survival were severe and aggravated by reduced irradiance associated with inputs of fine sediments from record floods in the southeastern embayment near the Wooramel River mouth and from increased sediment destabilization and detrital loads following the death of seagrasses (Short et al. 2011; Kendrick et al. 2019). Shark Bay is at risk from further climate change impacts linked to ocean warming and acute temperate extremes due to its location in a climate transition zone and due to the increasing seawater temperature, extended warm periods, and more frequent and severe extreme weather events linked to climate change, which are becoming important drivers of rapid ecosystem change in coastal ecosystems (Frölicher et al. 2018).

13.3.2 Carbon Dioxide Emissions from Climate-Driven Seagrass Loss at Shark Bay

Seagrass meadows in Shark Bay experienced a net loss of approximately 22% in habitat extent following the 2010/2011 marine heatwave (Arias-Ortiz et al. 2018; Fig. 13.3). As a result of the collapse of seagrass ecosystems, a portion of the organic carbon stocks within Shark Bay's seagrass soils, containing up to 1.3% of the total organic carbon stored within seagrass meadows worldwide, was potentially released to the atmosphere (Arias-Ortiz et al. 2018). Seagrass loss can entail the erosion and remineralization of their soil carbon stocks, and, within Shark Bay alone, Arias-Ortiz et al. (2018) estimated that between 2 and 9 Tg $CO_{2\text{-eq}}$ could have been released to the atmosphere during the 3 years following the 2010/2011 marine heatwave. This amount is roughly equivalent to the annual CO_2 output of 800,000 homes, 2 average coal-fired power plants, or 1,600,000 cars. That estimate was derived by applying a decay model of soil organic carbon (Lovelock et al. 2017) to the stocks measured in unimpacted seagrass meadows of the Bay, but has not been validated by in situ measurements of carbon stock losses in the heatwave affected meadows. Here, we directly estimate the erosion of seagrass soil organic carbon (C) in the 6 years following the heatwave by comparing the stocks prior to and after the heatwave event. Soil carbon stocks from ten sites impacted by the marine heatwave were sampled in 2017 using the same methods as Arias-Ortiz et al. (2018) and the results compared with pre-marine heatwave data from vegetated sites (Fig. 13.3). We also identified potential drivers of soil carbon loss and quantified the potential remineralization of organic carbon and associated $CO_{2\text{-eq}}$ emissions (obtained by multiplying C loss values by 3.67 that is the molecular ratio of CO_2 to C) in the 6 years following the heatwave related to its exposure to oxic conditions (Lovelock

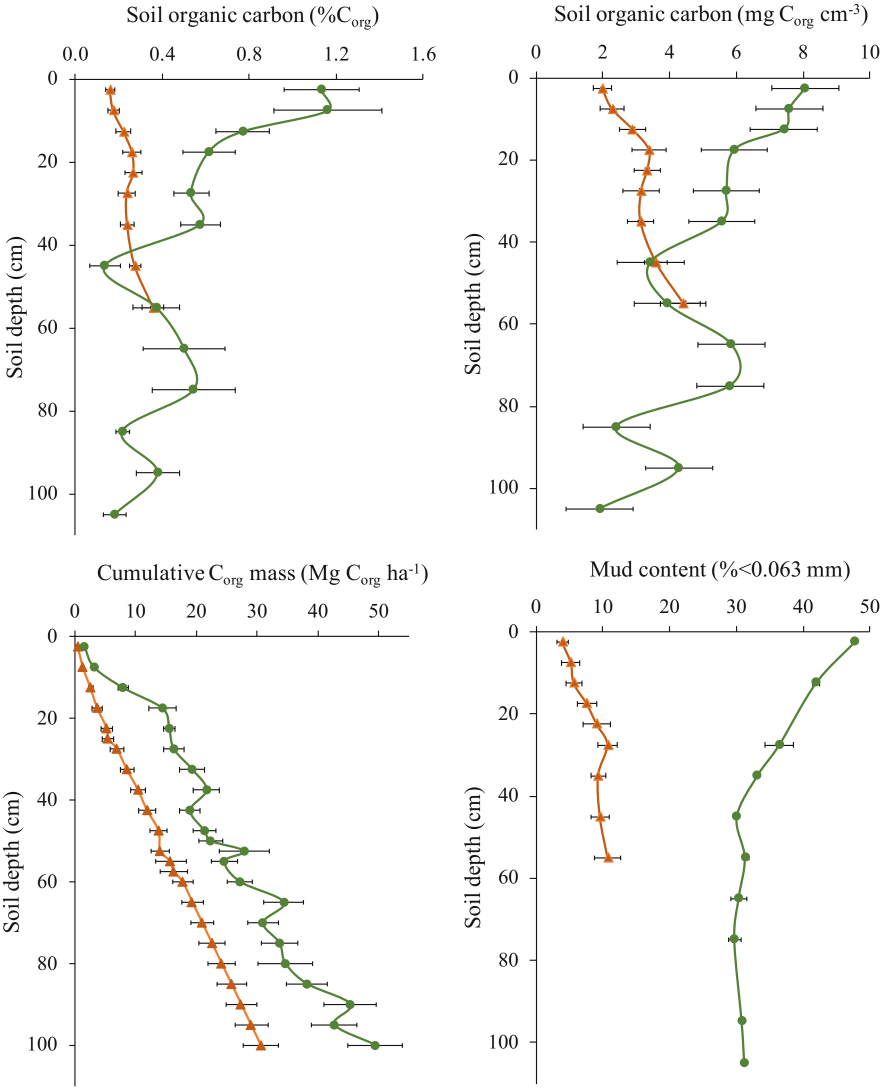


Fig. 13.4 Soil characteristics along depth in the cores from seagrass meadows (green) and bare but previously vegetated sites prior to the 2010/2011 marine heatwave in Shark Bay (orange). Soil organic carbon contents (in %C_{org} and mg C_{org} cm^{-3}), cumulative organic carbon mass downcore (Mg C_{org} ha^{-1}) and % mud content (% 0.063 mm). Data are average ± standard error of mean

et al. 2017). The results obtained showed that soil organic carbon stocks in bare but previously vegetated sites (31 ± 3 Mg C ha^{-1}) were lower than in nearby vegetated sites (45 ± 4 Mg C ha^{-1}), suggesting that ~15 Mg C ha^{-1} have been eroded following seagrass loss in 2011 (Fig. 13.4). The up to fivefold higher mud content (silt and clay particles <0.063 mm) in seagrass (35 ± 1.6%) compared to bare soils

(7.5 ± 0.5%) suggests that erosional processes linked to wave and tidal energy caused the resuspension and erosion of soil carbon at the bare sites. Seagrass canopies enhance sedimentation and reduce resuspension by altering hydrodynamic energy (Gacia et al. 1999), and, hence, following canopy loss the seagrass organic-rich soil deposits become exposed to erosional processes. This is particularly important in Shark Bay, owing to the shallow habitat occupied by seagrasses (1–8 m depth) and the strong swell and currents induced by wind and tides that prevail over the year in the region (Burling et al. 2003). Indeed, waves and currents in exposed locations may hinder or preclude the re-establishment of the meadows (Van Katwijk et al. 2009), which together with expected recurrence of marine heatwaves in Shark Bay poses concern for the natural long-term recovery potential of seagrass meadows in this subtropical region.

The fate of the eroded soil organic carbon remains unknown, but, assuming that 50–100% of the soil carbon eroded has been exposed to oxic conditions since 2012, we estimated cumulative emissions of 21–41 Mg $CO_{2\text{-eq}}$ per ha^{-1} over 6 years following seagrass loss. Within Shark Bay, the ~1000 km^2 loss of seagrass habitat (Arias-Ortiz et al. 2018) could have resulted in cumulative emissions of 2–4 Tg $CO_{2\text{-eq}}$ from the remineralization of soil organic carbon alone, increasing emissions from land-use change in Australia by 4–8% per annum. These estimates are within the lower range of potential emissions previously modelled by Arias-Ortiz et al. (2018) and do not account for potential methane and nitrous oxide emissions resulting from organic matter remineralization (Al-Haj and Fulweiler 2020; Murray et al. 2020), nor the emissions from the decomposition of dead seagrass biomass. After the event, phytoplankton and bacterial blooms were observed in Shark Bay as a consequence of increased nutrient inputs to the water column, suggesting altered water quality resulting from the degradation of seagrass biomass and the resuspension of fine sediments and associated nutrients (Nowicki et al. 2017). The predicted increase in frequency of extreme climate change events (Oliver et al. 2018) could continue to irreversibly damage one of the world largest blue carbon sink, resulting in continued CO_2 emissions from the exposed soils.

13.3.3 Impacts of a Marine Heatwave on Ecosystem Dynamics at Shark Bay

Sudden or disruptive extreme weather events can have severe ecological consequences at the ecosystem level, threatening the viability of populations and causing collapses in community structure toward degraded states (Wernberg et al. 2013). In Shark Bay, trophic cascade effects linked to seagrass loss also impacted marine food webs, including dugongs, dolphins, cormorants, fish communities, and invertebrates (Fig. 13.5). A 65% decrease in dugong abundance was reported following the marine heatwave, suggesting a displacement of dugongs searching for seagrass food elsewhere (Nowicki et al. 2019). The survival and reproduction of dolphins was impacted, causing a decline in female reproductive rates that still persists post-heatwave, owing to low prey availability leading to increased foraging

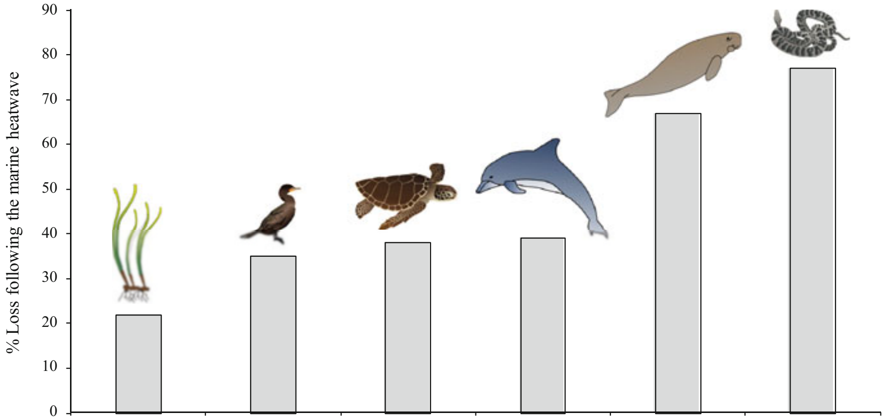


Fig. 13.5 Percentage loss of seagrass meadow extent in Shark Bay following the 2010/2011 marine heatwave (22%; Arias-Ortiz et al. 2018) and associated changes in landscape-level density of cormorants (35%), green turtles (38%), dolphins (39%), dugongs (67%), and sea snakes (77%) within Shark Bay (data from Nowicki et al. 2019). Symbols are from the Integration and Application Network, University of Maryland Center for Environmental Science (http://ian.umces.edu/imagelibrary/)

time and associated greater shark predation on calves (Wild et al. 2019). Mass mortalities across lower trophic levels during the marine heatwave, including invertebrate and fish communities (Pearce et al. 2011), likely contributed to the decrease in dolphins' fitness.

Although the collapse of foundation seagrass ecosystems at Shark Bay has allowed colonization of some bare areas by opportunistic and ephemeral tropical seagrasses (Kendrick et al. 2019; Strydom et al. 2020), the rate and trajectory of recovery towards the climax seagrass community remains unknown, as does the rate and trajectory of recovery of the associated ecosystem functions and services, such as support of biodiversity. The return of 125 km^2 of climax seagrass ecosystems in a small region of Shark Bay provides some optimism on future seagrass trajectories, and it seems likely that succession of seagrass species would take place over the next decades in the absence of severe disturbances. In addition, seagrass losses across Shark Bay were not homogeneous, with major losses within seaward populations and minor losses within landward populations (Fig. 13.3). The presence of resilient meadows along the shoreline, which likely experienced more severe heat stress during the 2010/2011 heatwave (Strydom et al. 2020), suggests that temperature tolerant populations are present in situ. However, projections of future increase in the frequency of marine heatwaves (Frölicher et al. 2018) suggest that intervals between heatwaves might be shorter than the timespan required for climax seagrass ecosystems to recover (several decades). This trend suggests the likely tropicalization of Shark Bay's seagrass assemblages and ultimately the collapse of the current climax seagrass ecosystem.

13.4 Future Perspectives and Management Strategies

The tropicalization of the oceans worldwide is evident and will continue to occur and be exacerbated under predicted future climate change scenarios (Frölicher et al. 2018). This will impact the structure and functioning of seagrass ecosystems, through mass mortality events and alterations to the ecological niches of seagrass species. Although seagrasses are declining in temperate regions, rapid poleward shifts in tropical and temperate seagrasses are expected with future warming, including colonization into currently cooler regions. Both the replacement of climax seagrass ecosystems in temperate regions by tropical species (Kendrick et al. 2019) and the expansion of temperate seagrass in the Arctic (Marbà et al. 2018) have already been reported. The occurrence of seagrass species assemblages along the shores of all continents except Antarctica (Short et al. 2011), and the important role of human activities in enhancing connectivity within and among oceans (Crook et al. 2015), likely will facilitate the tropicalization process and redistribution of seagrasses. For example, the arrival of exotic tropical seagrass species in the Mediterranean Sea facilitated by the Suez Canal, followed by the rapid expansion of tropical *Halophila* spp. meadows in the warmer eastern Mediterranean Basin and their recent colonization toward the colder western basin (Hoffman 2014), provides evidence of the seagrass plasticity to adapt to new habitats. However, the unprecedented velocity of climate change raises concern about the capacity of seagrasses to adapt and survive anthropogenic climate change (Loarie et al. 2009). The evidence points to an irreversible collapse of climax seagrass ecosystems worldwide, involving the loss of ecosystem complexity at the warmer edges of the geographical distribution of temperate species; however the net balance in terms of future seagrass ecosystem extent and complexity remains unknown.

Among all the impacts of tropicalization processes on seagrass ecosystems, the consequences for the global carbon cycle are of major concern. Seagrass meadows have stored 4–8 Pg C of globally in their soils over thousands of years, and their loss can entail the remineralization of these ancient sedimentary organic carbon deposits into CO_2, fuelling anthropogenic climate change (Fourqurean et al. 2012). The carbon sequestration potential of seagrasses is limited, and therefore the conservation of seagrasses to avoid emissions from soil carbon is crucial to avoid negative climate feedbacks. Indeed, climax seagrass communities in temperate regions, which are at higher risk from marine heatwaves, have disproportionally higher carbon stocks compared to tropical species (Fourqurean et al. 2012), raising further concern. With increasing frequency of marine heatwaves, the stability of seagrass carbon stocks is being compromised, further underlining the need to reduce greenhouse gas emissions and the implementation of conservation strategies to maintain natural carbon sinks.

Current management for seagrass conservation includes reducing nutrient loading in coastal areas from localized sewage and agricultural fields, the declaration of marine protected areas embedding seagrass, promoting responsible boating practices such as avoiding anchoring on top of seagrass and propeller-scarring, replacement of moorings consisting of a chain scouring the meadows by environmentally friendly ones, and through the dissemination of the significance of seagrass (Kenworthy et al. 2007). These actions are appropriate to diminish the impacts of localized stressors, such as eutrophication and meadow fragmentation, but less effective to cope with climate change threats such as marine heatwaves, owing to the devastating and sudden effects of these impacts (Orth et al. 2006). Protection of seagrasses from climate change should predate irremediable tipping points in ecosystem functioning and collapse and result from synchronized research efforts that inform management to implement conservation and restoration strategies driven by government, industry, academic institutions, nonprofit organizations, and local communities. The need for such a strategic effort was recognizable since the onset of seagrass mass mortality events induced by marine heatwaves in the twentieth century, but as far as we are aware, no strategies have been implemented.

In the face of climate change threats, management can aim to maintain or enhance the resilience of seagrasses (Kilminster et al. 2015). Heatwaves primarily impacted climax seagrass communities in temperate and subtropical regions, characterized by slow growth rates and high levels of resistance to disturbance but limited capacity to recover. Once lost, their capacity to recover largely depends on the import of seeds or seedlings from persistent meadows. As a result, conservation actions should largely aim to diminish local impacts aggravating those of global change to enhance their resilience. Following mass mortality events such as those induced by marine heatwaves, conservation actions could aim to remove excessive dead seagrass biomass to avoid further threats linked to severe phytoplankton and bacterial blooms, and sulfide toxicity as a result of the degradation of seagrass biomass and subsequent eutrophication processes (Arias-Ortiz et al. 2018). Indeed, management to maintain herbivory at natural levels can contribute to the recovery of seagrasses (Atwood et al. 2015). The restoration of impacted areas with seeds and seedlings can enhance recovery, but the success of seagrass revegetation efforts has been limited to sites with preexisting or prevailing favorable habitat conditions (Fonseca 2011). As a result, the potential for restoration of climax seagrass ecosystems in temperate and subtropical regions facing tropicalization is questionable and worsened by high costs linked to seagrass restoration which limit its implementation over large temporal and spatial scales (Bayraktarov et al. 2016).

Notwithstanding existing barriers, previous studies showed that seagrass ecosystem recovery after extreme climatic events is enhanced by species diversity and genotypic diversity (Hughes and Stachowicz 2004; Reusch et al. 2005), and thereby management actions could focus on revegetating areas with heatwave-resilient seagrass genotypes. Sourcing propagation material from resistant meadows within areas impacted by marine heatwaves could enhance the success of revegetation efforts, but also it could be further enhanced by sourcing propagation material from warmer climates within the distribution limits of the species of interest, or from specific locations with extreme warm conditions linked to geomorphic settings where seagrasses are growing at their physiological limits. Identifying resistant seagrass genotypes to marine heatwaves to supplement the genetic diversity and resilience of existing meadows arises as a challenging but promising solution against climate change threats. Revegetation with heatwave-resilient seagrass genotypes could also contribute to overcome the unprecedented velocity of climate change that raises concern on the natural capacity of seagrasses to adapt and survive anthropogenic climate change.

13.5 Conclusions

Seagrass meadows are facing the impacts of seawater warming and marine heatwaves, which are resulting in mass mortality events and alterations in the ecological niches of seagrass species. Foundation seagrass species forming climax ecosystems, typical of temperate climates, are largely suffering the consequences, with increasing cases of seagrass ecosystem collapses after sudden extreme climate events. Shifts in species composition and mass mortality events lower ecosystem complexity and weaken the ecosystem services they provide, including the release of significant amounts of CO_2 at global scales. With increasing recurrence of marine heatwaves, the resilience of seagrass meadows is being compromised, underlining the need to implement conservation strategies. Conservation strategies for seagrasses should preempt irreversible, climate change-driven tipping points in ecosystem functioning and result from synchronized efforts involving science, policy, and stakeholders. Management should aim to maintain or enhance the resilience of seagrasses and using propagation material from heatwave-resistant meadows to restore impacted regions arises as a challenging but promising solution against climate change threats. Although increasing scientific evidence points to severe impacts of extreme climate events on seagrass ecosystems, the occurrence of seagrass assemblages across the planet and the capacity of humans to modify the environment sheds some light on the capability of some seagrasses to adapt to changing ecological niches.

Acknowledgments O.S. was supported by an ARC DECRA DE170101524. AA-O was supported by the NOAA C&GC Postdoctoral Fellowship Program administered by UCAR-CPAESS under award #NA18NWS4620043B. GAK was supported by an ARC Discovery DP180100668. We thank the editors Pep Canadell, Rob Jackson, and Detlef Schulze for their comments that improved this chapter.

References

Al-Haj AN, Fulweiler RW (2020) A synthesis of methane emissions from shallow vegetated coastal ecosystems. Glob Chang Biol 26:2988–3005

Alheit J, Bakun A (2010) Population synchronies within and between ocean basins: apparent teleconnections and implications as to physical–biological linkage mechanisms. J Mar Syst 79:267–285

Arias-Ortiz A, Serrano O, Masqué P, Lavery PS, Mueller U, Kendrick GA, Rozaimi M, Esteban A, Fourqurean JW, Marba N, Mateo MA, Murray K, Rule MJ, Duarte CM (2018) A marine heatwave drives massive losses from the world's largest seagrass carbon stocks. Nat Clim Chang 8:338

Atwood TB, Connolly RM, Ritchie EG, Lovelock CE, Heithaus MR, Hays GC, Fourqurean JW, Macreadie PI (2015) Predators help protect carbon stocks in blue carbon ecosystems. Nat Clim Chang 5:1038–1045

Bayraktarov E, Saunders MI, Abdullah S, Mills M, Beher J, Possingham HP, Mumby PJ, Lovelock CE (2016) The cost and feasibility of marine coastal restoration. Ecol Appl 26:1055–1074

Beca-Carretero P, Guihéneuf F, Marín-Guirao L, Bernardeau-Esteller J, García-Muñoz R, Stengel DB, Ruiz JM (2018) Effects of an experimental heat wave on fatty acid composition in two Mediterranean seagrass species. Mar Pollut Bull 134:27–37

Bufarale G, Collins LB (2015) Stratigraphic architecture and evolution of a barrier seagrass bank in the mid-late Holocene, Shark Bay, Australia. Mar Geol 359:1–21

Burling MC, Pattiaratchi CB, Ivey GN (2003) The tidal regime of Shark Bay, Western Australia. Estuar Coast Shelf Sci 57:725–735

Cai W, Wang G, Santoso A, McPhaden MJ, Wu L, Jin FF, Timmermann A, Collins M, Vecchi G, Lengaigne M, England MH, Dommenget D, Takahashi K, Guilyardi E (2015) Increased frequency of extreme La Niña events under greenhouse warming. Nat Clim Chang 5:132–137

Caputi N, de Lestang S, Feng M, Pearce A (2009) Seasonal variation in the long-term warming trend in water temperature off the Western Australian coast. Mar Freshw Res 60:129–139

Crook DA, Lowe WH, Allendorf FW, Erős T, Finn DS, Gillanders BM, Hadwen WL, Harrod C, Hermoso V, Jennings S, Kilada RW, Nagelkerken I, Hansen MM, Page TJ, Riginos C, Fry B, Hughes JM (2015) Human effects on ecological connectivity in aquatic ecosystems: integrating scientific approaches to support management and mitigation. Sci Total Environ 534:52–64

Cullen-Unsworth LC, Nordlund LM, Paddock J, Baker S, McKenzie LJ, Unsworth RK (2014) Seagrass meadows globally as a coupled social–ecological system: implications for human wellbeing. Mar Pollut Bull 83:387–397

de los Santos CB, Krause-Jensen D, Alcoverro T, Marbà N, Duarte CM, van Katwijk MM, Perez M, Romero J, Sanchez-Lizaso JL, Roca G, Jankowska E, Perez-Llorens JL, Fournier J, Montefalcone M, Pergent G, Ruiz JM, Cabaco S, Cook K, Wilkes RJ, Moy FE, GMR T, Seglar X, de Jong DJ, Fernandez-Torquemada Y, Auby I, Vergara JJ, Santos R (2019) Recent trend reversal for declining European seagrass meadows. Nat Commun 10:1–8

Dowling R (1991) Tourism and the natural environment Shark Bay, Western Australia. Tour Recreat Res 16:44–48

Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N (2013) The role of coastal plant communities for climate change mitigation and adaptation. Nat Clim Chang 3:961–968

Duke NC, Kovacs JM, Griffiths AD, Preece L, Hill DJ, Van Oosterzee P, Mackenzie J, Morning HS, Burrow D (2017) Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. Mar Freshw Res 68:1816–1829

Feller IC, Friess DA, Krauss KW, Lewis RR (2017) The state of the world's mangroves in the 21st century under climate change. Hydrobiologia 803:1–12

Feng M, Biastoch A, Böning C, Caputi N, Meyers G (2008) Seasonal and interannual variations of upper ocean heat balance off the west coast of Australia. J Geophys Res Oceans 113:C12025

Feng M, McPhaden MJ, Xie S-P, Hafner J (2013) La Nina forces unprecedented Leeuwin current warming in 2011. Sci Rep 3:1277

Fonseca MS (2011) Addy revisited: what has changed with seagrass restoration in 64 years? Ecol Restor 29:73–81

Fourqurean JW, Duarte CM, Kennedy H, Marbà N, Holmer M, Mateo MA, Apostolaki ET, Kendrick GA, Krause-Jensen D, McGlathery KJ, Serrano O (2012) Seagrass ecosystems as a globally significant carbon stock. Nat Geosci 5:505–509

Frölicher TL, Fischer EM, Gruber N (2018) Marine heatwaves under global warming. Nature 560:360–364

Gacia E, Granata TC, Duarte CM (1999) An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows. Aquat Bot 65:255–268

Henson SA, Beaulieu C, Ilyina T, John JG, Long M, Séférian R, Tjiputra J, Sarmiento JL (2017) Rapid emergence of climate change in environmental drivers of marine ecosystems. Nat Commun 8:1–9

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328:1523–1528

Hoffman R (2014) Alien benthic algae and seagrasses in the Mediterranean Sea and their connection to global warming. In: The mediterranean sea. Springer, Dordrecht, pp 159–181

Hughes AR, Stachowicz JJ (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proc Natl Acad Sci 101:8998–9002

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JB, Kleypas J, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017) Coral reefs in the Anthropocene. Nature 546:82–90

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS, Torda G (2018) Global warming transforms coral reef assemblages. Nature 556:492–496

Hyndes GA, Heck KL Jr, Vergés A, Harvey ES, Kendrick GA, Lavery PS, McMahon K, Orth RJ, Pearce A, Vanderklift M, Wernberg T, Whiting S, Wilson S (2017) Accelerating tropicalization and the transformation of temperate seagrass meadows. Bioscience 66:938–948

Jordà G, Marbà N, Duarte CM (2012) Mediterranean seagrass vulnerable to regional climate warming. Nat Clim Chang 2:821–824

Kelleway JJ, Saintilan N, Macreadie PI, Skilbeck CG, Zawadzki A, Ralph PJ (2016) Seventy years of continuous encroachment substantially increases 'blue carbon'capacity as mangroves replace intertidal salt marshes. Glob Chang Biol 22:1097–1109

Kendrick GA, Nowicki RJ, Olsen YS, Strydom S, Fraser MW, Sinclair EA, Statton J, Hovey RK, Thomson JA, Nurkholder DA, McMahon KM, Kilminster K, Hetzel Y, Fourqurean JW, Heithaus MR, Orth RJ (2019) A systematic review of how multiple stressors from an extreme event drove ecosystem-wide loss of resilience in an iconic seagrass community. Front Mar Sci 6:455

Kenworthy WJ, Wyllie-Echeverria S, Coles RG, Pergent G, Pergent-Martini C (2007) Seagrass conservation biology: an interdisciplinary science for protection of the seagrass biome. In: Seagrasses: biology, ecology and conservation. Springer, Dordrecht, pp 595–623

Kilminster K, McMahon K, Waycott M, Kendrick GA, Scanes P, McKenzie L, O'Brien KR, Lyons M, Ferguson A, Maxwell P, Glasby T, Udy J (2015) Unravelling complexity in seagrass systems for management: Australia as a microcosm. Sci Total Environ 534:97–109

Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC, Connell SD, Johnson CR, Konar B, Ling SD, Micheli F, Norderhaug KM, Pérez-Matus A, Sousa-Pinto I, Reed DC, Salomon AK, Shears NT, Wernberg T, Anderson RJ, Barrett NS, Buschmann AH, Carr MH, Caselle JE, Derrien-Courtel S, Edgar GJ, Edwards M, Estes JA, Goodwin C, Kenner MC, Kushner DJ, Moy FE, Nunn J, Steneck RS, Vásquez J, Watson J, Witman JD, Byrnes JEK (2016) Global patterns of kelp forest change over the past half-century. Proc Natl Acad Sci 113:13785–13790

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. Nature 462:1052–1055

Lovelock CE, Fourqurean JW, Morris JT (2017) Modeled CO_2 emissions from coastal wetland transitions to other land uses: tidal marshes, mangrove forests, and seagrass beds. Front Mar Sci 4:143

Marbà N, Duarte CM (2010) Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. Glob Chang Biol 16:2366–2375

Marbà N, Krause-Jensen D, Masqué P, Duarte CM (2018) Expanding Greenland seagrass meadows contribute new sediment carbon sinks. Sci Rep 8:1–8

Marín-Guirao L, Ruiz JM, Dattolo E, Garcia-Munoz R, Procaccini G (2016) Physiological and molecular evidence of differential short-term heat tolerance in Mediterranean seagrasses. Sci Rep 6:28615

Marín-Guirao L, Entrambasaguas L, Dattolo E, Ruiz JM, Procaccini G (2017) Molecular mechanisms behind the physiological resistance to intense transient warming in an iconic marine plant. Front Plant Sci 8:1142

Mateo MA, Romeo J, Pérez M, Littler MM, Littler DS (1997) Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*. Estuar Coast Shelf Sci 44:103–110

McPhaden MJ, Zebiak SE, Glantz MH (2006) ENSO as an integrating concept in earth science. Science 314:1740–1745

Montefalcone M, Vassallo P, Gatti G, Parravicini V, Paoli C, Morri C, Bianchi CN (2015) The exergy of a phase shift: ecosystem functioning loss in seagrass meadows of the Mediterranean Sea. Estuar Coast Shelf Sci 156:186–194

Murray R, Erler DV, Rosentreter J, Wells NS, Eyre BD (2020) Seasonal and spatial controls on N2O concentrations and emissions in low-nitrogen estuaries: evidence from three tropical systems. Mar Chem 221:103779

Nowicki RJ, Thomson JA, Burkholder DA, Fourqurean JW, Heithaus MR (2017) Predicting seagrass recovery times and their implications following an extreme climate event. Mar Ecol Prog Ser 567:79–93

Nowicki R, Heithaus M, Thomson J, Burkholder D, Gastrich K, Wirsing A (2019) Indirect legacy effects of an extreme climatic event on a marine megafaunal community. Ecol Monogr 89: e01365

O'Brien KR, Waycott M, Maxwell P, Kendrick GA, Udy JW, Ferguson AJ, Kilminster K, Scanes P, McKenzie LJ, McMahon K, Adams MP, Samper-Villarreal J, Collier C, Lyons M, Mumby PJ, Radke L, Christianen MJA, Dennison WC (2018) Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. Mar Pollut Bull 134:166–176

Oliver EC, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV, Benthuysen JA, Feng M, Gupta AS, Hobday AJ, Holbrook NJ, Perkins-Kirkpatrick SE, Scannell HA, Straub SC, Wernberg T (2018) Longer and more frequent marine heatwaves over the past century. Nat Commun 9:1–12

Orth RJ, Carruthers TJ, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Olyarnik S, Short FT, Waycott M, Williams SL (2006) A global crisis for seagrass ecosystems. Bioscience 56:987–996

Pearce A, Feng M (2007) Observations of warming on the Western Australian continental shelf. Mar Freshw Res 58:914–920

Pearce AF, Lenanton R, Jackson G, Moore J, Feng M, Gaughan D (2011) The "marine heat wave" off Western Australia during the summer of 2010/11 (p. 40). Western Australian fisheries and marine research laboratories

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, Clark TD, Colwell RK, Danielsen F, Evengård B, Falconi L, Ferrier S, Frusher S, Garcia RA, Griffis RB, Hobday AJ, Janion-Scheepers C, Jarzyna MA, Jennings S, Lenoir J, Linnetved HI, Martin VY, McCormack PC, McDonald J, Mitchell NJ, Mustonen T, Pandolfi JM, Pettorelli N, Popova E, Robinson SA, Scheffers BR, Shaw JD, Sorte CJB, Strugnell JM, Sunday JM, Tuanmu M-N, Vergés A, Villanueva C, Wernberg T, Wapstra E, Williams SE (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human Well-being. Science 355:eaai9214

Pendleton L, Donato DC, Murray BC, Crooks S, Jenkins WA, Sifleet S, Craft C, Fourqurean JW, Kauffman JB, Marbà N, Megonigal P, Pidgeon E, Herr D, Gordon D, Baldera A (2012) Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. PloS One 7:e43542

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel CV, O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ (2013) Global imprint of climate change on marine life. Nat Clim Chang 3:919–925

Reusch TB, Ehlers A, Hämmerli A, Worm B (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proc Natl Acad Sci 102:2826–2831

Seddon S, Connolly RM, Edyvane KS (2000) Large-scale seagrass dieback in northern Spencer gulf, South Australia. Aquat Bot 66:297–310

Shields EC, Parrish D, Moore K (2019) Short-term temperature stress results in seagrass community shift in a temperate estuary. Estuar Coasts 42:755–764

Short FT, Polidoro B, Livingstone SR, Carpenter KE, Bandeira S, Bujang JS, Calumponge HP, Carruthers TJB, Coles RG, Dennison WC, Erftemeijer PLA, Fortes MD, Freeman AS, Jagtap TG, Kamal AHM, Kendrick GA, Kenworthy WJ, La Nafie YA, Zieman JC (2011) Extinction risk assessment of the world's seagrass species. Biol Conserv 144:1961–1971

Strydom S, Murray K, Wilson S, Huntley B, Rule M, Heithaus M, Bessey C, Kendrick GA, Burkholder D, Fraser MW, Zdunic K (2020) Too hot to handle: unprecedented seagrass death driven by marine heatwave in a world heritage area. Glob Chang Biol 26:3525–3538

Sullivan BK, Trevathan-Tackett SM, Neuhauser S, Govers LL (2018) Host-pathogen dynamics of seagrass diseases under future global change. Mar Pollut Bull 134:75–88

Unsworth RK, McKenzie LJ, Nordlund LM, Cullen-Unsworth LC (2018) A changing climate for seagrass conservation? Curr Biol 28:R1229–R1232

Van der Werf GR, Morton DC, DeFries RS, Olivier JG, Kasibhatla PS, Jackson RB, Collatz GJ, Randerson JT (2009) CO2 emissions from forest loss. Nat Geosci 2:737–738

Van Katwijk MM, Bos AR, De Jonge VN, Hanssen LSAM, Hermus DCR, De Jong DJ (2009) Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Mar Pollut Bull 58:179–188

Vergés A, Steinberg PD, Hay ME, Poore AG, Campbell AH, Ballesteros E, Heck KL, Booth DJ, Coleman MA, Feary DA, Figueira W, Langlois T, Marzinelli EM, Mizerek T, Mumby PJ, Nakamura Y, Roughan M, van Sebille E, Gupta AS, Smale DA, Tomas F, Wernberg T, Wilson SK (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B Biol Sci 281:20140846

Waycott M, Duarte CM, Carruthers TJ, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL Jr, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci 106:12377–12381

Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, De Bettignies T, Bennett S, Rousseaux CS (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Chang 3:78–82

Wernberg T, Bennett S, Babcock RC, De Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA, Wilson S (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353:169–172

Wild S, Krützen M, Rankin RW, Hoppitt WJ, Gerber L, Allen SJ (2019) Long-term decline in survival and reproduction of dolphins following a marine heatwave. Curr Biol 29:R239–R240

Wyatt AS, Hewitt CL, Walker DI, Ward TJ (2005) Marine introductions in the Shark Bay world heritage property, Western Australia: a preliminary assessment. Divers Distrib 11:33–44

Correction to: Ecosystem Collapse on a Sub-Antarctic Island

Dana M. Bergstrom, Catherine R. Dickson, David J. Baker,
Jennie Whinam, Patricia M. Selkirk, and Melodie A. McGeoch

Correction to:
Chapter 2 in: J. G. Canadell, R. B. Jackson (eds.),
***Ecosystem Collapse and Climate Change,* Ecological Studies 241,**
https://doi.org/10.1007/978-3-030-71330-0_2

The original version of Chapter 2 was inadvertently published with incorrect last name of the co-author. The name "Jennie Winham" has now been corrected to "Jennie Whinam".

The updated online version of this chapter can be found at
https://doi.org/10.1007/978-3-030-71330-0_2

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0_14

Index

© Springer Nature Switzerland AG 2021

J. G. Canadell, R. B. Jackson (eds.), *Ecosystem Collapse and Climate Change*,
Ecological Studies 241, https://doi.org/10.1007/978-3-030-71330-0