ECOLOGY, BIODIVERSITY AND CONSERVATION

Invading Ecological Networks

EBC



Invading Ecological Networks

Until now, biological invasions have been conceptualised and studied mainly as a linear process: from introduction to establishment to spread. This volume charts a new course for the field, drawing on key developments in network ecology and complexity science. It defines an agenda for Invasion Science 2.0 by providing new framings and classification of research topics and by offering tentative solutions to vexing problems. In particular, it conceptualises a transformative ecosystem as an open adaptive network with critical transitions and turnover, with resident species learning heuristically and fine-tuning their niches and roles in a multiplayer eco-evolutionary game. It erects signposts pertaining to network interactions, structures, stability, dynamics, scaling and invasibility. It is not a recipe book or a road map, but an atlas of possibilities: a 'hitchhiker's guide'.

CANG HUI is a professor of mathematical biology and holds the South African Research Chair in Mathematical and Theoretical Physical Biosciences at Stellenbosch University. He is a trustee of the International Initiative for Theoretical Ecology. He has published widely on biological invasions and ecological networks.

DAVID M. RICHARDSON is Director of the Centre for Invasion Biology at Stellenbosch University. He is a member of the Species Survival Specialist Group on Invasive Organisms for the International Union for Conservation of Nature. His main expertise is in invasion ecology, and particularly alien tree invasions. He has published extensively on invasive species and restoration ecology.

ECOLOGY, BIODIVERSITY AND CONSERVATION

General Editor Michael Usher, University of Stirling

Editorial Board Jane Carruthers, University of South Africa, Pretoria Joachim Claudet, Centre National de la Recherche Scientifique (CNRS), Paris Tasman Crowe, University College Dublin Andy Dobson, Princeton University, New Jersey Valerie Eviner, University of California, Davis Julia Fa, Manchester Metropolitan University Janet Franklin, University of California, Riverside Rob Fuller, British Trust for Ornithology Chris Margules, James Cook University, North Queensland Dave Richardson, University of Stellenbosch, South Africa Peter Thomas, Keele University Des Thompson, NatureScot Lawrence Walker, University of Nevada, Las Vegas

The world's biological diversity faces unprecedented threats. The urgent challenge facing the concerned biologist is to understand ecological processes well enough to maintain their functioning in the face of the pressures resulting from human population growth. Those concerned with the conservation of biodiversity and with restoration also need to be acquainted with the political, social, historical, economic and legal frameworks within which ecological and conservation practice must be developed. The new Ecology, Biodiversity, and Conservation series will present balanced, comprehensive, up-to-date, and critical reviews of selected topics within the sciences of ecology and conservation biology, both botanical and zoological, and both 'pure' and 'applied'. It is aimed at advanced final-year undergraduates, graduate students, researchers, and university teachers, as well as ecologists and conservationists in industry, government and the voluntary sectors. The series encompasses a wide range of approaches and scales (spatial, temporal, and taxonomic), including quantitative, theoretical, population, community, ecosystem, landscape, historical, experimental, behavioural and evolutionary studies. The emphasis is on science related to the real world of plants and animals rather than on purely theoretical abstractions and mathematical models. Books in this series will, wherever possible, consider issues from a broad perspective. Some books will challenge existing paradigms and present new ecological concepts, empirical or theoretical models, and testable hypotheses. Other books will explore new approaches and present syntheses on topics of ecological importance.

Ecology and Control of Introduced Plants Judith H. Myers and Dawn Bazely Invertebrate Conservation and Agricultural Ecosystems T. R. New

Risks and Decisions for Conservation and Environmental Management Mark Burgman Ecology of Populations Esa Ranta, Per Lundberg, and Veijo Kaitala Nonequilibrium Ecology Klaus Rohde The Ecology of Phytoplankton C. S. Reynolds Systematic Conservation Planning Chris Margules and Sahotra Sarkar Large-Scale Landscape Experiments: Lessons from Tumut David B. Lindenmayer Assessing the Conservation Value of Freshwaters: An International Perspective Philip J. Boon and Catherine M. Pringle Insect Species Conservation T. R. New Bird Conservation and Agriculture Jeremy D. Wilson, Andrew D. Evans, and Philip V. Grice Cave Biology: Life in Darkness Aldemaro Romero Biodiversity in Environmental Assessment: Enhancing Ecosystem Services for Human Well-Being Roel Slootweg, Asha Rajvanshi, Vinod B. Mathur, and Arend Kolhoff Mapping Species Distributions: Spatial Inference and Prediction Janet Franklin Decline and Recovery of the Island Fox: A Case Study for Population Recovery Timothy J. Coonan, Catherin A. Schwemm, and David K. Garcelon Ecosystem Functioning Kurt Jax Spatio-Temporal Heterogeneity: Concepts and Analyses Pierre R. L. Dutilleul Parasites in Ecological Communities: From Interactions to Ecosystems Melanie J. Hatcher and Alison M. Dunn Zoo Conservation Biology John E. Fa, Stephan M. Funk, and Donnamarie O'Connell Marine Protected Areas: A Multidisciplinary Approach Joachim Claudet Biodiversity in Dead Wood Jogeir N. Stokland, Juha Siitonen, and Bengt Gunnar Jonsson Landslide Ecology Lawrence R. Walker and Aaron B. Shiels Nature's Wealth: The Economics of Ecosystem Services and Poverty Pieter J. H. van Beukering, Elissaios Papyrakis, Jetske Bouma, and Roy Brouwer

Birds and Climate Change: Impacts and Conservation Responses James W. Pearce-Higgins and Rhys E. Green Marine Ecosystems: Human Impacts on Biodiversity, Functioning and Services Tasman P. Crowe and Christopher L. J. Frid Wood Ant Ecology and Conservation Jenni A. Stockan and Elva J. H. Robinson Detecting and Responding to Alien Plant Incursions John R. Wilson, F. Dane Panetta and Cory Lindgren Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story Joris P. G. M. Cromsigt, Sally Archibald and Norman Owen-Smith National Park Science: A Century of Research in South Africa Jane Carruthers Plant Conservation Science and Practice: The Role of Botanic Gardens Stephen Blackmore and Sara Oldfield Habitat Suitability and Distribution Models: With Applications in R Antoine Guisan, Wilfried Thuiller and Niklaus E. Zimmermann Ecology and Conservation of Forest Birds Grzegorz Mikusiński, Jean-Michel Roberge and Robert J. Fuller Species Conservation: Lessons from Islands Jamieson A. Copsey, Simon A. Black, Jim J. Groombridge and Carl G. Jones Soil Fauna Assemblages: Global to Local Scales Uffe N. Nielsen Curious About Nature Tim Burt and Des Thompson Comparative Plant Succession Among Terrestrial Biomes of the World Karel Prach and Lawrence R. Walker Ecological-Economic Modelling for Biodiversity Conservation Martin Drechsler Freshwater Biodiversity: Status, Threats and Conservation David Dudgeon Joint Species Distribution Modelling: With Applications in R Otso Ovaskainen and Nerea Abrego Natural Resource Management Reimagined: Using the Systems Ecology Paradigm Robert G. Woodmansee, John C. Moore, Dennis S. Ojima and Laurie Richards The Species-Area Relationship: Theory and Application Thomas J. Matthews, Kostas A. Triantis and Robert J. Whittaker Ecosystem Collapse and Recovery Adrian C. Newton Animal Population Ecology: An Analytical Approach T. Royama Why Conserve Nature? Perspectives on Meanings and Motivations Stephen Trudgill

Invading Ecological Networks

CANG HUI

Stellenbosch University

DAVID M. RICHARDSON

Stellenbosch University



CAMBRIDGE UNIVERSITY PRESS

University Printing House, Cambridge CB2 8BS, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314-321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi - 110025, India

103 Penang Road, #05-06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of the University of Cambridge.

It furthers the University's mission by disseminating knowledge in the pursuit of education, learning, and research at the highest international levels of excellence.

www.cambridge.org

Information on this title: www.cambridge.org/9781108478618 DOI: 10.1017/9781108778374

© Cang Hui and David M. Richardson 2022

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 2022

Printed in United Kingdom by TJ Books Limited, Padstow Cornwall

A catalogue record for this publication is available from the British Library.

ISBN 978-1-108-47861-8 Hardback ISBN 978-1-108-74596-3 Paperback

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.

Imagin'd rather oft than elsewhere seen, That stone, or like to that which here below Philosophers in vain so long have sought, In vain, though by their powerful Art they bind Volatile Hermes, and call up unbound In various shapes old Proteus from the Sea, Drain'd through a Limbec to his native form. John Milton, Paradise Lost, III, 599–605

Contents

	Preface	page xi
	Acknowledgements	xvii
1	Invasion Science 1.0	1
	1.1 Welcome to the Anthropocene	1
	1.2 The Making of a Discipline	7
	1.3 A Unified Invasion Framework	11
	1.4 Pathways and Propagules	12
	1.5 Invasion Dynamics	20
	1.6 Invasiveness and Invasion Syndromes	29
	1.7 From Trees to Networks	38
2	Relentless Evolution	50
	2.1 Learning through Games	50
	2.2 Interaction Strength	62
	2.3 Coexistence and Invasion	69
	2.4 Interaction Rewiring	77
	2.5 Interaction Kernel	81
	2.6 Co-evolution of Traits	85
	2.7 Invasion Hypotheses	97
3	Network Assembly	109
	3.1 Succession and Assembly	109
	3.2 Network Topology and Architecture	121
	3.3 Three Types of Network	131
	3.3.1 Overview	131
	3.3.2 Competitive Communities	137
	3.3.3 Antagonistic Networks	142
	3.3.4 Mutualistic Networks	149
	3.4 Network Emergence	153
	3.4.1 Structural Emergence Models	153
	3.4.2 Co-evolution and Invasion	167

x · Contents

	3.4.3 Ecological Fitting	175
	3.4.4 Open Network Emergence	183
4	Regimes and Panarchy	205
	4.1 Open Adaptive Systems	205
	4.2 Multifaceted System Stability	209
	4.3 Stability Criteria	217
	4.4 Collapses and Panarchy	230
	4.5 Persistent Transition at Marginal Instability	244
5	Network Transitions	265
	5.1 The Forecasting Conundrum	265
	5.2 Early Warning Signals	272
	5.3 Temporal Turnover of Ecological Networks	278
	5.4 Weather Vane of Network Transitions	287
	5.5 Peculiarity of Rarity	299
	5.6 Advice from a Caterpillar	307
6	Network Scaling	318
	6.1 The Rise of Alien Biomes	318
	6.2 Spatial Scaling Patterns	324
	6.3 Dissecting Spatial Communities	338
	6.4 Meta-network Dynamics	347
	6.5 Stability Criteria of Meta-networks	354
	6.6 Percolation Transition	356
7	Rethinking Invasibility	370
	7.1 Invasion Science 2.0	370
	7.2 Eco-evolutionary Dynamics of an Open	
	Adaptive Network	377
	7.3 Network Invasibility	383
	7.4 Central-to-Reap, Edge-to-Elude	385
	7.5 Management in a VUCA World	394
	Glossary	405
	Index	419

Color plates are to be found between pages 206–207

Preface

The I Ching or Book of Changes, published about three thousand years ago, is among the oldest of the Chinese classics. It posits that all things are interlinked and changing, and therefore that the state of any system is in constant flux and transition, while the rules of change are observable in the midst of the diverse patterns of flux exhibited in the interlinked natural world. Indeed, our planet's biosphere, comprising all living things and their interactions, is experiencing unprecedented change, most of it attributable to humans. This rapid change has created a wave of selection, transforming global ecosystems and moulding their structures and functions. Within a few decades we could have entirely new climates and radically altered species compositions and distributions - the emergence of novel networks of biotic interactions extending across multiple scales. The agenda in ecology, however, is largely mired in thoughts of restoring balance and equilibrium. We hope that this book will stimulate readers to think deeply about the concept and ramifications of constant change in our natural world and to ponder the rules of change in our rapidly changing ecosystems.

Alien species, those that have been moved to new areas through human actions, are both drivers and the passengers of the current global change. Although many introduced species fail to establish footholds in new regions, many flourish in their new homes to such an extent that they transform recipient ecosystems. The novel experiences and nonequilibrial dynamics associated with biological invasions, and the complex responses of recipient ecosystems, provide us with a natural experiment to gain an understanding of the rules of change in this emerging transformative ecology. We envisage that the transformative structure and function of an open adaptive ecosystem, driven by eco-evolutionary processes, biological invasions and other drivers of change, will become the mainstay of ecology.

Species do not live alone but share their spaces with many others, both long-time residents and newcomers, the latter often dumped in their

xii · Preface

new homes without co-evolved partners by human activities. Introduced species and the changes they cause to biotic interactions are both key drivers of community succession and assembly. Along the conceptual spectrum of an ecological community, Frederic Clements (1916) proposed the metaphor of a superorganism evolving towards a stable 'climax state'. He further argued that 'climax' formations could arise, grow, mature, die and reproduce. In opposing the ideas of Clements, Henry Gleason (1926) depicted ecological communities as artefacts shaped by these residing species which happened as merely a coincidence and behave in an individualistic manner. Ecological communities are, of course, neither a superorganism nor an artefact, but an entangled web of biotic interactions. As Charles Darwin (1859) so eloquently portrayed at the end of *On the Origin of Species*,

It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us.

We view 'ecological networks' as entangled webs of distinct, interdependent and complex biotic interactions among co-occurring species in a landscape; such webs are also called ecological interaction networks. They are the veins of an ecological community, with the emphasis on the strength and structure of biotic interactions rather than the identity of its residing species. To describe an ecological network, we need to delineate its boundaries, enumerate the resident species and define and elucidate the entangled interactions. When asked to define the boundary of an ecological community, Samuel Scheiner quipped, 'That's where an ecologist stops the car.' Although dispersal barriers, such as rivers, gorges or fences, do create clear edge effects on the distribution of biodiversity, their boundaries seldom coincide neatly with those of ecological networks. As is the case in the concepts of meta-population and meta-community, smaller ecological networks can be connected to form, or are embedded within, much bigger spatial networks - meta-networks. Importantly, delimiting the boundary of ecological networks not only affects how we label a species, resident or alien, but also defines the complexity and impact of the entangled biotic interactions.

Network ecology focusses on understanding the functions that emerge from the complexity of biotic interactions; each residing species is thus conscripted into a community by virtue of its functional traits (typically invoking Eltonian niches), not by its identity per se. Mark Davis and colleagues (2011) have argued that we should judge a species not by its origin but rather by its functional roles in an ecosystem. Such views, when considered from the perspective of network ecology and conservation science, represent a paradigm shift from the classic species-centric view towards one focussed on the safeguarding ecosystem functioning and services in the Anthropocene. All crises beget opportunities. Faced with massive ongoing extinctions and failed conservation attempts, such as the Aichi Biodiversity Targets, Chris Thomas (2017) called for ecologists to embrace opportunities created by biological invasions and other facets of global change to deal with anticipated species losses. Such challenges force us to confront critical questions. Can we replace a community of native species with one comprising a mixture of native and alien species while ensuring the same or even more desirable functioning and services? What makes an alien species different from a resident native species?

Ecological networks are far more than just ensembles of co-occurring species. Species interact with each other in a network not simply through trait matching; Dan Janzen (1985) coined the term 'ecological fitting' for this. Species also co-adapt and co-evolve relentlessly, as J. N. Thompson puts it (2013). This is not a jigsaw puzzle, but a melting pot. It is messy and unpredictable. We cannot simplify the ways of change in an ecological network as actions and reactions. As Robert Holt opined, parsimony is the rule of reasoning, but not necessarily the way of nature. Ecological networks, to us, are therefore multi-agent, complex and adaptive systems. Ecosystems facing biological invasions are, consequently, ideal models for studying the structure and function of an open, complex, adaptive and dynamic network.

The young and vibrant discipline of invasion science has a wide range of focal research agendas and uses diverse approaches to address theoretical and practical issues. The field is, however, converging on a few unifying frameworks that serve to unite and clarify concepts and define the most pressing questions (Wilson et al. 2020). One of the most widely accepted frameworks in invasion science is a species-centric linear scheme that conceptualises barriers as mediators of progression of the species through different invasion stages (Richardson et al. 2000). Building on the mantra of this barrier construct, a unified framework for invasion biology was proposed to elucidate the factors that drive this progression along a linear introduction–naturalisation–invasion continuum (Blackburn et al. 2011).

xiv · Preface

This has served as a roadmap for both theoretical and applied studies. Management-focussed work has sought effective intervention strategies to curb or slow progression along the invasion continuum. In adopting this invasion construct, substantial effort has gone into applying correlative statistics to identify the functional traits that allow species, or groups of species, to overcome different barriers. Macroecological approaches are often applied to compare, for example, the niches of alien species in their invaded versus their native ranges; the traits of aliens and those of ecologically similar native species; or to identify traits and environmental factors associated with alien species of contrasting invasion stages. Such research has, to some extent, unified management practices and has yielded reasonable, albeit often unsatisfying, insights into invasion dynamics. This invader-centric phase is unpacked when we describe what we term Invasion Science 1.0 in Chapter 1.

The other chapters of this book explore the potential of a new agenda for invasion science, and perhaps also for global change biology more broadly. In particular, we try to build on tentative steps taken to address key questions pertaining to biological invasions using concepts and tools developed in the fields of network science for complex systems. In a complex system, feedback loops can push a network towards a state of paradox – although patterns derived from observations are highly structured in retrospective views (e.g., invasive traits can be clearly identified from comparative studies), predictions based on such observed structures often perform poorly and have high levels of uncertainty. This is akin to weather forecasts, earthquake predictions or shares in the stock market. Retrospectively, clear patterns emerge from interpolation, but forward extrapolation normally fails. In this new paradigm, we explore such failures, expose their potential causes and propose a way forward.

In tackling the state of paradox facing Invasion Science 1.0, in line with rapid advances in community, network, evolutionary and systems ecology, we tentatively suggested in our earlier book *Invasion Dynamics* the need to shift the metaphor of biological invasions from one based on the linear invasion continuum scheme to one that invokes complex adaptive networks (Hui and Richardson 2017). In the section of our book titled 'Invasion Science 2050' we suggested that such a restructuring is 'not just a call for next-generation quantitative methodologies to improve detection and measurement of feedback loops in ecology' but also 'an appeal for a paradigm shift in ecology and invasion science to embrace adaptive cycles and network thinking'. As the first step in this direction we offered a tentative blueprint of Invasion Science 2.0 in a

paper titled 'How to Invade an Ecological Network' (Hui and Richardson 2019). There, we unpacked the practical difficulties and challenges that emerge when seeking to marry concepts and tools from network ecology and invasion ecology. We also demonstrated the potential of this network–invasion synergy by providing a simple generic model. This book expands substantially on this thesis.

We plan to expand our vision for Invasion Science 2050 (Hui and Richardson 2017, 2019) and elucidate the core conceptual issues that need to be considered in the transition towards Invasion Science 2.0. After cherry-picking the key concepts of Invasion Science 1.0 in Chapter 1, the remaining six chapters of the book expand on six core concepts that are essential for understanding how ecological networks harbour numerous interacting species, adapt and respond to biological invasions, as well as the role of each species, native or alien, in this complex multiplayer game. In a nutshell, we hope to show how biotic interactions operate as the building blocks of ecological networks (Chapter 2); the emergence of network complexity and architecture (Chapter 3); how biological invasions modify and break the network complexity-stability relationship, and push the system regime towards marginal instability (Chapter 4); network dynamics, as well as invasion performance, at marginal instability; (Chapter 5); how the response of network structure and function to biological invasions plays out over ranges of spatial and temporal scales (Chapter 6); and finally to ponder on the concept of network invasibility as the sweet-spots in the functional trait space to achieve elevated invasion performance in an adaptive ecological network (Chapter 7).

In 1889, King Oscar II of Sweden established a prize for the *n*-body problem in mathematics and physics,

Given a system of arbitrarily many mass points which attract each other according to Newton's laws, try to find, under the assumption that no two points ever collide, a representation of the coordinates of each point as a series in a variable which is some known function of time and for all of whose values the series converges uniformly.

We now face a similar but perhaps even more complex *n*-species problem in ecology. To paraphrase King Oscar II's letter: given an ecological network of arbitrarily many species which engage with each other according to trait-mediated density-dependent inter- and intraspecific biotic interactions, under the assumptions that new species can invade this ecological network and that the resident species can become

xvi · Preface

extinct or be extirpated, we need to predict, for a meaningful time span, the population dynamics of each species, including both the invaders and those resident species, and the evolutionary dynamics of their functional traits. This is the subject of our book. It is not a recipe book, but a hitchhiker's guide, a cloud atlas, to the adventures of future ecology.

References

- Blackburn TM, et al. (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26, 333–339.
- Clements FE (1916) Plant Succession: An Analysis of the Development of Vegetation. Washington, DC: Carnegie Institute of Washington Publication Sciences.
- Darwin CR (1859) On the Origin of Species by Means of Natural Selection. London: John Murray.
- Davis M, et al. (2011) Don't judge species on their origins. Nature 474, 153-154.
- Gleason HA (1926) The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53, 7–26.
- Hui C, Richardson DM (2017) Invasion Dynamics. Oxford: Oxford University Press.
- Hui C, Richardson DM (2019) How to invade an ecological network. Trends in Ecology & Evolution 34, 121–131.
- Janzen D (1985) On ecological fitting. Oikos 45, 308-310.
- Richardson DM, et al. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* **6**, 93–107.
- Thomas CD (2017) Inheritors of the Earth: How Nature Is Thriving in an Age of Extinction. London: Penguin Books.
- Thompson JN (2013) Relentless Evolution. Chicago: University of Chicago Press.
- Wilson JRU, et al. (2020) Frameworks used in invasion science: progress and prospects. NeoBiota 62, 1–30.

Acknowledgements

We are grateful to so many colleagues and friends who have over the years discussed and collaborated with us, either casually or formally, on topics that somehow shaped our thinking on issues covered in this book. Many students and postdoctoral fellows have passed through our labs; their sparks of inspiration and inquisitiveness spurred us on to dig deeper into this topic. These include, in alphabetical order, Ashleigh Basel, Cecile Berthouly-Salazar, Oonsie Biggs, Tim Blackburn, William Bond, Luz Boyero, Åke Brännström, Chris Broeckhoven, Marc Cadotte, Jonathan Chase, Susana Clusella-Trullas, Franck Courchamp, Richard Cowling, Helen de Klerk, Ulf Dieckmann, Genevieve Diedericks, Benjamin du Toit, Allen Ellis, Marcela Espinaze, Franz Essl, Gordon Fox, Llewellyn Foxcroft, Mirijam Gaertner, Laure Gallien, Richard Gibbs, Lev Ginzburg, Dominique Gravel, Jessica Gurevitch, Xiaozhuo Han, Fangliang He, Steve Higgins, Marinel Janse van Rensburg, Jonathan Jeschke, Jan-Hendrik Keet, Ingolf Kuhn, Christian Kull, Sabrina Kumschick, Bill Kunin, Vitalis Lagat, Pietro Landi, Gilbert Langat, Guillaume Latombe, Jaco Le Roux, Jingjing Liang, Sandy Liebhold, Sandra MacFadyen, Denise Mager, Anne Magurran, Mario Marial, Sonja Matthee, Melodie McGeoch, John Measey, Guy Midgley, Joe Miller, Ony Minoarivelo, Mozzamil Mohammed, Jane Molofsky, Assumpta Nnakenyi, Ana Novoa, Savannah Nuwagaba, Anton Pauw, David Phair, Luke Potgieter, Petr Pyšek, Andriamihaja Ramanantoanina, Axel Rensberg, Mark Robertson, James Rodger, Mathieu Rouget, Núria Roura-Pascual, Helen Roy, Nate Sanders, Jeff Sanders, Wolf-Christian Saul, Maria Schelling, Ross Shackleton, Min Su, Lawal Suleiman, John Terblanche, Jessica Toms, Anna Traveset, Brian van Wilgen, Nicola van Wilgen, James Wilsenach, Sofia Vaz, Peter Verburg, Joana Vicente, Vernon Visser, Sophie von der Heyden, Klaus von Gadow, Olaf Weyl, John Wilson, Darragh Woodford, Theresa Wossler, Yinghui Yang, Dongxia Yue, Feng Zhang and Zihua Zhao.

We have surely missed some names here. Forgive us.

xviii · Acknowledgements

The opportunities for research and friendly collaboration across traditional disciplinary boundaries provided by sixteen years of funding to the DSI-NRF Centre of Excellence for Invasion Biology (C·I·B) cannot be overstated. It has been an exhilarating ride. We also acknowledge financial support from South Africa's National Research Foundation (grants 85417 and 89967 in particular), the Australian Research Council (grant DP200101680), the UK's Natural Environment Research Council (grant NE/V007548/1) and the Oppenheimer Memorial Trust (grant 18576/03).

We appreciate the great editorial support from Dominic Lewis, Michael Usher, Samuel Fearnley and Aleksandra Serocka at Cambridge University Press. We are also grateful to Jonathan Downs, Vanessa du Plessis, Larisse Bolton and Charndré Williams for their assistance in preparing the reference lists and handling copyright issues.

Lastly, we thank our families, Beverley, Keira and Zachary Hui, and Corlia and Sean Richardson, for their patience and tremendous support during the writing of this book, especially through the extended period of time over the lockdown due to the COVID-19 pandemic.

1 • Invasion Science 1.0

This [invasion] velocity is proportional to the square root of the intensity of selective advantage and to the standard deviation of scattering in each generation.

(Fisher 1937)

1.1 Welcome to the Anthropocene

At the time of writing this book, we have witnessed an extreme case of biological invasion. A virus, through an evolutionary leap, has jumped onto a new host species, Homo sapiens, and has taken advantage of the new host's ambitions and mobility in the zealous phase of globalisation, causing a worldwide pandemic and economic meltdown. The 2019 coronavirus outbreak (COVID-19) is a showcase of the core of invasion science. A list of questions spring to mind. Why this particular virus, and not others? Why now? How fast can it spread? How is its spread mediated by climatic and other environmental factors? What are its vectors and pathways of transmission? Which regions and populations are most susceptible? How much damage can it cause to public health and economies? What factors cause substantial variation in mortality between human populations in different countries? How can we control it? Can we forecast and prevent future outbreaks of emerging infectious diseases? While the whole world scrambles to make sense of COVID-19 and to combat the biggest crisis for humanity since World War II (WWII), we embark on a journey to address these questions to cover many more taxa and situations - the invasion of any biological organism into novel environments.

All species have the means to shift their progeny, either via direct movement or through vector-mediated dispersal. The incentive to move has driven Earth's biota to cover all possible niches, from the Antarctic to the Arctic, from the Himalayas to the Mariana Trench. Most propagules,

2 · Invasion Science 1.0

however, move slowly and over short distances. On very rare occasions do propagules catch a ride on ocean rafts or hurricanes, or become attached to a seabird. Such propensity and limitation of dispersal are key factors behind the world's distinct biotic zones. This process of natural dispersal and spread of species was altered by early hominids. Hunter-gatherer societies had deep knowledge of the animals and plants around them and started to cultivate many species to ensure a sustainable supply of food and fibre. When humans began colonising the entire planet, cultivated plants and animals moved with them, the result being a growing list of species able to thrive in human-dominated environments, with the capacity to transform landscapes. Not only did humans intentionally move many species with them to supply their needs, but their movements also resulted in the accidental movement of many species. These include species associated with useful organisms, such as yeasts, viruses and other microorganisms, and many other types of pest and weed that simply 'hitched a ride' on diverse means of transport. Human selection has resulted in a rather unique assemblage of species, distinct from those that occur in natural communities and which are filtered by natural selection.

Human-mediated movement of species has accelerated dramatically in the era of globalisation, in terms of quantity, distance and speed. Technological innovations have revolutionised ways in which we transport goods. Stretching from Xi'an to Rome, the Silk Road connected the Eurasian supercontinent as early as the first century BC, carrying goods on the backs of horses and camels. Islamic merchants created the Spice Route in the seventh century, thereby connecting the Mediterranean Sea and the Indian Ocean. Global trade started in earnest in the Age of Discovery, when European explorers connected East and West with the Americas in the fifteenth century. Global trade scaled up after the first Industrial Revolution in the eighteenth and nineteenth centuries when global production chains began compartmentalising (e.g. meat export from South America). The trajectory has been interrupted only by two World Wars and the COVID-19 pandemic. After WWII, globalisation resumed its march with the mainstream transport of cars, ships and planes (global export totalling US\$62 billion in 1950), only being slowed temporarily by the Iron Curtain during the Cold War. A milestone of this globalisation was the launch of the World Trade Organisation in 1995, when global exports reached US\$5 trillion. Globalisation then soared over the next two decades, with bumps along the way during the 2008 recession and the COVID-19 pandemic,



Figure 1.1 Global GDP, in international dollars (2011 price), and world population, in the past two millennia. Based on data from ourworldindata.org under CC-BY Licence.

reaching close to US\$19 trillion in 2014. Real gross domestic product (GDP) per capita in the United States in 2014 was four times the size it was in 1950. The human population increased from 2.5 billion in 1950 to 7 billion in 2012 (Figure 1.1), and is projected to reach 10 billion in 2050. Not only has our ecological footprint overshot the planet's carrying capacity, but there are also emerging global crises that are threatening the whole of humanity (e.g. climate change, biodiversity loss and the pandemic).

With the rising dominance of humans in the biosphere, previously characteristic floras and faunas in regional biotic zones have been mixed and reshuffled, resulting in a major homogenisation of the world's biota. The accumulation of non-native species across the globe is continuing with no sign of a slowing of the rate of new records of naturalisation and invasion (Seebens et al. 2017). Putting aside biases in taxonomy and sampling effort, the trend in the global rate of new records of established non-native species is overwhelming (Figure 1.2). Geographic and taxonomic variations in the dynamics and rate of non-native establishment reflect the role and history of regional countries in global trade. With the rise of global trade, the rate of establishment of non-native species has increased steadily, as stowaways, contaminants and pets since 1800, and



Figure 1.2 Global temporal trends in the rates of first records of the establishment of non-native species. Global temporal trends in first record rates (dots) for all species (a) and taxonomic groups (b–q) with the total number of established non-native species during the respective time periods given in parentheses. Data after 2000 (grey dots) are incomplete because of the delay between sampling and publication, and therefore not included in the analysis. As first record rates were recorded on a regional scale, species may be included multiple times in one plot. (a) First record rates are the number of first records per year during 1500-2014. (b–q) First record rates constitute the number of first records per 5 years during 1800-2014 for various taxonomic groups. The trend is indicated by a running median with a 25-year moving window (red line). For visualisation, 50-year periods are distinguished by white/grey shading. From Seebens et al. (2017) under CC-BY Licence.

accelerated further after 1950 – with the sole exception of mammals and fishes, which exhibit a hump-shaped curve, perhaps due to the regulations on farming for the game and fur industry. The establishment of non-native plant species has maintained a high rate since 1900 (Figure 1.2), coinciding with acclimatisation and colonisation activities in European diasporas. Technology has enabled us to move species around the world in new ways, quickly and in huge numbers; and changing fashions, fads and desires of human societies are continuously modifying and expanding the catalogue of translocated species – not just for essential goods but also for peculiar luxuries and hobbies. We need new ways of categorising and managing the new assemblages of biota that occur in different environments. Not only do we need to understand how many species are moved around the world by humans, but we also need to understand how these species interact with other species and how the added species and the changes that they bring affect the functioning of ecosystems, and thereby influence our well-being, both positively and negatively.

Biological invasions are by no means the only driver of the massive global-scale environmental changes that we are seeing. Invasive species interact in complex ways with other key builders and shapers of novel ecosystems such as agriculture, urbanisation, altered biogeochemical cycles, excessive carbon emission and pollution. For instance, of the documented 291 records of plant species extinction (Le Roux et al. 2019), agriculture, urbanisation, grazing, habitat degradation and destruction, together with biological invasions, are found to be implicated. The exact role of each of these factors is difficult to discern in most cases, but each surely has its own distinct temporal pattern and role to play (Figure 1.3). With these burgeoning factors affecting the planet's biosphere, we are witnessing pervasive alterations to physical systems, disturbance regimes and biogeochemical cycles, leading to a downward spiral in the integrity and health of ecosystems, accompanied by biodiversity loss and ecosystem transformation. In some cases, biological invasions are directly responsible for the decline of native biota, e.g. native plant species in Mediterranean-type ecosystems have been severely affected by nonnative plants, particularly by Australian acacias (Figure 1.4; Gaertner et al. 2009). Recent reviews on the role of biological invasions in reducing the biodiversity of recipient ecosystems overwhelmingly support this view of the detrimental role of invasive species, more so at local than regional levels (Figure 1.5; Chase et al. 2018). These forces of change sometimes reinforce each other at different spatial and temporal scales, often with lags, leading to complex and intertwined challenges to the well-being of humanity and ecosystems (Díaz et al. 2015; Essl et al. 2015a). On this wagon of humanity, many hitchhiker species proliferate, creating harmful impacts on human well-being. The huge number of species that have been transported by us in different quantities and rates, intentionally or not, directly or not, define the subject and context of invasion science (Pyšek et al. 2020a).

6 · Invasion Science 1.0



Figure 1.3 Primary drivers of plant extinctions over the last 300 years shown as area graphs to visualise the temporal changes in the relative contribution of the 11 identified primary extinction causes. Data from Le Roux et al. (2019).



Figure 1.4 Effect size (95% Cl) of invasion on species richness for different (a) unit sizes and (b) taxonomical groups in Mediterranean-type ecosystems. Q-test shows significant different effect sizes (heterogeneity) between unit sizes and between species. From Gaertner et al. (2009), reproduced with permission.



Figure 1.5 Results of a meta-analysis of scale-dependent responses to a number of different ecological drivers. Points represent the log response ratio comparing species richness in control to treatments in a given comparison measured at the smallest (x-value) and largest (y-value) scale. The solid line indicates the 1:1 line expected if effect sizes were not scale dependent. Points above and below this line indicate effect sizes that are larger or smaller, respectively, as scale increases; points in the upper left and lower right quadrants represent cases where the direction of change shifted from positive to negative, or vice versa, with increasing scale. The dashed line indicates the best fit correlation, which is significantly different than the 1:1 line (P < 0.01), indicating that overall, effect sizes tend to be larger at smaller scales than at larger scales. Colours for points indicate categorisations into different ecological drivers. From Chase et al. (2018), reproduced with permission.

1.2 The Making of a Discipline

Although the human-mediated translocation of species has been documented anecdotally since antiquity, the concept of biological invasions is a very recent construct. Many naturalists in the 1800s wrote of non-native species, but it was only in the mid-1900s that the scale of human-mediated movements of species and the growing importance of the implications of such movement became apparent. Pioneers of ecology in the nineteenth century – among them Charles Darwin, Augustin and his son Alphonse de Candolle, Joseph Dalton Hooker and Charles Lyell – explored the role and performance of a small number of non-native species in competition with indigenous ones. Lyell (1832) wrote,

8 · Invasion Science 1.0

every species which has spread itself from a small point over a wide area, must, in like manner, have marked its progress by the diminution, or entire extirpation, of some other, and must maintain its ground by a successful struggle against the encroachments of other plants and animals.

Such appreciation of invasive spread leading to species extinctions predates the rise of global change biology in the late twentieth century (Wilkinson 2002). When writing about the European thistle cardoon, *Cynara cardunculus*, in his journal of research into the geology and natural history of the various countries visited by HMS *Beagle*, Darwin (1839) commented,

I doubt whether any case is on record, of an invasion on so grand a scale of one plant over the aborigines [of South America].

Following these early accounts of non-native species, many ecologists in the early twentieth century began synthesising the scattered knowledge of the ecology of non-natives, unknowingly taking the first tentative steps towards creating a framework for conceptualising biological invasions. Albert Thellung, in his 1912 Habilitation thesis *La Flore Adventice de Montpellier*, offered an early population-based definition of naturalisation which implied the notion of penetration of environmental barriers. He also devised concepts to classify the nonnative flora of Montpellier in France according to their degree of naturalisation, introduction pathways and residence time (Kowarik and Pyšek 2012). Unfortunately, such work did not have much, if any, influence on the emerging field of ecology, and the ideas were only rediscovered in the late twentieth century, as the underpinning concepts of invasion science began coming under intense scrutiny.

Charles Elton's (1958) classic book *The Ecology of Invasions by Animals* and *Plants* is recognised as a milestone in the development of the field now known as invasion science (Richardson and Pyšek 2007, 2008). Already expressed in Elton's (1927) book on *Animal Ecology*, the Eltonian niche is an important concept for formulating a species' position in an ecological network using its functional traits, as will be elaborated in later chapters. Following this line of thinking, Elton (1958) speculated that island assemblages are filtered for a small portion of colonisers, which subsequently cannot fully explore the island's resources and are therefore more susceptible to invasions than those on the mainland. However, the publication of Elton's book was not immediately followed by a significant rallying of research effort. Unlike some other books on environmental topics, Elton's book on invasions had a negligible impact on public perceptions and launched no major actions (Hobbs and Richardson 2010). At about the same time as Elton's book appeared, geneticists began synthesising concepts pertaining to the evolution and genetics of colonising species (Baker and Stebbins 1965). These insights provided crucial stepping stones to the development of the central tenets of invasion science, including the determinants of invasion success, lifehistory trade-offs, generalist versus specialist strategies, general-purpose genotypes, adaptive phenotypic plasticity, mating systems and the influence of bottlenecks on genetic variation (Barrett 2015). Perhaps the most important linkage of Elton's (1958) classic volume to the theme of our book is his notion that decreased diversity leads to decreased stability. This complexity-stability relationship has stimulated long-lasting debates in ecology with substantial inputs from many figures in the field, including Robert MacArthur, Robert May and G. Evelyn Hutchinson. As will be shown in Chapter 4, ecological networks facing biological invasions typically violate this relationship but simultaneously reveal their trajectory of transition and turnover.

In 1980, the third international conference on mediterranean-type ecosystems, termed MEDECOS, was held in Stellenbosch, South Africa. The invasion of fynbos vegetation by non-native trees, a prominent topic of discussion at this meeting, conflicted with the dominant view of the time, which was that human-induced disturbance was the prerequisite for invasion into pristine ecosystems. A proposal drafted at the Stellenbosch meeting led to an international programme on the ecology of biological invasions under the auspices of the Scientific Committee on Problems of the Environment (SCOPE) (Mooney 1998). Its first five-year plan (1982-1986) revisited Elton's key assumptions and generalisations, reviewed the status of invasions worldwide and addressed three key questions relating to invasiveness, invasibility and management. The SCOPE programme attracted some of the world's top ecologists and comprised national, regional and thematic groups covering all aspects of invasions (Drake et al. 1989). Through the SCOPE programme, invasion science has firmly established itself as an exciting and relevant research field within global change biology (Simberloff 2011). In 1996, an influential conference in Trondheim, Norway, concluded that invasions had become one of the most significant threats to global biodiversity and called for a global strategy to address the problem (Mooney 1999; Sandlund et al. 1999). This led to the launch of the Global Invasive Species Programme (GISP Phase 1) in 1997, with more transdisciplinary goals than the SCOPE programme, acknowledging the need for work on economic valuation, stakeholder participation and pathway analysis and management (Mooney et al. 2005). The Convention on Biological Diversity (CBD), Article 8(h), calls on member governments to control, eradicate or prevent the introduction of those non-native species that threaten ecosystems, habitats or species. In 2000, the IUCN published their guidelines for the prevention of biodiversity loss caused by non-native invasive species. The 1990s saw the blossoming of invasion science, with the number of publications growing rapidly in all related fields (Vaz et al. 2017). In 2018 the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) launched a thematic assessment of invasive non-native species and their control.

Invasion science, as is the case with any emerging discipline, has exhibited different phases. From 1950 to 1990, studies on biological invasions were rather sparse, with fewer than ten publications per year according to the ISI Web of Science. In 1999, the journal *Biological Invasions* was launched, with its founding editor James T. Carlton (1999) stating,

[the aim of] *Biological Invasions* [the journal] ... is to seek the threads that bind for an evolutionary and ecological understanding of invasions across terrestrial, fresh water, and salt water environments. Specifically, we [the journal] offer a portal for research on the patterns and processes of invasions across the broadest menu: the ecological consequences of invasions as they are deduced by experimentation, the factors that influence transport, inoculation, establishment, and persistence of non-native species, the mechanisms that control the abundance and distribution of invasions, and the genetic consequences of invasions.

The period 1990 to 2010 saw the rapid rise of invasion science and its multidisciplinary tentacles (Richardson et al. 2011; Vaz et al. 2017). During this phase, competing concepts, hypotheses, models and know-ledge frameworks have been proposed and debated, and consensus has been reached on many fronts; we call this 'Invasion Science 1.0'. Knowledge systems developed during this period accumulated mainly through individual case studies and comparative studies, with the focus being on the invader itself. Developments in the study of invasions at this time must be considered within the context of the intellectual landscape of the day. Indeed, following the Clements–Gleason debate, the Gleasonian individualistic notion that species function independently from the influence of others was implicitly accepted by most researchers as the foundation on which to build frameworks and concepts about

ecological communities (Mascaro et al. 2013). As a result, Invasion Science 1.0 sought synergies mainly with population ecology, initially, and macroecology, more recently. The toolbox assimilated via this route served the field reasonably well, until problems began emerging early in the new millennium. As detailed later in this chapter, the growing frustration from contextual complexity and the lack of genuine predictability in invasion science, tentatively due to Gleason's individualistic view, has driven many to search for alternatives, especially with the rise of network science, and call for the synergy between invasion science and community and network ecology; we call this 'Invasion Science 2.0' – the focus of this book. To start off, however, we use the rest of this chapter to delve into Invasion Science 1.0 and discuss its key concepts, achievements and shortcomings.

1.3 A Unified Invasion Framework

With the flourishing of invasion science in the new millennium, a number of frameworks emerged that were grasped by researchers to guide research on the ecology and management of invasions (Wilson et al. 2020a). Several protocols were proposed to synthesise the current understanding of invasiveness and invasibility into simple flow-chart models for assessing the risk of newly introduced species becoming invasive. The Australian Weed Assessment scheme (originally proposed by Pheloung et al. 1999) has been the most widely applied of these protocols. Phase 2 of GISP (2006-2010) set out to improve the scientific basis for decision-making to enhance the ability to manage invasive species; assess the impacts of invasions on major economic sectors; and create a supportive environment for the improved management of invasions. This initiative stimulated many new directions in research to elucidate the multiple dimensions of the impacts of invasive species and to utilise existing knowledge and incorporate new ideas and methodologies to inform options for management (e.g., Richardson et al. 2000; Clout and Williams 2009; Wilson et al. 2017). Substantial progress was made towards deriving general models of invasion, such as the 'unified framework for biological invasions' (Blackburn et al. 2011), which sought to merge insights from many previous attempts to conceptualise key aspects of invasion dynamics for all taxa (Figure 1.6; Table 1.1). This model, reinforcing the utility of conceptualising the many processes implicated in the phenomena of biological invasions using a series of barriers along an introduction-naturalisation-invasion continuum, has

12 · Invasion Science 1.0



Figure 1.6 The unified framework for biological invasions. The framework recognizes that: the invasion process can be divided into a series of stages; that in each stage there are barriers that need to be overcome for a species or population to pass on to the next stage; that species are referred to by different terms depending on the stage in the invasion process they have reached; and that different management interventions are feasible at different stages. Different parts of this framework emphasise views of invasions that focus on individuals, populations, processes or species. The unfilled block arrows describe the movement of species along the invasion framework with respect to the barriers; alphanumeric codes associated with the arrows relate to the categorisation of species with respect to the invasion pathway given in Table 1.1. From Blackburn et al. (2011); reproduced with permission.

been widely applied (Wilson et al. 2020b). It provided an objective framework for linking theoretical and applied aspects in invasion science, and reinforced the foundations for a standard lexicon of terms for the field of invasion science (Richardson et al. 2011).

1.4 Pathways and Propagules

The premise of any biological invasion is the introduction of non-native propagules via invasion pathways that are required to breach ecological barriers and physical distance. Elton (1958) summarised his view in a chapter called 'The Invasion of the Continents', on pathways and the breakdown of geographic isolation through human-induced movement of organisms around the world. He likened the continents to great tanks of water, connected by narrow tubing blocked by taps. Using this

Table 1.1 A	categorisation .	scheme for	populatio	ons in	the un	ified f	ramework
of biological ir	wasions. From	Blackburr	ı et al. (2	2011).			

Category	Definition
А	Not transported beyond limits of native range
B1	Individuals transported beyond limits of native range, and in captivity or quarantine (i.e., individuals provided with conditions suitable for them, but explicit measures of containment are in place)
B2	Individuals transported beyond limits of native range, and in cultivation (i.e., individuals provided with conditions suitable for them but explicit measures to prevent dispersal are limited at best)
B3	Individuals transported beyond limits of native range, and directly released into novel environment
C0	Individuals released into the wild (i.e., outside of captivity or cultivation) in location where introduced, but incapable of surviving for a significant period
C1	Individuals surviving in the wild (i.e., outside of captivity or cultivation) in location where introduced, no reproduction
C2	Individuals surviving in the wild in location where introduced, reproduction occurring, but population not self-sustaining
C3	Individuals surviving in the wild in location where introduced, reproduction occurring and population self-sustaining
D1	Self-sustaining population in the wild, with individuals surviving a significant distance from the original point of introduction
D2	Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction
Е	Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence

analogy, he conceptualised the processes of biological invasions as interlinked tanks of propagule sources via introduction tubes (Figure 1.7),

Fill these tanks with different mixtures of a hundred thousand different chemical substances in solution... then turn on each tap for a minute each day... the substances would slowly diffuse from one tank to another. If the tubes were narrow and thousands of miles long, the process would be very slow. It might take quite a long time before the system came into final equilibrium, and when this happened a great many of the substances would have been recombined and, as specific compounds, disappeared from the mixture, with new ones from other tanks taking their places. The tanks are the continents, the tubes represent human transport along lines of commerce.



Figure 1.7 Elton's vision of global biological invasions across continents via invasion pathways. Artwork by Lorraine Blumer. Copyright: DSI-NRF Centre of Excellence for Invasion Biology. Reproduced with permission.

Six such introduction tubes, now known as invasion pathways, have been described (Table 1.2; Hulme et al. 2008) and adopted by the CBD. Invasion management targeting surveillance, mitigation and rapid response can efficiently target related invasion pathways and associated non-native taxa, before the species can gain foothold in new territories. Except for the unaided pathway of natural dispersal, the rest reflect clear management negligence and surveillance gaps that should be targeted by various different agencies (Hulme 2015). When combined with the unified framework (Section 1.3), biological invasions via different pathways were found to have different levels of invasion performance (Wilson et al. 2009). For instance, of those non-native plant species introduced to Central Europe, the pathways of release and contamination have resulted in higher than expected proportions of naturalised and invasive species, whereas the pathways of escape and stowaway do not (Pyšek et al. 2011). Each pathway also faces its own cataloguing issues as multiple pathways can be involved in one invasion, while the contribution of each pathway to non-native species introduction varies in terms of geographic, taxonomic and temporal contexts (Essl et al. 2015b).

Table 1.2 Six invasion pathways and related policy issues. Several key science and policy issues that should be considered if invasion pathways are to be successfully managed to prevent the introduction of invasive non-native species. From Hulme (2015) with modified examples.

Pathway	Example	Science issues	Policy issues
Release Escape	The Asian Carp was introduced to the southern United States to clean commercial ponds in the 1970s but considered invasive by US FWS in 2006 and threatening the Great Lakes ecosystem. Wild pet trade, for	Improved risk assessment tools to quantify the likelihood of economic, environmental and social impact of species with no prior history of introduction outside their native range. Identify current	Legislation that holds parties undertaking assisted colonisation responsible for any costs arising from the impacts and management of such introductions (e.g., assurance bonds).
	example, Burmese python <i>Python</i> <i>bivittatus</i> (Kuhl) in Florida.	commercial activities affecting risk management in the wild pet trade, reasons for non-compliance and ways to change such behaviours.	approach to the trade in wild pet species, based on sound risk assessment yet also offering significant commercial benefits.
Contaminant	As a result of adult beetles or larvae hidden in wooden pallets on a ship, the Polyphagous Shot Hole Borer <i>Euwallacea</i> <i>fornicatus</i> is rapidly killing trees in South Africa by transmitting the fungus <i>Fusarium</i> <i>euwallaceae</i> .	Enhanced next- generation DNA tools and biosystematic data to allow rapid screening of live commodities for cryptic pathogens and parasites.	Extend existing policies on risk prevention of emerging diseases to address the threats posed to biodiversity and ecosystem function.

(cont.)

16 · Invasion Science 1.0

Table 1.2 (cont.)

Pathway	Example	Science issues	Policy issues
Stowaway	Tourists might carry SARS-CoV-2 and cause the COVID-19 pandemic.	Analyse the risks from increasing tourist numbers, changes in countries of origin of tourists and shifts in location and types of tourism activities.	Robust codes of practice for tourism operators, aiming to prevent the introduction and movement of invasive non-native species.
Corridor	Canal development, for example, rabbitfish <i>Siganus</i> <i>luridus</i> introduced through Suez Canal.	Better prediction of the invaders that might be facilitated by corridors, the potential costs of future impacts and the value of practical measures to mitigate impacts.	International legislation to support environmental risk assessments of major infrastructure projects that include transboundary consequences.
Unaided	Lyme disease outbreak in Canada from bacteria <i>Borrelia</i> <i>burgdorferi</i> transmitted through bites by immature blacklegged ticks (the vector has extended its northern range potentially due to climate change).	New modelling tools to predict how wind and sea currents as well as extreme weather events can lead to long-distance dispersal of non- native species.	Polluter pays principle applied where countries fail to contain or eradicate an invasive non-native species with potential to cause detrimental impacts should it spread beyond national borders.

For example, the invasion of marine species in Western Europe is predominantly driven by shipping and aquaculture, whereas in the Eastern Mediterranean countries marine invasions are largely the result of the human-mediated opening of corridors, in this case largely the Suez Canal (Figure 1.8a). After WWII, aquaculture gradually declined as an (a) Marine species



Figure 1.8 Geographic, taxonomic and temporal variation in the importance of the main pathways of introduction for non-native (a) marine species, (b) freshwater species or (c) terrestrial arthropods in Europe. The size of the pie charts indicates the approximate numbers of non-native species per recipient country of first introduction. Temporal trends of new introductions (the right panels) are given as black lines (the right axes). The pathway 'Suez Canal' (a) refers to Red Sea species that moved unaided into the Mediterranean via the Suez Canal. From Essl et al. (2015b), reproduced with permission.

$18 \cdot Invasion Science 1.0$

important pathway for freshwater invasions, while the pathway through the pet trade, terrarium and aquarium is on the rise (Figure 1.8b). The release of non-native terrestrial arthropods for biocontrol was a reasonable practice in Europe until 2000 (green belt in Figure 1.8c), probably due to the implementation of the EPPO (European and Mediterranean Plant Protection Organization) standard in 1999.

In reality, multiple pathways can facilitate invasions from different source areas at different stages, while propagules are transferred through these pathways at different rates and times in different contexts. This web of pathways facilitates recurrent bridgehead effects of invasions and gives rise to a pathway network. For instance, three quarters of the nonnative ant species intercepted by US air and maritime ports between 1914 and 2013 are from countries into which the species were previously introduced, via similar or other pathways from its native range (Figure 1.9; Bertelsmeier et al. 2018). This further increases the genetic diversity of the introduced species and potentially improves their invasion performance in their new homes. However, a fully-fledged Pathway Network Analysis for most types of biological invasions is still not feasible because of limited data availability and resolution problems. Comprehensive pathway network analyses are undertaken to trace disease-related, protein-coding genes with gene expression data; these analyses use powerful statistical approaches and software developed to identify critical pathways for drug design and disease treatment (Khatri et al. 2012). Such pathway network analyses may be feasible in invasion science when the field has fully embraced data science and informatics, and when new methods are in place to collect and manage large volumes of high-resolution data and geographic and taxonomic coverage at a pace relevant to management.

The total number of non-native propagules introduced to an area through a pathway network, known as the propagule pressure (Lockwood et al. 2005), is the best-supported driver of invasion establishment and success. Although invasion performance is often caused by a chain of demographic actions (Gurevitch et al. 2011), early demographic advantage can provide a long-lasting boost to invasion dynamics, and often leaves an imprint on subsequent invasion dynamics (related to transient dynamics; Stott et al. 2011; Caswell 2019). Propagule pressure typically trumps any niche processes and filters imposed in the recipient ecosystems (Carr et al. 2019). According to a recent meta-analysis (Cassey et al. 2018), the relationship between propagule pressure and non-native population



1.4 Pathways and Propagules • 19

Figure 1.9 Percentage of primary v. secondary introductions of the most frequently intercepted ant species in the United States. The proportion of interceptions from the species' native countries is shown above the x-axis (in grey) and the proportion of interceptions from countries in the non-native range below the x-axis (in colour). The colour code indicates the origin of the secondarily intercepted species. Species were visually grouped on the x-axis according to their native range (Dataset S1). Af, Africa; As, Asia; Eu, Europe; N. Am, North America; L. Am, Latin America; Oc, Oceania. From Bertelsmeier et al. (2018); reproduced with permission.

establishment success is consistently strong, showing a logistic form against the log-transformed propagule size (Figure 1.10). Such a saturation shape resembles the relationship between population viability and initial population size (McGraw and Furedi 2005), suggesting a mirror image between invasion and extinction (Figure 1.11; Colautti et al. 2017). As such, biological invasions are better formulated as an open and non-equilibrial system (Hui and Richardson 2019). Constant propagule influx is crucial to erase the genetic bottleneck anticipated for most invasive species as only a small sample of propagules are actually introduced (Simberloff 2009), although the impact of such obvious genetic bottlenecks on establishment might be weaker than previously thought because of rapid local adaptation (Dlugosch and Parker 2008).



Figure 1.10 Estimated relationship of establishment success with propagule pressure and 95% credible interval (shaded). Dashed lines are individual experimental relationships based on a logistic model with random variation in the intercept and slope among individual experiments. Data points are raw data from 14 relationships from 11 studies that experimentally tested associations between propagule pressure and establishment probability. From Cassey et al. (2018), under CC-BY Licence.

1.5 Invasion Dynamics

With invasion pathways and propagule pressure clarified, many researchers have focused their efforts on investigating the behaviour and mechanisms underlying the diverse forms of invasion dynamics. Invasion dynamics are highly stochastic and context dependent, making attempts to synthesise knowledge and predict particular cases challenging to say the least (Pyšek et al 2020b). This is not only a result of the spatiotemporal complexity of any given ecosystems but also the stochastic nature of invasive spread itself. The two demographic processes involved in spreading - growth and dispersal - both contribute to demographic stochasticity and contextual dependence (Hui et al. 2011b). Demographic rates such as the population growth rate of an invader can be scale-dependent and often exhibit specific spatial covariance structures in the invaded range (Gurevitch et al. 2016; Hui et al. 2017). The dispersal of an invader, often depicted as the dispersal kernel (probability distribution of dispersal distance), can also be anisotropic and reflect context-dependent movement strategies (e.g., good-stay, bad-disperse dispersal behaviour;

1.5 Invasion Dynamics · 21



Figure 1.11 Extinctions and invasions conceptualised 'Through the Looking Glass' of evolutionary ecology. Extinctions (left side) represent population decline over time, while biological invasions (right side) represent an increase in abundance. Both invasions and extinctions reflect a common set of elements (central column) because subtle but influential ecological and genetic differences (outer columns) can cause opposite population growth trajectories. From Colautti et al. (2017), reproduced with permission.

Hui et al. 2012). The availability of natural enemies and dispersal barriers, as well as the novel ecological and evolutionary experiences facing each non-native organism (Schittko et al. 2020), make each turn a decision that affects the future possibilities of its invasion performance and dynamics. For instance, in the early 1900s when acclimatisation societies introduced the common starling, *Sturnus vulgaris*, into North America, southeastern Australia and the Western Cape of South Africa, the different propagule pressures, geographies and climates of the three regions (Okubo 1980: Phair et al. 2018). Despite such challenges, progress has been made that allows us to grasp the processes and mechanisms behind a plethora of invasion dynamics (Hui and Richardson 2017). Here we highlight only a few aspects that are especially relevant to later chapters.

Once geographic barriers have been breached, via human facilitation, non-native organisms embark on their invasion and spread in recipient ecosystems. Patterns of invasion dynamics are diverse but

22 · Invasion Science 1.0

can be summarised into different types for convenience (Hui and Richardson 2017), although the reality is much fuzzier around these thematic curves. Essentially, invasion dynamics can be divided into transient and asymptotic phases, where the former is highly flexible but the latter more consistent, reflecting the potential within a given habitat (see invasion curves in Figure 1.12a). In the invasion science literature, the curve of a specific invasion is often found to have multiple phases (Figure 1.12b), with a lag phase after introduction



Figure 1.12 A variety of possible invasion dynamics. The invasion expansion of a non-native species is often documented as the distance from the advancing range front to the point of introduction over time. (a) Invasion dynamics are divided into two phases: a transient phase that is highly context-dependent which converges gradually to an asymptotic phase during which spread occurs at constant velocity. (b) Invasion dynamics are divided into a lag phase (no expansion for a period after introduction), and then slow and fast phases during which expansion occurs at a constant velocity. (c) A typical logistic curve for highly mobile species with an acceleration phase and a saturation phase as invasible space is occupied. (d) Boom-and-bust invasions are often caused by the collapse of local demographic processes, or by the encounter of an efficient natural enemy that has switched to target the non-native resource species when the non-native resource reaches an abundance threshold.

and before invasive expansion, and a biphasic range expansion of a slow phase followed by a fast phase. Over a longer period, the trajectory resembles a logistic curve and can be divided into acceleration and saturation phases (Figure 1.12c). For some invaders, success is transient, and its population size may follow a boom-and-bust trajectory, eventually settling at a much lower level, while the invaded range can percolate back from a continuous range to multiple smaller scattered local populations (Figure 1.12d). Such diverse forms of invasion dynamics – the duration, timing and speed of different phases – can be explained by different constraints and limiting factors through the invaded range, not only behaviourally by individuals of the non-native species but also ecologically and evolutionarily by its niche dynamics.

In terms of spreading dynamics, physicists and modellers have made great strides in elucidating the phenomenon of particle diffusion and dispersion in a suspension matrix. The Brownian movement of pollen grains in water, driven by the collision of numerous water molecules and the pollen, has enjoyed the attention of many renowned physicists, including Albert Einstein (1905). Collectively, such random movements of particles can be studied using specific models of partial differential equations known as reaction-diffusion models. Adolf Eugen Fick (1829-1901) described two laws of diffusion in 1855. Fick's first law relates the diffusive flux to the concentration, assuming a steady state (Fick 1855). It postulates that the flux goes from regions of high concentration to regions of low concentration, with a magnitude proportional to the concentration gradient (i.e., spatial derivative); in simplistic terms, a solute moves from a region of high concentration to a region of low concentration across a concentration gradient. Fick's second law predicts how diffusion causes the concentration to change with respect to time. Based on Fick's second law, Ronald Fisher (1937) developed the now famous reaction-diffusion model which depicts the advancing wave of advantageous genes in the context of population dynamics

$$\frac{\partial n}{\partial t} = m(1-n) + D\frac{\partial^2 n}{\partial x^2},\tag{1.1}$$

where *n* represents the population density and is a function of time *t* and location *x* (thus more explicitly, n(t, x)). The left of this equation describes the time derivative of population density. The first term on the right depicts a simple logistic growth, with *r* reactivity (here, the

intrinsic rate of growth). The second term on the right depicts diffusion as a second order derivative of population density over space, known as the Laplacian operator; this term describes how uneven population densities (i.e., density gradients) in a local area are smoothed out. The diffusion cannot even out constant gradients of densities (e.g., at the range front), and consequently propels the population to spread along the direction of the gradient, forming a travelling wave. Fisher (1937) derived the travelling wave solution of the system. He concluded that the spreading velocity 'is proportional to the square root of the intensity of selective advantage [r] and to the standard deviation of scattering in each generation $[\sigma]$ ', as $\nu = \sigma \sqrt{2r}$, or 'equivalently to the square root of the diffusion coefficient when time is measured in generation', as $v = 2\sqrt{rD}$. This milestone not only provides a way to estimate the diffusion rate based on movement records (e.g., from ringing and mark-recapture data) as $D = \sigma^2/2$ but also derives a commonly used estimate of spreading velocity that has been the backbone of many models of spread ever since. A classic example is by Okubo (1980) who used this model to explore the invasive spread of common starlings, Sturnus vulgaris, in North America. This has resulted in such developments as velocity estimates under biotic interactions, density dependence (e.g., Allee effect), heterogeneous habitats, drift/convection in environments and biotic interactions (see review by Hui et al. 2011b).

A major challenge facing diffusion-type models is related to Reid's (1899) paradox of rapid northward plant migration after the last glacial maximum. In Reid's words, 'the oak, to gain its present most northerly position in northern Britain after being driven out by the cold, probably had to travel fully six hundred miles, and this, without external aid, would take something like a million years' (see updated review by Davis and Shaw 2001; Figure 1.13). This is probabilistically impossible when estimated based on r and D measured for today's oak populations, while the unrealistically high levels of population growth rate and diffusion models to accommodate Reid's paradox has led to a systematic shift in paleoecology away from the use of population ecology models that partition observed velocity into demographic factors of population growth and dispersal in driving such range shifts (Clark et al. 1998).

Two mechanisms have received substantial support in invasion science for explaining such an augmented spreading velocity, as anticipated by Reid's paradox. First, the forms of dispersal kernels can be diverse. While the standard deviation of dispersal distances is only a representative shape



Figure 1.13 Ranges, as indicated by pollen percentages in sediment, of spruce (*Picea*) and oak (*Quercus*) in eastern North America at intervals during the late Quaternary. The continental ice sheet is shown in blue; pollen proportions are shown in shades of green. The shoreline is not drawn to reflect changes in sea level. (a) Spruce pollen representing three extant species plus the extinct *P. critchfieldii*. More recent data show that spruce was abundant further south in the Mississippi valley during the Last Glacial Maximum than shown here. Both southern and northern range boundaries of spruce shifted northward. (b) Oak pollen representing some or all of the 27 extant *Quercus* species in eastern North America. Oak expanded from the southeast but continued to grow near locations of full-glacial refuges. From Davis and Shaw (2001); reproduced with permission.

metric for Gaussian-type kernels, it fails to capture the 'average' for highly skewed, often fat-tailed, dispersal kernels. For instance, extremely rare dispersal events of non-native species over large distances can occur, often mediated by human activities that skew the dispersal kernel (e.g., Suarez et al. 2001). To accommodate rare long-distance dispersal events, models with stratified dispersal kernels (i.e., a combination of different modes of dispersal) have been proposed, especially to explain biphasic range expansion (Figure 1.12b; Shigesada and Kawasaki 1995). More explicit modelling, however, needs to implement realistic dispersal kernels directly. This can be handled flexibly by using integral equations. Integral equations have a long history in mathematics (Fredholm 1903); they were first applied in invasion ecology by Van den Bosch (1992) and Kot et al. (1996). A generic form of an integrodifference equation is

$$n(x, t+1) = \int k(x, y) f(n(y, t)) n(y, t) dy.$$
 (1.2)

26 · Invasion Science 1.0

where the population density n(x, t + 1) at time t + 1 in location x can be calculated as the integral (or the summation) of propagules from all possible locations in the previous time step n(y, t) multiplied by the percapita population growth rate during one time step f(n(y, t)), and weighted by the dispersal kernel k(x, y) that depicts the chance of a propagule moving from location y to location x within one time step. A vector format of such equations is easily extended to accommodate population structures of species with complex life-cycles and life stage-dependent dispersal modes. In such models, dispersal kernels are typically implemented as only distance dependent k(d), with the distance d = ||x - y||, while more realistic movement can be captured directly by considering explicitly the beginning and end locations, y and xrespectively. One important way to boost up the rate of spread comes with the realisation that the movement of most organisms, especially those that disperse via means other than gravity, follows the pattern of Lévy flights (e.g., $k(d) \sim d^{-3/2}$ in Figure 1.14 for the common starling). Unlike Gaussian-type kernels with finite mean and variance, such a power-law dispersal kernel is of infinite variance, meaning that the movement can have diverse characteristic length, and is highly flexible



Figure 1.14 The inverse power function of the dispersal kernel for all movements of European starling *Sturnus vulgaris* within Britain during the breeding season. Dispersal kernels are produced using a 2 km distance class; that is, all records are binned to the dispersal distance class of < 2 km, 2–4 km, 4–6 km, and so on. From Hui et al. (2012); reproduced with permission.