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'.

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ECOLOGY, BIODIVERSITY AND CONSERVATION

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.

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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

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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 non-equilibrial 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 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).

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 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.

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We have surely missed some names here. Forgive us.

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