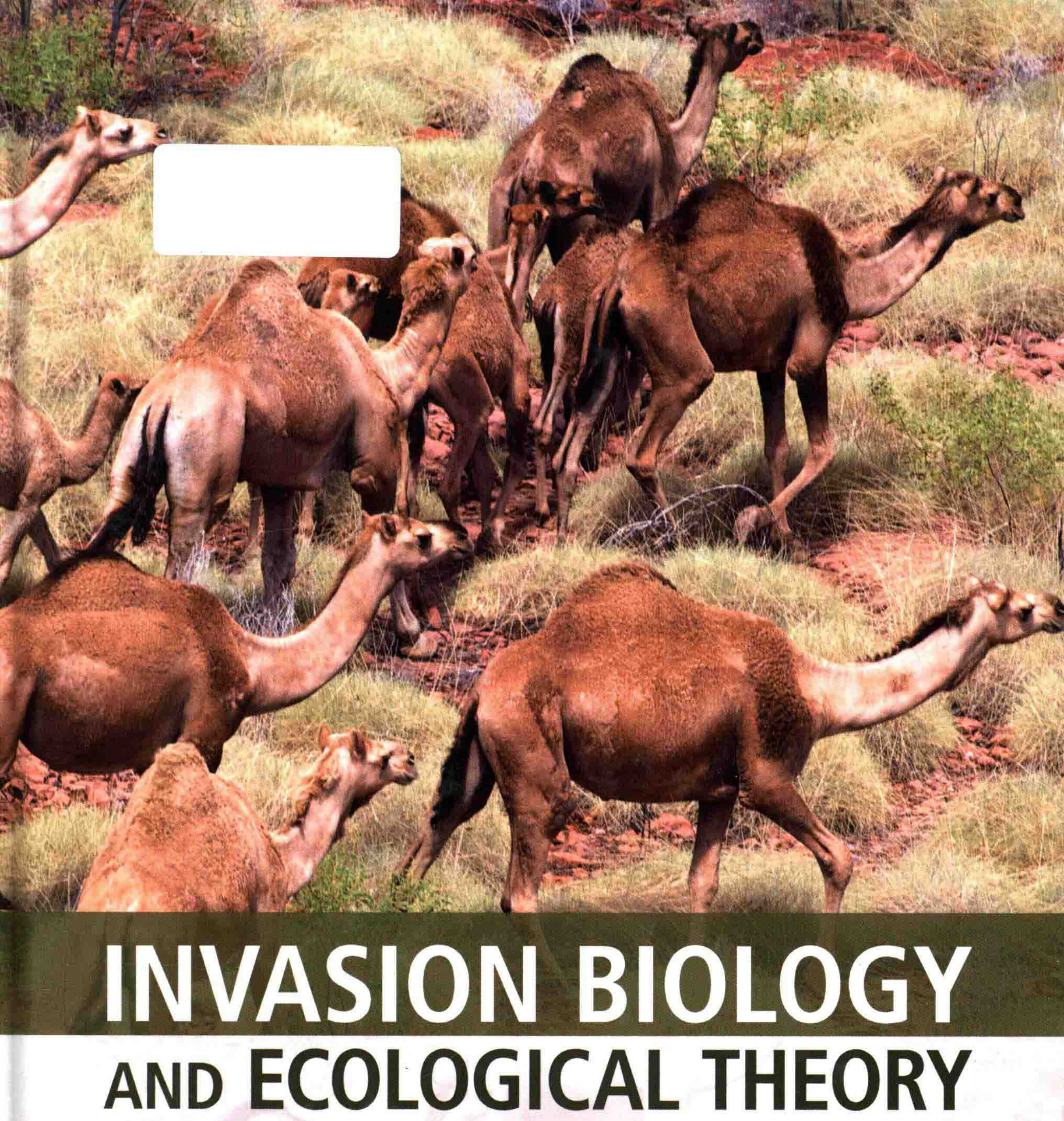

INVASION BIOLOGY AND ECOLOGICAL THEORY

Insights from a Continent in Transformation

EDITED BY Herbert H. T. Prins
and Iain J. Gordon

With a foreword by Charles J. Krebs

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Invasion Biology and Ecological Theory

Insights from a Continent in Transformation

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Invasion Biology and Ecological Theory

Insights from a Continent in Transformation

Many conservationists argue that invasive species form one of the most important threats to ecosystems the world over, often spreading quickly through their new environments and jeopardising the conservation of native species. As such, it is important that reliable predictions can be made regarding the effects of new species on particular habitats and ecosystems.

This book provides a critical appraisal of ecological theory using case studies of biological invasions in Australasia. Each chapter is built around a set of 11 central hypotheses from community ecology, which were mainly developed in North American or European contexts. The authors examine the hypotheses in the light of evidence from their particular species, testing their power in explaining the success or failure of invasion, and accepting or rejecting each hypothesis as appropriate. The conclusions have far-reaching consequences for the utility of community ecology, suggesting a rejection of its predictive powers and a positive reappraisal of natural history.

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Foreword

Alas, the poor ecologist who is expected to follow the laws of scientific inference that have arisen from physics and chemistry. Erect hypotheses, make predictions, see if they are supported by evidence obtained by observations or manipulative experiments. Perhaps it would be easier if, instead of 30 million species, we had only 118 elements in the periodic table to study or only a few forces in physics to design hypotheses around. So how do we cope? We can deal with autecology or the ecology of individual organisms because we have a strong base in physiology and simple things like metabolic rates are constrained by how evolution has proceeded. We can deal with populations because they typically have a restricted nexus of interactions, as Andrewartha and Birch (1984) told us. But things are getting more complicated since the interactions can involve competition, predation, disease, food supplies, climate, and social effects. Perhaps we can cope with this amount of complexity, but it is certainly complex enough to allow many ecologists to argue extensively about the factors causing populations to rise or fall. In principle we can sort out these arguments at the population level by field or laboratory experiments, and this approach will often work to provide evidence-based explanations. But when we move up to community and ecosystem ecology problems multiply if only because experimental manipulations become more difficult and certainly more expensive. It is partly a reflection of why aquatic community ecology has progressed more than terrestrial community ecology – large-scale experiments in rivers and lakes are more prevalent than they are in terrestrial ecosystems. But it may also be partly a reflection of hypotheses that are not operational.

In an ideal universe we might be able to work out some of these problems but the arrival of human influences has added yet more complexity. Invasion biology is now one of the leading fields of community ecology both because of its intrinsic interest as a test case of how much we understand community interactions and even more because many species invasions have consequences written very large in dollars and cents.

The complexities of community and ecosystem ecology have spawned a number of approaches to ecology that have been less helpful than we might have thought 60 years ago. Simple ideas – diversity promotes stability – have morphed into widely accepted hypotheses that weigh heavily on how the terms involved are defined and measured. If there are really 70 different stability concepts (Grimm and Wissel 1997) and at least a dozen different measurements of diversity, it is small wonder there is confusion mixed with controversy over attempts to test this kind of hypothesis. Much of this confusion has been augmented by mathematical models that make assumptions about ecological concepts that differ in important ways from their mathematical parameterisation.

Enter this book – a bold attempt by Herbert Prins and Iain Gordon to formulate a set of 11 hypotheses that can be tested with empirical examples from Australasia. They have brought together 34 scientists with solid field experience to write 18 chapters on specific examples of invasions with the explicit demand to test the 11 hypotheses in each example if possible. They have used both ancient and modern invaders to broaden the dataset. The results are spectacularly interesting for those of us who are interested in natural history, but they also provide a strong warning for ecologists who think time's arrow always points in the direction of theoretical progress and more precise generalisation.

But relax. If you do not like the conclusions reached here, you have the well-utilised rationalisation that we cannot expect ecological examples from Australasia to apply to theories that are designed to be applied to important parts of the globe (i.e. England). Of course I jest, but evolution is the biggest jester of all in our search for ecological wisdom, as illustrated so well in Darwin's two-creators comments. We do not know the breadth of ecological generalisation.

But we press on. Theory must continually be revised on the basis of evidence from field studies, and this book is a good example of how this change can be driven by specialist knowledge from diverse fields. How much we will be able to understand invasions by defining the niche of a species is just one of the open questions addressed here. As I was reading the evaluation of Hypothesis 3 in Chapter 22, I remembered a conversation I had with Robert MacArthur in 1969. He told me that he had abandoned the concept of the niche because it was not measurable by any realistic set of parameters.

Where next? If the arguments made by the authors of this book are accepted, we should be much more careful about giving predictions of what invasions associated with climate change will do to communities and ecosystems. Predictions about invasive species seem to be successful only after the fact, and the operational message ought to be simply to use every measure possible to restrict the human transport of organisms from one part of the world to another. There are many practical management issues we can, as ecologists, recommend about invasive species, but we should not pretend to have the wisdom that exists only in the closed systems of mathematics. Walk slowly, we have much to do.

Charles J. Krebs
Vancouver, B.C.
11 December 2012

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Grimm, V. and C. Wissel (1997). Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* **109**:323–334.

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1 Testing hypotheses about biological invasions and Charles Darwin's two-creators rumination

Herbert H. T. Prins and Iain J. Gordon

Some of today's most pressing issues deal with invasions by alien species into natural or man-made ecosystems such as agricultural landscapes. Invasions are not a new phenomenon having been a part of the relationship between man and the environment ever since humans moved out into the savannas; however, they became part of the ecological agenda in the middle of the last century. The foundations of invasion ecology stem from Charles Elton, who, in his book, *The Ecology of Invasions by Animals and Plants* (published in 1958) attempted to draw together three stands of ecology – faunal history, ecology, particularly population ecology, and conservation. Elton's book had some traction at the time (e.g. Baker and Stebbins 1965), however, few ecologists paid much attention to invasions during the 1960s even though island biogeography theory (MacArthur and Wilson 1967) did provide theoretical frameworks for how new species fitted into the resident species communities on islands. It was not until the 1970s that invasion ecology began to gain traction in the literature (e.g. Baker 1974; Embree 1979) and continues to this day (Richardson 2011). There have been recent attempts to create unified theoretical frameworks for understanding the invasion process (Blackburn *et al.* 2011) and the traits that determine the degree to which a species can invade a new ecosystem or the degree to which an ecosystem can be invaded by a new species (Richardson and Pysek 2006). These developments provide a foundation upon which to assess the degree to which hypotheses concerning biological invasions relate to real-world case studies that are proliferating in the literature.

For several reasons, Australasia, including the continent of Australia, offers a great opportunity to test hypotheses that were formulated mainly in Europe and North America. First and foremost is the fact that many excellent, scientifically trained ecologists have worked in this area of the world: clearly the legacy of Herbert Andrewartha's (1907–92), but there followed (the New Zealander) Graeme Caughley (1937–94), (the American) Eric Pianka (born 1939) and (the Canadian) Charles Krebs (born 1936). Most of the chapters in this book are written by ecologists who work in Australasia where a large amount of ecological research takes place: we could have easily doubled the number of authors if we had invited more to contribute. Second, most of Australia's

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ecologists are acutely aware of the fact that the continent is being invaded by new species, although one ecologist recently pleaded for the release of African mega-herbivores to solve Australia's fire threats (Bowman 2012), as if Australia's ecological problems are not serious enough. The science of invasion ecology has a high standing in Australia, not least because CSIRO (Commonwealth Scientific and Industrial Research Organisation) has devoted a substantial amount of resources to studying and combating biological invasions. It is not only because of ecological invasions taking place in this part of the world that we focus on Australasia (a term coined already in 1756 meaning 'south of Asia') but also because the region forms a biogeographical unit; it lies to the east of the Wallace Line and is characterised by a very peculiar flora and fauna. Indeed, Wallace's Line has been attracting the attention of biogeographers and ecologists for one-and-a-half centuries; it forms the antithesis of the concept of invasions.

The third reason is that ecological theory should be generally applicable – otherwise it is not proper theory within the realm of the natural sciences. Therefore, hypotheses, largely generated through observations of species' interactions in Laurasian ecosystems (i.e. those that evolved on the former supercontinent Laurasia in the north), should be transferable to Australasian ecosystems (which derived from the supercontinent Gondwana in the south; see Chapter 11). Due to its very isolated location, Australasia has evolved a unique flora and fauna that offers a geographic context to independently test hypotheses that were formulated elsewhere. We, as authors and editors, are aware that this comes as close as possible to testing ecology's basic tenets apart from going, literally, to the depths of the oceans. The fauna and flora of Australasia does indeed appear to come from a very different world; to quote Charles Darwin (diary for 19 January 1836):

> I had been lying on a sunny bank and was reflecting on the strange character of the animals of this country compared to the rest of the World. An unbeliever in everything beyond his own reason might exclaim, 'Surely two distinct Creators must have been at work; their object is the same and certainly the end in each case is complete'. Whilst thus thinking, I observed the conical pitfall of a Lion-Ant: a fly fell in and immediately disappeared; then came a large but unwary Ant. His struggles to escape being very violent, the little jets of sand described by Kirby were promptly directed against him. His fate however, was better than that of the fly's. Without doubt the predacious Larva belongs to the same genus but to a different species from the [European] kind. Now what would the Disbeliever say to this? Would any two workmen ever hit on so beautiful, so simple, and yet so artificial a contrivance? It cannot be thought so. The one hand has surely worked throughout the universe. A Geologist perhaps would suggest that the periods of Creation have been distinct and remote the one from the other; that the Creator rested from his labour. (Darwin on-line; see the comment on this text by Armstrong 2002).

To facilitate the reader's understanding of Australasia's uniqueness and its distinct geological and climatological history, we have included two chapters in this book, by Stannard (Chapter 11) and by McLaren and her co-authors (Chapter 12), providing information on its very long isolation from other continents. Especially for those ecologists who never have had the pleasure of visiting the unique and distinct continent of Australia and the adjacent oceanic or continental islands, these chapters may be essential for appreciating Charles Darwin's 'Two-Creators Idea'. They also provide justification for our notion that we can use Australasia as an independent test arena for evaluating ecological hypotheses that were formulated elsewhere.

The foundations of ecology

The field of ecology has been fortunate to attract some of the great minds of the eighteenth to twentieth centuries, such as Alexander von Humboldt (1769–1859; the first person who understood that vegetation varies with altitude, climate or soil, and who explored what determines the species that make up a community and their relative abundance (Stokstad 2009)), Justus von Liebig (1803–73; who discovered the Law of the Minimum), Charles Darwin (1809–82; who developed important ideas about co-existence and competition), Ernst Haeckel (1834–1919; who coined the term 'ecology'), Alfred Wallace (1823–1913) and Eugenius Warming (1841–1924) (both fathers of biogeography), Christen Raunkiaer (1860–1938; who initiated classification of plant life-forms and who was the first quantitative ecologist), Joseph Grinnell (1877–1939; who coined the term 'niche') and Arthur Tansley (1871–1955; who adopted the term 'ecosystem' and defined it as 'the whole system ... including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment'). In the 1930s to 1960s a transition took place when great ecologists such as Charles Elton (1900–91; who redefined the term 'niche'), Vero Wynne-Edwards (1906–97) and Herbert Andrewartha started long-term observations and executed carefully designed experiments to test important concepts such as density dependence. They, along with Henry Allan Gleason (1882–1975), slowly moved away from thinking about the benefit for the species, incorporating neo-Darwinian theory in highlighting the consequences of behaviour for the fitness of individuals.

The great breakthrough took place through the merger of mathematics with ecology in the work of Pierre Verhulst (1804–49; who devised the formulae for carrying capacity), Karl Pearson (1857–1936; who started looking for empirical evidence of Darwinian selection), Alfred Lotka (1880–1949; famous for his book *Elements of Physical Biology* published in 1925), Vito Volterra (1860–1940; of the Lotka–Volterra equations taken further by C. S. (Buzz) Holling in 1959), Ronald Fisher (1862–1960; famous for his book *Statistical Methods for Research Workers* (1925) and many other very important publications). This led to the golden age of ecology in the 1950s to 1960s when Evelyn Hutchinson (1903–91), Robert MacArthur (1930–72) and Edward O. Wilson (1929–) published their seminal works on ecology. It was mainly MacArthur who stressed the importance of hypothesis testing and thus was a driving force for changing ecology from a descriptive domain of knowledge (i.e. natural history) to a 'proper' science with an important branch, namely theoretical ecology. But, if ecology is a proper natural science, then it must follow the scientific method. This method, discovered in the seventeenth century, is described as 'a method or procedure that has characterised natural science, consisting in systematic observation, measurement, and experiment, and the formulation, testing, and modification of hypotheses' (*Oxford English Dictionary* online, 2013). Wikipedia explains the method further by stating:

The chief thing which separates a scientific method of inquiry from other methods of acquiring knowledge is that scientists seek to let reality speak for itself, and contradict their theories about it when those theories are incorrect. Scientific researchers propose hypotheses as explanations of phenomena, and design experimental studies to test these hypotheses via predictions which can be derived from them. These steps must be repeatable, to guard against mistake or confusion in any particular experimenter. Theories that encompass wider domains of inquiry may bind many independently derived hypotheses together in a coherent, supportive structure. Theories, in turn, may help form new hypotheses or place groups of hypotheses into context.

Whilst the scientific method is the basis upon which the edifice of science is built, much of the field of ecology appears to be based on weak inference rather than strong inference. In weak inference there are correlations between observations that describe patterns in the world rather than structured experiments that test hypotheses about how the world works (strong inference; e.g. Horn 1971). *In science* strong inference is seen to be more powerful because weak inference is more prone to error in interpretation.

Apart from investigating invasions, in this book we also explore whether the field of ecology holds to the scientific method. In 1973 the then-president of the British Ecological Society, Amyan MacFadyen, asked the same question and his verdict, although couched carefully, was not too favourable. He wrote:

There are those who argue that ecology, like human history, is concerned with unique events and that these are not supposed to be open to the 'scientific method'. Is this true and does 'scientific method' referred to in this context differ from its meaning in other sciences? (MacFadyen 1975)

We may fear that we enter some

sort of nihilistic postmodern view of ecology, where there is no truth, only stories, and the choice among stories is a question of individual taste (and power). To the degree that we reject the notion of falsifiability as a criterion for ecological theory, we reject the claim of ecology to be an empirical science, and consign it to the humanities. One of the essential differences between science and other forms of knowledge is that science makes claims about the world in the form of predictions that serve as testable hypotheses. (Weiner 1995)

In this book we enshrine the notion of falsifiability to the extent that we place falsifiable hypotheses central in all the biological chapters.

A key purpose of this book is thus, to test whether modern ecological theory is based on 'the scientific method', 'strong inference' and coherent theories that have been tested, or, whether ecology remains a descriptive science, based on weak inference, correlations and ad hoc hypotheses? We, the editors, can test this because we have enough test cases in this book to evaluate this question. We thus use the field of invasion ecology as our test-bed for this investigation.

Theodoropoulos (2003) claimed invasion biology to be a pseudoscience. The problem with Theodoropoulos' attack on invasion biology, though, is that he frames his analysis not in a context of examination of evidence and theory but within psychoanalysis. We quote:

The psychologies of prejudice and xenophobia have been well studied, and [my book] illuminates the psychopathologies that are at the root of invasion biology and why it is so uncritically

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