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Trends in Ecology & Evolution

Figure 1. Bob May (Right) Chatting to Sean Nee (Left) in 1994.

out of a lecture to find that they had managed to litter the ground floor lobby with marigold petals. I was worried that he would admonish me for not teaching them better manners but instead he clapped his hands in delight.

It never occurred to Bob that he might actually retire one day – he came into the office regularly and remained active in every sphere until it became impossible for him to do so. It was painful for all of us to watch such an agile mind become slowly clouded but he was loved and looked after by his many friends in the last years of his life – Paul Harvey and John Krebs, in particular – and his constant companion of almost 60 years, Judith. I have left mention of Judith till the last because she was the most special part of Bob's life. They met on a double date while he was a postdoc at Harvard and she was an undergraduate at Brandeis, married in 1962 and had a daughter, Naomi. Judith pursued a career in publishing, and together they lived a rich life full of tender understanding towards each other. The last time I visited Bob, he did not seem to recognize any of us for the most part, but there was a moment when he took her hand and said – Judith, you are such a lovely person, I am so lucky to have you.

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Science & Society

Invasion Science and the Global Spread of SARS-CoV-2

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Emerging infectious diseases, such as coronavirus disease 2019 (COVID-19), are driven by ecological and socioeconomic factors, and their rapid spread and devastating impacts mirror those of invasive species. Collaborations between biomedical researchers and ecologists, heretofore rare, are vital to limiting future outbreaks. Enhancing the crossdisciplinary framework offered by invasion science could achieve this goal.

SARS-CoV-2 as a Biological Invasion

A sinister combination of ecosystem alteration, wildlife exploitation, and global connectedness is increasing the risks of novel infectious disease emergence and spread [1,2]. This combination of factors goes far in explaining recent viral epidemics and pandemics such as severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2; the virus responsible for COVID-19 disease; 2019–ongoing), Zika (2015–2016), H1N1 (2009), and SARS (2002–2004), and forewarns of others in the future. Accordingly, societal efforts must be directed toward managing not only the pathogens themselves, but also the environmental factors that facilitate their emergence, spread, and impacts. In addition to resolving the immense socioeconomic and cultural challenges to this goal, clearly we must develop a crossdisciplinary research program to address the consequences of increasing global connectedness and

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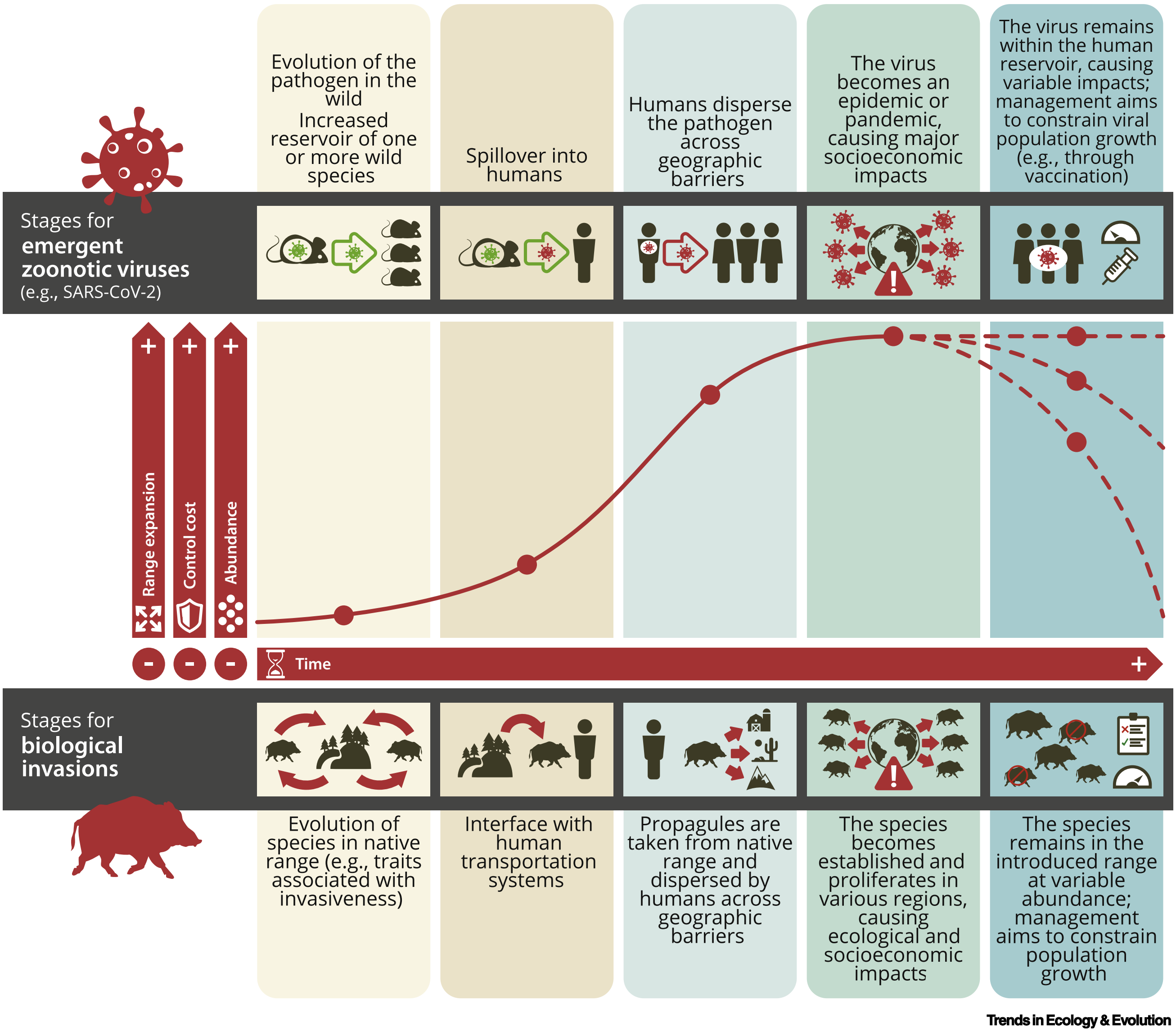

Figure 1. Stages of a Zoonotic Viral Epidemic Compared with those of a Biological Invasion. Similar stage-based processes affect the spread of infectious zoonotic pathogens (such as severe acute respiratory syndrome coronavirus 2; SARS-CoV-2) and nonpathogenic invasive organisms, demonstrating the need for a common set of international management actions (e.g. early detection, rapid response, eradication or containment, and mitigation) appropriate to each stage of the process.

alteration of biological systems. This collaborative effort must include the study of biological invasions, that is, the spread and proliferation of organisms in new regions.

SARS-CoV-2 should be viewed as a biological invasion, although infectious human diseases are rarely treated as such. Despite the longstanding debate on how to classify viruses as living organisms, this viral outbreak has traits typical of an invasive species: sudden emergence, rapid proliferation and spread, adaptation to new environments (or hosts), large-scale geographic dispersal via human transportation networks, and significant impacts, in this case on human health and well-being. Its management requires consideration of stage-based processes and expansion phases similar to those of invasions of nonpathogenic organisms (Figure 1). Thus, we contend that the field of invasion science [3] is positioned to contribute substantively to understanding the drivers and mechanisms of the spread, and factors promoting outbreaks, of novel infectious pathogens such as SARS-CoV-2.

The Spread of Novel Organisms and the Role of Invasion Science

Invasion science inherently examines the connectedness between natural and anthropogenic systems by integrating perspectives of, *inter alia*, ecology, biogeography, population dynamics, evolutionary biology, risk analysis, human history, and environmental management to understand the spread and impact of introduced organisms in non-native contexts. The study of invasions has traditionally focused on species *per se*, but ecologists have advocated extending its focus more generally to hybrids, microbes, viruses, genetically modified organisms, and synthetic life, which are all subject to biological constraints, evolutionary change, and opportunities to interface with global transportation networks [3–5].

A major insight from invasion science is that the coevolutionary relationships between introduced organisms and their environments are key to understanding their invasion success and impact [5,6], with novel organisms (those without evolutionary analogues in their recipient environment) having the greatest potential to cause disruption [5–7]. The introduction of novel organisms can create evolutionary mismatches in which members of the recipient community have no adaptations to these organisms and, thus, are highly vulnerable to their impact; the analogy to disease immunology is evident.

It is not known what proportion of introduced novel organisms will proliferate and cause substantial damage. Many have subtle or apparently minimal impacts on their environment. Others can remain innocuous for periods of time before suddenly becoming invasive (or virulent) in response to environmental change. Biological invasions are growing in frequency worldwide [8], and the impacts of even a small proportion (but an escalating absolute number) of these can be so disruptive and costly that the issue is of societal importance, including to human health and well-being [9]. At a time of unprecedented globalization, managing the threat of invasive novel organisms requires internationally coordinated rapid response plans. Poor preparedness and delayed response to invasions can lead to inadequate biosecurity measures and potentially devastating costs, as the world has witnessed with SARS-CoV-2.

A Crossdisciplinary Approach to Biosecurity

We believe the COVID-19 pandemic can provide a powerful impetus for ecologists, epidemiologists, sociologists, and biomedical researchers to develop an expanded invasion science that makes broader contributions to global biosecurity by embracing the philosophy of the One Health Initiative, the goal of which is to achieve optimal public health outcomes by monitoring and managing the interactions between humans, animals, and their environment [10]. Burgeoning studies have combined wildlife epidemiology with biogeography and community ecology, and ecologists recognize the compatibility of concepts of disease ecology and biological invasions [11–13]. Indeed, ecological research has revealed complex, indirect effects that invasions can have on human disease risk [9,14]. Invasion science, a broad field devoted to understanding the processes behind the spread and impact of novel organisms, is positioned to help prevent, control, and potentially eradicate harmful invasive organisms, such as SARS-CoV-2, thereby allowing a more sustainable human existence within an increasingly altered natural world.

Biomedical research on emergent infectious diseases would benefit from what invasion science can offer in terms of, for example, (i) a consolidated array of frameworks for studying the consequences of eco-evolutionary novelty, specifically the release of organisms lacking ecological analogues in their recipient environments [4]; (ii) expanding knowledge of the eco-evolutionary factors that determine the success of transitions between stages of invasion (Figure 1), which are influenced by a combination of human activities, environmental conditions, and their feedbacks [4,11,12]; and (iii) a rich literature on the context-dependent dynamics and predictive modeling of organismal spread and their effects.

However, although some invasion biologists have advocated greater integration of their field with human epidemiology, published evidence of crossdisciplinary research applied to emergent infectious diseases remains relatively meager. Ogden and colleagues [12] noted the scarcity of examples where the application of human epidemiology to biological invasions or invasion biology to emerging infectious diseases has resulted in improved prevention or control. Undoubtedly, there is a need for further advancement of crossdisciplinary approaches toward applied research and management of invasive human pathogens.

Owing to international sharing of spatiotemporal data, the spread of SARS-CoV-2 is the most meticulously mapped biological invasion ever documented on a global scale [15]. This unprecedented rapid sharing of information, particularly from the early stages of an invasion, is not only an extraordinary opportunity for advancing the frontiers of invasion biology and epidemiology, but also demonstrates the potential for global cooperation in biosurveillance of all types of novel organismal threat. Emerging infectious diseases, and invasive organisms in general, are increasing in frequency with no sign of saturation [2,8] and their prediction, prevention, and control are a societal priority. A crossdisciplinary invasion science offers valuable

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underexploited frameworks and insights that can facilitate such initiatives and we hope that the COVID-19 pandemic will serve to catalyze greater collaboration.

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Book Review

Causality Meets Mathematics: In Defense of the Mathematization of Evolutionary Biology

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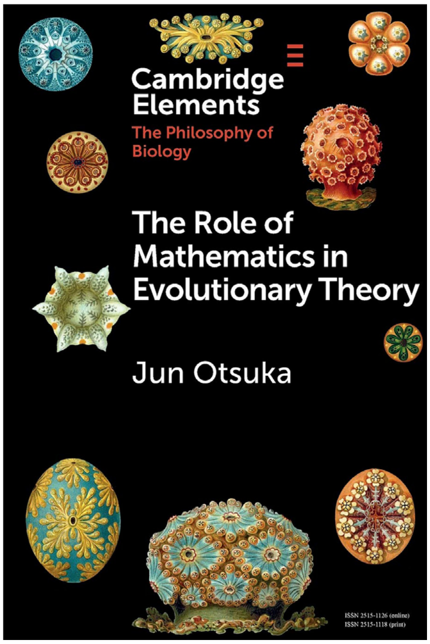

Few evolutionary biologists will be surprised by the opening statement in this book: ‘Like any other advanced science, contemporary evolutionary theory is highly mathematized’ [1]. What may be more surprising is the extent of the debate and disagreement that has surrounded the meaning of mathematics in evolutionary biology, spanning most of the past century to this day. This book – written by a philosopher of science closely involved with the debate – takes a perspective at the intersection of philosophy, mathematics, and biology. While a practicing biologist can continue their research without being aware of most of the questions this book centers on, I would unreservedly recommend it to anyone with an interest in the theoretical underpinnings of their field.

The book can be roughly divided into two halves. The first half provides a historical account of the debate and the second shifts the focus towards a proposed resolution. The story begins, as many stories do, with Darwin’s *On the Origin of Species* [2], notable for instigating one of the greatest scientific revolutions in history without the use of any explicit mathematics. While mathematical work in the early 20th century by scientists, such as Fisher, Wright, and Haldane, solved several problems Darwin’s theory had to face, new challenges of a different kind followed.

These challenges are exemplified by the Price equation [3], which is – despite having a biological motivation – a mathematical identity that is always true for any evolving population, not reliant on empirical validation. The Price equation is thought by many to be the most fundamental of mathematical theorems describing evolutionary change [4,5]. But if evolutionary theory is founded on a mathematical identity that is an *a priori* logical and mathematical truth, how can it ever tell us anything new or make predictions about the real world? Here, biology seems to profoundly differ from physics, which too is a mathematical science but one in which the mathematical foundations are not logical truths or tautologies and instead rely on empirical validation.

The reader is introduced to the ‘received view’, which seems to resolve the issue,