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Postcolonial Ecologies of Parasite and Host: Making Parasitism Cosmopolitan

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Abstract. The interest of F. Macfarlane Burnet in host–parasite interactions grew through the 1920s and 1930s, culminating in his book, *Biological Aspects of Infectious Disease* (1940), often regarded as the founding text of disease ecology. Our knowledge of the influences on Burnet's ecological thinking is still incomplete. Burnet later attributed much of his conceptual development to his reading of British theoretical biology, especially the work of Julian Huxley and Charles Elton, and regretted he did not study Theobald Smith's *Parasitism and Disease* (1934) until after he had formulated his ideas. Scholars also have adduced Burnet's fascination with natural history and the clinical and public health demands on his research effort, among other influences. I want to consider here additional contributions to Burnet's ecological thinking, focusing on his intellectual milieu, placing his research in a settler society with exceptional expertise in environmental studies and pest management. In part, an ''ecological turn'' in Australian science in the 1930s, derived to a degree from British colonial scientific investments, shaped Burnet's conceptual development. This raises the question of whether we might characterize, in postcolonial fashion, disease ecology, and other studies of parasitism, as successful settler colonial or dominion science.

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By 1936, F. Macfarlane Burnet could see that since World War I, ''the most characteristic development of epidemiology has been the adoption of what may be called a more oecological point of view, in which the activities of the two organisms concerned – man and the pathogenic micro-organism – are both considered from the point of view of survival of the species'' (Burnet, 1936, p. 100). Given the paucity of contemporary work on the subject, one might suppose that Burnet was indulging in wishful thinking, but in his own mind the ecological pattern was clear. Through framing all infectious disease in terms of host–parasite interactions, or the relations of prey and predator, he believed he could make general microbiology as biological as it was microbial. ''All epidemiological problems can be most profitably studied along oecological lines, as an interaction between two or more species of living organism,'' Burnet declared. ''Such considerations hold as much for pathogenic bacteria and viruses as for sheep and parrots or mice and men'' (p. 102). At the time, the Australian virologist was beginning to write *Biological Aspects of Infectious Disease*, which was not published until 1940 (Burnet, 1968; Sexton, 1991). His book would become the key text in the development of disease ecology and one of the more influential monographs in twentieth-century biomedicine (Anderson, 2004).

Coined in the 1930s, the term ''disease ecology'' connoted a specific analytic framework for understanding the interactions of microorganisms and macrobial hosts, even as it implied a distinctive, and perhaps more distinguished, disciplinary affiliation for those microbiologists among its advocates. For philosophically inclined medical scientists like Burnet, ecological modeling of disease could align clinical service with theoretical biology and natural history, allowing them to make an unbidden microbial offering to the evolutionary synthesis emerging in the 1940s (Huxley, 1942; Mayr and Provine, 1980; Smocovitis, 1992). Always a minority interest within general microbiology, disease ecology nevertheless suggested a means through which routine diagnostic services might be elevated into the intellectually creditable realm of evolutionary biology. Burnet envisaged evolutionary biology as making sense of disease processes in the field, providing an integrative, though not holistic, framework for comprehending organismal competition and equilibrium. He showed little interest in social medicine (Rosen, 1947; Galdston, 1954; Porter, 1992), that other integrative or configurative framework popular between the wars – for he was a biologist, not a sociologist or political economist. Nor did he care for the remnants of geographical medicine (Valencius, 2000; Barrett, 2000), or geomedicine as the Germans called it, regarding such explanation of disease patterns as too environmentally reductive, restrictive, and static – and therefore insufficiently Darwinian. Rather, disease ecology, he believed, would transform epidemiology from mere microbe hunting into a biologically interactive, and hence more complex and dynamic – and larger scale, even global – scientific enterprise (Anderson, 2004). Of course, the intellectual and practical ambitions of disease ecology would not be fully realized until the 1980s, at the end of Burnet's life, when it served to frame the emergence of diseases such as acquired immune deficiency syndrome (AIDS).

Although prepared to cite selectively some influences and antecedents, Burnet immodestly asserted the novelty of his synthesis and the unique scope of his treatment of disease ecology. He claimed not to have read bacteriologist Theobald Smith's related *Parasitism and Disease* (1934), but later admitted that many of Smith's formative ideas had filtered through to him.[1] More generously, Burnet (1940) acknowledged the profound impact of Julian Huxley's speculative biology on his thinking, especially through the ecological section of *The Science of Life* (1931), a revered source. Burnet (1940) happily deferred also to the work of Charles Elton, particularly his *Ecology of Animals* (1933), aware no doubt of Elton's close connection to Huxley.[2] But otherwise the Australian microbiologist was careful to cover his tracks. Surely the inclinations toward natural history of John C.G. Ledingham, his Ph.D. supervisor at the University of London, and Christopher J. Andrewes, his closest friend there, had exerted some influence.[3] Presumably, the naturalistic studies of Charles Nicolle (1930) of inapparent, asymptomatic infections shaped his thoughts, even if only in translation.[4] Burnet must have known, too, about Major Greenwood's search for a more complex epidemiology after World War I, though he never mentioned it.[5] From Huxley he would have heard of Ronald Ross's mathematical modeling of mosquito populations and their link to malaria incidence (Wells et al., 1931; see Ross, 1905, 1911). Elton (1933)

[1] According to his student Frank Fenner, interviewed by Warwick Anderson, 29 July 2002, Canberra.

[2] Burnet and Elton also were connected through friendship with Howard Florey, the Australian professor of pathology at Oxford.

[3] Ledingham, who succeeded C.J. Martin, a patron of Australian science, as director of the Lister Institute in London, was an expert on asymptomatic disease carriage, or inapparent infection. Andrewes pursued interests in influenza, the common cold, and virus immunity. See Sankaran, 2006.

[4] Burnet seems to have read widely in German, but not so much in French, yet Ledingham, Hans Zinsser, and Karl Friedrich Meyer (1936), his parasitologically minded friend in San Francisco, must have drawn his attention to Nicolle's studies – as would the award to Nicolle of the 1928 Nobel Prize in physiology or medicine (Pellis, 2006). For the extensive correspondence between Burnet and Meyer from the early 1930s, mostly about psittacosis, see the K.F. Meyer papers, 76/42 cz, Bancroft Library, University of California at Berkeley.

[5] As Greenwood (1916, p. 244), based at the London School of Hygiene and Tropical Medicine, put it: "It is high time that epidemiology is extracted from its present humiliating position as the plaything of bacteriologists and public health officials, or as, at the best, a field for display of antiquarian research." See Mendelsohn, 1998.

certainly directed his attention, perhaps somewhat belatedly, to Vito Volterra's and Alfred J. Lotka's esoteric explanations of the population fluctuations of predators and prey, or parasites and hosts (Volterra, 1926; Lotka, 1925). But Burnet refrained from citing them.

To compensate for Burnet's selectivity – which shaded into evasiveness – we must register more completely his own ecology of knowledge (Rosenberg, 1979), describing the "local biology" of Melbourne and environs, his comfortable intellectual niche. In particular, this means giving more credit to the enthusiasm for philosophical biology and the emergence of ecological theories occurring in southeastern Australia during the interwar period. It requires us to look more closely at what constitutes colonial science, or proto-national science, or even "dominion" science, in the first half of the twentieth century, shifting ground from the usual concentration on tropical medicine, which was generally (at least until World War II) a science of European sojourners, rather than settlers. It implies enlarging the scope of "empire" in our analysis of the development of disease ecology in the 1930s. The focus on the complexities and ambiguities of knowledge making – what may be called "border biology" (Kohler, 2002, p. 294) – at one intensively colonized site, a settler colonial borderland, thus offers a critical post-colonial perspective on the emergence of disease ecology (Anderson, 2009, 2014). In making parasites visible in Australia, a federation of former colonies and still a British dominion between the wars, Burnet was able to reframe human infectious disease of all sorts in terms of host–parasite interactions – the parasite, or rather his situated knowledge of the parasite, thus became cosmopolitan. As, indeed, did he.

Parasitology, Animal Ecology, and Human Pathology

"Where did the modern, ecological understanding of epidemic infectious disease come from?" asks J. Andrew Mendelsohn. Not from general ecology or parasitology, he assures us. "How indeed to imagine," he writes (1998, pp. 301–302), "that the fledgling ideas and methods of upstart population ecology, or the premises of parasitology, which were of uncertain relevance to bacterial and viral disease… could have conquered bacteriology." Mendelsohn argues instead that the challenge of frightening disease outbreaks after World War I, especially the influenza pandemic, compelled epidemiology to become biologically complex and competent. John Farley anticipates Mendelsohn in dismissing parasitology. "Twentieth-century parasitology," he writes (1992, p. 406), "came to resemble nineteenth-century helminthology; hermetically confined by cultural circumstances, neither managed to share its resources with the medical search for an understanding of disease." In the nineteenth century, August Hirsch (1881–1883) had urged nascent bacteriologists to transform germ theory into the parasitic theory of infectious disease. But the study of parasites often did not appeal to those committed to identifying and tracking bacteria. Late in the nineteenth-century, Patrick Manson, Smith, Ross and others described the vectors and intermediate hosts of a number of parasites, yet such knowledge seemed inapplicable to bacteriology – at least to nearly everyone except Smith, as we shall see. After 1900, bacteria and parasites routinely were differentiated. Bacteria were generally contagious, whereas strict parasites, needing to pass through a vector or intermediate host, were not. According to Manson, bacteria could thus be cosmopolitan, whereas parasites depended on the geographical dispersion of insects and other hosts. That "the bacterial diseases should be cosmopolitan is easily understood," wrote the founder of tropical medicine, "the germ passes from host to host without metamorphosis, and practically uninfluenced by the usual media of transmission" (Manson, 1899, p. 59; see Li, 2002). Such germs were not geographically limited, and therefore not the substance of tropical medicine. The study of bacteria and parasites thus became institutionally segregated, with parasitology confined to tropical medicine, a segment of public health, and agriculture (Foster, 1965; Worboys, 1983; Farley, 1992).

In contrast, other historians of science gravitate towards the tropics to discern the roots of ecological thought in general medicine. According to Michael Worboys (1988, p. 22), tropical medicine "required detailed knowledge of the taxonomy of vector species and ecological management, which found application in the tropical environment." It was the most obvious source for ecological thinking in infectious diseases research. Similarly, Helen Tilley (2011, esp. p. 185) points out that tropical medicine in Africa, structured around the lifecycles of parasites, became the conduit though which ecological thought entered medical discourse. No doubt experience in tropical medicine, especially in dealing with malaria, did turn some medical scientists toward ecology (see Strong, 1935). For example, Frank Fenner, one of the more influential Australian infectious disease experts after World War II, shifted during the war in Palestine and the South Pacific away from anatomical studies to malaria research – so enthusiastic was he about the mosquito vector, he acquired the nickname ''Noffie.'' Working closely with entomologists Ian Mackerras and Francis Ratcliffe in the Australian malaria research program confirmed in Fenner an ecological sensibility that shaped profoundly his post-war research. Thus he arrived in the late 1940s at the laboratories of leading disease ecologists Burnet and René Dubos, at the Rockefeller Institute, already ecologically minded (Anderson, 2013). Yet Burnet himself evinced little interest in tropical medicine.

Burnet, however, was familiar with the foundational work of Theobald Smith, who was among the few who sought to broaden the scope of parasitology to encompass all bacteriology. Committed to comparative pathology, to tracing the communication lines between diseases of humans and other animals, and immersed in German ecological thought (Nyhart, 2009), Smith was arguing as early as 1900 that bacteria functioned effectively as parasites (Dolman and Wolfe, 2003). ''After the opening of that vast domain of parasitism,'' he reflected (Smith, 1900, p. 166), ''it became possible to begin an analysis and interpretation of the phenomena of infectious diseases.'' Thus ''bacteriology is essentially a study of two realms,'' the Harvard pathologist wrote, ''that of the parasite and that of the host, of two organizations, widely different, acting upon one another and entering into complex, reciprocal relations'' (Smith, 1904, p. 818). The distraction of bacterial taxonomy and preoccupation with their role in pathogenesis had obscured their true biological identity. In the interwar years, based then at the Rockefeller Institute, Smith (1921, p. 101) interrupted his studies of animal pathology to vent again from this ''biological viewpoint.'' While it was ''customary to distinguish between parasitic invasion and bacterial infection'' (p. 102) such a distinction applied only to extremes. Rather, it was ''best to class all living invasive organisms as parasites, subject more or less to the same host mechanisms of repression and destruction'' (p. 102). Smith urged more study of the ''dynamic relations between host and parasite'' (p. 107). Admired for his vast knowledge of biology, and a keen reader of journals like *Science*, *Nature*, and the *Quarterly Review of Biology*, Burnet must have been aware of Smith's repeated efforts to make parasites cosmopolitan.[6] Probably he also noticed the neglect of such pleas. Even so, the Australian's ecological models would turn out different from Smith's understanding of

[6] After 1935, Burnet came to know Hugh K. Ward, the professor of bacteriology at the University of Sydney, who had worked closely at Harvard with Hans Zinsser, a friend of Smith. Burnet likely also read Huff (1938). A protégé of Zinsser, Smith, and Richard P. Strong, Huff, based at the University of Chicago, was ''tracing the origins and evolutionary histories of disease-producing organisms'' (p. 196).

biological interaction. The American comparative pathologist had favored adaptation and harmony, the declining virulence of parasites and the establishment of equilibrium with their hosts (Smith, 1900; Méthot, 2012). Instead, Burnet would come to emphasize competition and struggle, in keeping with other trends – at least outside the United States – in animal ecology in the 1930s.

Burnet readily admitted to learning about animal ecology through reading Huxley's extensive review of the field in *The Science of Life*. With H.G. Wells and G.P. Wells, Huxley defined ecology as the study of the "balances and mutual pressures of species living in the same habitat" (Wells et al., 1931, p. 578). Their sweeping survey of ecological knowledge was based largely on A.G. Tansley's investigations of plants and Elton's arguments about animals. Significantly, they deliberately called the bacillus of pneumonic plague a "parasite," and they speculated lightly on host–parasite interactions in the production of infectious disease. "The bacteria are the most important of any parasites," they observed in passing (p. 556). "By variation in the virulence of a parasite and the resistance of a host, and by other circumstances, the relations between a human population and the bacterial population inside it may be altered," they noted (p. 625). "Violent epidemic disease seems to be the natural and inevitable result of overcrowding," Huxley and his co-authors averred. "When a certain density of population is reached, the disease, hitherto a smouldering and sporadic thing, becomes a fulminating epidemic – spreading with maximum rapidity through the entire population" (p. 599). They chose not to elaborate but Burnet must have been intrigued.

In his account of ecology in *The Science of Life*, Huxley relied heavily on his former student Elton's *Animal Ecology* (1927), for which he had written the introduction.[7] In this breezy overview of the emerging discipline, Elton set out his understanding of what he called "scientific natural history" (Elton, 1927, p. 1; see Crowcroft, 1991; Anker, 2001). He emphasized the interactions of animals with one another and with their environment, but warned that it was "necessary to speak in generalities, since so little is known at present about the rules governing the regulation of animal numbers" (p. 120).[8] Later, in *The Ecology of*

[7] Tantalizingly, Huxley (1927, p. xv) mentioned that "disease was envisaged more and more as a phenomenon of general biology." But Elton does not take this up in the book.

[8] In the 1920s, Elton was surprisingly reluctant to incorporate microbiology into his concepts of animal ecology. In one essay, however, Elton (1925) related rodent population fluctuations to plague epidemics, without considering the dynamics of host-parasite interactions.

Animals (1933), Elton was able to expatiate on the regulation of populations and the interactions of organisms in their surroundings. In this text, the Oxford don supplied his readers with several ecological analyses plucked from tropical medicine, including the impact of air travel on the dispersion of yellow fever, a mode of transmission that came to fascinate Burnet. Additionally, Elton now referred to mathematical studies of the fluctuations of numbers of predators and prey.[9] He focused on the theories of Alexander John Nicholson, whose arcane calculus recently had determined the chances of parasites searching for and finding their hosts in different population densities. Burnet was acquainted with Nicholson, who was working not far from him in Canberra, Australia's primitive bush capital.

Antipodean Ecological Visions

In Australian settler society, Burnet inevitably became deeply immersed in ecological thought. As environmental historian Tom Griffiths (1997, p. 10) puts it, "a settler society, whether or not numerically dominant, was an invading, investing, transforming society with an internal frontier, both natural and cultural." Accordingly, Griffiths writes, "for Australian settlers, 'ecology' and 'empire' represented the competing realities of geography and history, land and culture, and stood for a fundamental, persistent tension between origins and environment in Australian life" (p. 11). In the early-twentieth century, the arid continent – with its poor soils, deserts, recurrent droughts and floods – was regarded by agricultural scientists and veterinarians as a challenging environment, even a hostile one, for introduced crops and animals. Marginal agricultural and pastoral regions were turning into desert; pests and plagues were killing off much of what remained. How to cultivate and settle this land, how to manage the imbalance between European crops and animals and the Australian environment, was a matter of intense biological discussion (Mulligan and Hall, 2001).

In southern Australia between the wars, the "sciences of settling," as Libby Robin (1997, p. 65) calls them, mostly were concerned with control of agricultural and pastoral pests. Across southern regions, agricultural and veterinary scientists, along with entomologists, sought to understand the interactions of parasites with their plant and animal

[9] Kingsland (1985) claims that Huxley showed Elton Volterra's *Nature* article in 1926, but its impact is not evident till Elton's 1933 publication—after he had become familiar with Nicholson's work.

hosts. In contrast, north of Capricorn, specialists in the new tropical medicine, investigating racial adaptation and racialized disease threats, became the main scientists of white settlement, but increasingly they were isolated in the tropics, dwindling in numbers (Anderson, 2006). Whether in tropical medicine, agriculture, animal husbandry, or entomology, all this research focused on the quality and quantity of biological populations, human, animal, and plant. In 1926, the federal government established the Council for Scientific and Industrial Research (CSIR) in order to promote applied biological research, principally in the southern regions of the continent. The Empire Marketing Board, set up by British colonial secretary Leo Amery in the same year, concentrated initially on developing trade within the empire and dominions, but soon emphasized the imperial planning of research, supporting in particular after 1928 the CSIR's studies in economic entomology (Schedvin, 1984, 1987). The CSIR's introduction of the Cactoblastus moth from Argentina in the late 1920s almost miraculously had eliminated the scourge of prickly pear, saving the brigalow country of Queensland and New South Wales, and beginning a new era in the biological control of agricultural pests (Rolls 1984; Frawley and McCalman 2004). In Melbourne, the young medical scientist and amateur naturalist, Burnet, was paying attention.

The seeds of Australian ecological research had come from England, but they grew differently on the southern continent. In Cambridge, and later Oxford, Tansley combined systematic botanical work with continental European vegetation mapping techniques, developing the science of plant ecology. In 1904, he set up the British Vegetation Committee, which embarked on a systematic survey of British plants, and in 1913 he helped to establish the British Ecological Society. His book, *Elements of Plant Biology*, published in 1922, proved remarkably influential (Tansley, 1947; Anker, 2001; Ayres, 2012). After World War I, Tansley and a demonstrator in the Botany Department at Cambridge, Samuel Wadham, organized an ecology club, leading bicycle parties out to inspect the local fens (Godwin 1985, p. 146). In 1926, Wadham came to the University of Melbourne to take up the chair of agriculture, and began infusing the study of Australian crops with ecological methods.[10] Through the 1930s, Wadham mixed socially with reserved and reticent Burnet; they frequently went bushwalking with the Wallaby Club in the

[10] As Wadham wrote to Tansley (5 October 1931): "It has been very interesting during the last few years to watch the development of scientific efforts in a hundred different directions in a relatively new country" (1/2/20/1, box 2, Samuel Wadham papers, 1964.0014, University of Melbourne Archives).

hills around Melbourne (Humphreys, 2000; Attwood, 1993). At Melbourne, Wadham trained Herbert Andrewartha and Charles Birch, both of whom in the late 1930s worked at the Waite Agricultural Research Institute at Adelaide, investigating the population dynamics of agricultural pests – Andrewartha on apple thrip, and Birch on the grasshoppers devastating the wheat belt of South Australia (Mulligan and Hall, 2001).[11] There they could collaborate with the botanists at the University of Adelaide, especially the ecologist Bentley Osborn, who would succeed Tansley as Sherardian professor of botany at Oxford. At Adelaide, Anthrewartha and Birch developed their theory that components of the environment, not just density and competition, influence population numbers. Their major work, *The Distribution and Abundance of Animals*, was not published till 1954, when it provoked international debate within ecology.[12] By the 1950s, Burnet had moved on, but *The Distribution and Abundance of Animals* would reshape the ecological thinking of microbiologist Frank Fenner, a close friend of Andrewartha (Fenner, 2006). It drew Fenner ever closer to environmentalism.

In 1929, Francis Ratcliffe arrived from Oxford to join the CSIR economic entomology division in Canberra. He had studied with Elton and with Huxley, who was preoccupied at the time writing the ecology sections of *The Science of Life*. The great southern land fascinated him, though his initial impression of its human population was poor. ‘‘The Australian,’’ he wrote to his mother, ‘‘is a foul-mouthed, incorrigibly lazy waster, whose chief pastimes are drinking and betting on horses.’’ It took a few years before the fastidious Ratcliffe lost ‘‘the hustling habits of the London man,’’ and adapted to the harsh cultural environment.[13] The young ecologist lost no time in making contact with Wilfred E. Agar, the philosophical professor of zoology at the University of

[11] Birch had also studied with Wilfred Agar (1943) at Melbourne, but only later came to appreciate his teacher's enthusiasm for the philosophy of Alfred North Whitehead. It was after Kenneth F. Newman, a philosopher at the University of Adelaide, prompted Birch to read Whitehead that he turned to Agar for further instruction (Steffes 2008).

[12] The earliest published formulation of the density-independence theory probably is Davidson and Andrewartha (1948). At the University of Sydney, Birch later taught Robert May, a prominent disease ecologist in Princeton and London (Gay, 2013). V.A. Bailey was still professor of physics when May was a student at Sydney.

[13] Ratcliffe to Mother, 4 October 1929; and to Mother, 17 October 1929, box 8, Francis Ratcliffe papers, MS 2493, National Library of Australia, Canberra.

Melbourne, who offered him a job, which he reluctantly declined.[14] Ratcliffe was committed to labor in provincial Canberra, along with A.J. Nicholson. In 1929, Ratcliffe observed that Nicholson, who soon took over the economic entomology division, ‘‘has just taken up what is in my opinion a very important line of investigation: working out, from a purely mathematical point of view, the effect of the relation between animals – host and parasite, preyer and preyed-upon.’’[15] Immersing himself in the small biological community in southeastern Australia, Ratcliffe would strengthen the connections of figures like Nicholson, Agar, Wadham, and later Fenner, with Huxley, Elton, and other British ecologists.

In the years before World War II, Ratcliffe exuberantly investigated the population patterns of flying foxes (or fruit-eating bats) as well as termites and pests of stored wheat (Robin, 1997; Mulligan and Hall, 2001). He also ventured deep into the outback to assess the limits of agriculture in Australia, causing him to write that environmental classic, *Flying Fox and Drifting Sand* (1947), prescribed reading for generations since of Australian children. ‘‘We seemed to be looking around the bend of the earth,’’ Ratcliffe (1947, p. 260) wrote of his experiences in the Never–Never, ‘‘later I was to be really scared – scared that something in my mind would crack, that the last shreds of my self-control would snap and leave me raving mad.’’ The Australian outback tended to have that effect on sensitive English ecologists. During World War II, Ratcliffe joined Fenner in the Australian army’s malaria research program in Cairns, North Queensland, under the command of the formidable tropical medicine specialist Neil Hamilton Fairley (Anderson, 2013). In the 1950s, back in Canberra, they would collaborate on a classic investigation of the attempt to eradicate rabbit pests by introducing the myxoma virus, perhaps still the most rigorous and illuminating study of the co-evolution of parasite virulence and host resistance (Ratcliffe and Fenner, 1965; Fenner and Fantini, 1999). Fenner (1999, p. 639) believed it was ‘‘the best natural experiment on the co-evolution of viral virulence and host resistance available for a disease of vertebrates.’’

[14] A well-connected cytologist, Agar had read zoology at Cambridge at the beginning of the century, coming under the influence of William Bateson. Through the 1930s he became preoccupied with animal psychology and biological philosophy, particularly the theories of Whitehead (Agar, 1936, 1938), which he shared with his colleagues.

[15] Ratcliffe to People, 29 March 1929, box 8, Francis Ratcliffe papers, MS 2493, National Library of Australia, Canberra.

A zoologist from Birmingham, England, Nicholson led the CSIR's economic entomology division in Canberra through the 1930s.[16] Studying blowflies, the major parasite of sheep, he became convinced that competition within and between species determined population numbers or density. Nicholson had read carefully the mathematical studies of Lotka (1925) and Volterra (1926) on biological associations between species and the regulation of population, but many of their assumptions seemed to him to lack rigor and to dismiss the actual dynamism of population interactions. While Nicholson agreed that a density-dependant regulatory mechanism governed animal population, which led to fluctuations around an equilibrium, his model was more intricate than earlier mathematical explanations, factoring in competition within species. For Nicholson, there were two processes of selection working on populations, one eliminating the less fit in periods of environmental adversity, the other a struggle for existence among organisms in balance with their environment – and it seemed to him that the latter was the more powerful in determining their distribution and abundance. Natural selection might produce adaptive characteristics, but it did not regulate populations. As Sharon Kingsland (1985, p. 120) points out, "Nicholson made a sharp distinction between natural selection as a disruptive mechanism and competition as a regulatory mechanism" (see also Mackerras, 1996; Kingsland, 1996). In this sense, Nicholson's theory epitomized the increasing emphasis on competition in pre-war animal ecology, a trend that made its insights more obviously compatible with studies of human pathology.

For years, Nicholson toiled over his zoological calculations with an old friend, Victor A. Bailey, the professor of physics at Sydney, who corresponded regularly with Lotka. Nicholson and Bailey made sure to send drafts of their labors to Agar in Melbourne. "It is desirable that you should have some leisure when dealing with this work," Nicholson warned him in 1929. "It is most interesting and novel," Agar responded, "but extremely stiff reading! Most biologists have very little mathematical training and easily get lost when any but the simplest mathematical relations are discussed." Agar would have been happier if Nicholson had restricted his analysis to insects and deferred more general consideration of host–parasite interactions.[17] Not published until 1933,

[16] Nicholson had worked at the University of Sydney with Launcelot Harrison, an entomologist interested in host-parasite interactions, who had studied zoology at Cambridge and was acquainted with Huxley. Harrison died young, in 1928. Nicholson was also familiar with the theoretical inquiries of W.R. Thompson (1930).

[17] Nicholson to Agar, 3 January 1929; and Agar to Nicholson, 5 March 1929, box 1, A.J. Nicholson papers, MS 130, Basser Library, Australian Academy of Science, Canberra.

Nicholson's article, "The Balance of Animal Populations," concluded that competition, especially between hosts and their parasites, determines species density and maintains animals in a state of balance with their environment (see also Nicholson and Bailey, 1935; Bailey, 1931). "Competition always *tends* to cause animals to reach, and to maintain, their steady densities," he wrote. "Factors such as climate and most kinds of animal behaviour, whose action is uninfluenced by the densities of animals, cannot themselves determine animal densities, but they may have an important influence on the values at which competition maintains these densities" (Nicholson, 1933, p. 176). In his analysis, Nicholson acknowledged the assistance of Bailey and Agar, friend and colleague of Burnet.[18] Before publication, both Ratcliffe and Agar had urged Nicholson to submit the article to Elton. "I cannot myself tell whether your theory will turn out right or wrong," Elton wrote to Nicholson, "but that does not seem to me the whole point: the paper introduces a new viewpoint which must be put forward for discussion as soon as possible."[19] In the 1930s, Nicholson's modeling of host–parasite interactions exerted considerable influence on ecologists worldwide – and Burnet certainly was impressed.[20]

Disease Ecology as Dominion Science

Writing *Biological Aspects of Infectious Disease* in Melbourne during the late 1930s, Burnet pondered Nicholson's descriptions of host–parasite interactions, seeking to weave these insights into the pattern of infectious diseases. Evidently, influences beyond animal population ecology also were shaping Burnet's thinking. In particular, the practicalities of disease investigation at the Hall Institute, which fulfilled a service role for the adjacent Royal Melbourne Hospital, meant that his interest in the biological complexity of latent infections such as psittacosis, and epidemics such as influenza, regularly was stimulated (Anderson, 2004). Nonetheless, the influence of Nicholson and Elton was marked, especially in the concern with density, competition, and uneasy equilibrium.

[18] Burnet, too, shared Agar's interests in the biological aspects of Whitehead's philosophy and in eugenics: see Anderson and Mackay (2014).

[19] Elton to Nicholson, 28 December 1929, box 1, A.J. Nicholson papers, MS 130, Basser Library, Australian Academy of Science, Canberra.

[20] Though Nicholson admitted to Bailey: "A tapeworm is a real parasite, our parasites are not; they are really a special type of predator" (24 February 1932, box 1, A.J. Nicholson papers, MS 130, Basser Library, Australian Academy of Science, Canberra).

Thus Burnet (1940, p. 23) began his ecological text with the observation that there is:

> A conflict between man and parasites which, in a constant environment, would tend to result in a virtual equilibrium, in which both species would survive indefinitely. Man, however, lives in an environment constantly being changed by his own activities, and few of his diseases have attained such an equilibrium.

Examining a number of common diseases, including malaria (but not limiting himself to the tropics), Burnet sought a biological explanation of the relations between human populations and their parasites, a category in which he included viruses and bacteria. While Smith had generalized host–parasite relations in order to promote comparative pathology, Burnet did so explicitly to open up an ecological perspective. "Infectious disease can be thought of with profit along ecological lines as a struggle for existence between man and microorganisms of the same general quality as many other types of competition between species in nature" (Burnet, 1940, p. 3). In the introduction to this book on infectious disease, Burnet thus asked his readers to consider the prickly pear and the rabbit in Australia. Infectious disease, he claimed (p. 4), was just the "manifestation of the interaction of living beings" in a changing environment. Microbiology could be considered a branch of "animal ecology [which] deals with the activity of animals as individuals and as species, their mode of feeding and of reproduction, the environmental conditions necessary for their well-being, and the enemies with which they have to contend" (p. 4). Human disease ecology therefore was concerned with population density and competition. Natural selection disrupted, Burnet argued, while competition regulated.

In this essay, I have tried briefly to put the study of host–parasite interactions in a relatively undisciplined Australian intellectual environment or cultural topography, to show how parasites became cosmopolitan in disease ecology – in a sense, to locate the parameters of their dislocation. Yet Burnet and Fenner are not part of the conventional history of Australian ecological thinking – and general Australian ecological thinking is not yet part of the emerging international history of disease ecology. As historians we often have been limited by disciplinary and geographical barriers invisible to the scientists we study. To be sure, Burnet and Fenner are recognized as key figures in the development of the biology of infectious disease, but historians of science have tended to discern only those intellectual influences on them derived from North Atlantic biology or tropical medicine, ignoring local knowledge and connections. To an extent, I have tried to do for disease ecology what Richard Grove, in *Green Imperialism* (1995), once did for conservation biology – that is, to relocate the action in the history of science from North Atlantic shores to the borderlands of the imperial and post-colonial world. I have tried to recuperate disease ecology as one of many dominion sciences, as emerging from one of many imperial intellectual networks (Jones and Anderson, 2015; Pietsch, 2013). In other words, I am calling for more historical realism in the history of biology, recognition of other places, the places of others, as locales of knowledge-making, and not just as sites of resource extraction and passive intellectual reception. In order to understand how parasites became cosmopolitan in disease ecology, we too, as historians, need to become cosmopolitan – to rescue other histories from the violence of exclusion, just as Burnet once saved parasitism for biomedicine (Serres 2007).

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