



Article

Conceptualizing histories of multispecies entanglements: Ancient pathogen genomics and the case of *Borrelia recurrentis*

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Abstract

This article explores the conceptual and cultural implications of using pathogen ancient DNA (aDNA) collected in archaeological contexts to understand the past. More specifically, it examines ancient pathogen genomics as a way of conceptualizing multispecies entanglements. The analysis focuses on the 2018 sequencing of *Borrelia recurrentis* bacteria retrieved from a medieval graveyard in Oslo, Norway. *B. recurrentis* is associated with louse-borne relapsing fever (LBRF), known to have killed several million people in Europe during the past millennium, and it is still encountered in parts of East Africa. The article demonstrates that while aDNA research often foregrounds multispecies entanglements, its epistemic tools cannot easily address the ontological blurriness of pathogens and their embeddedness in vibrant material processes. The article draws on feminist posthumanities work on microbes and materiality to highlight conceptual openings that a theorization of ancient pathogens could engender.

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Introduction

This article investigates the ways in which ancient pathogen genomics is shaping the cultural understanding of historical processes of change. It asks what is at stake epistemically when the past is conceptualized through reconstructed microbial or viral sequences. Ancient pathogen genomics studies microbial and viral material retrieved from archeological contexts in order to trace the evolution of specific diseases. The field brings together two phenomena that have caught public attention during the past decade. First, the rise of high-throughput technologies has allowed the analysis of ancient DNA (aDNA) retrieved from historical and pre-historical remains as well as from environmental samples – the theme of this special issue. Surrounded by considerable excitement both within the biosciences and in cultural discourse, aDNA studies have engendered analyses of increasingly old specimens, such as prehistoric hominins and extinct animal species (Cappellini et al., 2018; Ermini et al., 2015; Llamas et al., 2017). Cultural fascination with aDNA has shaped popular imaginaries of evolution as well as reinforced assumptions of epistemic authority assigned to genetic knowledge in society (Turner, 2007; Oikkonen, 2019). Second, our relationship to bacteria and viruses has become an object of growing biomedical and political interest through the rise of antimicrobial resistance (Brown and Nettleton, 2017; Landecker, 2015) as well as emerging infectious diseases (Caduff, 2015; Lakoff, 2017; Porter, 2019). These more-than-human phenomena have made it clear that we need to invent new ways of living with pathogens. At the same time, increasing knowledge about the centrality of bacteria and viruses to healthy biological processes, such as our symbiotic relationship with microbes in the digestive tract, has highlighted the importance of understanding how human and nonhuman species mold one another (Ironstone, 2019; Lorimer, 2017; Paxson and Helmreich, 2014).

Research in ancient pathogen genomics has identified and sequenced pathogens behind historically significant diseases such as plague, the 1918–1919 “Spanish Flu” influenza, tuberculosis, cholera, salmonella, and smallpox (Arning and Wilson, 2020; Duchêne et al., 2020; Spyrou et al., 2019). Some of these results, such as the sequencing of the *Yersinia pestis* bacteria behind plague, have raised considerable media interest. Ancient pathogen DNA is typically retrieved from mummified remains, dental calculus, and coprolites (fossilized feces) or from environmental samples, for example ice cores (Arning and Wilson, 2020). As with hominin and animal aDNA, proponents of aDNA research view ancient pathogen DNA as a source of knowledge unavailable through historical records, anatomical study of skeletal remains, or modern pathogen genomes. Ancient pathogen

genomes may serve as a source of information on extinct bacterial or viral lineages not preserved in the currently circulating strains, or they may be used to help identify pathogens behind vague descriptions of symptoms in historical records (Spyrou et al., 2019: 329). For example, in the case of an 800-year-old grave in Trondheim in Norway, ancient pathogen analysis suggested that “salmonellosis was a deadly invasive disease of humans for centuries before its first recognition by physicians” (Zhou et al., 2018: 2424). Ancient pathogen genomics has also provided information on the co-presence and co-circulation of multiple pathogens in specific historical contexts (Arning and Wilson, 2020; Duchêne et al., 2020). Some have argued that ancient pathogen genomics has also potential relevance for biomedicine by allowing scientists to understand processes through which bacteria and viruses evolve over time and thus better estimate the ecological conditions and genetic mechanisms through which modern strains may increase in virulence (i.e. how easily they infect and harm organisms) (Duchêne et al., 2020; Houldcroft et al., 2017; Spyrou et al., 2019).

This article centers on a key point made by some proponents of ancient pathogen genomics: that ancient pathogen genomics could be used to elucidate how human evolution is entangled with the evolution of pathogens. For example, in an overview of the promises and challenges of ancient pathogen genomics, Kelly M. Harkins and Anne C. Stone write: “A driving force behind the field of ancient pathogen genomics is the necessity to characterize how human interactions with commensal organisms, pathogens, and hosts impact human evolution. Today, populations and individuals differ in susceptibility to disease as a direct result of our evolutionary history with pathogens” (Harkins and Stone 2015: 137). Crucially, the human-nonhuman co-evolution outlined by Harkins and Stone involves more than two biological entities, humans and pathogens. It also involves a range of “hosts”: nonhuman animal species. These include so-called *disease vectors* – species through which bacteria or viruses enter other species – such as mosquitoes in the case of malaria or Zika virus. They also include species through which *zoonosis* – the crossing of mutating pathogens across species – may take place, as in the case of avian influenza viruses or the currently circulating SARS-CoV-2. In short, it is assumed that evolution cannot be understood without a detailed examination of more-than-human multispecies dynamics.

This article seeks to understand the cultural and epistemic implications of aDNA approaches to more-than-human coevolution. It asks what kinds of knowledges are produced through the study of ancient pathogens, and how these emerging epistemic practices shape the understanding of human-pathogen entanglements. More specifically, the article asks what kinds of conceptual openings and closures take place in approaching patterns of historical change through bacterial or viral genomes. Rather than a critique of ancient pathogen genomics, the article offers an analysis of its epistemic role as a mode of inquiry into historical processes.

My exploration of ancient pathogen genomics starts with a specific case study: a 2018 scientific report of the first successful sequencing of ancient *Borrelia*

recurrentis from human remains in a 15th-century grave in Norway. Compared to publicly discussed cases such as *Y. pestis* medieval genomes or the recovery of “Spanish Flu” influenza virus, the case of *B. recurrentis* seems to have attracted little media attention. However, *B. recurrentis* provides an illuminating viewpoint into the cultural and historical implications of ancient pathogen knowledge because the bacterium is associated with louse-borne relapsing fever (LBRF), known to have killed several million people in Europe during the past millennium. The case produced genetic information about the presence of an ancient pathogen in a specific historical location (medieval Scandinavia). It also involved a vector – the human body louse – highlighting the multispecies dynamics structuring the evolution of diseases. Using the case as a starting point, the article explores the conceptual implications of using pathogen aDNA to approach more-than-human processes of historical change.

The article is structured as follows. The next section introduces my theoretical and methodological starting point, feminist posthumanities theorization of multi-species relations, and outlines how its toolkit can be used to unpack the conceptual implications of approaching multispecies evolution through pathogen aDNA. The following section introduces the case study and situates it within the technological and epistemic engagements of aDNA research. The section “Multispecies entanglements as a historical force” explores how multispecies evolution is conceptualized in the sequencing of the ancient *B. recurrentis* samples as part of processes of historical change. The section “Conceptualizing pathogens” elaborates on the role of bacteria and viruses as evolutionary actors, identifying a tension between pathogens as evolving and unstable in scientific research and pathogens as agential entities in cultural expectations surrounding aDNA. Throughout these sections, I argue that the cultural significance of ancient pathogen genomics is in many ways ambiguous: while it foregrounds our entanglements with other forms of life, its ways of conceptualizing pathogens cannot easily accommodate the multitude of vibrant materialities that play a constitutive role in historical processes. This points to the need for interdisciplinary conceptual work in the study of multispecies pasts.

Theoretical framework

The article approaches *B. recurrentis* and LBRF through theoretical tools developed within feminist posthumanities. I use feminist posthumanities as an umbrella term that includes the so-called feminist “new materialist” rethinking of matter as active, the rethinking of multispecies relationships as entangled in feminist environmental studies, and feminist science and technology studies’ (STS) analyses of technologies as constitutive of more-than-human relations (Åsberg and Braidotti, 2018; Åsberg et al., 2011; Hird and Roberts, 2011). I focus here on the first two, as the ways in which feminist posthumanities scholars view material processes and interspecies dynamics as productive of historical change are useful for understanding what is at stake conceptually when history is approached through pathogen aDNA. Crucially, these two areas of theorization draw on rich histories beyond

feminist scholarship, especially indigenous studies' longstanding engagement with vibrant matter and interspecies relations (TallBear, 2017).

It should be noted that feminist posthumanities is by no means the only theoretical framework through which conceptualizations of past microbes and viruses could be analyzed fruitfully. In addition to indigenous studies, feminist posthumanities scholarship resonates with the so-called material turn in archaeology, such as “symmetrical archeology” that grants equal empirical weight to nonhuman species and material things as participants in the situated coproduction of phenomena (Olsen et al., 2012; Olsen and Witmore, 2015), or the “entrainment” of often unpredictable material processes, situated human engagement, and cultural and political valuation (Bauer and Kosiba, 2016). Like feminist posthumanities analyses, materially oriented archaeological approaches have explored the co-productive entanglements of humans and plants (Lodwick, 2019; van der Veen, 2014) and humans and environments (Grauer, 2020). Discussions on how archeologists negotiate materiality and its theorization (Edgeworth, 2012; Pétursdóttir and Olsen, 2018) also resonate with many of the methodological concerns of feminist posthumanities. While I hope to contribute to these archaeological debates, my analysis engages explicitly with feminist posthumanities because of its rich engagement with *interspecies biology as lively coproduction*. That is, feminist posthumanities literature allows me to theorize biology as open-ended interspecies entanglements, which is crucial for unpacking the epistemic and ontological implications of ancient pathogen genomics.

Feminist posthumanities literature has sought to explore how matter in its multiple forms – biological entities, technologies, cultural artefacts – is lively, not-fully-predictable, and productive. For example, Jane Bennett's book *Vibrant Matter* focuses on “the capacity of things – edibles, commodities, storms, metals – not only to impede or block the will and designs of humans but also to act as quasi agents or forces with trajectories, propensities, or tendencies of their own” (Bennett, 2010: viii). Through a range of examples from waste management to stem cell research, Bennett theorizes “a vibrant materiality that runs alongside and inside humans to see how analyses of political events might change if we gave the force of things more due” (Bennett, 2010: viii). In a similar vein, Deboleena Roy explores “what matter, molecules, bodies, and organisms such as grass *are capable of doing*” (Roy, 2018: 29). Roy argues that focusing on the vitality and complexity of matter makes it possible to “rethink matter in terms of flux, motion, and capabilities, and reframe biology in terms of events and processes” (Roy, 2018: 29).

This focus on material processes that “run alongside and inside humans” (Bennett) and that are characterized by “flux, motion, and capabilities” (Roy) helps highlight that pathogens are much more than genetic codes in an aDNA database. Microbes and viruses are evolving and materially complex entities that have unexpected vibrant capacities to steer co-evolutionary processes. For example, Roy (2018) explores how bacteria edit their own genomes. Roy suggests that important questions center on the effects of bacterial editing: “how are bacteria

changed, how are labs changed, how are institutions changed, and how are we as human scientists changed when bacteria begin to write?” (Roy, 2018: 121). In the case of *B. recurrentis* studied in this article, a central aspect of the liveliness of bacteria is the ability of *B. recurrentis* to engender a variety of surface proteins, which is the reason why the disease it causes – louse-borne relapsing fever – is characterized by multiple relapses.

The constitutive role of multispecies relations in societies is another key theme in feminist posthumanities. Several scholars have drawn on biologist Lynn Margulis’ work on symbiogenesis, which highlights the productive role of symbiotic relationships between species as an evolutionary force, and places bacteria at the heart of the evolution of life (e.g. Margulis 1993). Feminist theorist Donna Haraway has developed the concept of “becoming with” to capture the productive entanglements of species and other life forms. Foregrounding the blurriness of bodily boundaries, Haraway describes how “[o]rganisms are ecosystems of genomes, consortia, communities, partly digested dinners, mortal boundary formations”, and how they are inseparable from their ecological and multispecies contexts (Haraway, 2008: 31). Likewise, Myra Hird (2009) has developed the idea of “microontologies” to understand our constitutive entanglement with microbial communities both within and around us. Commenting on bacterial editing like Roy above, Hird explores how bacterial communities may shape evolutionary processes through communication and self-regulation, “mak[ing] use of a collective epigenetic memory that can, for instance, track previous encounters with antibiotics” (Hird, 2009: 42). For Hird, the entanglements between species – such as humans and the multiplicity of microorganisms – constitute an ontologically productive force that generates biological diversity and evolutionary change. In the case of *B. recurrentis* and LBRF explored in this article, multispecies relations involve the entanglements of and interactions across bacteria, humans, and lice. From a feminist posthumanities viewpoint, these three entities are not stable actors but co-constitute one another in a dynamic process through which immunities and vulnerabilities, as well as material changes in each entity, emerge.

The focus of this article is theoretical and explorative rather than empirical, as my goal is to outline key conceptual and cultural issues that have arisen with the extension of aDNA techniques to microbial and viral evolution. The case of *B. recurrentis* provides a starting point for this exploration. In terms of materials, my discussion reflects on the original scientific report on ancient *B. recurrentis* by Guellil et al. (2018) and science communication around it, as well as scientific articles on both modern *B. recurrentis* cases and genetic analysis of other ancient pathogens. I read these materials through the key themes outlined above: vibrant living matter and multispecies relations. My method involves identifying constructions of interspecies relations and processes of historical change in both scientific and popular texts. However, the intention is not to equate scientific and popular accounts, which represent different conceptual and epistemic logics. Rather, reading scientific and popular texts side by side helps make visible the wider cultural stakes in how aDNA projects enter cultural discussions about history. My analysis

is guided by the questions: How are pathogens conceptualized in these materials? How are their relationships with other life forms, such as humans, imagined? Through these questions, the article addresses the conceptual implications of understanding history through ancient pathogens and suggests some ways in which those epistemic parameters could be expanded in cultural debates about the past.

The case

Louse-borne relapsing fever (LBRF) has been associated with millions of deaths throughout European history, including outbreaks during the Irish Famine and in the aftermath of World War I (Cutler, 2010). The name of the disease reflects its most prominent characteristic: a pattern of periods of remission and relapse after the initial infection. LBRF is transmitted through a vector, the human body louse, which also operates as a vector in other historically significant diseases such as plague and typhus. While there are indications that ancient and medieval European societies suffered from LBRF, the disease got its distinct name, relapsing fever, after an outbreak in Edinburgh in the 1840s. The ability of the specific type of bacteria involved in *Borrelia* infections – spirochetes – to cause disease was first described in 1873, and the causative link between a vector and the outbreak of relapsing fever was shown in the early years of the 20th century (Cutler, 2010). While LBRF has mostly disappeared in Europe following improvements in living conditions and subsequent decline in human body lice populations, it is still a public health concern in some countries in East Africa, and cases of LBRF have been documented in Europe among refugees from those areas (Badiaga and Brouqui, 2012; ECDC, 2015).

Researchers at the University of Oslo and the Norwegian Institute for Cultural Heritage Research collected and sequenced the first *B. recurrentis* aDNA genome in 2018 (Guellil et al., 2018). The aDNA was retrieved from the skeletal bones of a woman buried along with a child in a 15th-century grave in a medieval graveyard south of St. Nicolay's Church in Oslo. After the initial identification of ancient bacterial material resembling the deposited *B. recurrentis* reference genome, additional pathogen DNA was retrieved from teeth, enabling the reconstruction of the ancient genome. According to the team that conducted the analysis, the fact that *B. recurrentis* was present in “relatively high quantities” in the remains suggested that the woman had died “at the height of bacteremia” (Guellil, 2018: 10426).

The comparison of the bacterial aDNA to modern bacterial sequences did more than simply identify the medieval “European” pathogen. The comparison also located material differences between the modern “African” sequences and the medieval “European” sequence, which offered a basis on which the evolution of *B. recurrentis* into separate lineages over centuries and across space could be sketched. Crucially, this enactment of differences between old and new geographically situated pathogen strains echoes the organizing logics of aDNA research, in which ancient and modern samples, such as sequences from early hominins and

modern humans, are compared in order to produce evolutionary histories (Ermini et al., 2015; Llamas et al., 2017; Oikkonen, 2019). In this framework, ancient pathogen knowledge (like all aDNA knowledge) is understood to be *material* in the sense that it is discoverable in the remains at the archaeological site. At the same time, it is also *digital* in the sense that it accrues meaning through its life in the genomic database and its comparison to other sequences (Oikkonen, 2019; Turner, 2007).

While ancient pathogen genomics is past-oriented, the comparisons of modern and past pathogen strains also engage futures. The identified differences between the *B. recurrentis* aDNA sample and six modern samples of East African origin previously sequenced by Marosevic et al. (2017) pointed to potentially significant structural changes in the microbial genomes in the two lineages. These involved genes that encode mechanisms of *antigenic variation*, the ability of the microbe to alter its surface features and thus repeatedly evade the immune system and cause the relapses, so that “each new wave of infection, in this case febrile relapse, is characterized by a new serotype [i.e. an immunologically significant new variant]” (Guellil et al., 2018: 10424). The researchers observed that the medieval genome seems to have less antigenic variation than the modern genomes of East African origin. They suggest that this could explain why current East African strains are characterized by five relapses, whereas historical records typically mention one or two. The researchers also note that both the modern and medieval strains embody features – such as the shrinking of certain parts of the genome compared to a closely related spirochete, *B. duttonii* – that suggest specialization to specific ecological conditions. In terms of public health, such structural changes in the pathogen genome could potentially shape the future of LBRF as a re-emerging disease in regions outside East Africa, where *B. recurrentis* has been absent in the body lice population for decades (on re-emerging outbreaks, see Antinori et al., 2016; ECDC, 2015).

Multispecies entanglements as a historical force

My analysis centers on the ability of *B. recurrentis* aDNA and other pathogen aDNA genomes to illuminate the historical processes through which humans and nonhuman species have shaped one another. Research on pathogen aDNA often highlights how human and pathogen evolutionary trajectories are entangled, and point to key events – societal changes, migration of people – through which humans and pathogens affect one another. For example, a recent review of ancient pathogen genomics published in the journal *Current Biology* describes how, in the case of “*S. enterica* and *Y. pestis*, the ancient presence of virulence factors indicates that subsequent decline in their incidence and disease severity was most likely driven by changes in human behaviour and pathogen ecology” (Duchêne et al., 2020: R1224). Another review published in *Microbial Genomics* asks “how have human–microbe interactions influenced the evolution of each species” and suggests that “aDNA studies have precipitated a major revision to our understanding of

recent human and bacterial evolution, for example the spread of steppe ancestry across Eurasia, and the plagues carried with it” (Arning and Wilson, 2020: 15).

These examples show how ancient pathogen genomics engages with insights from ecology, epidemiology, archaeology, history, and other disciplines. At the same time, such examples suggest that the evolutionary trajectories of each species are often conceptualized as ontologically distinct. That is, species and organisms, such as microbes, humans, and non-human vectors like lice or mosquitos, are approached as *ontologically separable* from their mutual entanglements – they are entities that interact, as in the account of “human-microbe *interactions*” above (Arning and Wilson, 2020: 15; emphasis mine). In the case of *B. recurrentis* aDNA, the original article and science communication show points of connection between human cultural and social history and the molecular evolution of *B. recurrentis*. The scientists note that *B. recurrentis* “is known for its involvement in devastating historical epidemics” (Guellil et al., 2018: 10422), a framing that posits the microbe as an actor involved in a historical event with consequences for human societies. At the same time, the paper portrays the microbe as an object of evolutionary pressure, evident in how “*B. recurrentis* shows accelerated rates of genome degradation caused by adaptation to host-restricted vectors and functional trade-offs, resulting in a degraded genome, reduced genome size, low coding content, and increased virulence” (Guellil et al., 2018: 10425). While the points where the entangled trajectories of humans and microbes materialize in epidemics are constructed as life-threatening moments for humans as individuals and communities, microbial evolution appears as curiously separate from human biology. For example, the intricate immunological processes inside human bodies that have emerged from the necessity of living with particular pathogens in different historical contexts fall outside this conceptual framework. The ways in which living with pathogens affects human biology across generations, and how this, in turn, shapes pathogens as vital, biological entities, evades genetic analysis.

In the rest of this section, I outline some ways in which a conceptualization of pathogen aDNA as part of vibrant, more-than-human processes could provide new vistas onto the co-production of change over time. This requires approaching species and pathogens as ontologically inseparable and locating vibrant and productive materiality beyond the microbial or viral genome in a range of embodied processes. To begin with, *B. recurrentis* and human bodies are entangled in very specific ways. The work of Kyla Schuller (2018) sheds light on these human-microbial relations. Schuller has examined the complex material dynamics of a related bacterium, *Borrelia burgdorferi*, which causes the North American variant of Lyme disease. Both *B. recurrentis* and *B. burgdorferi* are spirochetes, which move in a twisting motion and are thus able to penetrate parts of the human body, such as the brain and the nervous system, that cannot be reached by most microbes. Furthermore, it has been argued that spirochete colonies may lay dormant inside the body, protected by a biofilm, for long periods of time until they reawaken. For this reason, “spirochete infections are likely relations for the long haul” (Schuller, 2018: 51). Highlighting the constitutive role of relations between

species, Schuller perceptively describes how “[t]he individual human body is entangled in spirals with spirochetes, unfolding and enfolding in dynamic relation with the bacteria in ways that challenge conventional notions of infection, disease, and health” (Schuller, 2018: 52).

Schuller’s way of conceptualizing spirochete infections suggests that *B. recurrentis*, like *B. burgdorferi*, is entwined with human bodies much more thoroughly than suggested by aDNA sequences and genetic knowledge, or by accounts of disease outbreaks as historical events. Schuller’s analysis draws attention to how spirochete and human materialities shape one another in a process that may not have a clear endpoint or key climactic moment. In the case of *B. recurrentis*, the relapsing nature of the illness points to this cyclicity, which, like the spirochete, moves forward in time while swirling. This highlights the conceptual constraints of approaching illness through aDNA: While the focus on antigenic variation in the *B. recurrentis* aDNA study captures the cyclicity of the disease, it cannot show how that cyclicity takes shape through a constitutive inseparability of living microbial and human matter.

Explicating the experiences of Lyme patients, Schuller highlights how matter – both embodied and bacterial – is active and surprising, evident in the range of “sensory, affective, cognitive, and muscular-skeletal symptoms experienced by hundreds of thousands of Lyme patients for months and years” after the initial infection (Schuller, 2018: 52). This draws attention to how the human-spirochete entanglements operate as a productive force that engenders not-fully-predictable material and affective outcomes. It also resonates more generally with Myra Hird’s (2009) exploration, introduced above, of symbiotic entanglements of bacteria and human and nonhuman animal species as constitutive of variation.

While drawing on Schuller’s and Hird’s analyses of how bacteria may linger and engender material change, I want to draw attention to how materialities beyond the embodied processes inside living human bodies are also part of this productive dynamic. Such materialities include vectors (here, the human body louse) as well as particular arrangements of material relations reflecting structural poverty, absence of medical attention, poor hygiene, and overcrowded living quarters. Crucially, economic circumstances do not translate into an infection in a straightforward manner but are part of the not-fully-predictable dynamic that may, or may not, engender an infection. In the case of the woman and the child in the Oslo grave, the site of the burial away from the church points to poverty and low social status (Avset, 2018). These material circumstances can be viewed as part of the vibrant dynamic that produces a specific disease outcome. In recent years, these material and multispecies entanglements have been a concern in other vector-borne diseases such as Zika, in which living conditions (especially the presence of stagnant water) and the complex and difficult-to-control entanglements of humans, mosquitos, and viruses engender unexpected material outcomes: cases of microcephaly among children born to some women infected with the Zika virus during pregnancy (Day, 2018; Oikkonen, 2017). While interdisciplinary scientific projects have explored the complex relations between biological and societal factors, the

vibrancy and ontological inseparability of these situated elements are addressed less frequently.

How, then, to conceptualize material processes and multispecies entanglements as productive? In addition to the feminist posthumanities scholarship introduced earlier, three approaches may provide some suggestions. First, Steve Hinchliffe (2015) points out that the crossing of new viral strains across species is not a matter of a single event but rather a series of interactions over time and across space that sometimes (but not always) leads to a development of a new strain that can be transmitted among another species (such as humans). This highlights how exposure to disease is often a matter of either *quantity* or *quality* of microbial material or *length* of exposure rather than an absolute presence or absence of pathogens. Likewise, immunities that emerge from infection are partial and situated (Oikkonen, 2018). Second, Eben Kirksey (2015) explores how new kinds of variants and symbiotic and co-productive entanglements between plants, animals, and microbes emerge at unexpected sites following ecological disaster. Kirksey highlights the productive power of these newly shaped symbiotic relationships through the term *emergent ecologies*. This emphasis on emergence as an unpredictable material process captures the processual nature of multispecies entanglements within an evolutionary frame. Third, Neel Ahuja (2016) examines unpredictable life and multispecies travels as not only an evolutionary but also a historical force. Ahuja shows how human history is shaped by attempts to interfere with multispecies relations and the material articulation of life through such relations. Like Kirksey, Ahuja argues that multispecies life cannot be fully managed, and that the biological is often inseparable from its societal and political manipulation. Read together, the three accounts point to a multiplicity of vibrant processes that may – or may not – materialize in a disease outbreak or in a new microbial or viral strain.

As to LBRF and *B. recurrentis*, these observations make visible the conceptual boundaries of genetic analysis. As aDNA analysis targets a necessarily limited number of strains of preserved DNA, the focus is on reconstructing temporal trajectories between past and modern samples to capture material changes recorded in DNA. Even when aDNA projects are able to collect a large number of samples – a challenging task due to the degradation of biological material – the material encounters and constitutive entanglements of species, pathogens and material conditions that *precede* genetic change tend to evade analysis.

Conceptualizing pathogens

A further issue key to understanding vibrant multispecies dynamics concerns the conceptualization of pathogens as entities. There is a long cultural history of portraying pathogens as anthropomorphic, independent agents that – if we are to believe the storylines of popular fiction and films – seek to outwit humans and take over the world (Wald, 2008). The news coverage of recent epidemics such as Zika, or current ones such as COVID-19, often also implicitly positions the pathogen as an independent agent that threatens society (e.g. Brives, 2020; Oikkonen,

2017). This reflects visual traditions in which the threatening virus or bacterium appears as separated from its surroundings, floating in the space-like interiority of the body (Haraway, 1991: 203–230). Some of the publicly celebrated discoveries of ancient pathogens have followed this same anthropomorphizing narrative. For example, an article in *The New York Times* on the 2015 sequencing of *Y. pestis* aDNA states that “Bacteria can change history” and that “After acquiring the ability to infect fleas, *Yersinia pestis* may have begun to spread more readily from one rodent to another, eventually causing widespread epidemics” (Zimmer, 2015). Likewise, a 2019 *Science Magazine* article on a new *Y. pestis* aDNA discovery describes how “a single strain was responsible for the Black Death, from Italy to the United Kingdom” and “the bacterium persisted locally in Europe, perhaps in rodent hosts, where it evolved into diverse strains that caused later epidemics” (Gibbons, 2019). My point here is not to evaluate the accuracy of these statements, but to draw attention to the ease with which they slip into a culturally recognized model of thinking of pathogens as agential entities.

Anthropomorphic undercurrents in how microbes and viruses are conceptualized are reinforced by cultural representations of genes as agential. By this, I do not mean to equate genes with pathogens. Rather, the anthropomorphizing discourses around genes in society provide a culturally familiar framework through which ancient pathogen genomes are made sense of. The idea of genes as evolutionary actors has a long history that includes influential accounts such as Richard Dawkins’ (1989) concept of the “selfish gene” – the gene as an agent that uses living organisms as means of its own reproduction. In cultural discourse around ancient pathogens like *Y. pestis* or *B. recurrentis*, popular ideas of genes and pathogens as agential merge into one another. As a result, the pathogen emerges as if it was an evolutionary actor similar to the selfish gene. For example, an *Ars Technica* article on Guellil et al.’s discovery talks about “hiding from the immune system” as “one possible evolutionary solution” for a pathogen (Smith, 2018).

This is, of course, not how ancient pathogen genomics discusses either genes or pathogens. Genes are not actors, but entities approached through statistical models, distribution of variation across samples, and gene flow – migration of organisms and their genes – between geographically located populations. Likewise, pathogens lack conscious agency and intentionality. There is, then, a clear tension between the popular portrayal of pathogens (and genes) as agential actors and the scientific understanding of pathogens as complex and genetically evolving entities that change over time through gradual adjustments to evolving ecological and material conditions. Furthermore, Guellil et al.’s article shows that genetic knowledge is constructed rather than discovered. The authors suggest that there are “discrepancies” between the *B. recurrentis* reference sequence and the aDNA and modern samples that “can be linked to the deposition of an incomplete assembly of the original reference genome strain A1, since both our medieval European strain and the modern African strains show the same variations” – that is, the reference genome may have an error (Guellil et al., 2018: 10423). This

highlights how reconstructed genome sequences are compiled and enacted objects rather than natural ones (M'charek, 2014).

At the same time, pathogens as entities arise from multispecies entanglements and subsequent flows in genetic and other biological material across life forms (Hird, 2009). Schuller (2018) provides some ways of theorizing further this ontological blurriness. Through *B. burgdorferi*, Schuller illustrates how species fold into one another so that species boundaries cease to exist in any meaningful manner: "Entanglement with spirochetes makes particularly salient how new, microbial notions of subjectivity and personhood are unfolding in the contemporary moment in which the nervous system and sensory experience are elements of a multispecies choreography that exceeds the spatiotemporal purview of the singular self" (Schuller, 2018: 63). Schuller highlights that spirochete infections indicate a move "from genetic, neural, and hormonally determined notions of singular-subject formation to a multi-life-form idea of the subject and the sensorium" (Schuller, 2018: 62). In this conceptualization, bodily and species boundaries disappear in an intricate neurological, immunological, and affective dynamic that keeps generating not-fully-predictable change.

Furthermore, the blurriness of microbes and viruses arises from their inseparability from their ecological contexts – that is, the ontology of pathogens is *enacted* through their relations to other species and material realities in specific circumstances. The work of Astrid Schrader (2010) and Claire Waterton (2017) illustrates this ontological inseparability. Schrader (2010) examines a micro-organism called *Pfiesteria piscicida*, which is known for its association with fish kills in North Carolina estuaries in the United States. In specific environmental conditions, which involve the presence of large numbers of fish, *Pfiesteria piscicida* forms toxic colonies that move with water; without those conditions, it does not appear to be toxic. Waterton (2017), in turn, explores a participatory communal project, the Loweswater Care Project, in the Lake District in the United Kingdom, which set out to improve local water quality. In the heart of the project are cyanobacteria, which, like Schrader's *Pfiesteria piscicida*, are toxic in only some ecological conditions and to some species. Waterton shows how the nature of cyanobacteria's existence emerges as an open question in the project. Schrader's and Waterton's studies show how micro-organisms are defined through their ecological contexts and multispecies entanglements, and how they are in this sense ontologically blurry. Both studies also show how the ways in which we approach and conceptualize micro-organisms enact them in particular ways. This also applies to ancient pathogen genomics, which enacts (rather than simply reflects) a particular microbial or viral ontology and multispecies ecology.

What would it mean to think of *B. recurrentis* as ontologically dependent on ecological contexts? For one, it would highlight the way in which the pathogenicity of *B. recurrentis* – and indeed its very existence – relies on the vector, the human body louse, which in turn relies on the human body. Crucially, this would shift the focus from *B. recurrentis* as pathogens to *B. recurrentis* as entangled and vibrant life forms. The ability of *B. recurrentis* to cause illness is inseparable from the ways

in which it interacts with lice as well as human bodies; those interactions, in turn, are made more likely through the material circumstances connected to poverty and social marginalization. This highlights the intricate ways in which *B. recurrentis* unfolds with its environments, and how such moments of unfolding engender a range of embodied outcomes, including outbreaks in some historically specific locations or situated bodies, and a dormant disease elsewhere.

Viewing microbes and viruses as blurry and contextual has implications for how we understand communities, in the past as well as the present. Stephanie Fishel's (2017) theorization of what she calls "the microbial state" provides some tools for unpacking these implications. Fishel suggests that we should rethink states in light of recent immunological and microbiological research that highlights the openness of embodied material processes and the entanglements of human biology with more-than-human life. National and communal borders emerge as inseparable from their ecological contexts, and there simply is no point where the inside becomes the outside. In the case of communities affected by *B. recurrentis*, this means that the spirochete is no outsider but embodies the inseparability of humans and microbes, on the one hand, and pathogens and potentially harmless microbes, on the other. At the same time, the comparisons between aDNA and modern samples highlight how past societies and belonging expand materially to the future. The ways in which outbreaks come and go, and microbial strains split (in this case, between Europe and Africa), show how community is materially present outside its borders. For example, the genetic detail of the medieval European strain is partly, but not wholly, present in the lineage that engendered the modern strains identified in the samples from individuals from Africa. Yet genetic knowledge cannot be taken as an epistemically superior way of unpacking this temporal and spatial leakiness of community. While ancient pathogen genomics opens up ways of making visible the circulation and impact of past pathogens, approaches theorizing vibrant and entangled materiality, including (but not limited to) those arising from feminist posthumanities, help us conceptualize the constitutive entanglements of pathogens and other entities as historical phenomena from which futures unfold.

Conclusion

Ancient DNA has received a lot of public attention because it is associated with materiality that is perceived in cultural discourse as more permanent and stable than material archaeological artefacts and objects. This perception arises, paradoxically, from the fact that genomic knowledge is digital. The idea of an indestructible "code" is powerful as it posits aDNA beyond the (historically crumbling) materiality that archaeologists and historians trace. Crucially, the idea of DNA as unambiguous and indestructible is misleading because, despite advances in high-throughput sequencing, aDNA work is relational: this is shown by how Guellil et al.'s paper found out that the *B. recurrentis* reference genome was likely missing a section.

Instead of turning away from the idea of aDNA as material, this article has embraced the possibility of rethinking materiality more broadly, bringing together

a range of material processes and exploring them as constituting a productive dynamic with possibly open-ended outcomes. In the case of LBRF, these materialities include *B. recurrentis* bacteria, human body lice, immunological and neurological processes inside living human bodies, and the larger ecological and economic circumstances, such as the material conditions arising from structural poverty. These materialities are vibrant, as when the spirochete and human neurological and cellular processes shape one another inside the living body, with the bacteria altering its proteins, engendering the cyclical pattern of relapsing fever. Also, the socioeconomic and cultural circumstances are more than stable context. They bring together body lice, human bodies, and microbes in a particular historical dynamic that has material outcomes: disease cases affecting individual bodies or communal outbreaks.

I have argued that while ancient pathogen genomics has foregrounded the past entanglements of humans, microbes and viruses, and non-human vectors, the task of unpacking these entanglements conceptually is beyond the epistemic reach of genetic frameworks. I have suggested that such conceptual work requires approaching ancient pathogens and their constitutive entanglements as lively and productive rather than as a record of the past. The article has highlighted two themes that would emerge from this conceptual work: multispecies entanglements as a historical force, and reconceptualization of pathogens as ontologically blurry entities. While aDNA research makes multispecies entanglements visible, its epistemic tools cannot easily unpack the ontological blurriness and vibrant co-production that emerge from such entanglements.

Finally, the article has suggested that bringing aDNA into dialogue with historical, social, and archaeological research is important but not enough as such. In order to avoid falling back on familiar epistemic models (whether historical or aDNA), aDNA sequences could be seen as an opportunity to rethink historical processes of transformation and our relationship with other life forms conceptually. How are our lives – or life in general – conditioned by multispecies entanglements? In what ways do our futures rely on past trajectories of becoming with other species?

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