Recent decades have brought countless outbreaks of infectious disease among wildlife. These events appear to be increasing in frequency and magnitude, but to objectively evaluate whether ecosystems are experiencing rising rates of disease, scientists require historical data on disease abundance. Specimens held in natural history collections represent a chronological archive of life on Earth and may, in many cases, be the only available source of data on historical disease patterns. It is possible to extract information on past disease rates by studying trace fossils (indirect, fossilized evidence of an organism’s presence or activity, including coprolites or feces), sequencing ancient DNA of parasites, and examining sediment samples, mumified remains, study skins (preserved animal skins prepared by taxidermy for research purposes), liquid-preserved hosts, and hosts preserved in amber. Such use of natural history collections could expand scientific understanding of parasite responses to environmental change across deep time (that is, over the past several centuries), facilitating the development of baselines for managing contemporary wildlife disease.

In a nutshell:

- Defining a baseline state for infectious disease is vital to natural resource management and policy; without such a baseline, managers attempting to maintain or recover the health of ecosystems under their stewardship are “shooting in the dark.”
- Unfortunately, historical data on diseases are rare; while naturalists have been collecting high-quality data on free-living species for generations, parasitic species have been less rigorously documented.
- Natural history collections are a potentially valuable and underutilized source of data on historical disease patterns.
- Using parasitological dissection, DNA sequencing, advanced imaging technology, and archaeological and paleontological tools, disease ecologists can take advantage of natural history collections to track disease changes across deep time, providing historical context that can inform management about contemporary disease problems.

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We believe that natural history collections have the potential to be a prized resource for ecologists interested in tracking long-term shifts in parasitism and disease. Here, we aim to draw attention to this potential trove of data and to reduce barriers to the use of natural history collections for this purpose. Collections personnel are increasingly interested in facilitating such research; some are already collaborating with public health agencies to respond to emerging infectious diseases (DiEuliis et al. 2016; Schindel and Cook 2018), while others are using archival samples to study long-term change in human diseases (Emery et al. 2012). However, few of these existing collaborative efforts have involved ecologists focused on wildlife disease, despite the substantial promise of natural history collections for supplying information on ecological (DiEuliis et al. 2016) and evolutionary (Holmes et al. 2016) changes in parasitism of non-human animals.

The use of natural history collections in disease research has its challenges. While digitization promises broad availability of collections data via the internet, not all such data are currently available in searchable, public databases. Disease researchers may also be concerned about whether specimens represent an unbiased sample of their populations of origin (Wehi et al. 2012). Variability in sampling effort and preservation techniques, as well as decay over time, might affect the likelihood of detecting disease in a way that creates artifactual relationships between disease prevalence and time (eg Morrison 2001). Moreover, biological collections can be expected to favor preservation of some parasitic species over others, and cannot be assumed to be a complete record of the parasite fauna of a particular host species.

If these constraints can be accounted for, natural history collections allow otherwise impossible studies that extend deep into the past, providing the kind of historical context that is too often absent in disease ecology. This paper highlights the many ways in which information on parasitic infections can be extracted from natural history collections. Our focus is on detection of parasites within or associated with host tissue and by-products, and we do not discuss dedicated parasite collections, such as the US National Parasite Collection at the Smithsonian Institution’s National Museum of Natural History or the Parasitic Worms Collection at the Natural History Museum, London. Parasite collections can serve as valuable reference material, particularly because they contain hosts of known infection status, providing a positive control by which to test the effectiveness of some of the methodologies reviewed below (these parasite collections are discussed in other recent reviews; eg DiEuliis et al. 2016; Bell et al. 2018). We define natural history collections broadly, to include specimens collected over the past several centuries, including paleobiological and archaeobiological specimens. We highlight methods currently in use, as well as novel, untested methods with potential applications to natural history collections. By combining our areas

![Figure 1. A vast number of specimens appropriate for parasitological studies are stored in natural history museums throughout North America and Europe. Here, data from some of the most prominent museums in North America and Europe are shown, including specimens from (a) vertebrate, (b) invertebrate, and (c) paleobiological collections. In (a), data on fishes are from only four museums and were extracted from the websites of those museums, whereas data on reptiles, amphibians, birds, and mammals are from 14 museums and were extracted from Holmes et al. (2016) and Giere et al. (2018). In (b), data on invertebrates (inclusive of insects) are from only five museums and were extracted from the websites of those museums and from Giere et al. (2018). In (c), data are from only five museums and were extracted from museum websites and Giere et al. (2018). The y-axis label in (a) (Total number of specimens [in millions]) also applies to (b) and (c). AMNH = American Museum of Natural History; Berkeley = Berkeley Natural History Museum; Berlin = Natural History Museum, Berlin; CAS = California Academy of Sciences; CM = Carnegie Museum; FMNH = Field Museum of Natural History; Harvard = Harvard University Museum of Comparative Zoology; KU = University of Kansas Biodiversity Institute; LACM = Natural History Museum of Los Angeles County; Michigan = University of Michigan Museum of Zoology; MNHN = Muséum National d’Histoire Naturelle, Paris; NHM = Natural History Museum, London; UF = Florida Museum of Natural History; USNM = Smithsonian Institution National Museum of Natural History.](diagram)
of expertise in empirical ecological research (CLW and DTJL) and natural history collection management (AH and DTJL), we outline the sweeping potential of natural history collections for reconstructing parasite assemblages of the past.

### Archaeo- and paleoparasitology

Natural history museums often separate biological collections (ie modern specimens) from archaeological/paleontological collections (ie older specimens collected from excavations). Because of this segregation, it can be easy for disease ecologists to overlook the fact that archaeological and paleontological collections contain a vast diversity of faunal remains. Use of such resources extends the time range available for study into the millions of years, permitting both a vastly increased sample pool and broadened temporal scope; in particular, this scope could facilitate the development of a pre-Anthropocene “baseline” for rates of parasitism that would provide crucial information about whether diseases are emerging in a given host or geographic area.

Evidence of parasitism can be recovered from purposeful interments or burials accomplished by geologic forces. For example, a study of sediment samples collected from human and bovine remains from middle Neolithic to Roman Iron Age Germany revealed the presence of eggs of the liver fluke *Fasciola hepatica* (Dittmar and Teegen 2003). High numbers of parasite eggs or whole individuals may also exist in ground deposits; for instance, sediment samples taken from around the hearth of a ~1000 CE (common era) farmhouse in Greenland contained the flea *Pulex irritans*, and the lice *Pediculus humanus* and *Damalinia ovis*, suggesting not only ectoparasite presence but also possible cultural activities such as delousing by firelight (Panagiotakopulu et al. 2007). Other researchers have used deposits from latrines and human occupation sites to assess fluctuations in the abundance of human parasites across time (Araújo et al. 2015). These data should be treated with caution, given that an object as small as a parasite egg may be susceptible to disturbance (eg movement by groundwater), reducing confidence in its temporal and spatial origin. However, in combination with thorough field notes, site maps, and site data, it may be possible to use these sediment collections to explore past parasite distributions; many museums possess collections of archaeological soil thin sections suitable for such purposes.

While these examples entail purposeful interment and a focus on human disease, animals buried by sediment deposition, frozen by natural forces, or intentionally mummified may also contain well-preserved parasites. For example, the gut contents of a frozen Siberian mammoth (*Mammuthus sp*) yielded a previously undescribed species of extinct botfly, *Cobboldia rusanovi* (Grunin 1973), and specimens of the tick *Rhipicephalus sanguineus* and the louse fly *Hippobosca longipennis* were identified in the fur and ears of a mummified Egyptian dog dating to the 4th century CE (Figure 2; Huchet et al. 2013).
Trace remains – such as desiccated or mineralized feces, known as coprolites – can provide information about the intestinal parasite burdens of long-dead animals (Figure 3; Reinhard and Bryant 1992). Far fewer animal than human coprolites have been examined for infection (Richardson et al. 2012), but we know from studies of human coprolites that this material can yield a high diversity of parasites. Most of the existing studies of parasites in animal coprolites have detected the presence of helminth eggs through light microscopy, following thin sectioning or rehydration (see WebTable 1). Because the host taxon is not always identifiable, the most useful coprolite specimens may be those clearly associated with animal remains. For example, coprolites were removed during a partial necropsy of Peruvian mummified Chiribaya shepherd dogs (Richardson et al. 2012). Numerous mammal species – including some primates, lagomorphs, ungulates, and carnivores – are known to make use of latrines, or sites of repeat defecation. If collected as archaeological or paleobiological material, the contents of such latrines could become useful sources of parasitological data.

A prime candidate for latrine study may be woodrat (Neotoma spp) middens, which consist of fecal pellets, urine, and plant and bone materials, and are deposited by generation after generation of woodrats repurposing existing middens. Layers can be radiocarbon dated, and contain fecal samples already being used in paleo-ecological studies focused on plant community composition and climate change (e.g. Cole and Arundel 2005). More than 1800 rodent middens have been radiocarbon dated, forming a near-continuous sample of middens to at least 50,000 years ago (Webb and Betancourt 1990). There are, to our knowledge, no published paleoparasitological analyses of Neotoma middens, but such work would allow reconstruction of long timelines of parasite presence and abundance, providing an ideal means of exploring host–parasite relationships in the context of a changing climate. A recent study of southern viscacha (Lagidium viscacia) middens in South America demonstrated the validity of this approach, with parasite eggs being discovered in coprolites from eight out of 10 fossil middens dating to 10,000–2500 years before present (BP; Beltrame et al. 2016).

Even human latrines can reveal information about the distribution of animal parasites. Eggs of the fish tapeworms Diphyllobothrium spp have been described in archaeological contexts in Peru, Chile, the US, France, Germany, Switzerland, and Israel (Le Bailly et al. 2005). Diphyllobothrium’s definitive hosts include humans, with fish serving as second intermediate hosts. During the ancient Roman period, garum – an uncooked, fermented fish sauce – was traded throughout the Roman Empire. Trade in garum may have been responsible for expansion of the fish tapeworm’s range from an endemic focus in Scandinavia to a pan-European distribution (Blake et al. 2017).

Another archaeological gastrointestinal product – raptor pellets – may also contain abundant evidence of parasitism. Even very old pellets can yield evidence of parasitic infection; nematode and tapeworm eggs identifiable to genus have been found in 4000-year-old raptor pellets collected at archaeological sites in Patagonia (Beltrame et al. 2011). Because raptor pellets decompose quickly, preservation is uncommon unless pellets are deposited in dry, unexposed locations, such as caves and rock shelters. Fortunately, many species of owls use the same caves and rock shelters as multi-generational long-term roost sites for years to millennia. The potential for parasitological study is exemplified by the Homestead Cave faunal assemblage, which consists of a deposit of owl pellets spanning 11,270 years (Grayson 2000). This dataset has not been analyzed for parasite presence, but could be a rich source of material.

It may come as a surprise to many ecologists that parasites themselves are sometimes fossilized (Leung 2017). For example, the remains of putative hooks of flatworms, possibly of species within the Monogenea or Cestoda, have been reported in the fossilized bodies of Devonian juvenile fish (Upeniece 2001), and a 44-million-year-old fossil louse collected in Germany is so well preserved that bird feather barbules are visible in its foregut (Figure 4; Wappler et al. 2004). Exquisitely preserved fossil marine cymothoid fish “lice” have also been found in situ with their fish hosts from 168-million-year-old deposits (Nagler and Haug 2017). Fossilized traces of parasite activity may also be used to diagnose parasitic infection. For instance, etched markings on the oral surface of a late Cretaceous echinoid are similar to attachment scars created by parasitic foraminifers (Neumann and Wisshak 2006). It has also been suggested that lesions on the mandibles of Tyrannosaurus rex specimens may have been caused by a
Natural history collections as archives of parasites

*Trichomonas gallinae*-like protozoan, which leaves similar lesions on the mandibles of modern raptors (Wolff *et al.* 2009). The protozoal parasite that causes malaria leaves telltale signs on the skeletal remains of humans, suggesting that disease pathology might be a useful indicator of infection for some parasites (Smith-Guzmán 2015). The plausible span for study of parasites in fossilized remains stretches back to the Devonian, approximately 400 million years BP.

As fancifully illustrated in the 1993 movie *Jurassic Park*, amber has excellent preservative properties, and preservation in amber may provide the rare opportunity to observe and quantify ancient blood-borne parasites. A new species of trypanosomatid, *Paleoleishmania proterus*, was described through microscopic examination of an early Cretaceous sand fly from an amber deposit (Poinar and Poinar 2004); *Paleohaimatus calabresi* has been detected microscopically in mammalian red blood cells from an amber-encased tick (Poinar 2005); in addition, oocysts and sporozoites of *Plasmodium dominicana* have been detected in a Tertiary *Culex* mosquito (Poinar 2017).

**Imaging technology**

Since its introduction in the 1970s, x-ray computed tomography (CT) has permitted high-resolution imaging of soft tissues, including those of living organisms. This technique is now sometimes used in place of histological analysis (i.e., microscopic examination of thin-sectioned tissues), and may have application to the study of parasitism in natural history collection specimens.

During CT imaging, x-ray beams scan axial slices of a given specimen, and the device measures attenuation of the x-ray beam across space to produce a display of digital voxels (similar to pixels but in three dimensions rather than two). The three-dimensionality of the data captured allows the resultant scan to be rotated and sectioned, permitting imaging from multiple perspectives (Goldman 2007). In addition to being less destructive than histology or dissection, CT creates an objective record of findings. Recently, CT machines with high-resolution imaging capability (micro-CT) have been developed. Smaller in size than traditional CT scanners, micro-CT scanners produce scans within 5–30 minutes at a relatively low cost, making these devices more accessible for researchers scanning animals or objects.

Micro-CT has not yet been deployed for parasite detection or identification in natural history collection specimens, but several examples illustrate its promise. Micro-CT permitted the first images of intact marine crabs infested with rhizocephalan barnacles (Figure 5). These parasitic barnacles consist of both an external and internal portion, with the latter akin to a “root system” that extends throughout the host’s body (Noever *et al.* 2016). CT scans can be used to diagnose parasitic infection in living organisms, suggesting that similar diagnoses could be made of specimens in natural history collections. For example, micro-CT has provided evidence of *Paragonimus* infection progress in living dogs (Lee *et al.* 2007) and, in human clinical settings, CT can reliably detect many parasite species (eg Seon *et al.* 2015). New micro-CT-based research has even revealed the intimate relationship between the liver fluke *Dicrocoelium* and the brains of their ant intermediate hosts (Colwell *et al.* 2017), resolving parasites no larger than ~40 μm in diameter; whether such small parasites...
can be detected by CT in natural history collection specimens remains to be seen.

Increasingly, highly resolved CT scans of specimens are being made publically available through portals such as iDigBio (www.idigbio.org); for example, the goal of the iDigBio oVert Project is to digitize >20,000 fish specimens, representing >80% of the living genera of vertebrates. These data, freely available online, could serve as a valuable resource for taxa for which diagnosis of infection is possible via CT scan.

### Ancient DNA

Until recently, the earliest DNA sequences originated from 110,000–130,000 years BP, but in 2013, paleontologists sequenced DNA from a Pleistocene horse fossil dated to 560,000–780,000 years BP (Orlando et al. 2013). The potential for geologic-time genetic analysis is increasing with technological advancement, and techniques for such analysis might be translated to specimens in natural history collections, which are typically younger than fossils but are often detrimentally affected by fixatives, preservatives, or decay. Techniques for analyzing ancient DNA (aDNA) may be broadly defined as DNA sequencing from sources that yield only fragmented, damaged, single-stranded, or low-concentration DNA, and where special techniques such as target enrichment (ie targeting specific portions of the genome) and next-generation sequencing are required to amplify DNA sequences and avoid contamination (Hofreiter 2012).

aDNA offers opportunities to study the ecology of historical microorganisms, which are otherwise undetectable in natural history specimens (eg through dissection or micro-CT; Hofman et al. 2015). aDNA approaches hold several advantages over alternatives. First, small samples of infected tissues are generally adequate for molecular investigation (Bianucci et al. 2015), resulting in limited damage to specimens. Moreover, protocols exist for non-destructive sampling of pathogen DNA from a variety of sources, including bones and teeth, greatly expanding the number of specimens available for examination (Rohland and Hofreiter 2007; Foote et al. 2011). An additional advantage of modern aDNA techniques is that researchers do not need to know what parasite species are present in order to isolate and identify sequences, given that a shotgun sequencing approach obviates the need for primers, allowing characterization and identification of unexpected species (Zink et al. 2002). Published protocols exist for multiplex polymerase chain reaction (PCR) amplification of aDNA, permitting researchers to identify multiple pathogens using only a single sample (Stiller and Fulton 2012).

aDNA retrieval and amplification has been widely applied to paleoparasitological identification (Hofman et al. 2015), particularly in human archaeological materials. For example, the remains of Eleonora of Toledo, wife of Cosimo I de’Medici, who lived in 16th-century CE Italy, yielded *Leishmania infantum* and *Mycobacterium tuberculosis* aDNA, providing a disease diagnosis for a notable historical figure (Bianucci et al. 2012). Recent studies have made more sophisticated inferences based on historical infection patterns; for instance, a study of latrine contents dating from 500 BCE (before common era) to 1700 CE yielded mitochondrial genome haplotype frequencies for human intestinal parasites, providing data to assess the likelihood of various potential dispersal pathways from the evolutionary center-of-origin (Jensen et al. 2018).

The parasites of non-human animals have also been identified with aDNA techniques (Hofman et al. 2015). Wood et al. (2013) simultaneously used microscopy and aDNA to examine Holocene coprolites of three extinct moa species and found that aDNA provided a considerable advantage over morphological parasite identification in terms of taxo-
nomic resolution. There has been particular interest in the use of aDNA techniques to study "emerging diseases", as aDNA data can help to resolve if the presence of such a disease is the result of an invasion, environmental change, or adaptation of the parasite. Consider the disease chytridiomycosis (caused by the fungal parasite Batrachochytrium dendrobatidis), which has decimated amphibian populations worldwide. The origin of the disease was elucidated with aDNA screens for fungal spores on the skin of liquid-preserved frog specimens (Weldon et al. 2004) and, since then, aDNA analysis of amphibian specimens from natural history collections has also resolved the historical prevalence of the chytrid parasite (Ouelette et al. 2005; Talley et al. 2015). Similarly, aDNA techniques have been used to assess the history of geographic expansion and origin for Pseudogymnoascus destructans, the fungal parasite that causes white-nose syndrome in bats (Campana et al. 2017). aDNA may even allow identification of the parasites of parasites; Amanzoughene et al. (2016) used quantitative PCR to screen for Borrelia, Bartonella, Acinetobacter, Rickettsia, and Yersinia pestis in human head lice (Pediculus humanus capitis) from archaeological sites in Moa and the Judean Desert dating to the Roman period (6th century BCE–1st century CE).

DNA sequencing can identify microorganisms from their unique genetic signatures, but such identification becomes more difficult post-mortem. In death, cells rupture, resulting in fragmentation, base alteration, cross-linking, and other damage to DNA molecules (eg Morozova et al. 2016). Specimens also vary in DNA quality depending on their age, treatment, and fixative, with formalin fixation presenting a special challenge. For example, of seven specimens of the tapeworm Ligula spp tested, amplification of long DNA fragments was successful only in ethanol-preserved specimens; formalin-fixed specimens yielded DNA fragments of 450 base pairs or fewer, and extraction product success declined as time since collection increased (Li et al. 2000). However, technology for extracting degraded DNA has progressed in recent years, allowing amplifiable DNA to be obtained from fixed tissues by changing the method of tissue digestion, adding new processes, and incorporating DNA repair enzymes (Zhang 2010). With this emerging ability to extract DNA from formalin-fixed specimens, vast possibilities exist for obtaining information on parasites of the past (Wandeler et al. 2007).

Parasitological examination of biological specimens

Dissection is the primary stock-in-trade of parasite ecologists. Through dissection, most of the metazoan (eg flatworm, roundworm, arthropod) parasites of a vertebrate or invertebrate host can be detected and sometimes identified with nothing more than a light microscope. Fortunately for parasite ecologists interested in the history of infection in their focal host, liquid preservatives fix not only host tissue but also parasite tissue. Metazoan endoparasites are still detectable in liquid-preserved hosts tens or even hundreds of years after the specimen is collected, making these hosts veritable “parasite time capsules” that reflect the parasite assemblages of a particular host in its time and place of collection.

Although dissection could be used to reconstruct the parasite assemblages of any of the tens of millions of liquid-preserved vertebrate and invertebrate specimens held by natural history collections around the world, such dissections have been only sparsely documented in the literature. Examination of museum specimens of Puget Sound English sole (Parophrys vetulus) collected between 1930 and 2016 provided corroborative evidence of historical records documenting a long-term rise in prevalence of the parasitic nematode worm Clavinema mariae (Howard et al. 2019). That this approximately eightfold increase in abundance of an economically important parasite went entirely unnoticed until the publication of Howard et al.’s (2019) report illustrates the power of data on long-term change in parasite abundance. Another example of this phenomenon comes from dissections of museum specimens of lake trout (Salvelinus namaycush), which revealed that the parasitic nematode Cystidicola stagnatura was present in trout in the Great Lakes prior to 1925, but that the worms disappeared with the decline in abundance of their trout host after 1925 (Black 1983).

Dissection does not merely detect large or adult-stage parasites; small, larval parasites can also be observed. For example, Johnson et al. (2003) dissected preserved North American amphibian specimens and confirmed that historical cases of amphibian limb malformation were – like contemporary cases – associated with infection by metacercariae (300–350 μm in length; Johnson et al. 2004) of the trematode Ribeiroia ondatrae. Myxospores of the myxozoan parasite Myxidium immersum were found in eight specimens of endemic Australian frog species but never in specimens collected before 1966, suggesting that the parasite may have been introduced when the cane toad (Rhinella marina) arrived in Australia in 1935 (Hartigan et al. 2010). Myxospores are minute, barely multicellular structures, and yet their integrity is maintained in liquid-preserved hosts.

In some instances, parasitic infection might leave telltale signs on skeletons or skins – a fortunate circumstance for scientists interested in reconstructing past patterns of infection, given that these specimens are not only common in natural history collections, but also resilient and easy to examine without causing damage. For example, ectoparasites cling to their hosts’ fur, feathers, or skin, even after death of both parasite and host. These parasites can be collected by simple combing, and their morphological integrity can be maintained for decades after the host specimen’s preparation. Bird lice specialists have been examining study skins for more than a century (Mey 2002). Researchers examined occult bat (Myotis occultus) ectoparasites on 52 field-captured bats (“fresh hosts”) and 150 preserved bat specimens held at the University of New Mexico’s Museum of Southwestern Biology (Albuquerque, NM); of the 16 ectoparasite species identified,
11 were found on both museum specimens and fresh hosts, two only on museum specimens, and three only on fresh hosts (Valdez et al. 2009).

Dissection allows detection of the full complement of metazoan parasites infecting a vertebrate host, but it is also destructive or semi-destructive. Specimens are irreplaceable, and curators must balance the promise of parasitological data versus the preservation of a specimen for future use. In some cases there is substantial redundancy in natural history collections (eg contents of research trawls), which allows for flexibility, permitting a subset of specimens from a particular time and place to be destructively sampled. Partial parasitological dissection, in which the viscera are destroyed but the remainder of the body stays intact, can yield information about the majority of metazoan parasites of vertebrates while preserving the external morphological integrity of the specimen. Curators and researchers should work together to assess whether the information yielded by dissection would justify the damage done to a specimen. New technologies, such as advanced imaging, may yield an equal amount of parasitological information while better preserving specimen integrity.

Conclusions

Natural history collections offer a unique opportunity: access to the ecology of long-vanished ecosystems. Some of the methods we describe for reconstructing the abundance and diversity of parasites of the past are well established in archaeology and medicine, such as the examination of coprolites and CT-aided diagnosis of parasitic infection, while other approaches remain largely untapped, such as systematic analysis of preserved animal gut contents and parasitological dissection of liquid-preserved specimens. We encourage disease ecologists to share their research goals with collections professionals and to explore the potential utility of natural history collections for tracking disease changes through time. For many ecosystems, this approach may be the only means of developing accurate baselines for the management of contemporary wildlife disease.

Acknowledgements

We thank D Grayson for advice and literature suggestions; C Hawks for comments; I Palmer and N Vollmer for literature suggestions; D Rhodes and D Thomas for technical expertise on Neotoma middens and Raman spectroscopy, respectively; JS Meschke and H Keister for discussions about the implications of disease study in natural history museums; and K Helgen, C Potter, J Mead, and D Lunde for introducing AH to the possibilities of disease study in natural history collections. We also thank TAM Ewin, R Portela Miguez, C Quaisser, and P Mayer for sharing their estimated collection specimen counts, and W O’Donnell, J Luke, A Ong, K Morrissey, D High, M Farrar, and L Hayes for encouragement and support. CLW was supported by a Sloan Research Fellowship from the Alfred P Sloan Foundation, a University of Washington (UW) Innovation Award from the UW President’s Innovation Imperative, and a grant from the UW Royalty Research Fund.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2017/suppinfo