Spillover of zoonotic pathogens: A review of reviews

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Spillover of zoonotic pathogens: A review of reviews

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Abstract

Zoonotic spillover and subsequent disease emergence cause significant, long-lasting impacts on our social, economic, environmental and political systems. Identifying and averting spillover transmission is crucial for preventing outbreaks and mitigating infectious disease burdens. Investigating the processes that lead to spillover fundamentally involves interactions between animals, humans, pathogens and the environments they inhabit. Accordingly, it is recognized that transdisciplinary approaches provide a more holistic understanding of spillover phenomena. To characterize the discourse about spillover within and between disciplines, we conducted a review of review papers about spillover from multiple disciplines. We systematically searched and screened literature from several databases to identify a corpus of review papers from ten academic disciplines. We performed qualitative content analysis on text where authors described either a *spillover pathway*, or a *conceptual gap* in spillover theory. Cluster analysis of *pathway* data identified nine major spillover processes discussed in the review literature. We summarized the main features of each process, how different disciplines contributed to them, and identified specialist and generalist disciplines based on the breadth of processes they studied. Network analyses showed strong similarities between concepts reviewed by 'One Health' disciplines (e.g. Veterinary Science & Animal Health, Public Health & Medicine, Ecology & Evolution, Environmental Science), which had broad conceptual scope and were well-connected to other disciplines. By contrast, awas focused on processes that are relatively overlooked by other disciplines, especially those involving food behaviour and livestock husbandry practices. Virology and Cellular & Molecular Biology were narrower in scope, primarily focusing on concepts related to adaption and evolution of zoonotic viruses. Finally, we identified priority areas for future research into zoonotic spillover by studying the *gap* data.

KEYWORDS

data science, environment and public health, one health, review, zoonoses

Cecilia A. Sánchez and Joy Venkatachalam-Vaz contributed equally.

1 | INTRODUCTION

Pathogens that originate from animals and spill over to infect humans are increasing and represent 75% of emerging human pathogens (Jones et al., 2008; Taylor et al., 2001). Zoonotic pathogen spillover and subsequent disease emergence have widespread and long-lasting impacts on environmental, social, economic and political systems (Bender et al., 2006; Huber et al., 2018; Martins et al., 2015). For example, the ongoing COVID-19 pandemic is a major public health crisis that has caused more than 160 million cases and more than 3.3 million deaths, as of 13 May 2021. It is expected to cost trillions in USD and suppress global economic growth, the consequences of which are typically borne by the most vulnerable in society (Egger et al., 2021; United Nations Conference on Trade & Development, 2020). Understanding the processes involved in pathogen spillover is crucial for informing pandemic prevention and mitigating the burden of infectious diseases (Bogich et al., 2012). However, the processes that enable pathogen spillover across species are complex and remain poorly understood.

Spillover transmission fundamentally involves animals, humans and the environments with which they interact. Accordingly, literature across multiple academic disciplines investigates spillover processes, from virology (Holmes, 2009) to anthropology (Muehlenbein, 2016) to environmental sciences (Myers & Patz, 2009). It is increasingly recognized that transdisciplinary approaches are useful for investigating the complex web of factors that promote spillover transmission (Kelly et al., 2017; Plowright et al., 2017). For example, the One Health initiative acknowledges that human, animal and environmental health are inextricably linked and focuses on integrative research (Daszak et al., 2000, 2007; Kelly et al., 2017). At the same time, research suggests that communication between disciplines involved in spillover research could be improved (Daszak et al., 2007; Parkes et al., 2005; Wilcox & Colwell, 2005). By sharing disciplinary knowledge, researchers could avoid duplication of efforts and draw from a larger pool of data, methods and theoretical approaches, ultimately producing a more holistic picture of the complex nature of spillover. For example, melding approaches from social and natural sciences can help identify causal links between drivers and disease emergence (Plowright et al., 2008).

We conducted a review of reviews to characterize the shape of the inter-disciplinary discourse about spillover. Review papers about spillover can provide a broad overview of different spillover processes, present hypotheses or claims about pathways that lead to spillover and identify knowledge gaps in this area of research. Our goals were to (a) describe the main processes of spillover discussed in review literature and identify key elements in each process, (b) identify prominent disciplines discussing spillover and compare the foci of each discipline across and within these spillover processes, (c) assess conceptual overlap between disciplines to identify shared interests and (d) summarize conceptual gaps identified by review authors. We used a systematic search to assemble a corpus of review papers about pathogen spillover from wildlife or livestock into human populations. We extracted text segments of disease spillover

Impacts

- Zoonotic disease 'spillover' from animals to humans poses a threat to global health. Research collaborations between academic disciplines are challenging, but important for understanding the complex processes that lead to spillover.
- Nine major spillover processes emerge in this review of concepts drawn from multiple disciplines, highlighting similarities and differences in the interests of life sciences, social sciences and 'One Health' disciplines.
- Key knowledge gaps about spillover remain; understudied areas present opportunities for collaborative research and could spark novel interdisciplinary approaches to tackle these open questions.

pathways from this corpus and coded each segment qualitatively. ext, we performed a hierarchical cluster analysis to group-related pathways into conceptual clusters (spillover processes) and descriptively summarized each cluster. We examined the relative focus of disciplines across conceptual clusters, important codes for disciplines and clusters and the similarity of disciplines based on shared codes. Further, we descriptively summarized author-identified gaps in spillover research. Our work highlights understudied areas that present opportunities for collaborative, interdisciplinary research approaches.

2 | METHODS

2.1 | Search strategy

We identified review papers about zoonotic disease spillover using a systematic literature search (Figure 1). We identified peer-reviewed published studies (i.e. no grey literature) on zoonotic disease spillover on 8 February 2018. We queried the databases Web of Science, PubMed, Anthropology Plus, EconLit, Sociological Collection and the journal Annual Reviews using the following search strings: ('emerg* infect*' OR spillover OR zoonotic OR zoonos*) AND (disease). These databases were chosen for their coverage of a vast range of topics and scientific disciplines. The Web of Science search was restricted by language (ENGLISH), document type (REVIEW) and index (SCI-EXPANDED, SSCI, A&HCI). It was also restricted by timespan (1992–2018); the range minimum marks the publication year of *Emerging Infections: Microbial Threats to Health in the United States* (Institute of Medicine, 1992). The PubMed search was restricted by language, document type and timespan (same as previous). The Anthropology Plus, EconLit and Sociological Collection searches were restricted by language and timespan (same as previous); no option was available to choose reviews. The Annual Reviews search was restricted by language
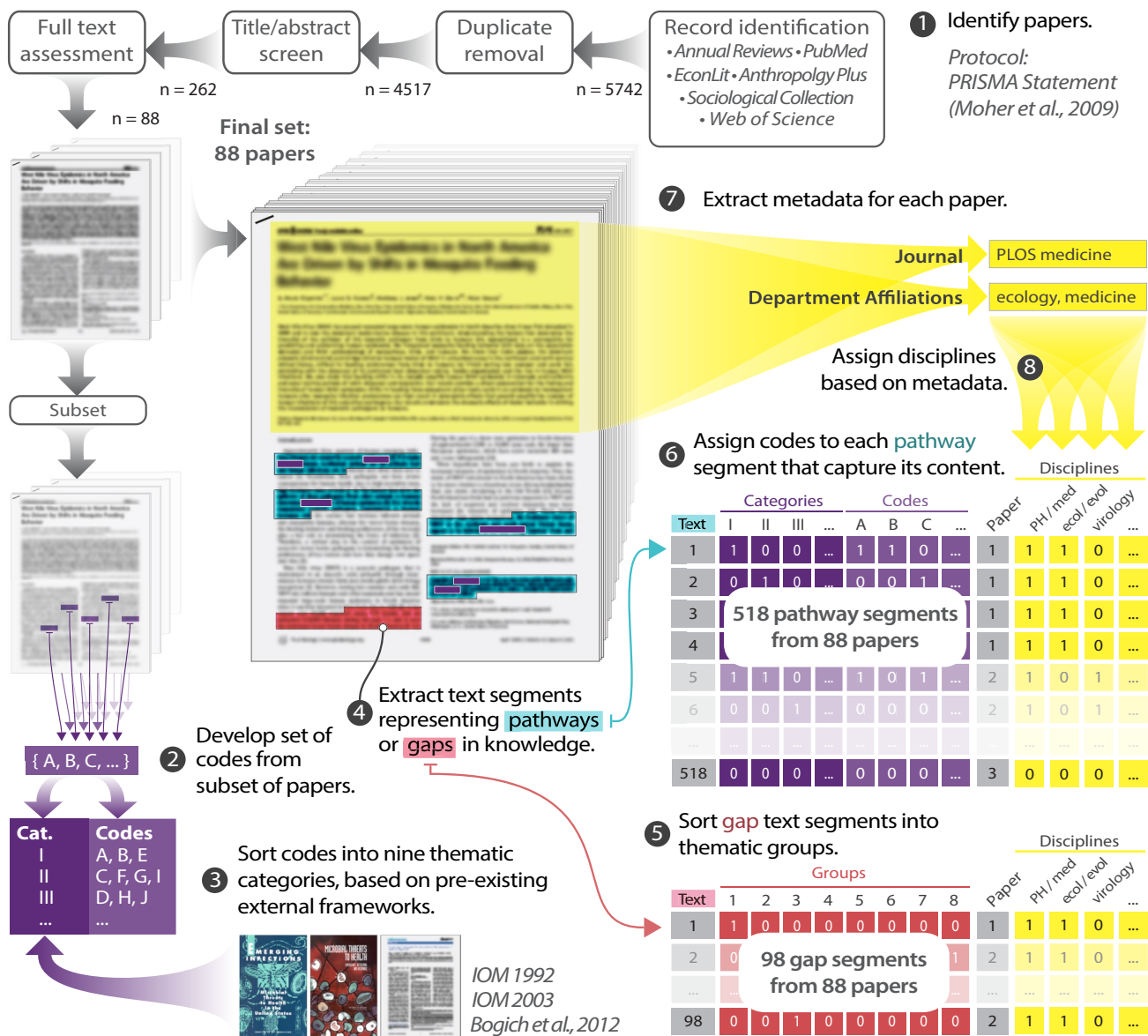
FIGURE 1 Conceptual figure describing the process used in this paper to identify and code spillover processes described in multiple disciplines. (1) We performed a systematic search across several databases to identify papers related to emerging infections, spillover, zoonoses, and disease. (2) We read a subset of papers from the corpus to develop a set of 68 codes commonly used to describe processes that lead to spillover, which we (3) grouped into nine summary categories derived from (Bogich et al., 2012; Institute of Medicine, 1992, 2003). (4) Returning to the full corpus, we read each paper in full, extracting text segments representing descriptions of spillover pathways or perceived gaps in spillover theory. (5) We assigned gaps to descriptive groups based on content similarity. (6) We assigned codes to each pathway reflecting its content. (7) We extracted metadata (journal and author department affiliations) for each paper and assigned each paper to one or more of ten disciplines based on the metadata

and timespan (same as previous); all papers are reviews. Search results for all databases were exported using an automated process as comma-separated values (.csv) or .xml files; .xml files were converted to .csv using an online converter. Annual Review results were exported manually into a .csv file. Search results were concatenated, and duplicate papers were removed using R (R Core Team, 2019) and manual identification.

After removal of duplicate papers, two authors (CAS, JV-V) screened paper titles and abstracts using the 'metagear' package in

R (Lajeunesse, 2016; R Core Team, 2019) to select review papers about processes allowing pathogens to spill over from wildlife or livestock into humans. Papers were excluded if they met any of the following criteria: (a) not a review paper (e.g. a case study reporting a single disease transmission event), (b) does not review processes of disease spillover (e.g. papers about financial spillover), (c) focus of paper is narrow in scope (e.g. spillover processes limited to a single pathogen, host or geographic region), or (d) focus of paper is spillover from companion animals (e.g. pet dogs, cats) to humans. Criterion (c)

TABLE 1 An example of a pathway text segment extracted from a review paper in the corpus of spillover literature and the codes we assigned to the pathway

Pathway text segment	Assigned code	Category	Relevant text
'Expansion of agriculture promotes encroachment into wildlife habitats, leading to ecosystem changes and bringing humans and livestock into closer proximity to wildlife and vectors, and the sylvatic cycles of potential zoonotic pathogens. This greater intensity of interaction creates opportunities for spillover of previously unknown pathogens into livestock or humans and establishment of new transmission cycles'. (Jones et al., 2013)	(changes in) agriculture	Agriculture & Food Industry Changes	'expansion of agriculture'
	(changes in) community composition	Population & Community Ecology	'bringing humans and livestock into closer proximity to wildlife and vectors'
	(changes in) geographic overlap	Population & Community Ecology	'bringing humans and livestock into closer proximity to wildlife and vectors'
	(changes in) interspecies contact	Population & Community Ecology	'greater intensity of interaction'
	encroachment	Land Use Changes	'encroachment into wildlife habitats'

was chosen to maximize the likelihood of identifying review papers that would describe spillover mechanisms that would be broadly applicable, rather than system-specific ones.

After title and abstract screening, CAS and JV-V conducted full-text readings of the remaining papers. Adopting Plowright et al. (2017) definition of spillover, 'the processes that enable a pathogen from a vertebrate animal to establish infection in a human', we accordingly excluded papers about the persistence or spread of pathogens in human populations after spillover, or papers focusing on the surveillance, control or prevention of emerging diseases. Papers that remained after full-text screening comprised our final corpus.

2.2 | Data extraction and qualitative coding

We used qualitative content analysis to examine our corpus of spillover review literature (Hsieh & Shannon, 2005). We first read each review paper and extracted text segments that described either a *spillover pathway* or a *conceptual gap* in spillover theory (Figure 1). Pathway text segments (hereafter, pathways) described an observed or hypothesized mechanism for disease spillover from animals to humans. We did not extract pathways that described spillover mediated by human technology (i.e. xenotransplantation, bioterrorism, laboratory infection). Gap text segments (hereafter, gaps) described a research question or problem that review authors perceived as insufficiently addressed in the spillover literature.

Pathway data were analysed by qualitatively coding extracted text (Hsieh & Shannon, 2005). In an initial coding cycle, a subset of papers from the corpus (*n* = 30) were read to identify common words or phrases used to describe processes that lead to spillover. From these, we developed a set of 68 codes, which we used to code the rest of our pathways. These codes were sorted into nine thematic categories which we created by adapting pre-existing frameworks for conceptualizing spillover (Bogich et al., 2012; Institute of Medicine, 1992, 2003). Further details on codes and categories can be found in Figure S1 and Table S1.

We assigned codes to each pathway that captured its content (Table 1) and produced a binary matrix showing the codes assigned to each pathway (Figure 1). This pathway–code matrix comprised the fundamental data we later used to identify clusters of pathways. We did not assign codes to gaps.

We recorded the paper in which extracted text segments were published. Papers in the corpus were assigned to one or more of the following ten disciplines: Anthropology; Cellular & Molecular Biology; Ecology & Evolution; Environmental Science; Food & Agriculture; Microbiology & Immunology; Parasitology; Public Health & Medicine; Veterinary Science & Animal Health; and Virology. Two authors (CAS and JV-V) assessed and independently assigned one or more of the above disciplines to each paper. Disciplinary assignments were based on the journal in which a paper was published and the departmental affiliations of the authors. We subsequently compared assignments; any disagreements were discussed until consensus was achieved. All text segments from a paper were assigned to the same disciplines as the paper from which they were extracted.

2.3 | Cluster analysis

All analyses were performed in the R computing environment v 3.6.1 (R Core Team, 2019). Following Guest and McLellan (2003), we used hierarchical cluster analysis to group pathways into conceptually similar clusters. Specifically, we constructed a pairwise distance matrix from our pathway–code matrix and used the 'hclust' function in the 'stats' package to perform agglomerative clustering on this distance matrix. We used Ward's hierarchical clustering method to minimize within-cluster variation (Murtagh & Legendre, 2014).

We next visualized the results of our hierarchical cluster analysis as a dendrogram with the 'dendextend' package (Galili, 2015). Any dendrogram can be cut at a height (h) to yield a set of clusters; a smaller h (i.e. a cut that is closer to the leaves or tips) yields many small, specific clusters, whereas a larger h yields few large, diffuse

clusters with more dissimilarity among pathways within a cluster. Our goal was to choose a value of *h* that would divide the tree into clusters of pathways, with each cluster representing a major spillover process discussed in the literature. We chose an intermediate value of *h* because it produced a set of clusters that were conceptually distinct and had a high degree of coherence within each cluster, without producing clusters that were too specific. After cutting the dendrogram, we re-read all pathways in each cluster and summarized each cluster descriptively. Gaps were also grouped into conceptually similar clusters, but rather than analysing them using qualitative coding and hierarchical clustering, we read the extracted text segments and identified major themes. We then sorted each gap into one of the themes and descriptively summarized each thematic group.

2.4 | Disciplinary foci, similarity and co-assignment

To identify and compare conceptual foci across disciplines, we created a bar plot of pathway frequency by cluster and discipline. Bars are scaled to account for the number of pathways in each cluster and discipline.

We created a heatmap to visualize the frequency of each code within a cluster (i.e. the proportion of pathways in that cluster which were assigned that code; Warnes et al., 2019). For comparison, we also created a second heatmap to visualize code frequency within each discipline (i.e. the proportion of pathways in that discipline that were assigned a given code).

To examine how often two disciplines were assigned to the same papers, we created a network diagram connecting 10 nodes that corresponded to our 10 disciplines. Edges connected disciplines that had shared papers. Edge weights (numerical values assigned to each edge) were proportional to the number of times two connected disciplines were assigned to the same paper.

We created a second network diagram to identify disciplinary similarity in content. Nodes again corresponded to disciplines, and edges connected disciplines that had shared codes. Edge weights were calculated using cosine similarity, such that thicker edges represented higher similarity between disciplinary content. Cosine similarity is a similarity measure between 0 and 1 based on the frequency of terms shared by two documents ($sim(x, y) = \frac{x \cdot y}{\|x\|\|y\|}$; see Supporting Information for details; Han et al., 2012). We used the 'wordspace' package (Evert, 2014) to calculate cosine similarity values (CSVs) for all possible discipline pairs based on shared codes. For clarity in distinguishing edge weights, we used four colours to plot the edges. The range of data values for each colour were determined by dividing CSVs into quartiles.

3 | RESULTS

Our search produced a corpus of 88 review papers about emerging diseases, zoonotic diseases and spillover (File S1; Figure S2). Most papers were assigned to one or more of three disciplines: Public Health & Medicine, Veterinary Science & Animal Health, and Ecology & Evolution. From this corpus, we extracted 518 pathways and 98 gaps. [Correction added on 28 May, 2021 after first online publication : Supplemental file Fig S1 was published inadvertently and has been renamed as File S1 in this version.]

We cut the hierarchically clustered dendrogram of pathways at an intermediate height (*h* = 3), producing nine clusters (Figure 2). We believe this cut-off provided a suitable balance between creating a few clusters that are so broad as to obscure variation in the data, and creating many clusters that are so specific that it is difficult to drawn general conclusions. These clusters represented general *spillover processes*, enabling pathogen transmission from animals to humans (summarized in Table 2). A spillover process consisted of several interacting elements (e.g. environmental change, host and pathogen traits, human behaviour) that can create conditions that enable cross-species transmission—a spillover event. For instance, the *Global Movement* cluster generally described how the large-scale movement of humans, goods and animals can facilitate spillover by bringing susceptible humans into unfamiliar environments where they encounter novel zoonotic pathogens, or by bringing animals or animal products, along with their pathogens, into unexposed populations.

The ten disciplines in our study differed in their degree of specialism (i.e. most pathways grouped into a small number of clusters) versus generalism (i.e. pathways grouped into many clusters; Figure 3). For example, Public Health & Medicine and Veterinary Science & Animal Health were generalist disciplines, with pathways well-distributed across all clusters and no focus on a particular spillover process. Microbiology & Immunology was also a relatively generalist discipline, with a similar number of pathways assigned to five diverse clusters. Cellular & Molecular Biology and Virology were specialist disciplines, focusing largely on spillover processes involving viral adaptation. Anthropology was the most specialized discipline, only contributing to six out of the ten clusters. Most of its pathways were in the *Food & Livestock* cluster, followed by *Global Movement* and *Environmental Contact*. No Anthropology pathways were classified into the *Biodiversity & Community*, *Land Conversion*, and *Viral Adaptation* clusters. Ecology & Evolution, Environmental Science, Parasitology, and Food & Agriculture were neither particularly generalist nor specialist.

The cluster heatmap (Figure 4, left panel) shows the relative frequency of each code (i.e. the proportion of pathways in a given cluster that were assigned that code. The most common codes in a cluster are an indicator of the main features that represent the key components of its corresponding spillover process. Overall, each cluster—except for *Global Movement*—was brought together by one to three popular codes that appeared widely among pathways in that cluster, while the other codes were relatively rare. All clusters except *Global Movement* had at least one code that occurred in the majority (≥60%) of pathways in that cluster.

Comparing patterns of codes assigned to pathways further revealed content explored by disciplines (Figure 4, right panel). For example, '(changes in) reservoir host abundance and distribution', '(changes in) geographic overlap', and '(changes in) interspecies
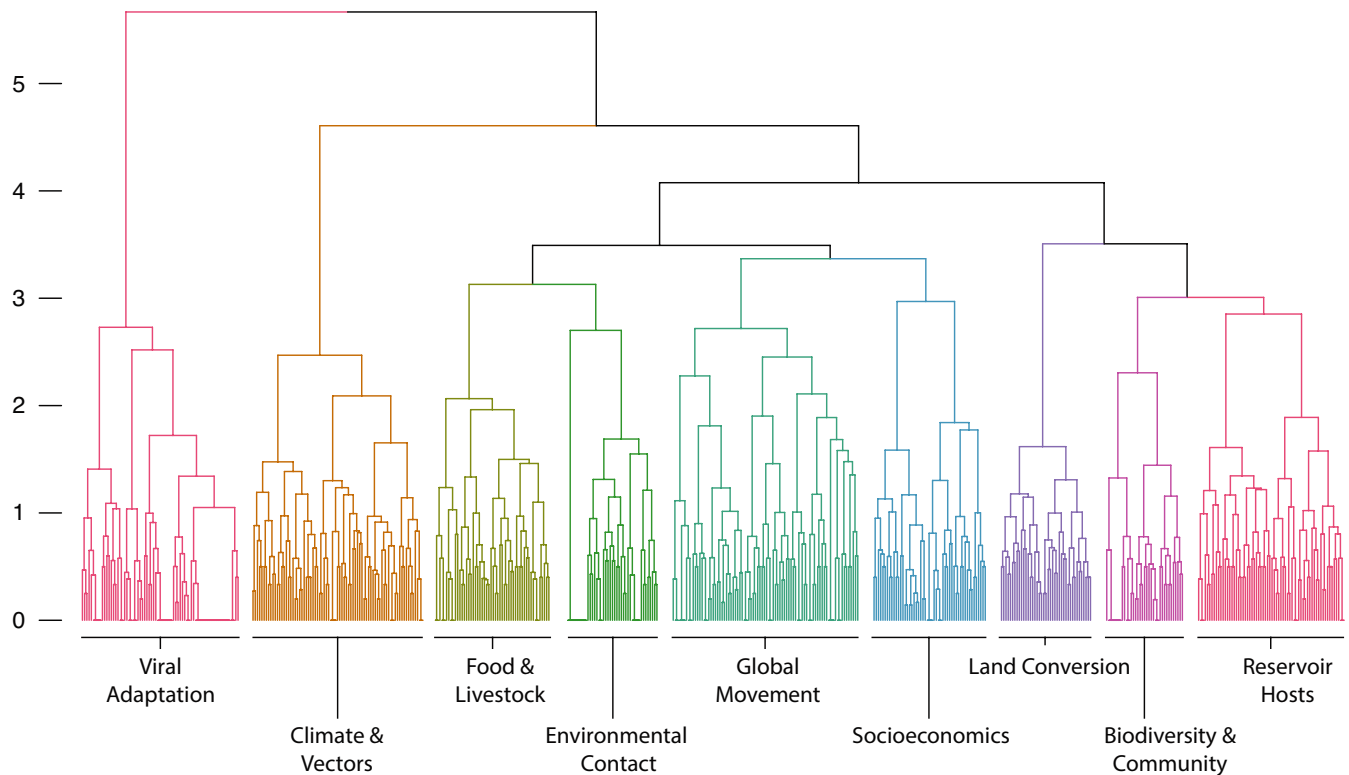
FIGURE 2 Dendrogram generated from 518 spillover pathways extracted from a corpus of 88 papers. Each leaf represents a single extracted pathway. To generate the dendrogram, each pathway was assigned codes reflecting its content; these data were then used to generate a distance matrix. We performed a hierarchical cluster analysis on the matrix to group similar pathways. The dendrogram was cut to divide the tree into nine clusters (or subtrees), each of which is represented by a different colour. The algorithm used orders subtrees so that tighter subtrees are on the left. The constituent pathways in each cluster were then re-read to identify their subject content, which is provided in a descriptive name under each cluster

contact' were common codes—they were assigned to pathways from many disciplines. Other codes were limited to a small number of disciplines, such as 'helminth pathogen' (Parasitology), 'agricultural practices' (Anthropology; Food & Agriculture), and 'viral pathogen' (Cellular & Molecular Biology; Virology; Microbiology & Immunology). We identified three main groups of disciplines with similar code patterns: a social science group (Anthropology; Food & Agriculture; Parasitology), a life sciences group (Cellular & Molecular Biology; Microbiology & Immunology; Virology), and a One Health group (Ecology & Evolution; Environmental Science; Public Health & Medicine; Veterinary Science & Animal Health).

3.1 | Disciplinary co-assignment and similarity

We examined the frequency with which two disciplines were assigned to the same review paper (Figure 5, left panel). Papers within four disciplines (Public Health & Medicine, Veterinary Science & Animal Health, Ecology & Evolution, and Environmental Science) were commonly also assigned to other disciplines in this group. Papers assigned to Anthropology were rarely co-assigned to Public Health & Medicine, Parasitology, and Ecology & Evolution, and never co-assigned to any of the other disciplines; however, note that there were few papers classified as Anthropology, as shown by the small node size.

We observed differences in disciplinary similarity, as measured by CSVs based on codes (Figure 5, right panel). CSVs ranged from 0.38 to 0.97 (interquartile range: 0.65–0.86). Anthropology was the least similar to other disciplines, with all but one of its edge weights falling below the 1st quartile. Parasitology was also relatively less similar to other disciplines. In contrast, Public Health & Medicine was highly similar to other disciplines, with five of its edge weights above the 3rd quartile. Public Health & Medicine, Veterinary Science & Animal Health, Ecology & Evolution, and Environmental Science were all strongly similar to each other.

3.2 | Conceptual gaps

We extracted 98 gap text segments from the corpus in which review authors identified missing knowledge or under-explored concepts about spillover. We grouped similar concepts together to yield eight broad groups of gaps. Five groups of gaps addressed a spillover process corresponding to a conceptual cluster, while two groups drew attention to concepts that were not captured in any clusters. The last group of gaps critiqued current approaches to spillover research, calling for more holistic frameworks for conceptualizing spillover.

The five clusters with associated groups of gaps were *Climate & Vectors, Reservoir Hosts, Viral Adaptation, Biodiversity & Community,*

TABLE 2 Summary of nine conceptual clusters about zoonotic spillover discussed in review literature of multiple academic disciplines

Cluster	Summary of spillover process	Code frequency (% of pathways)	Example pathway text segment
Viral Adaptation (n = 71)	Novel zoonotic pathogens can arise when a pathogen evolves to be able to infect a new host Viruses have high mutation rates and error prone replication, making them particularly likely to undergo host shifts and adapt to achieve higher fitness in the new host species Increasing contact and mixing between species can enhance pathogen exposure to humans and select for adaptations that enable host switching	pathogen adaptation & evolution (73%) host switching & host range (68%) viral pathogen (61%) drug resistance (15%)	"Viruses generally have multiple genes involved in cellular tropism and host range, that encode non-structural or structural viral proteins. Modification of such genes by mutation or their acquisition by recombination or reassortment opens the way to a change in host range and to disease emergence" (Domingo, 2010)
Climate & Vectors (n = 77)	Climate variation can lead to emergence by triggering shifts in the geographic range, abundance, or behaviour of arthropod vectors Rising temperatures allow vectors to expand their range into higher elevations and more temperate latitudes Major climate events such as heavy rainfall can lead to sudden surges in vector densities and emergence of vector-borne diseases	vector transmission (84%) reservoir abundance & distribution (45%) temperature (38%) climate change (34%) precipitation (25%) geographic overlap (19%) global warming (18%) seasonality (16%)	"It is well known that the mosquito life cycle is affected by temperature, meaning that a slight (1–2C) increase in average summer temperature may allow mosquitoes to inhabit temperate zones, often carrying with them zoonotic agents for which they serve as vectors" (Cascio et al., 2011)
Food & Livestock (n = 52)	Intensive livestock rearing lead to changes in disease dynamics at the wildlife–livestock–human interface, thereby increasing the risk of spillover Livestock can serve as 'bridge hosts' by mediating transmission of wildlife pathogens into humans Large-scale livestock production can entail crowding, confinement, mixed animal farming, and higher contamination. These conditions favour pathogen replication and lead to higher within- and cross-species transmission	agricultural practices (71%) livestock abundance & distribution (65%) food preferences, preparation, or storage (46%) interspecies contact (33%) human abundance & distribution (27%) food availability & distribution (27%) geographic overlap (23%) reservoir abundance & distribution (21%) animal trade & transport (15%)	"…the emerging trend is for more extensive and outdoor livestock rearing to comply with increasing public demand for organic production and management practices to improve animal welfare. Such free-ranging livestock in close contact with both the environment and wildlife may constitute an opportunity for emerging parasitic infections" (Broglia & Kapel, 2011)
Environmental Contact (n = 41)	Emergence of helminths and protozoa is more commonly mediated through direct contact with contaminated food, water, soil or animal products rather than reservoir hosts. Contact with animal tissue and fluids during hunting or butchering is a common risk factor	hunting behaviour (71%) food preferences, preparation, or storage (56%) interspecies contact (41%) encroachment (29%) agricultural practices (15%)	"The changing use of water in modern agriculture, the food industry and by human communities may also lead to an increased spread of waterborne parasitic diseases…contaminated water is an important source of human infection either by direct consumption or by the use of contaminated water in food processing or preparation" (Broglia & Kapel, 2011)

TABLE 2 (Continued)

Cluster	Summary of spillover process	Code frequency (% of pathways)	Example pathway text segment
Global Movement (n = 84)	The large-scale movement of humans, goods, and animals facilitates spillover by creating novel opportunities for spillover transmission. Worldwide travel and tourism can take susceptible humans into unfamiliar environments where they encounter novel zoonotic pathogens. The trade of livestock, wildlife, plants, food items, and other goods can inadvertently transport associated pathogens, thus introduce them to unexposed populations	tourism & travel (35%) global transportation (32%) geographic overlap (31%) human abundance & distribution (31%) global trade (23%) animal trade & transport (20%) human susceptibility (19%) interspecies contact (15%)	"Ships, aeroplanes or other vehicles can disseminate vectors of microorganisms, such as birds and insects" (Soto, 2009)
Socioeconomics (n = 51)	Human susceptibility to emerging zoonosis increases due to crowding, forced migration, or unhygienic living conditions. Displaced populations living in temporary living conditions may not have access to clean water or infrastructure to manage waste. Rodent and insect reservoirs are thought to thrive in these conditions. War, civil unrest, or improper governance can lead to a breakdown in public health measures that could mitigate spillover	public health infrastructure & sanitation (61%) close contact transmission (43%) non-close contact transmission (43%) food preferences, preparation, or storage (29%) helminth pathogen (27%) protozoan pathogen (25%) water management (22%) poverty (20%) agricultural practices (18%) human abundance & distribution (18%) war & conflict (16%)	"Unplanned migration due to war or natural disasters has played a large part in introducing infectious diseases into humans. Refugee camps, resettlement areas, and temporary shelters are often characterized by crowded living conditions, poor sanitation, and populations having poor nutrition status, limited access to clean water and medical care, as well as being poorly vaccinated, and lacking separation from insects and animals in the environment" (Ka-Wai Hui, 2006)
Land Conversion (n = 41)	Anthropogenic land conversion leads to spillover as humans, reservoir hosts, and vectors become densely aggregated across the landscape. Agricultural land can attract wildlife by providing food and shelter, often supporting high densities of zoonotic reservoir hosts and humans in close proximity to one another. As wildlife habitat is removed, reservoir hosts may crowd into shrinking patches of suitable land, increasing disease prevalence and risk of spillover into adjacent human settlements. Land conversion can increase the length of ecotonal areas along that facilitate interspecific contact and exposure to disease	land use (95%) land conversion for agriculture (78%) agricultural practices (63%) deforestation (54%) encroachment (49%) geographic overlap (49%) human abundance & distribution (41%) interspecies contact (39%) urbanization (37%) community composition (24%) reservoir abundance & distribution (22%) livestock abundance & distribution (20%) attraction of wildlife & commensals (17%)	"Human population growth and modern agricultural practices have enticed human settlers into clearing patches within ecosystems of maximally high biodiversity, such as tropical rain forests, converting substantial areas into cultivated fields and pastures. Commercial farming operations inserted into clearings in forest habitats juxtapose and intermingle humans and livestock with native animal populations, and, coincidentally, with whatever zoonotic pathogens exist within these natural nidi" (Childs et al., 2007)

TABLE 2 (Continued)

Cluster	Summary of spillover process	Code frequency (% of pathways)	Example pathway text segment
Biodiversity & Community (*n* = 35)	Changes in the species diversity and composition of host or vector communities can influence the risk of pathogen spillover Higher biodiversity might facilitate spillover by bringing humans in contact with a diverse pool of wildlife species Conversely, declines in biodiversity and loss of certain species from an ecological community can create a niche that favours pathogen prevalence, transmission, or adaptation to new hosts	biodiversity (91%) reservoir host abundance & distribution (71%) community composition (57%) interspecies contact (49%) reservoir competence (37%) land use (29%) pathogen prevalence (26%)	"Loss of biodiversity can exacerbate the risk of pathogen spillover. In low diversity communities, vectors attain higher pathogen prevalences because they feed more frequently on primary reservoirs. Conversely, vectors in high biodiversity communities feed on a wider range of hosts, some of which are poor pathogen reservoirs, often resulting in lower pathogen prevalence at ecological community level..." (Jones et al., 2013)
Reservoir Hosts (*n* = 66)	Changes in reservoir host abundance and distribution can increase spillover risk. Host abundance might increase due to improved food availability; changes in climate can increase vegetative food supplies, while human-modified areas can provide backyard feeders and trash. Abundance is in turn linked to zoonotic disease transmission via increased human encounters with abundant hosts	interspecies contact (65%) reservoir abundance & distribution (53%) (changes in) geographic overlap (23%) urbanization (21%) viral pathogen (21%) vector borne transmission (15%)	"Populations of urban-adapted hosts can reach densities in urban and suburban areas that are much higher than observed in undisturbed areas. Moreover, an abundance of certain resources is available in the city areas throughout the year via human waste or intentional feeding by citizens. These can additionally support thriving urban-adapted animal populations and can lead to increased contact with humans" (Pfäffle et al., 2013)

Note: The clusters were identified via hierarchical cluster analysis of up to 68 codes assigned to pathway text segments that were extracted from a corpus of review papers related to spillover. Code frequency within each cluster (i.e. the proportion of pathways in that cluster which were assigned that code) is provided for codes with ≥15% frequency.

FIGURE 3 Bar plots showing relative disciplinary foci across conceptual clusters. Disciplines are displayed vertically and clusters are displayed horizontally, in the same order as the dendrogram. Bar height is the number of pathways that a discipline contributed to a cluster, scaled by the number of pathways in each cluster and each discipline. Disciplines vary in their degree of specialism (focusing on a small number of clusters) versus generalism (no main focus) [Correction added on May 28, 2021 after first online publication : Figure 3 was wrongly formatted and was corrected in this version].
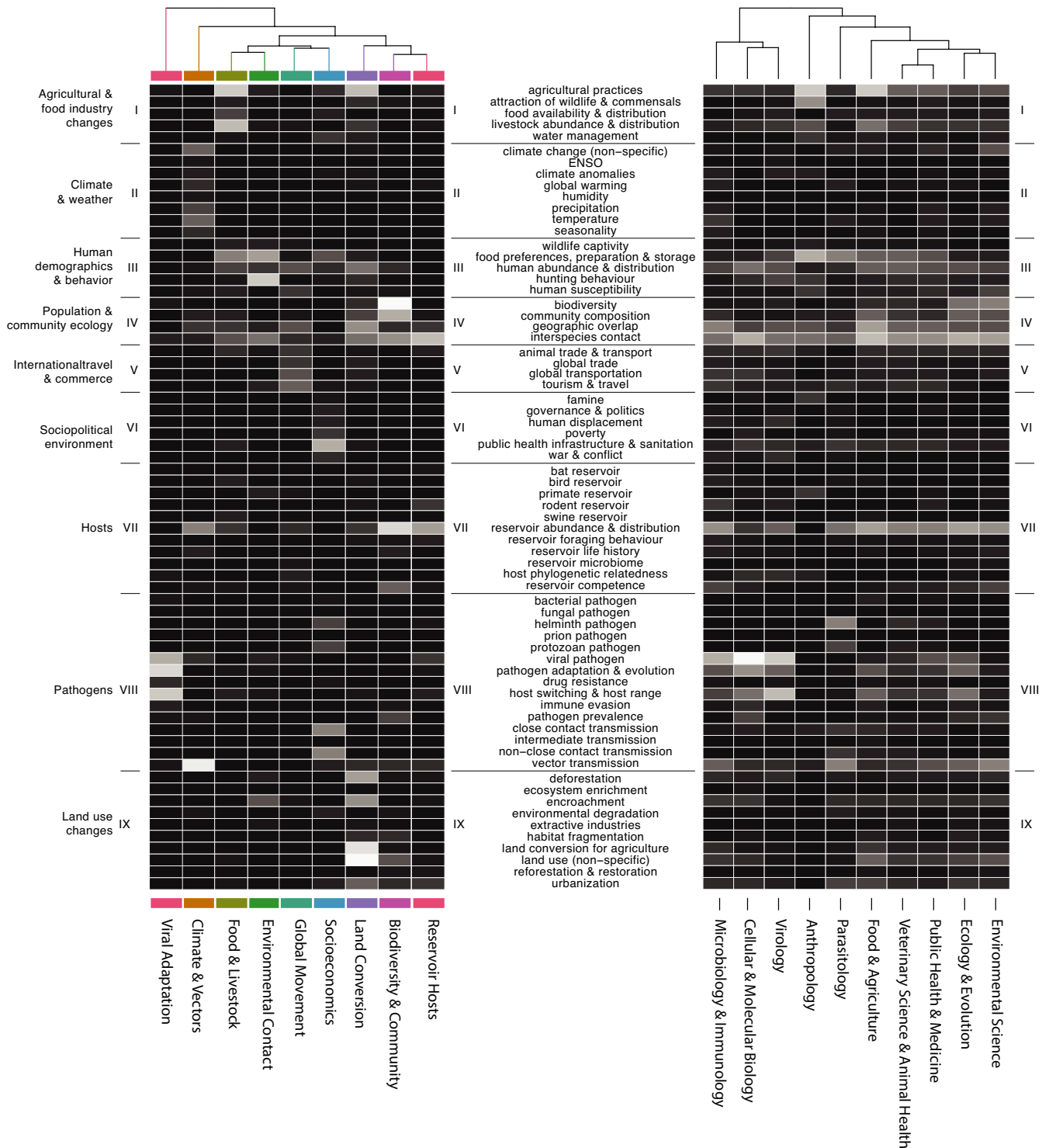
FIGURE 4 Comparing patterns of codes assigned to pathways reveals content explored by clusters and disciplines. Heatmaps show the relative frequency of codes within each cluster (left panel) and discipline (right panel). Cell shading represents the proportion of pathways in a cluster or discipline that were assigned a specific code; a lighter cell means that a code was often assigned to pathways for a given cluster or discipline. Clusters and disciplines are ordered hierarchically, represented by the vertical dendrograms

and *Land Conversion*. Review authors reported a lack of knowledge about how climate influences vector physiology, behaviour and distribution. They also noted that while the direct impacts of climate and weather have been explored, the effects of climate on other socioeconomic, behavioural and environmental factors may indirectly affect vector-borne disease risk. Reservoir host-related gaps asked how factors such as host immunity, within-host pathogen dynamics and population-level prevalence could affect spillover risk. Review authors highlighted the importance of identifying traits that allow hosts to tolerate infection and transmit pathogens to other species.
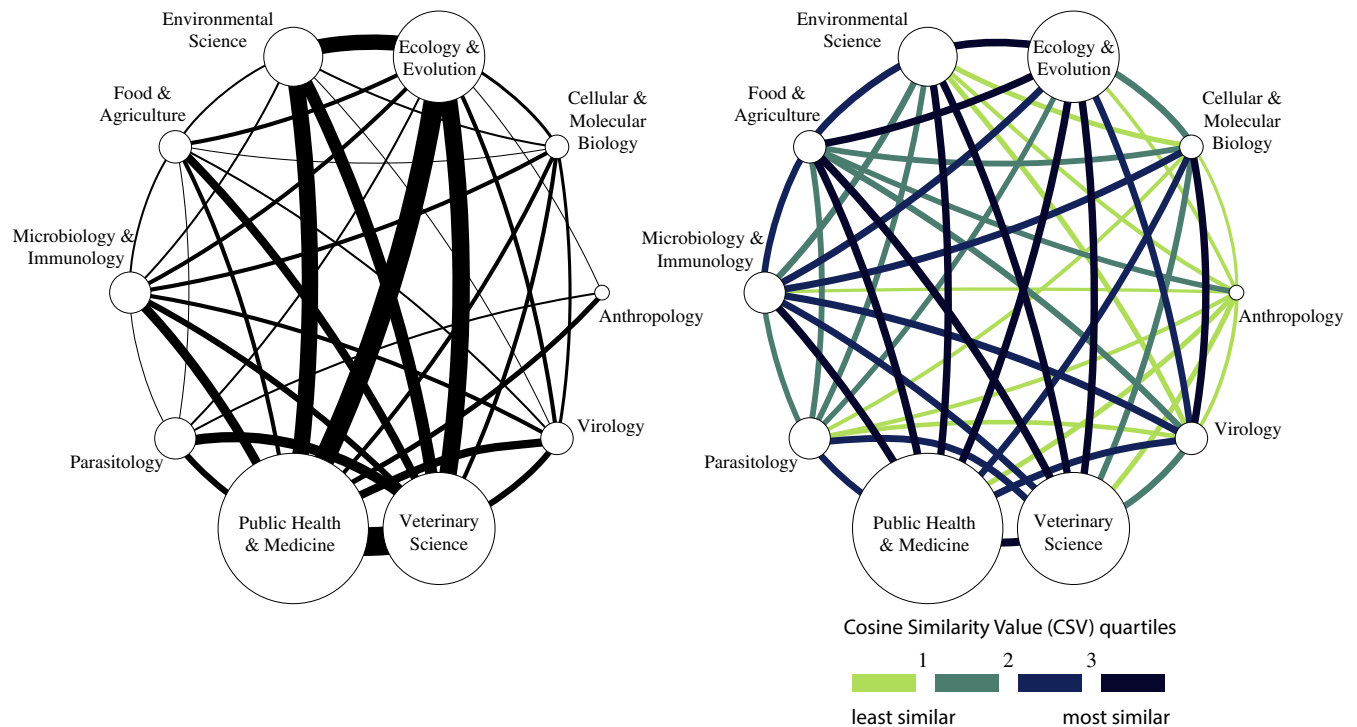
FIGURE 5 Network diagrams depicting the disciplinary co-assignment to review papers (left panel) and similarity between disciplines (right panel). In both networks, nodes represent the ten disciplines assigned by paper metadata, with node size representing the numbers of papers in that discipline (note that papers could be assigned to multiple disciplines). In the left panel, the weight of each edge (thickness of line connecting disciplines) is proportional to the number of times that these two disciplines were assigned to the same paper. In the right panel, edges are weighted and coloured by cosine similarity between disciplines, with thicker, darker lines representing greater similarity between disciplines. Cosine similarity values below the 1st quartile are green (least similar), values between the 1st and 2nd quartiles are light blue, values between the 2nd and 3rd quartiles are medium blue, and values above the 3rd quartile are dark blue (most similar)

For example, Mandl et al. (2015) noted that, 'Studies to date have focused primarily on viral detection and diversity, rather than on illuminating the nature of the host-virus equilibrium extant in their wild animal reservoirs'. Virus adaptation gaps identified the need to understand which traits allow pathogens to more easily switch to new host species, including humans. Regarding biodiversity, authors have sought to determine whether there is a general causal relationship between biodiversity and spillover risk, and to better understand that relationship where it exists. While spillover literature primarily focuses on changes to host diversity, review authors noted that changes to microbial communities also warrant attention. Research concerning the effects of anthropogenic factors could distinguish different types, scales and rates of change. Authors suggested focusing on mechanistic processes rather than general trends. Kilpatrick and Randolph (2012) pointed out that, 'although correlations exist between land use and disease incidence or measures of risk, rigorous and mechanistic analyses that identify causal factors…are absent in most cases'. Anthropogenic changes like urbanization and expansion were considered widely studied, compared with counter-urbanization, shrinking cities, reforestation and restoration.

Two groups of gaps dealt with concepts not addressed by our clusters. Some authors suggested that knowledge of past outbreaks gleaned through paleopathology and archaeology could inform studies of current zoonoses. Archaeological materials might provide

information about parasite transmission routes, and factors associated with spillover, such as diet, dwellings, culture and environment. Another novel suggestion was to study all members of the 'pathosphere' (i.e. the set of all disease-causing organisms) to identify all potential sources of human disease. Understanding the diversity of pathogens to which humans are exposed could be useful for predictive models.

Finally, a major gap identified was the need to integrate across disciplines to address the complexity of spillover processes. Studying combinations of factors across biological, veterinary, medical, agricultural and social sciences could better predict how these factors together predict spillover risk. Jones et al. (2013) asserted that 'A priority for research therefore should be a holistic perspective on pathogen dynamics at the wildlife–livestock–human interface, based on an interdisciplinary approach to the examination of biological, ecological, economic and social drivers of pathogen emergence'. Authors often advocated for the inclusion of social forces and the mechanisms by which they influence spillover processes. A better understanding of interactions between numerous factors was also considered important. A related recommendation was to study how spillover risk responds as multiple factors vary over space and time. Host and vector populations, transmission rates, infection prevalence and several other

factors were suspected to drive much of the dynamics of disease emergence.

4 | DISCUSSION

We performed a thematic analysis of spillover review literature using a combination of qualitative and quantitative techniques. The goal of our work was not to develop a new framework for conceptualizing spillover, as many exist already (Gortazar et al., 2014; Institute of Medicine, 2003; Lo Iacono et al., 2016; Plowright et al., 2017; Wood et al., 2012), but rather to broadly survey many disciplines with an interest in spillover and identify similarities and differences in their areas of focus. Our use of cluster analysis on qualitatively coded data allowed us to identify main spillover processes discussed in the literature, while examining specific codes allowed us to take a finer-scale look at concepts that were important in these processes.

We found that One Health disciplines (Veterinary Science & Animal Health; Public Health & Medicine; Ecology & Evolution; Environmental Science) were highly similar, based on codes applied to pathways in these disciplines. Additionally, these disciplines were broad, focusing on spillover concepts across a wide range of clusters. In contrast, Anthropology appeared distinct among disciplines studied here, tending to focus on a small number of clusters and uncommon codes. The relative uniqueness of Anthropology may be due to the failure to integrate anthropological perspectives into natural science frameworks for studying disease spillover. Infectious disease researchers have long recognized the value of incorporating social science theory into One Health and life sciences (Brown et al., 2015; Craddock & Hinchliffe, 2015; Janes et al., 2012; Wilcox & Colwell, 2005; Wolf, 2015). However, results from our heatmaps (Figure 4), network diagrams (Figure 5) and analysis of author-identified conceptual gaps show that there is little overlap between natural sciences and social sciences, despite the calls for interdisciplinary research. This disconnect between aspirations and practice may be due to the challenges of conducting interdisciplinary research. Though the potential benefits of collaboration between natural and social sciences are widely acknowledged, the numerous practical difficulties that arise when attempting to practice interdisciplinarity must be addressed (Keck & Lynteris, 2018; Lélé & Norgaard, 2005; Moon & Blackman, 2014; Wilcox & Colwell, 2005). Another explanation for this disconnect could be that commonly proposed frameworks for interdisciplinary research overlook lesser known, but still relevant, areas of anthropological study (Lapinski et al., 2015; Palsson et al., 2013; Wilcox & Colwell, 2005). Much of the anthropology and social science content analysed in our study focused on epidemiological transition models, paleoparasitology, health inequity and political ecology—concepts that are rarely included in One Health or life science approaches to conceptualizing spillover.

Finally, the weak connections we observed between Anthropology and other disciplines could be due to the greater number of natural science disciplines represented in our study compared to social sciences. It is possible that our search process might have led to unequal representation of disciplines. In addition to identifying few Anthropology papers, we also did not identify any economics papers in our search, despite searching the EconLit database. This could be due to a true paucity of social science papers about spillover, or a failure to detect these papers based on our search databases or search terms. Economics review papers in particular may tend to focus more on economic consequences of spillover (e.g. Ozili & Arun, 2020), rather than economic conditions facilitating spillover.

We recognize several limitations in our work. First, this study was a review of English-language review articles. It is possible that review papers, compared to primary literature, do not fully capture the academic discourse about spillover that is occurring within disciplines. Similarly, we excluded papers that focused on a single pathogen, host, or geographic region. This could lead to an underrepresentation of lesser-known or system-specific pathways to spillover. By only including papers written in English, we also may have missed pathways more relevant to pathogens in non-English speaking countries. Second, our text extraction process did not evaluate the weight of evidence available for each pathway; that is, both observed and hypothesized pathways were included in our dataset. Therefore, we cannot identify which spillover processes are in fact most common or most important in causing spillover events (which was not the goal of our study). Finally, we note that our choice of codes, method of assigning disciplines, and qualitative interpretations in this study are subjective, and may be biased towards ecological perspectives because of our training as ecologists.

Our research suggests several lines of potentially fruitful inquiry for future spillover research. We recommend that researchers focus on understudied clusters within spillover research; for example, the *Biodiversity & Community* cluster lacked diverse disciplinary input. By examining Figure 3 (bar plot of pathway frequency by cluster and discipline), researchers in individual disciplines may discover areas of spillover research that other academic disciplines have identified as relevant to spillover, but not well-represented in one's own. Similarly, by examining Figure 4 (heatmaps of code frequency by cluster and discipline), researchers could explore specific components of spillover processes (codes) that are less studied in their disciplines. In addition, integrating knowledge from other disciplines with one's own could help address conceptual blind spots. By examining Figure 5 (network diagrams of discipline co-assignment and similarity), perhaps in combination with Figure 3, researchers might identify prospective areas for productive interdisciplinary research. For instance, a fruitful collaboration might involve researchers in Ecology & Evolution (relatively strong in *Biodiversity & Community* but weak in *Socioeconomics*) and Parasitology (weak in *Biodiversity & Community* but strong in *Socioeconomics*). Finally, we note that while there are many areas of research in the spillover literature, as indicated by our clusters, there are also unique gaps that could benefit from attention (e.g. characterizing pathogen diversity, drawing on historical material). We hope this analysis of spillover

review literature will spark new interdisciplinary collaborations and attract attention to gaps in our understanding of disease transmission from animals to humans.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTION

All authors conceived and developed the study. CAS and JV-V collected and analysed data, designed figures and tables and drafted the manuscript. JMD obtained funding for the study and oversaw its completion. All authors revised the manuscript critically for intellectual content and approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

The data and code supporting the results are archived in Zenodo and available at http://doi.org/10.5281/zenodo.4757545.

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