A social–ecological approach to landscape epidemiology: geographic variation and avian influenza — Source link ↗

Graeme S. Cumming, Graeme S. Cumming, Celia Abolnik, Alexandre Caron ...+5 more authors

Institutions: James Cook University, University of Cape Town, University of Pretoria

Related papers:

- Stakeholder's practices and representations of contacts between domestic and wild pigs: a new approach for disease risk assessment?

- Natural resource management by rural citizens in developing countries: Innovations still required

- Role, distribution and perspective of camel breeding in the third millennium economies

- The challenge of participatory natural resource management with mobile herders at the scale of a Sub-Saharan African protected area

- Landscape diversity and associated coping strategies during food shortage periods: evidence from the Sudano-Sahelian region of Burkina Faso

A social–ecological approach to landscape epidemiology: geographic variation and avian influenza

Graeme S. Cumming* · **Celia Abolnik** · **Alexandre Caron** ·**Nicolas Gaidet** · **John Grewar** · **Eleonore Hellard** ·**Dominic A. W. Henry** · **Chevonne Reynolds**

G. S. Cumming (*) · E. Hellard ·D. A. W. Henry · C. Reynolds
DST/NRF Centre of Excellence, Percy FitzPatrick Institute, University of Cape Town, Rondebosch, Cape Town 7701, South Africa e-mail: graeme.cumming@uct.ac.za

Present Address:
G. S. Cumming
ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

C. Abolnik
Department of Production Animal Studies, Faculty of Veterinary Science, University of Pretoria, Onderstepoort, Pretoria 0110, South Africa

A. Caron · N. Gaidet
UPR AGIRs, CIRAD, Montpellier, France

A. Caron
UPR AGIRs, CIRAD-RP-PCP, Harare, Zimbabwe
Mammal Research Institute, University of Pretoria, Pretoria 0110, South Africa

J. Grewar
Department of Agriculture, Government of the Western Cape, Townsville, South Africa

Abstract

Context Landscape structure influences host–parasite–pathogen dynamics at multiple scales in space and time. Landscape epidemiology, which connects disease ecol-ogy and landscape ecology, is still an emerging field. *Objective* We argue that landscape epidemiology must move beyond simply studying the influence of landscape configuration and composition on epidemiological processes and towards a more comparative, systems approach that better incorporates social–ecological complexity. *Methods* We illustrate our argument with a detailed review, based on a single conceptual systems model, of geographic variation in drivers of avian influenza in Western Europe, Southeast Asia, and Southern Africa. *Results* Our three study regions are similar in some ways but quite different in others. The same underlying mechanisms apply in all cases, but differences in the attributes of key components and linkages (most notably avian diversity, the abiotic environment, land use and land cover, and food production systems) create significant differences in avian influenza virus prevalence and human risk between regions. Conclusions Landscape approaches can connect local- and continental-scale elements of epidemiology. Adopting a landscape-focused systems per-spective on the problem facilitates the identification of the most important commonalities and differences, guiding both science and policy, and helps to identify elements of the problem on which further research is needed. More generally, our review demonstrates the importance of social–ecological interactions and comparative approaches for landscape epidemiology.

Introduction

Recent years have seen increasing recognition of the influence of landscape structure on both plant and animal health. Global trends in land use change and related activities, such as deforestation, agriculture, irrigation, and urbanisation, have profound implications for the biophysical environment, the structuring of communities of other organisms, and the biotic interactions that drive populations and communities of parasites and pathogens (Patz et al. 2004). It is no coincidence in a time of massive anthropogenic landscape alteration that parasites and pathogens are increasingly emerging as health threats to the human population (Daszak et al. 2000, 2001b; Jones et al. 2013).

Ostfeld et al. (2005) noted that few studies had considered how landscape structure (composition and configuration) influences disease risk or incidence, and argued in favour of 'a true integration of landscape ecology with epidemiology'. Landscape epidemiology, which deals with this integration, focuses on 'how the temporal dynamics of host, vector, and pathogen populations interact spatially within a permissive environment to enable disease transmission' (Reisen 2010). Meentemeyer et al. (2012) stated that landscape epidemiology 'integrates concepts and approaches from disease ecology with the macroscale lens of landscape ecology', but also noted that although landscape epidemiology emerged in tandem with landscape ecology (Pavlovsky 1966; Galuzo 1975), it is still struggling to find its own identity.

Given the lack of a clear paradigm of landscape epidemiology, better integration between existing ideas in landscape epidemiology and other closely related areas of research (as discussed in the next section) seems desirable. We begin with a brief overview of landscape epidemiology and a discussion of the merits of a comparative social–ecological systems approach. We then present a detailed case study of avian influenza that illustrates how (1) consideration of social–ecological feedbacks can alter our understanding of landscape epidemiology, particularly where the socioeconomic environment varies in space, and (2) a comparative systems approach, in which a systems model is used to explore differences in effect sizes and

interactions between discrete landscapes, can contribute to understanding geographical and between-scale influences on epidemiology in ways that go well beyond simply considering the influences of landscape structure on pathogen occurrences.

Integrating landscape epidemiology and systems ecology

Landscape epidemiology is closely allied to 'spatial epidemiology', which has been defined as 'the study of spatial variation in disease risk or incidence' (Ostfeld et al. 2005) or 'the description and analysis of geographic variations in disease with respect to demographic, environmental, behavioral, socioeconomic, genetic, and infectious risk factors' (Elliott and Wartenberg 2004). We use 'landscape epidemiology' (Pavlovsky 1966) as the older of the two terms.

Landscape epidemiology has been recently reviewed by Reisen (2010) and Meentemeyer et al. (2012). Reisen (2010) adopted a biophysical definition of a landscape and focused on the creation by different interacting factors (hosts, landscapes, people) of a dynamic space, the 'nidus', in which pathogen transmission may occur. The properties of this space depend on the ecological attributes of the species involved in the interaction and the spatial structure of the broader landscape, including anthropogenic influences. Meentemeyer et al. (2012) emphasized the importance of scale and in particular, cross-scale processes and feedbacks. They argued that new dynamic models are needed to facilitate our understanding of epidemiological functional connectivity across landscapes and recognized the reciprocal feedbacks between human behaviour and disease dynamics as an integral component of landscape epidemiology. Many of the ideas that currently form the core of landscape epidemiology are summarized in the 10 propositions of Lambin et al. (2010) (Table 1).

Several papers have extended landscape epidemiological concepts and empirical evidence since the most recent comprehensive review of the topic (Meentemeyer et al. 2012). Robinson et al. (2013) provide a good example of a quantitative approach that connects dispersal models with landscape structure to understand the spread of chronic wasting disease through populations of white-tailed deer in the Midwestern USA. Lane-deGraaf et al. (2013) developed an

Table 1 Ten propositions for landscape epidemiology

Propositions
(1) Landscape attributes may influence the level of transmission of an infection
(2) Spatial variations in disease risk depend not only on the presence and area of critical habitats but also on their spatial configuration
(3) Disease risk depends on the connectivity of habitats for vectors and hosts
(4) The landscape is a proxy for specific associations of reservoir hosts and vectors linked with the emergence of multi-host diseases
(5) To understand ecological factors influencing spatial variations of disease risk, one needs to take into account the pathways of pathogen transmission between vectors, hosts, and the physical environment
(6) The emergence and distribution of infection through time and space are controlled by different factors acting at multiple scales
(7) Landscape and meteorological factors control not just the emergence but also the spatial concentration and spatial diffusion of infection risk
(8) Spatial variation in disease risk depends not only on land cover but also on land use, via the probability of contact between, on one hand, human hosts and, on the other hand, infectious vectors, animal hosts or their infected habitats
(9) The relationship between land use and the probability of contact between vectors and animal hosts and human hosts is influenced by land ownership
(10) Human behaviour is a crucial controlling factor of vector-human contacts, and of infection

After Lambin et al. (2010)

agent-based modelling framework for thinking about the relationships between landscape structure and parasite spread by long-tailed macaques, and Altman and Byers (2014) found a strong impact of anthropogenic landscape elements on trematode populations. Empirical evidence for the importance of landscape elements in disease dynamics has also been rapidly increasing; in the last 2 years, for example, land cover and land use patterns have been shown to influence (amongst others) the transmission risks of West Nile Virus, tick-borne babesiosis, and Lyme Disease in the USA (Tran and Waller 2013; Walsh 2013; Gardner et al. 2014), Nipah Virus in Bangladesh (Hahn et al. 2014), Scrub Typhus in Taiwan (Wardrop et al. 2013), and malaria in Senegal and South Africa (Ngom et al. 2013; Okanga et al. 2013).

Landscape epidemiology overlaps in important ways with many ideas in community ecology and biogeography. Most ecological communities are open, in the sense that they are connected by dispersal to regional pools of species (including hosts, parasites, and pathogens) and food webs (Polis et al. 1997, 2004). Community openness, coupled to spatial heterogeneity, has a variety of implications for community-level processes that can facilitate the coexistence of different host species and of hosts and their parasites and pathogens (Holt and Dobson 2007). The diversity of open systems may be enhanced by migration and habitat selection, which can enable the coexistence of similar species by regulating populations at different seasons; by a range of metapopulation processes, such as differences in colonization ability and responses to disturbance; and by source-sink dynamics, which can allow an inferior competitor to persist in one community if it is a superior competitor in a nearby community (Holt and Dobson 2007). These same principles are important for understanding the spread and maintenance of pathogens across landscapes.

From an interdisciplinary perspective, host–parasite–pathogen systems have all the characteristics of a complex adaptive system (Pearce and Merletti 2006; Norberg and Cumming 2008). Specifically, their dynamics cover a wide range of different but interacting scales, at different speeds; they are structured by gradients and influenced by membership in networks; and they typically include complex feedback loops, nonlinear relationships between cause and effect, and indirect effects such as trophic cascades (Plowright et al. 2008; Keesing and Young 2014; Moore et al. 2014). To make sense of such complexity, in-depth individual case studies of single host–parasite and/or host–pathogen systems—the traditional approach in epidemiology—are necessary but not sufficient.

Coping with complexity depends not only on better models of local and regional spatial interactions, but also on developing a comparative approach that facilitates quantitative analysis of multi-scale spatial

influences across different landscapes (Polis et al. 2004; Cumming 2011b, c). Scientific understanding of pathogen dynamics is often conditional on a particular set of study conditions and local parameters (e.g., local climate, available host species, movement patterns, and human environment). If these conditions do not represent the full range of conditions under which the pathogen is found, knowledge from one region may not be directly applicable to another region. For example, the 'global' model of Herrick et al. (2013) is based primarily on northern hemisphere rainfall data, with only three very general indices of anthropogenic influences; it is therefore unsurprising that it predicts that northern conditions are suitable for avian influenza viruses (AIVs). The challenge for landscape epidemiology is to move from such oversimplified interpolations and disconnected case studies to a more general framework, under which the relevance of studies at particular locations is clear because they are used to test and refine more general explanatory hypotheses (Pickett et al. 2007).

The problem of locally specific parameters is exacerbated by the classical focus of landscape epidemiology on a relatively small number of biophysical variables and on target populations rather than target communities. Individual organisms and their parasites and pathogens are embedded in communities of species, not just in single-species populations. Recent years have seen the incorporation of parasites more fully into food web analyses (Dobson et al. 2008; Lafferty et al. 2008) but these analyses often ignore the role of spatial heterogeneity (Polis et al. 2004). Similarly, although systems approaches have been applied quite widely in the One Health literature, they are mostly specific to a single system (Zinsstag et al. 2011). The epidemiology of many pathogens is strongly influenced by human management, landscape modification, and production systems for domestic animals (Myers et al. 2013); and the roles of wild animals as vectors and hosts create an equally strong ecological component. These different elements are seldom considered over broad spatial extents, or from a social–ecological systems perspective.

Systems perspectives often lead to quantitative models, but their deeper value comes from the ways in which they can be used to frame a problem and think through the important variables, interactions, and dynamics within a particular problem space. To demonstrate the value of a comparative, systems approach to host–pathogen interactions, and the importance of geographic comparisons
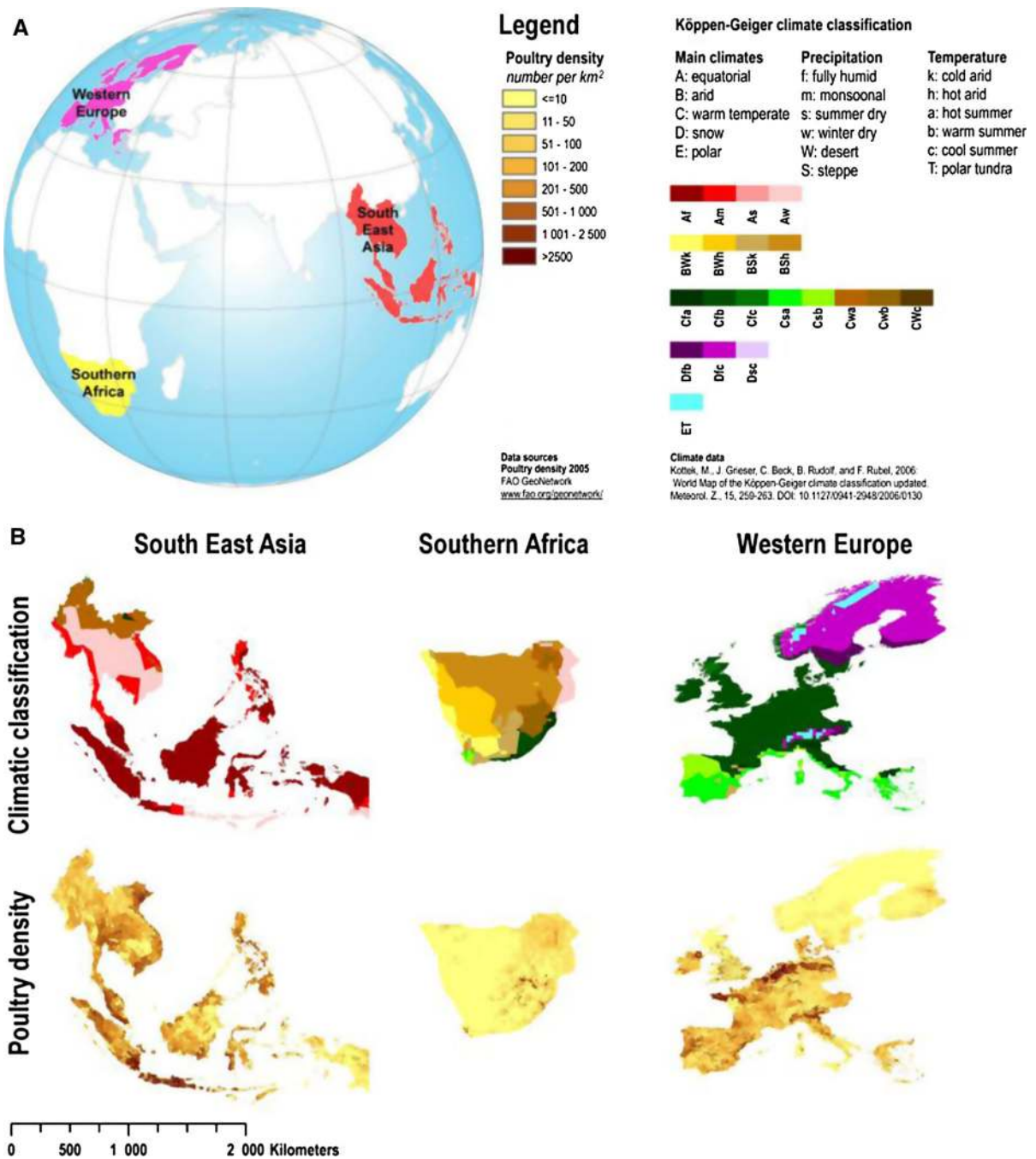
Fig. 1 Section **a** shows the geographic regions used in this ▶ review on a *global scale*. We defined Western Europe using the region called the Western European and Others Group (WEOG) in the unofficial regional groups of the United Nations, but excluding Turkey, Iceland, Australia, Canada, New Zealand and Israel. Countries in this region include Andorra, Austria, Belgium, Denmark, Finland, France, Germany, Greece, Ireland, Italy, Liechtenstein, Luxembourg, Malta, Monaco, Netherlands, Norway, Portugal, San Marino, Spain, Sweden, Switzerland and the UK of Great Britain and Northern Ireland. We defined Southern Africa as the region described by the UN scheme of geographic regions but including Zimbabwe and that part of Mozambique that is south of the Zambezi River (i.e., the region south of the *line* created by the Zambezi and Kunene Rivers). Countries in this region include Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe. We defined Southeast Asia as countries belonging to the Association of Southeast Asian Nations (ASEAN) but including East Timor. Countries in this region include Brunei Darussalam, Cambodia, Indonesia, Lao People's Democratic Republic, Malaysia, Myanmar, Philippines, Singapore, Thailand, Timor-Leste and Vietnam. Note that this regional definition includes both mainland and island nations. Section **b** shows the studied regions in more detail with both the climatic classification and the density of domestic poultry compared between regions. The regions in section **b** are to *scale* showing their comparison in land area

of both social and ecological system elements for landscape epidemiology, we use a detailed case study of the landscape epidemiology of avian influenza.

A comparative systems approach to landscape epidemiology: the example of avian influenza

Overview

AIVs are widespread and occur across a range of conditions of (amongst others) climate, host community composition, and transmission cycles. AIV research has concentrated on the fine-scale details of transmission (e.g., contact rates, details of viral shedding; Caron et al. 2009) with relatively little assessment of geographic, community-level, and anthropogenic variation. We compared AIV dynamics in Western Europe, Southern Africa, and Southeast Asia (Fig. 1). We did not try to include all areas that are considered geographically important for AIVs; our approach is illustrative, not exhaustive, and could easily be extended to other locations. We selected these particular locations because they are very different from one another, both socially and ecologically, and hence provide a suitable cross-section of global conditions to support generalisation.

A

Legend

Poultry density
number per km²

	<=10
	11 - 50
	51 - 100
	101 - 200
	201 - 500
	501 - 1 000
	1 001 - 2 500
	>2500

Data sources
Poultry density 2005
FAO GeoNetwork
www.fao.org/geonetwork/

Köppen-Geiger climate classification

Main climates	Precipitation	Temperature
A: equatorial	f: fully humid	k: cold arid
B: arid	m: monsoonal	h: hot arid
C: warm temperate	s: summer dry	a: hot summer
D: snow	w: winter dry	b: warm summer
E: polar	W: desert	c: cool summer
	S: steppe	T: polar tundra

Af Am As Aw
BWk BWh BSk BSh
Cfa Cfb Cfc Csa Csb Cwa Cwb Cwc
Dfb Dfc Dsc
ET

Climate data
Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel, 2006:
World Map of the Köppen-Geiger climate classification updated.
Meteorol. Z., 15, 259-263. DOI: 10.1127/0941-2948/2006/0130

B — South East Asia — Southern Africa — Western Europe

Climatic classification

Poultry density

0   500   1 000   2 000 Kilometers

We used a conceptual systems model (Fig. 2) to identify key commonalities and differences between regions. Processes are considered at three different scales: local, regional (including national and multi-national), and global. At the local scale, AIVs are influenced by wild and domestic birds, by other pathogens, and by the environment. The environment includes the abiotic template (e.g., rainfall, temperature, topography), biotic system elements (e.g., vegetation type, predators) and anthropogenic elements, most notably the dominant land uses and land cover types within the area. Land use and land cover

are driven by regional and global economic and institutional factors, including such things as commodity prices, regulations, and national and international policies (Geist and Lambin 2002). The ecological consequences of global economic processes, such as anthropogenic climate change, may also affect AIV distributions and prevalence.

Although some system elements are indirectly or weakly related to AIVs for much of the time, many interactions assume greater importance at particular times or under certain conditions. For example, water storage capacity is strongly driven by national policy and local demand, as expressed through domestic use, recreation, food production, and hydroelectric power (Grey et al. 2013). By providing key dry-season habitat and food resources for anatids, managed impoundments can be critical to the persistence and concentration of bird populations and the pathogens that they may carry.

There are significant differences between our three focal regions in the nature and relevance of the different components and the strengths of the different interactions between components. To illustrate the complexity of the problem in depth, and the many feedbacks between social and ecological systems, we first describe each model component and its immediate interactions individually and then synthesize these pieces to provide a comparative overview.

System components and interactions

This section details the contents of each of the model components displayed in Fig. 2, which provides a road-map for understanding the relevance of each subsection. We discuss each component in isolation first and then consider the ways in which they are connected within and across landscapes.

Influenza viruses

The influenza A virus is mainly found in wild ducks and shorebirds. It replicates in the respiratory and gastro-intestinal tracts, usually with no clinical symptoms, and is excreted into the environment through mucosal exudates or in the faeces. Other birds ingesting contaminated food or water become infected, thereby maintaining the infection cycle. Infections may last for several weeks. Of the 18 serotypes defined by the hemagglutinin surface antigens (Tong et al. 2013), the H5 and H7 serotypes cause highly pathogenic avian influenza (HPAI) in poultry, and are potentially zoonotic. The remaining avian influenza serotypes are referred to as low pathogenicity avian influenza (LPAI).

Few studies have focused on the susceptibility of different species to infection and to different serotypes (Costa et al. 2011). Juvenile birds are immunologically naïve and may be both highly susceptible to infection and prolific shedders of the virus (van Dijk et al. 2014). AIVs exhibit geographic differences; for example, H5N1 HPAI has been found in Southeast Asia and Western Europe but not in Southern Africa. In general, however, the biogeography of avian influenza is insufficiently well known to adequately compare patterns in AIV biodiversity across our three regions.

Wild bird community

The main natural maintenance hosts for low pathogenic avian influenza (LPAI) are birds in the family Anatidae (geese, swans, and ducks), of which there are c.162 species globally. Western Europe has lower overall avian diversity than the two other regions, but has a speciose and abundant anatid fauna that includes 51 anatid species: 3 swan species, 14 goose species, 18 freshwater duck species, and 16 sea duck species (British Trust for Ornithology 2014). Substantial populations of many of these are migratory, with movement corridors running north to the Arctic, east into Asia, and south into West and East Africa. Anatids may reach very high densities in Western Europe, particularly at pre-migration staging areas. Duck restocking for hunting is common, with several million hand-reared wild ducks (mostly mallards, *Anas platyrhynchos* Linnaeus, 1758) released each year (Söderquist et al. 2013).

Southeast Asia hosts around three quarters of the Asian region's 2700 bird species (Unwin 2011). For the area including Thailand, Vietnam, and Cambodia there are 37 anatid species: 2 swan species, 7 goose species, and 28 duck species (Bhushan et al. 1993). Unlike the two other regions, the Southeast Asian anatid community contains a mix of migratory species (e.g., Garganey *Anas querquedula* Linnaeus, 1758) that breed in temperate and boreal regions of Asia, and resident species (e.g., Lesser Whistling Duck *Dendrocygna javanica* Horsfield, 1821) that breed in tropical regions. Within the broader Asia–Pacific region there are three main flyways: Central Asian, East Asian–Australasian, and Central Pacific. The East Asian Flyway connects Southeast Asia to Australia and northern Asia. Some of
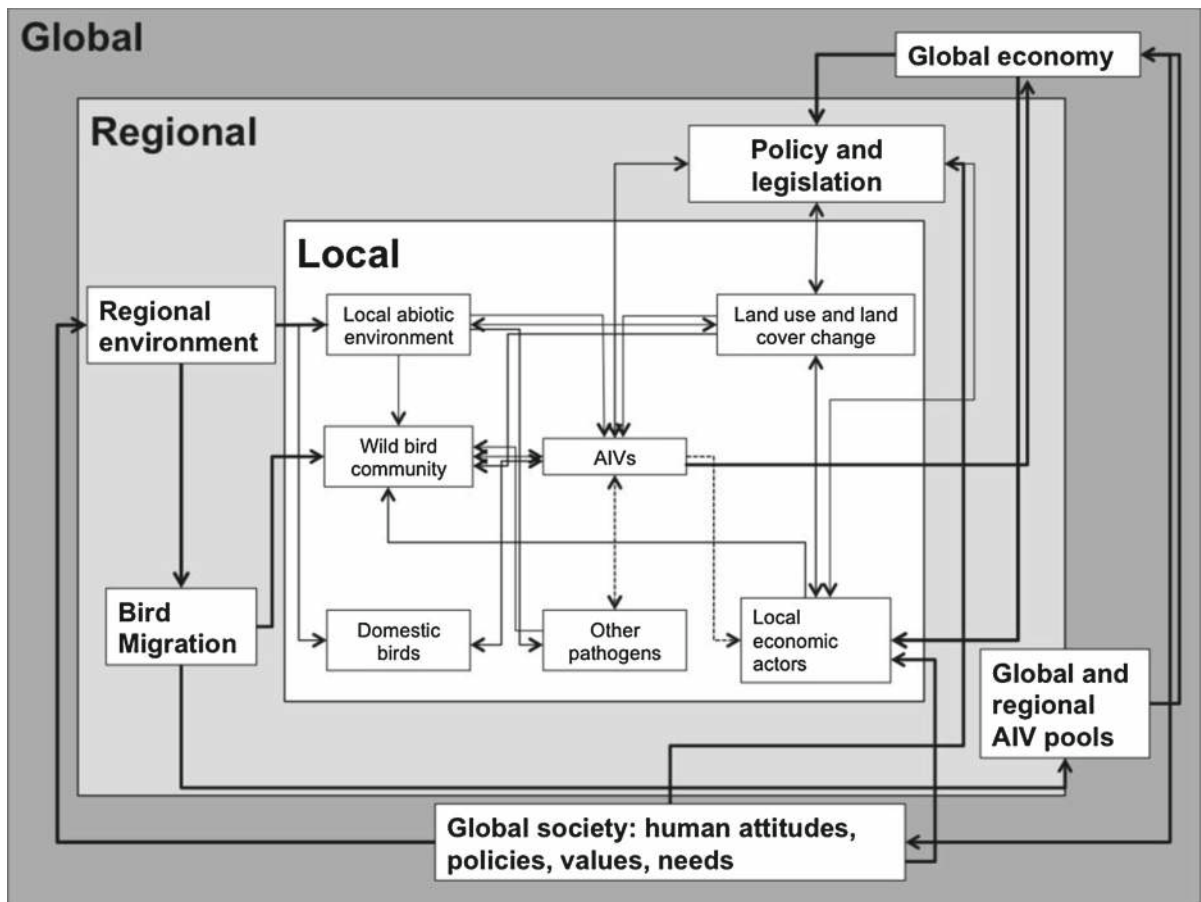
Fig. 2 Social–ecological systems model of avian influenza dynamics, showing what we consider to be the main components and interactions within the system. *Darker lines* indicate connections at broader scales, *dotted lines* indicate weaker linkages. Observed changes in AIV prevalence are a conse-quence of spatial and temporal variation generated across multiple different scales by a combination of social, economic, and ecological patterns and processes. The exact nature and strength of the different linkages within this model are less important than the general point that avian influenza viruses are components of a complex system that exhibits high variation in both space and time and contains many feedback loops both within and between different scales. Our understanding of the dynamics of avian influenza viruses in wild bird populations currently depends on regional snapshots of subsets of the different components of the model, rather than on a general and more integrated view such as the one presented here

the major flyways that extend into Europe, Africa, and the Americas also have their origins in northern Asia (Mundkur 2006), with some shared breeding and moulting sites, making Asia a potential mixing point for AIVs from around the world.

Southern Africa has c. 950 documented bird species of which a substantial component of songbirds, raptors, terns, and wading birds migrates annually to and from Western Europe. There are 16 indigenous, locally-breeding duck species in Southern Africa and a small population of feral Mallard Ducks. Southern Africa has no true geese and no swans. None of the Southern

African ducks, with the possible exception of the Knob-billed Duck *Sarkidiornis melanotos* Pennant, 1769, is a true migrant (Oatley and Prys-Jones 1986) and most Eurasian migratory anatids overwinter north of the equator. Moult migrations (annual, long-distance, directed movements to large waterbodies for the purpose of flightless moult) have been documented for Egyptian Geese (*Alopochen aegyptiaca* Linnaeus, 1766), and evidence for Red-billed Teal (*Anas ery-throrhyncha* Gmelin, 1789) and White-faced Whistling Duck (*Dendrocygna viduata* Linnaeus, 1766) suggests the occurrence of similar radial movement patterns

(Petrie and Rogers 1997b; Cumming et al. 2012a) as well as possible nomadic movements (Hockey et al. 2005). Ducks occur in Southern Africa at lower abundances than in Western Europe and Southeast Asia but show a variety of different breeding and moulting strategies, meaning that in many wetlands there are ducks present year-round as well as potentially high densities of wading birds, gulls, terns, and coots.

Abiotic components

Waterfowl are influenced by such abiotic factors as precipitation, climate (Fig. 1), topography, and wetland distribution (Owen and Black 1990) as well as vegetation and anthropogenic influences. Climate and water quality play key roles in the persistence and transmission of AIV in waterfowl communities (Breban et al. 2009; Roche et al. 2009). Western Europe has a diverse, heterogeneous landscape that is dominated by forests and woodlands, agriculture, and grassland. It has plenty of permanent surface water and a temperate climate. The high seasonal variation in temperature and precipitation is critical for waterfowl, which avoid winter by migrating out of the Palaearctic.

Southeast Asia has a tropical climate with a land mass dominated by agriculture, savannah, and tropical rainforests. While rainforest is generally a poor environment for waterbirds (with a few exceptions; e.g., White-winged Wood Duck *Carina scutulara* Müller, 1842), areas that have been cleared for agriculture, riverbanks, and large impoundments within forested areas may provide suitable habitat. Rice paddies, for example, may be extensively used by ducks (Gilbert et al. 2007). Rainfall is high and occurs throughout much of the year, and water levels influence waterfowl breeding and aggregation patterns. Many indigenous waterbird species are adapted to take advantage of the monsoonal floods that often occur May–September in low-lying areas. Annual average temperature and humidity in Southeast Asia are high, with little variation, meaning that some species can breed throughout the year. Asia's topography has a strong influence on its vegetation, and its mountains are high enough to function as geographical barriers that channel migratory birds into corridors or flyways.

Southern Africa has a semi-arid climate with dry, mild winters and hot, wet summers (apart from the Cape). There are large areas of semi-desert and relatively little forest, and its mountains are not high enough to channel migratory birds into corridors

(Hockey 2000). It has high spatiotemporal variation in precipitation (Tyson 1986; Dilley 2000) but not in temperature. Many waterfowl breed opportunistically in ephemeral water bodies (Hockey et al. 2005). Towards the end of the dry season, high densities of waterfowl can be found at some permanent wetlands as ephemeral wetlands dry down (Mundava et al. 2012).

Many varieties of AIV have been isolated from standing water, suggesting that it can act as both a source of contamination and a reservoir (Brown et al. 2007). The virus persists for longer at cooler temperatures (4–17 °C), slightly basic pH (7.4–8.2) and in fresh–brackish water (salinity from 0 to 20,000 ppm; Brown et al. 2007, 2009; Weber and Stilianakis 2008). Theoretical models of AIV prevalence have suggested that environmental persistence of the virus contributes more to transmission in temperate regions (Rohani et al. 2009; Van Dalen et al. 2010), while direct inter-individual transmission is more important in tropical regions (Gaidet et al. 2012a). However, the range of conditions for AIV persistence overlaps with conditions in Southern Africa during winter and part of summer.

The differing compositions and configurations of the abiotic elements in each of our three case study landscapes have important implications for the temporal elements of landscape epidemiology. Waterfowl live in highly mobile populations that may aggregate and disaggregate several times during a year. As the patterns of different landscape features (such as waterbodies and agricultural lands) change in time, they drive the movement of waterfowl and the resulting movement and transmission of their pathogens. Landscape variation in the abiotic elements of greatest relevance to avian influenza occurs at fine temporal scales (e.g., anthropogenic manipulation of water levels in dams), medium temporal scales (e.g., variations in rainfall within a season) and broad scales (e.g., annual seasonality and decadal weather patterns). Long-term, fine-scale data sets will be essential for understanding how this variation affects epidemiology.

Interactions between environmental factors and AIV prevalence

The prevalence of AIVs in waterfowl depends on the interaction between host ecology, ecological region and seasonal fluctuations in environmental factors. Standard approaches for predicting species occurrences (Cumming 2007a; Elith and Graham 2009;

Franklin 2010) do not necessarily translate well into a landscape epidemiology context to predict pathogen occurrences because of the additional complexities involved in having an animal, rather than a biophysical habitat, as the pathogen's habitat. In Southern Africa, for example, Cumming et al. (2011) found no clear annual pattern of AIV prevalence in waterfowl and explained this as a consequence of the dynamic nature of wetland resources and the flexibility of waterfowl movement strategies (Caron et al. 2011; Cumming et al. 2011, 2012b). In a sample of Afrotropical wetlands that included data from East and West Africa as well as Southern Africa, Gaidet et al. (2012a) showed that although variation in AIV prevalence was related to waterfowl density and the arrival of European migrants, it was not influenced by regional climatic conditions. By contrast, predictable peaks in AIV prevalence occur in Europe and North America in autumn, prior to migration (Wilcox et al. 2011; Latorre-Margalef et al. 2014; van Dijk et al. 2014). This pattern is a consequence of large pre-migration concentrations of waterfowl with high proportions of immunologically naïve juveniles (Latorre-Margalef et al. 2014; van Dijk et al. 2014).

Other studies have highlighted the role of specific environmental variables as important factors in AIV risk assessments. Liu et al. (2007) found that outbreaks of HPAI H5N1 in Eurasia occurred during or immediately after a rapid decrease in temperature. Temperature, NDVI (normalised difference vegetation index, a measure of vegetation greenness) and precipitation were found to be key environmental factors for creating accurate risk maps for H5N1 outbreaks in Europe (Gilbert and Pfeiffer 2012). Elevation, particularly in Southeast Asia, correlates with spatial variation in AIV prevalence in Thailand, Indonesia and Vietnam (Gilbert and Pfeiffer 2012) because agricultural land, which has higher risks of AIV transmission between wild and domestic birds, tends to be lower-lying. Paul et al. (2014) found that AIV prevalence was negatively associated with distance to the closest water body in the Red River Delta, Vietnam highlands and Madagascar. They also found a positive association between AIV and duck density in the Vietnam highlands and Thailand, and with rice landscapes in Thailand and Madagascar, confirming the important role of wetlands–rice–duck ecosystems in the epidemiology of AI in SE Asia. The influence of environmental variables on AIV prevalence depends on the landscape context (Si et al. 2010), and hence risk factors for one area may not be as relevant elsewhere (Williams and Peterson 2009). There is a clear need in this context for better hypotheses and theories that connect landscape structure and dynamics, in a general sense, to the prevalence of AIVs.

Domestic poultry farming

Domestic poultry is a potential source of both high and low pathogenic influenza viruses for human and wild bird populations. In most highly intensive poultry production systems, birds are caged and the risks of transmission from domestic to wild birds (or vice versa) are relatively low (Caron et al. 2010). Higher risks for wild–domestic contact are posed by free range poultry, backyard poultry, live bird markets, and systems such as ostrich farms and duck ponds in which birds are held in fenced outdoors enclosures (Songserm et al. 2006). Smith and Dunipace (2011) have argued, based on data from an AIV outbreak in Canada, that the potential contribution of backyard flocks to epidemic spread is small; but it is unclear whether this can be more generally assumed. Waste disposal from commercial farms may also be a route for viral transmission, suggesting a possible role for anthropogenic infrastructure in the landscape epidemiology of influenza viruses.

Poultry farm density, the type of poultry production system (e.g., free-range production), the related level of biosecurity, and movement patterns between farms (e.g., of birds, people, and vehicles) influence AIV transmission and maintenance. The highest farm density is in Southeast Asia, where heterogeneous levels of biosecurity give AIVs opportunities to spread (Songserm et al. 2006). Intensive production systems in Southeast Asia often include direct contact between people, ducks, and pigs, making this the most likely location for the emergence of new HPAI strains in domestic poultry.

Western Europe has a more intensive, less dense, and more secure poultry production system, making it less suitable for AIV maintenance and spread. There is a considerable amount of backyard and free range poultry production in intensively farmed European landscapes, but less mixing between different kinds of production system. Analysis of an AIV outbreak in the Netherlands found no evidence for a role for European backyard or free range poultry in the probability of

spread (Thomas et al. 2005; European Food and Safety Authority 2008). Poultry populations are highly clustered, with highest densities in Belgium and The Netherlands, the northwestern region of France, and Northern Ireland. Farms with broiler or layer chickens are the majority across EU member states (European Food and Safety Authority 2006).

Domestic production of non-gallinaceous species, such as ducks in Southeast Asia or ostriches in Southern Africa, can introduce a large population of alternative hosts for AIVs. The role of domestic ducks raised in large flocks in paddy fields is now accepted in the maintenance of AIVs (Desvaux et al. 2011) and recurrent AIV outbreaks in ostrich farms in South Africa have the potential to spread to poultry (Abolnik et al. 2007, 2012). Outbreaks of HPAI H5N2 in ostriches in 2004, 2006 and 2011 indicate that a change from low to highly pathogenic viral strains is possible in this species. Ostrich production occurs almost entirely outdoors (Fig. 3), where contact with wild birds (including wild waterfowl) is common.

Other pathogens and parasites

Infectious agents do not circulate in isolation; host individuals are co-infected by microorganisms that can interact with each other, either directly (Massey et al. 2004) or indirectly (Biancotto et al. 2008), with potentially serious consequences for microbial dynamics and host health (Abu-Raddad et al. 2006; Telfer et al. 2010), inter-individual or inter-population variations in pathogenicity (Ives et al. 2011), and disease control (Modjarrad and Vermund 2010).

Influenza viruses can synergistically interact with respiratory bacteria, such as *Pneumococcus* in humans (McCullers 2006) or *Haemophilus parasuis* in swine (Mussa et al. 2012), predisposing the host to, and worsening, bacterial infections. Co-infection of chickens or turkeys with LPAIV and Newcastle Disease Virus alters the replication dynamics of both viruses, although not the clinical signs (Costa-Hurtado et al. 2014). Commensal bacteria modulate host immune response against influenza A virus (Ichinohe et al. 2011). Little is known about geographic variation in internal microbial and parasite communities, but it seems likely that the structure and composition of the host microbiota (Yatsunenko et al. 2012) will differ between populations and geographical regions.

Policy and legislation

AIV regulation and control are coordinated at the global scale under the global strategy for the progressive control of HPAI, which is a joint effort of the Food and Agricultural Organisation of the United Nations (FAO), The World Organisation for Animal Health (Office International des Epizooties, OIE), and the World Health Organisation (WHO; FAO 2008). Policy and legislation for HPAI H5N1 are assumed to be effective in the control of other HPAI subtypes. All regional policies share the elements of ongoing surveillance, notification, rapid responses, stamping out HPAIVs by slaughtering infected birds, restricting movements on live birds, and improving sanitation. Vaccination is undertaken in Western Europe and parts of Southeast Asia. Implementation of polices at regional and national levels, however, depends on capacity.

In Western Europe, regulation of AIV is coordinated by the European Union under Council Directive 2005/94/EC. Commission regulation (EC) 798/2008 imposes veterinary certification requirements for the importation and transit through of poultry products within the European Union community. The EU has compulsory surveillance programs for AIV in both poultry and wild birds (Pittman and Laddomada 2007). Contrary to other regions, hunting activities are also important in monitoring and surveillance. Hunters provide bird samples for AIV testing and alert authorities of unusual bird mortality (Green and Elmberg 2014), and the hand-rearing and release of ducks for hunting also affects local AIV dynamics (Vittecoq et al. 2014). Within the region, compliance is high and response to outbreaks swift.

In Southeast Asia, a framework implemented by the Association of Southeast Asian Nations (ASEAN) for the control and eradication of HPAI in ASEAN countries is in effect (ASEAN 2010). The policy is similar to that of Western Europe, but the high number of birds in backyard production systems and disparity in socioeconomic status between member states translate into important differences in AIV control. For example, in member states with primarily backyard production systems, surveillance is difficult or absent (Rushton et al. 2005); and Cambodia, one of the poorest countries of the region, offers no compensation for culled poultry. This results in delayed or no

Fig. 3 Ostriches in quarantine, prior to slaughter, on a farm near Oudtshoorn, South Africa. The feeding trays are shared with a high abundance of potential bridge species, including not only doves, pigeons, and sparrows, but also bishop and weaver birds that typically nest in reedbeds or trees that overhang the water. Photo Graeme S. Cumming

reporting of potentially infected poultry (Rushton et al. 2005; ASEAN 2010).

Control measures for HPAI in Southern Africa were drafted at Southern African Development Community level through the OIE/FAO Regional Animal Health Centre (RAHC) in Gaborone, Botswana (RAHC 2013). Southern Africa has many of the same implementation issues as Southeast Asia, particularly in relation to capacity to implement surveillance programs and the difficult task of surveying widely dispersed backyard poultry.

In general, policy and legislation for AIV at global, regional and local levels are similar, particularly for HPAI. The more important uncertainty is whether local regulatory bodies can enforce existing policies. Regions such as the EU have the necessary capacity, but many countries in the Asian and African contexts are inadequately equipped to control AIV in domestic poultry. The longer an AIV circulates, the more it spreads and the greater chance it has to mutate. The

virus may then become endemic, creating a long-term problem, as with H5N1 HPAI in countries such as Bangladesh, China, Egypt, India, Indonesia, and Vietnam.

Policy and legislation are also highly relevant as drivers and modulators of land use and land cover change. It is beyond the scope of this article to review the huge body of work on the influence of institutions on agriculture and forestry; the interested reader is referred to Ostrom (2009) and Lambin and Geist (2006).

Landscape influences

The landscape epidemiology of AIV in wild birds is strongly influenced by landscape structure and context. Wetlands differ in their biophysical properties, the degree to which they provide suitable foraging, roosting, and breeding sites, their degree of human disturbance, and the predator populations in their

immediate surroundings. Similarly, the availability of food within the broader landscape and its variation in time are likely to be important drivers of the seasonal movements of ducks, particularly outside breeding and moulting periods (Cumming et al. 2013). Human agricultural activities provide year-round food for grazing species via irrigated agriculture, and adjacent waterbodies are often eutrophic and suitable for dabbling ducks (Mangnall and Crowe 2003; Cumming et al. 2013).

Water quality and quantity are influenced by changes in the distribution and amount of different habitat types in the upstream catchment, including growth or loss of forest, fire regimes, and agricultural fertilization and management practices (Tilman et al. 2001; Likens 2004). These broad-scale changes alter habitat suitability and affect the reproductive success of duck populations, potentially leading to subtle shifts in anatid community composition and abundance (Okes et al. 2008).

Anatid species that are disturbance-tolerant and relatively robust, such as Canada Geese (*Branta candensis* Linnaeus, 1758) and Egyptian Geese, are often favoured by human impacts on wetlands and their surroundings (e.g., creation of lawns and secure roosting sites at golf courses and on lakeshores; Okes et al. 2008). Other species that are less disturbance-tolerant and require particular kinds of habitat, such as the water lily-dependent African Pygmy Goose, often fare worse where human impacts are heavy (Okes et al. 2008).

Southern Africa is a water-scarce region (Seckler et al. 1998) in which water levels in impoundments are often maintained through the early part of the dry season and then rapidly lowered via irrigation towards the end of the dry season. Changes in river flow regimes and the loss of natural drydowns can have substantial impacts on aquatic ecosystems and the waterbirds that depend on them (Kingsford et al. 2004; Cumming et al. 2012b). Alterations to flow regimes affect not only the productivity of individual wetlands but also the likelihoods of such events as long distance dispersal, the formation of large aggregations of waterbirds, and the chance of individual birds opting to remain at a wetland through the dry season rather than disperse. Similarly, small impoundments created for irrigation and livestock are often scattered across arid landscapes and may provide year-round habitat for dabbling and potentially diving ducks (Petrie and Rogers 1997a).

The landscape-wide influence of water management is arguably lower in the wetter environments of Western Europe and Southeast Asia, although historic losses of floodplains in Europe must have had severe impacts on duck populations. In Western Europe, broad-scale landscape modification and intensive farming have had significant effects on waterfowl. For example, the expansion of the mute swan (*Cygnus olor* Gmelin, 1789) population is in part due to food subsidies provided by nitrogen and calcium rich croplands that are important in reproduction (Fouque et al. 2007). In the Camargue, France, division of the marshes and large inputs of freshwater have resulted in lower water salinity and longer flood periods, leading to losses of biological diversity and higher plant biomass favouring use by wintering waterfowl (Tamisier and Grillas 1994). A confounding issue is that loss of wetland habitat may at least initially favour larger aggregations and overcrowding of waterfowl at remaining wintering, breeding and stopover sites. This in turn may lead to higher probabilities of contact between domestic and wild birds (Vandegrift et al. 2010).

In Thailand, irrigation has enabled year-round or 'second harvest' rice cropping that supports higher densities of domesticated free-ranging duck populations that rely on postharvest rice fields for nutrition (Gilbert et al. 2006) while also helping to control snail populations. The co-occurrence of rice cultivation and wetlands connects domestic and wild duck populations and promotes AIV circulation, often enhanced by the captive rearing of waterfowl on wetland shores (Feare et al. 2010). In these areas, HPAI H5N1 outbreaks in domestic poultry are frequent, suggesting a possible causal link (Gilbert et al. 2008). Additionally, the conversion of forest to rice paddies increases the total habitat available for species that can host AIVs.

As these examples show, the anthropogenic impacts of aseasonal resource provision for some but not all prospective host species, combined with dampened overall variation in resource provision, can have profound implications for both hosts and pathogens. Although there are differences in the details of different anthropogenic impacts across our three case study regions, it is clear that human landscape modification is of central importance in understanding the landscape epidemiology of avian influenza.

Economic actors

Increasing affluence and global population growth have intensified consumer demand for livestock-

derived protein (Leibler et al. 2009). Poultry production is the fastest growing livestock subsector globally, with a current annual growth rate of 4.3 %. Per capita production growth for other meat products has been stagnant or negligible (FAOSTAT 2013). The poultry subsector produces over 99 Mt of meat (c. one third of total global meat production) and 69 Mt of eggs per annum (FAOSTAT 2013). Poultry production is geographically concentrated (Fig. 1) and >9 Mt of poultry meat are moved internationally each year (FAOSTAT 2013). Most chickens and turkeys are produced from commercial parent breeds that are confined in houses of 15,000–70,000 birds (Leibler et al. 2009). Although large commercial farms have good biosecurity and containment, the densities at which birds are housed facilitate rapid and efficient transmission of virulent AIVs (Vandegrift et al. 2010).

Poultry production per region varies greatly, with Western Europe producing almost three times more than Southern Africa and twice as much as Southeast Asia. Western Europe is one of the world's leading producers of eggs and poultry meat, with nearly 1.9 b broilers, 129 M turkeys, >100 M ducks and geese, and 150 M egg-laying birds (Windhorst 2007). France is the world's fifth largest producer of poultry meat (Fermet-Quinet and Bussière 2007), with 24,500 poultry farms and around 235 M birds. France also differs from most other poultry producing countries in that it supports hundreds of thousands of backyard poultry owners.

In contrast to other regions, waterfowl hunting is an important sporting activity in Western Europe, with >6.7 M registered hunters and >7.6 M waterfowl and 4.2 M shorebirds hunted annually (Hirschfeld and Heyd 2005; Mooij 2005). Mathevet (2000) demonstrated that the Camargue generates about €10 million annually through hunting activities and may even rival income generation from agricultural activities (Mathevet and Mesléard 2002). It is unclear whether hunters' perceptions of AIVs and associated risks have any influence on the hunting industry (and hence, on the economic values associated with wetlands).

Southeast Asia produces >2.9 Mt of poultry per annum (FAOSTAT 2013). Roughly 90 % of all poultry production in the region is in small extensive or backyard type operations (McLeod et al. 2005; Rushton et al. 2005). Poultry production systems in Southeast Asia are exceptionally diverse. Unlike the rest of Southeast Asia, the majority of poultry produced in Thailand is commercial (McLeod et al. 2005); produces 91 M broilers, 72 M native chickens, and 27 M ducks per annum and supports 24 M laying birds (Rushton et al. 2005). By comparison, Myanmar produces >93.7 M chickens and 11.2 M ducks per annum in small-scale, market-oriented systems (Burgos et al. 2010).

The poultry sector in Southern Africa is growing at 6 % per annum, faster than in the other two regions. It supports approximately 380 M birds that produce 1.6 Mt of meat and 0.5 Mt of eggs per annum. An estimated 60–70 % of all poultry is in smallholder free-range systems and traded in live bird markets (FAOSTAT 2013). South Africa dominates commercial production in the region, producing 1.4 Mt of poultry meat per annum. Very little duck meat (393 t in South Africa for 2012) and no turkey meat are produced, due to problems with seasonality of moulting (turkeys), water availability (duck production), and lack of consumer demand for these meats.

South Africa's ostrich industry is also relevant for avian influenza. South Africa has dominated global trade in ostrich products (meat, leather, and feathers) for well over a century (Mather and Marshall 2011) and is the current world leader in ostrich production, with 65 % of global market share (DAFF 2011). The South African ostrich production system is worth >1.2 b Rand (about 118 m US dollars) per annum. Ostrich production is largely outdoors, where domestic birds may come into contact with grazing wild waterfowl (Burger et al. 2012). HPAI outbreaks, such as the H5N2 outbreak of 2011, can have devastating consequences for the industry (Moore et al. 2014).

The differences in production systems between the three regions have important consequences for AIV maintenance, spread and evolution within the broader landscape. All support free-range poultry, but in varying degrees. Backyard systems with free-range ducks or chickens have little or no biosecurity. Domestic birds are free to mix with wild species, and frequently consist of multi-age flocks that can support persistent enzootic virus transmission (Gilbert et al. 2006, 2008). Domestic ducks in Southeast Asia are usually farmed in rice paddies, where they come into contact with wild waterfowl (Rushton et al. 2005), and kept inside the home during the night, increasing contact with humans (Vandegrift et al. 2010). Village poultry systems play an essential role in rural

livelihoods in Southeast Asia, and AIV outbreaks can be devastating to communities (Tiensin et al. 2007).

Differences in host susceptibility to AIV and the relative proportions of poultry species between the three regions also influence the ecology of AIV in these areas. Gallinaceous poultry (chickens and turkeys) are considered to be highly susceptible to infection with AIV strains, producing clinical disease varying from severe with high mortalities (HPAI) to mild with drops in egg production (LPAI). Ducks and ostriches (both domestic and wild) display few or no clinical signs, despite being effective propagators and disseminators of AIV (Perkins and Swayne 2002; Abolnik et al. 2012).

Poultry trade in and between some developing countries may carry a larger risk of viral spread due to infrequent testing, quarantine and poorly regulated trade (Vandegrift et al. 2010). Live animal markets are common in the developing world and play an integral role in the dynamics of influenza virus transmission and evolution. They have been implicated in a number of AIV outbreaks and in facilitating enzootic influenza virus transmission worldwide (Ito et al. 2001), including H5N1 in Hong Kong (Ellis et al. 2004) and in other parts of Asia (Cardona et al. 2009). Markets can also be hotspots for viral evolution because they bring together different species of animals from different geographical areas into an unsanitary environment, potentially facilitating reassortment between viruses (Webster 2004).

Macro-scale influences

At regional and global extents, and over longer time periods, a number of broad-scale factors contribute to the shifting mosaic of AIVs across European, African, and Asian landscapes. Climate change since the 1970s has already altered the breeding patterns and migration distances of European species (Lehikoinen et al. 2013). As climates become warmer, ducks are able to find sufficient winter food to remain at higher latitudes. If European and north Asian ducks reduce their migration distances, and if fewer individuals migrate, the likely consequence for AIVs will be a profound reduction in the global connectivity of different regions.

Although warmer water is less favourable for viral persistence, climate change will not necessarily reduce AIV prevalence. In arid areas, reductions in precipitation may lead to larger dry season aggregations of birds and greater competition for food (and hence, greater stress and greater susceptibility to infections). Conversely, increases in precipitation may increase available resources and/or contribute to predator release for highly mobile, opportunistic duck populations. In general, climate change is likely to introduce even greater variability into duck populations and movements, making monitoring and control of AIVs more difficult. Climate change will also have both direct and indirect effects on agriculture and related patterns of water management (Huntjens et al. 2011; Viviroli et al. 2011), again with relatively unpredictable consequences for waterbird populations and AIV transmission cycles (Both 2010; Slenning 2010).

Also at broader scales, technological innovations, global demand for food, and trends in agricultural economics have the potential to influence AIV dynamics. As farming systems in Africa and Asia shift from extensive to intensive models to meet global food demand (Pretty et al. 2011; Pingali 2012), areas of monoculture may become more appealing to grazing anatids; levels of fertilizer use (hence, impacts on waterbodies) are likely to increase; and irrigated agriculture may create additional habitat for ducks and hence for AIVs. Changes in farming practices (e.g., the use of alfalfa on fields, or shifts from rice farming to aquaculture) can further affect the ability of a given habitat to maintain AIVs.

The relevance of economic factors for epidemiology is receiving increased attention in the emerging field of epidemiological economics (Perrings et al. 2014). Epidemiological economics, or EE, focuses on the ways in which economic factors influence human decisions about how and with whom they interact. Since many local economic interactions demand contact, people's willingness to engage in certain kinds of economic activity may be altered by their perceptions of the risks associated with contact. For example, Fenichel et al. (2013) have demonstrated that perceptions of the risk of contracting highly pathogenic influenzas can have significant economic implications for airlines. Similarly, the perceptions of people and governments of food safety or quality can have important implications for AIV circulation. The AIV risk posed by poultry consumption led to drastic reductions in poultry consumption during the 2005–2006 HPAI H5N1 panzootic (Figuie and Fournier 2008) and governments adopted related policies (Figuié 2013). Such impacts are often short term, but

their consequences for food consumption habits can persist. At broader scales, and across landscapes, EE implies that macroeconomic incentives and policies that have implications for agricultural practices, human behaviour, migration, and ecosystem management—such as labour laws or agricultural subsidies— may also play important roles in both human and wildlife pathogen dynamics.

Lastly, regional and international economic competition and the growing global demand for meat may impact production systems. Shifts in cost: benefit ratios may make ostrich farming less sustainable in Southern Africa; and if global demand for duck meat increases, a duck production industry may develop. Changes in ostrich, duck, and poultry populations and farming practices could have significant influences on regional patterns of AIV occurrence.

Synthesis of regional patterns

There are common elements but also some important regional differences in the various influences on the epidemiology of AIVs (Table 2). Consideration of our systems model (Fig. 2) and the differences indicated in Table 2 suggests that important regional differences are to be expected in many of the cause–effect relationships that relate to avian influenza prevalence and dynamics. These differences will in turn lead to differences in transmission cycles and infection risks within both domestic and wild populations of birds, and in relation to people. As a result, we would expect different variables and different interactions to be more important in predicting and managing avian influenza in different regions.

In Western Europe, with its cold winters, less diverse bird fauna, thoroughly implemented control policies, and lower rates of land cover change, the primary drivers of avian influenza dynamics seem likely to be climate and the long-distance, migratory movements of waterbirds. Predictable bird movements make it easier to identify areas and seasons that increase the risk of spillover from wild to domestic birds. The more biosecure poultry sector and compliance of most stakeholders to EU policy minimise the threat of AIV to poultry, with rapid responses to outbreaks resulting in an almost negligible threat of local AIV zoonosis. Risk remains from exogenous introductions through poultry trade, wild bird migration, and potential introduction of a human-to-human transmissible strain via travel.

In Southeast Asia, with its warm, wet climate, diverse and highly mobile bird fauna, often poorly implemented control policies, and high numbers of backyard poultry, the primary drivers of avian influenza dynamics seem likely to be fine-scale farming practices (especially rice cultivation and domestic duck production) and domestic bird movements, particularly where these relate to domestic ducks and their interactions with wild waterfowl and people. As in the other regions, a pool of AIVs is maintained in wild birds. However, the recent massive expansion of the wild/domestic bird interface has created multiple and frequent opportunities for AIV spillover from wild to domestic birds. The heterogeneity of policy enforcement in Southeast Asia prevents an efficient control of AIV in domestic populations. Unlike other regions, the domestic bird/human interface is extensive and some cultural/traditional practices promote bird–human transmission leading to zoonotic avian influenza. This region has the highest risk of AIV emergence, maintenance and spread and little risk from exogenous AIV introduction.

In Southern Africa, with its arid climate, diverse bird fauna, lack of migratory ducks, well developed but not always well-implemented control policies, and faster rates of land cover change, the primary drivers of avian influenza dynamics seem likely to be broad-scale human agricultural and water management practices. These practices affect the populations and movements of wild birds. Thus far there appears to be low or no risk of introductions of AIV to gallinaceous poultry, since no outbreaks besides LPAI H6N2 (which originated from ostriches) have been recorded in the region. The ostrich farming regions are the key susceptible poultry production system in this region, but the lack of both migratory anatids and interactions between ducks and free-range chickens reduces the probability of wild bird introductions. Risks nonetheless arise from exogenous introductions via the illegal poultry trade and potential introduction of a human-to-human transmissible strain via travel.

In all three regions, our review suggests that broad-scale economic factors, such as global commodity prices and technological innovations that influence farming practices and land cover change, may have significant effects on communities of AIVs through their effects on the spatial pattern and the abundance

Table 2 Summary of regional differences in different model components and interactions

	Western Europe	Southern Africa	Southeast Asia
Components			
Wild anatids	Large migrating populations within the region connecting other regions; large populations of resident birds. Relatively large populations of swans and geese	Large populations of resident birds but no truly migratory ducks; no true geese; no swans; movements radial from moulting sites rather than north–south	Large migrating populations within the region and connecting other regions; high diversity of anatids but populations of relatively low abundance; no swans and only small goose populations
Domestic birds	Large populations with high biosecurity measures, lower stocking density in commercial farms	Small populations with heterogeneous biosecurity measures and ostrich production, low farm density	Large populations with heterogeneous biosecurity measures and large domestic duck production, high farm density
AIVs	AIVs are present worldwide—LPAI pool shared between regions—although Southeast Asia is current hotspot of emergence of HPAI		
Abiotic environment	Seasonality driven by temperature	Seasonality driven by rainfall (more erratic)	Higher rainfall and high temperature year-long with less variation
Other pathogens	Multi-pathogen systems present in all regions; differences must exist but not documented		
Policy	Regional policy implemented and respected	Regional policy, partial implementation (lack of capacity). Control in ostrich production rigorous and strict	Regional policy not fully implemented, resulting in heterogenous control policy across countries
Land-use change	Slow (developed region), cultivated areas declining	Fast (developing region), more and more cultivated areas. Competition between conservation and development	Ultra-fast (developing region), increasing area under cultivation. Fewer natural areas left
Water resources and management (See Cumming 2011a for a comparison of issues in major river basins in each area)	Plentiful wetlands, but pollution historically high (post-industrial), many wetlands lost and river morphology heavily altered with canals and levees. Increasing attention now being given to water management	Water-scarce region with high aridity and few natural lakes. Water management is recognised as important but often problematic; high demand from multiple stakeholders	Plentiful surface water but environmental problems with water quality, excessive extraction, and large impoundments; heavily altered flow regimes in many river basins
Economic actors	Formal; perception of AIV as public health risk with pandemic potential	Formal and informal adaptation to risk; perception of little/no HPAI risk to people	Formal and informal adapting to risk and policies; perception of low risk to people and general lack of public awareness
Interactions between components			
AIV/wild birds	AIV are present worldwide in wild bird—LPAI pool shared between regions to some extent		
AIV/domestic birds	Well-controlled, low AIV load in domestic birds but periodic LPAI and HPAI outbreaks reported in backyard poultry in multiple European countries	Well-controlled in South Africa but LPAI H6N2 pool enzootic in poultry; periodic introductions of LPAI only in ostriches	Not well-controlled, HPAI pool maintained in domestic ducks
Wild birds/domestic birds	Controlled to some extent; rapid and effective response to periodic introductions	Historically not a risk factor for chickens. Not controlled in ostrich farms where farming is extensive	Not controlled notably in paddy fields and wetlands with mixed wild captured and domestic waterfowl rearing
Abiotic environment/bird populations	Seasonality influenced by temperature leading to synchronised reproduction and movement of wild birds	Seasonality influenced by rainfall leading to less synchronised and more erratic reproduction and movements of wild birds	Less seasonal, less synchronous reproduction and movements of wild birds

Table 2 continued

	Western Europe	Southern Africa	Southeast Asia
Abiotic environment/AIV	AIV can persist for months or even years in the environment, favouring indirect transmission	AIV cannot persist for long in the environment, more important role of inter-host direct transmission	
Link between policy and land use change	Policy more in favour of sustainable development and conservation	Contradicting policies between development and conservation of biodiversity	Policy in favour of development at "any cost"

of both wild and domestic birds. Consideration of epidemiological patterns across the broader landscape thus offers an important interface (and an often-ignored scale of analysis) between global and continental drivers of change and the local and more specific details of host–pathogen interactions and transmission cycles.

Discussion

Comparisons between different regions suggest that the same cause–effect relationships may play out differently, and with different consequences for our understanding of the landscape epidemiology of AIVs, in different regions. This means that if we are to develop a general understanding of the mechanisms that underlie AIV transmission, we need to find ways of undertaking research that tests the same hypotheses in comparable ways in different regions. At the same time, assumptions that are derived from any single region must be considered as working hypotheses until they have been validated in other systems. For example, widely held assumptions based on northern hemisphere findings about the importance of migratory ducks or large congregation sites of shorebirds (Krauss et al. 2010) as the primary sources of AIVs were not substantiated for Africa (Cumming et al. 2011; Gaidet et al. 2012b) despite clear evidence of a Eurasian origin for AIVs entering Southern Africa (Abolnik et al. 2006). Regional differences combined with geographic connectivity emphasize the need for a global-to-local approach to disease surveillance and control, because a failure to respond appropriately in one region can have consequences for other regions.

Our case study of avian influenza provides some important insights not only for our understanding of avian influenza, but also more generally for the further development of landscape epidemiology. Analysis of disease in wildlife populations has suggested that (1) many wildlife diseases are related to anthropogenic activities (Daszak et al. 2001a), and (2) R0, the basic reproductive number, a parameter used to estimate the number of cases one case generates on average over the course of its infectious period, is highly sensitive to heterogeneity in the spatial structure of the host population and/or the ability of pathogens to use multiple different host species (Dobson and Foufopoulos 2001). Understanding and predicting the development and spread of pathogens across landscapes will require that the activities of people and the relevance of spatial structuring in host populations be taken into account. Broad-scale spatial analysis is therefore essential for understanding and interpreting host–pathogen dynamics.

Layered over direct influences on epidemiology are many feedbacks and further complexities. For example, as we have argued, the local impacts of people on landscape pattern are further influenced by a set of regional and global variables such as agricultural policies and global food prices. These influences often have non-trivial implications for landscape structure and the movements of animals. In the case of Nipah and Hendra viruses, for example, fruit bat vectors may fly long distances to feed on cultivated fruit trees. Agricultural phenology thus plays an important role in their epidemiology (Daszak et al. 2006). Feedbacks between broad-scale and local-scale influences, such as between climate trends, economic demand, and cropping systems, can have unexpected knock-on effects on zoonotic prevalence in a given region. In some cases, identifying cross-scale effects will simply require the adaptation of existing data sets (e.g., land use and land cover change data) to yield more

pathogen-specific information. In other cases, such as the interactions of pathogens with other pathogenic or non-pathogenic agents and with the microbiome, little is known and more research is needed.

Similar questions and gaps arise for many emerging zoonoses; the key to progress is to turn these problems to our advantage. We propose that general systems models, based on proposed mechanisms rather than broad-brush correlations, should become the standard starting point for enquiry into the landscape epidemiology of cosmopolitan pathogens. The second step, which we have not attempted in this review article, is to quantify the different hypothesized interactions within the model and confront them with data. The scope of the problem is such that this may demand the use of initially incomplete or partial data sets. Progress in developing a more general framework for the landscape epidemiology of any single widespread pathogen will require a level of willingness to see what we can do with what we have, in the interests of hypothesis development, and openness from the scientific community when evaluating what may seem to be counter-intuitive results from less widely studied regions. International collaborations, in which different experiences and seemingly contradictory findings are shared and discussed, will be vital for our broader understanding of globally distributed pathogens. Where pattern-based (correlative) analyses differ in their findings, regional differences in pathogen occurrences offer valuable opportunities for testing and comparing alternative causal explanations. This will mean adopting a multi-scale, systems-oriented perspective on pathogens and parasites (e.g., Cumming 2007b; Plowright et al. 2008) to fully embed landscape epidemiology within a global change research paradigm.

References

Abolnik C, Cornelius E, Bisschop SPR, Romito M, Verwoerd D (2006) Phylogenetic Analyses of genes from South Africa LPAI Viruses isolated in 2004 from Wild Aquatic Birds suggests Introduction by Eurasian migrants. In: Schudel A,

Lombard M (eds) OIE/FAO international scientific conference on avian influenza, Basel, Karger 2006, vol 124, pp 189–199

Abolnik C, Bisschop S, Gerdes T, Olivier A, Horner R (2007) Outbreaks of avian influenza H6N2 viruses in chickens arose by a reassortment of H6N8 and H9N2 ostrich viruses. Virus Genes 34:37–45

Abolnik C, Olivier AJ, Grewar J, Gers S, Romito M (2012) Molecular analysis of the 2011 HPAI H5N2 outbreak in ostriches, South Africa. Avian Dis 56:865–879

Abu-Raddad LJ, Patnaik P, Kublin JG (2006) Dual infection with HIV and malaria fuels the spread of both diseases in sub-Saharan Africa. Science 314(5805):1603–1606

Altman I, Byers JE (2014) Large-scale spatial variation in parasite communities influenced by anthropogenic factors. Ecology 95(7):1876–1887

ASEAN (2010) Prevention, control and eradication of avian influenza in ASEAN: strategies and success stories. Jakarta. http://www.asean.org. Accessed 9 March 2015

Bhushan B, Fry G, Hibi A, Mundkur T, Prawiradilaga DM, Sonobe K, Usui S, Taniguchi T (1993) A field guide to the waterbirds of Asia. Wild Bird Society of Japan, Tokyo

Biancotto A, Iglehart SJ, Lisco A, Vanpouille C, Grivel J-C, Lurain NS, Reichelderfer PS, Margolis LB (2008) Upregulation of human cytomegalovirus by HIV type 1 in human lymphoid tissue ex vivo. AIDS Res Hum Retrovir 24(3):453–462

Both C (2010) Flexibility of timing of avian migration to climate change masked by environmental constraints en route. Curr Biol 20(3):243–248

Breban R, Drake JM, Stallknecht DE, Rohani P (2009) The role of environmental transmission in recurrent avian influenza epidemics. PLoS Comput Biol 5(4):e1000346

British Trust for Ornithology (2014). http://www.bto.org/about-birds/birdfacts/bird-families/waterfowl. Accessed 27 Feb 2015

Brown JD, Swayne DE, Cooper RJ, Burns RE, Stallknecht DE (2007) Persistence of H5 and H7 avian influenza viruses in water. Avian Dis 50:285–289

Brown JD, Goekjian G, Poulson R, Valeika S, Stallknecht DE (2009) Avian influenza virus in water: infectivity is dependent on pH, salinity and temperature. Vet Microbiol 136(1–2):20–26

Burger CE, Abolnik C, Fosgate GT (2012) Antibody response and viral shedding profile of Egyptian geese (*Alopochen aegyptiacus*) infected with low pathogenicity H7N1 and H6N8 avian influenza viruses. Avian Dis 56(2):341–346

Burgos S, Otte J, Roland-Holst D (2010) In: FAO (ed) Poultry, HPAI and livelihoods in Myanmar—a review. FAO, Roma

Cardona C, Yee K, Carpenter T (2009) Are live bird markets reservoirs of avian influenza? Poult Sci 88(4):856–859

Caron A, Gaidet N, de Garine-Wichatitsky M, Morand S, Cameron EZ (2009) Evolutionary biology, community ecology and avian influenza research. Infect Genet Evol 9:298–303

Caron A, de Garine-Wichatitsky M, Gaidet N, Chiweshe N, Cumming GS (2010) Estimating dynamic risk factors for pathogen transmission using community-level bird census data at the wildlife/domestic interface. Ecol Soc 15(3):25

Caron A, Abolnik C, Mundava, Gaidet N, Burger CE, Mochotlhoane B, Bruinzeel L, Chiweshe N, de Garine-

Wichatitsky M, Cumming GS (2011) Persistence of low pathogenic avian influenza virus in waterfowl in a Southern African ecosystem. EcoHealth 8(1):109–115

Costa TP, Brown JD, Howerth EW, Stallknecht DE (2011) Variation in viral shedding patterns between different wild bird species infected experimentally with low-pathogenicity avian influenza viruses that originated from wild birds. Avian Pathol 40(2):119–124

Costa-Hurtado M, Afonso CL, Miller PJ, Spackman E, Kapczynski DR, Swayne DE, Shepherd E, Smith D, Zsak A, Pantin-Jackwood M (2014) Virus interference between H7N2 low pathogenic avian influenza virus and lentogenic Newcastle disease virus in experimental co-infections in chickens and turkeys. Vet Res 45(1):1

Cumming GS (2007a) Global biodiversity scenarios and landscape ecology. Landscape Ecol 22:671–685

Cumming GS (2007b) Global biodiversity scenarios and landscape ecology. Landscape Ecol 22(5):671–685

Cumming GS (2011a) The resilience of big river basins. Water Int 36(1):63–95

Cumming GS (2011b) Spatial resilience in social–ecological systems. Springer, Dordrecht

Cumming GS (2011c) Spatial resilience: integrating landscape ecology, resilience, and sustainability. Landscape Ecol 26(7):899–909

Cumming GS, Caron A, Abolnik C, Catolli G, Bruinzeel L, Burger CE, Cecchettin K, Chiweshe N, Mochotlhoane B, Mutumi G, Ndlovu M (2011) The ecology of influenza A viruses in wild birds in Southern Africa. EcoHealth 8(1):4–13

Cumming GS, Gaidet N, Ndlovu M (2012a) Towards a unification of movement ecology and biogeography: conceptual framework and a case study on Afrotropical ducks. J Biogeogr 39(8):1401–1411

Cumming GS, Paxton M, King J, Beuster H (2012b) Foraging guild membership explains variation in waterbird responses to the hydrological regime of an arid-region flood-pulse river in Namibia. Freshw Biol 57(6):1202–1213

Cumming GS, Ndlovu M, Mutumi GL, Hockey PA (2013) Responses of an African wading bird community to resource pulses are related to foraging guild and food-web position. Freshw Biol 58(1):79–87

DAFF (2011) In: Department of Agriculture, Fisheries and Forestry (ed) A profile of the South African ostrich market value chain. Department of Agriculture, Fisheries and Forestry, Pretoria

Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife—threats to biodiversity and human health. Science 287:443–449

Daszak P, Cunningham AA, Hyatt AD (2001a) Anthropogenic environmental change and the emergence of infectious diseases in wildlife. Acta Trop 78(2):103–116

Daszak P, Cunningham AA, Hyatt AD (2001b) Anthropogenic environmental change and the emergence of infectious diseases in wildlife. Acta Trop 78:103–116

Daszak P, Plowright R, Epstein J, Pulliam J, Abdul Rahman S, Field H, Smith C, Olival K, Luby S, Halpin K (2006) The emergence of Nipah and Hendra virus: pathogen dynamics across a wildlife–livestock–human continuum. In: Disease ecology: community structure and pathogen dynamics. Oxford University Press, Oxford, pp 186–201

Desvaux S, Grosbois V, Pham TTH, Fenwick S, Tollis S, Pham NH, Tran A, Roger F (2011) Risk factors of highly pathogenic avian influenza H5N1 occurrence at the village and farm levels in the Red River Delta region in Vietnam. Transbound Emerg Dis 58:492–502

Dilley M (2000) Reducing vulnerability to climate variability in Southern Africa: the growing role of climate information. Clim Change 45(1):63–73

Dobson A, Foufopoulos J (2001) Emerging infectious pathogens of wildlife. Philos Trans R Soc Lond B 356(1411):1001–1012

Dobson A, Lafferty KD, Kuris AM, Hechinger RF, Jetz W (2008) Homage to Linnaeus: how many parasites? How many hosts? Proc Natl Acad Sci USA 105:11482–11489

Elith J, Graham CH (2009) Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. Ecography 32(1):66–77

Elliott P, Wartenberg D (2004) Spatial epidemiology: current approaches and future challenges. Environ Health Perspect 112(9):998–1006

Ellis TM, Bousfield RB, Bissett LA, Dyrting KC, Luk GS, Tsim ST, Sturm-Ramirez K, Webster RG, Guan Y, Malik Peiris JS (2004) Investigation of outbreaks of highly pathogenic H5N1 avian influenza in waterfowl and wild birds in Hong Kong in late 2002. Avian Pathol 33(5):492–505

European Food and Safety Authority (2006) Scientific opinion of the panel on animal health and welfare on a request from the European Commission on migratory birds and their possible role in the spread of highly pathogenic avian influenza. EFSA J 357:1–46

European Food and Safety Authority (2008) Animal health and welfare aspects of avian influenza and the risk of its introduction into the EU poultry holdings: scientific opinion of the Panel on Animal Health and Welfare. EFSA J 715:1–161

FAO (2008) In: FAO (ed) The global strategy for prevention and control of H5N1 highly pathogenic avian influenza. FAO, Roma

FAOSTAT (2013). Statistical yearbook of the Food and Agriculture Organization of the United Nations. http://faostat3.fao.org/home/E. Accessed 9 March 2015

Feare CJ, Kato T, Thomas R (2010) Captive rearing and release of bar-headed geese (Anser indicus) in China: a possible HPAI H5N1 virus infection route to wild birds. J Wildl Dis 46(4):1340–1342

Fenichel EP, Kuminoff NV, Chowell G (2013) Skip the trip: air Travelers' behavioral responses to pandemic influenza. PLoS ONE 8(3):e58249

Fermet-Quinet E, Bussière C (2007) Small commercial and family poultry production in France: characteristics, and impact of HPAI regulations. FAO Smallholder Poultry Production Paper. Rome

Figuié M (2013) Global health risks and cosmopolitisation: from emergence to interference. Sociol Health Illn 35(2):227–240

Figuie M, Fournier T (2008) Avian influenza in Vietnam: chicken-hearted consumers? Risk Anal 28(2):441–451

Fouque C, Guillemain M, Benmergui M, Delacour G, Mondain-Monval JY, Schricke V (2007) Mute swan (Cygnus olor) winter distribution and numerical trends over a 16-year period (1987/1988–2002/2003) in France. J Ornithol 148(4):477–487

Franklin J (2010) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge

Gaidet N, Caron A, Cappelle J, Cumming GS, Balanca G, Hammoumi S, Cattoli G, Abolnik C, Servan de Almeida R, Gil P, Fereidouni S, Grosbois V, Tran A, Mundava J, Fofana B, Ould El Mamy AB, Ndlovu M, Mondain-Monval JY, Triplet P, Hagemeijer W, Karesh WB, Newman SH, Dodman T (2012a) Understanding the ecological drivers of avian influenza virus infection in wildfowl: a continental scale study across Africa. Proc R Soc B 279(1731):1131–1141

Gaidet N, Ould El Mamy AB, Cappelle J, Caron A, Cumming GS, Grosbois V, Gil P, Hammoumi S, Servan de Almeida R, Fereidouni SR, Cattoli G, Abolnik C, Mundava J, Fofana B, Ndlovu M, Hurtado RF, Newman SH, Dodman T, Balança G (2012b) Investigating avian influenza infection hotspots in old-world shorebirds. PLoS ONE 7(9):e46049

Galuzo I (1975) Landscape epidemiology (epizootiology). Adv Vet Sci Comp Med 19:73

Gardner AM, Lampman RL, Muturi EJ (2014) Land use patterns and the risk of West Nile virus transmission in central Illinois. Vector Borne Zoonotic Dis 14(5):338–345

Geist HJ, Lambin EF (2002) Proximate causes and underlying driving forces of tropical deforestation. Bioscience 52(2):143–150

Gilbert M, Pfeiffer DU (2012) Risk factor modelling of the spatio-temporal patterns of highly pathogenic avian influenza (HPAIV) H5N1: a review. Spat Spatio-temporal Epidemiol 3(3):173–183

Gilbert M, Chaitaweesub P, Parakamawongsa T, Premashthira S, Tiensin T, Kalpravidh W, Wagner H, Slingenbergh J (2006) Free-grazing ducks and highly pathogenic avian influenza, Thailand. Emerg Infect Dis 12(2):227–234

Gilbert M, Xiao X, Chaitaweesub P, Kalpravidh W, Premashthira S, Boles S, Slingenbergh J (2007) Avian influenza, domestic ducks and rice agriculture in Thailand. Agric Ecosyst Environ 119(3–4):409–415

Gilbert M, Xiao X, Pfeiffer DU, Epprecht M, Boles S, Czarnecki C, Chaitaweesub P, Kalpravidh W, Minh PQ, Otte MJ, Martin V, Slingen J (2008) Mapping H5N1 highly pathogenic avian influenza in Southeast Asia. Proc Natl Acad Sci USA 105(12):4769–4774

Green AJ, Elmberg J (2014) Ecosystem services provided by waterbirds. Biol Rev 89(1):105–122

Grey D, Garrick D, Blackmore D, Kelman J, Muller M, Sadoff C (2013) Water security in one blue planet: twenty-first century policy challenges for science. Philos Trans R Soc A 371(2002):20120406

Hahn MB, Gurley ES, Epstein JH, Islam MS, Patz JA, Daszak P, Luby SP (2014) The role of landscape composition and configuration on *Pteropus giganteus* roosting ecology and Nipah virus spillover risk in Bangladesh. Am J Trop Med Hyg 90(2):247–255

Herrick KA, Huettmann F, Lindgren MA (2013) A global model of avian influenza prediction in wild birds: the importance of northern regions. Vet Res 44(1):42

Hirschfeld A, Heyd A (2005) Mortality of migratory birds caused by hunting in Europe: bag statistics and proposals for the conservation of birds and animal welfare. Ber zum Vogelschutz 42:47–74

Hockey PAR (2000) Patterns and correlates of bird migrations in sub-Saharan Africa. Emu 100:401–417

Hockey PAR, Dean WRJ, Ryan PG (2005) Roberts' birds of Southern Africa. Russell Friedman Books CC, Pretoria

Holt RD, Dobson A (2007) Extending the principles of community ecology to address the epidemiology of host–pathogen systems. In: Collinge SK, Ray C (eds) Disease ecology: community structure and pathogen dynamics. Oxford University Press, Oxford, pp 6–27

Huntjens P, Pahl-Wostl C, Rihoux B, Schlüter M, Flachner Z, Neto S, Koskova R, Dickens C, Nabide Kiti I (2011) Adaptive water management and policy learning in a changing climate: a formal comparative analysis of eight water management regimes in Europe, Africa and Asia. Environ Policy Gov 21(3):145–163

Ichinohe T, Pang IK, Kumamoto Y, Peaper DR, Ho JH, Murray TS (2011) Microbiota regulates immune defense against respiratory tract influenza A virus infection. Proc Natl Acad Sci 108(13):5354–5359

Ito T, Goto H, Yamamoto E, Tanaka H, Takeuchi M, Kuwayama M, Kawaoka Y, Otsuki K (2001) Generation of a highly pathogenic avian influenza A virus from an avirulent field isolate by passaging in chickens. J Virol 75(9):4439–4443

Ives A, Ronet C, Prevel F, Ruzzante G, Fuertes-Marraco S, Schutz F,. Zangger , Revaz-Breton M, Lye L-F, Hickerson SM, Beverley SM, Acha-Orbea H, Launois P, Fasel N, Masina S (2011) Leishmania RNA virus controls the severity of mucocutaneous leishmaniasis. Science 331:775–778

Jones BA, Grace D, Kock R, Alonso S, Rushton J, Said MY, McKeever D, Mutua F, Young J, McDermott J (2013) Zoonosis emergence linked to agricultural intensification and environmental change. Proc Natl Acad Sci 110(21):8399–8404

Keesing F, Young TP (2014) Cascading consequences of the loss of large mammals in an African savanna. Bioscience 64(6):487–495

Kingsford RT, Jenkins KM, Porter JL (2004) Imposed hydrological stability on lakes in arid Australia and effects on waterbirds. Ecology 85(9):2478–2492

Krauss S, Stallknecht DE, Negovetich NJ, Niles LJ, Webby RJ, Webster RG (2010) Coincident ruddy turnstone migration and horseshoe crab spawning creates an ecological 'hot spot' for influenza viruses. Proc R Soc B 277(1699):3373–3379

Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, Dunne JA, Johnson PT, Kuris AM, Marcogliese DJ, Martinez ND, Memmott J, Marquet PA, McLaughlin JP, Mordecai EA, Pascual M, Poulin R, Thieltges DW (2008) Parasites in food webs: the ultimate missing links. Ecol Lett 11(6):533–546

Lambin EH, Geist HJ (2006) Land-Use and Land-Cover Change: local processes and global impacts. Springer, Berlin

Lambin EF, Tran A, Vanwambeke SO, Linard C, Soti V (2010) Pathogenic landscapes: interactions between land, people, disease vectors, and their animal hosts. Int J Health Geogr 9(54):1–13

Lane-deGraaf KE, Kennedy RC, Arifin SMN, Madey GR, Fuentes A, Hollocher H (2013) A test of agent-based models as a tool for predicting patterns of pathogen transmission in complex landscapes. BMC Ecol 13:35

Latorre-Margalef N, Tolf C, Grosbois V, Avril A, Bengtsson D, Wille M, Osterhaus AD, Fouchier RA, Olsen B, Waldenström J (2014) Long-term variation in influenza A virus

prevalence and subtype diversity in migratory mallards in northern Europe. Proc R Soc B 281(1781):20140098

Lehikoinen A, Jaatinen K, Vähätalo AV, Clausen P, Crowe O, Deceuninck B, Hearn R, Holt CA, Hornman M, Keller V, Nilsson L, Langendoen T, Tománková I, Wahl J, Fox AD (2013) Rapid climate driven shifts in wintering distributions of three common waterbird species. Glob Change Biol 19(7):2071–2081

Leibler JH, Otte J, Roland-Holst D, Pfeiffer DU, Soares Magalhaes R, Rushton J, Graham JP, Silbergeld EK (2009) Industrial food animal production and global health risks: exploring the ecosystems and economics of avian influenza. EcoHealth 6(1):58–70

Likens GE (2004) Some perspectives on long-term biogeochemical research from the Hubbard Brook ecosystem study. Ecology 85(9):2355–2362

Liu C-M, Lin S-H, Chen Y-C, Lin KC-M, Wu T-SJ, King C-C (2007) Temperature drops and the onset of severe avian influenza A H5N1 virus outbreaks. PLoS ONE 2(2):e191

Mangnall MJ, Crowe TM (2003) The effects of agriculture on farmland bird assemblages on the Agulhas Plain, Western Cape, South Africa. Afr J Ecol 41(3):266–276

Massey RC, Buckling A, French-Constant R (2004) Interference competition and parasite virulence. Proc R Soc B 271:785–788

Mather C, Marshall A (2011) Living with disease? Biosecurity and avian influenza in ostriches. Agric Hum Values 28(2):153–165

Mathevet R (2000) Les usages des zones humides camarguaises: enjeux et dynamique des interactions environnement/usagers/territoire. Université J. Moulin Lyon 3, Lyon

Mathevet R, Mesléard F (2002) The origins and functioning of the private wildfowling lease system in a major Mediterranean wetland: the Camargue (Rhone River Delta, Southern France). Land Use Policy 19(4):277–286

McCullers JA (2006) Insights into the interaction between influenza virus and *Pneumococcus*. Clin Microbiol Rev 19(3):571–582

McLeod A, Morgan N, Prakash A, Hinrichs J (2005) Economic and social impacts of avian influenza. In: Proceedings of the joint FAO/OMS/OIE/World Bank conference on avian influenza and human pandemic influenza, November 2005, pp 7–9

Meentemeyer RK, Haas SE, Václavík T (2012) Landscape epidemiology of emerging infectious diseases in natural and human-altered ecosystems. Annu Rev Phytopathol 50:379–402

Modjarrad K, Vermund SH (2010) Effect of treating co-infections on HIV-1 viral load: a systematic review. Lancet Infect Dis 10(7):455–463

Mooij JH (2005) Protection and use of waterbirds in the European Union. Beitr zur Jagd- und Wildforschung 30:443–454

Moore C, Cumming GS, Slingsby J, Grewar J (2014) Tracking socioeconomic vulnerability using network analysis: insights from an avian influenza outbreak in an ostrich production network. PLoS ONE 9(1):e86973

Mundava J, Caron A, Gaidet N, Couto F, Couto T, de Garine-Wichatitksy M, Mundy P (2012) Factors influencing long-term and seasonal waterbird abundance and composition at two adjacent lakes in Zimbabwe. Ostrich 83(2):69–77

Mundkur T (2006) Successes and challenges of promoting conservation of migratory waterbirds and wetlands in the Asia–Pacific region: nine years of a regional strategy. In: Boere GC, Gailbraith CA, Stroud DA (eds) Waterbirds around the world. The Stationery Office, Edinburgh, pp 81–87

Mussa T, Rodriguez-Cariño C, Sanchez-Chardi A, Baratelli M, Costa-Hurtado M, Fraile L, Dominguez J, Aragon V, Montoya M (2012) Differential interactions of virulent and non-virulent *H. parasuis* strains with naïve or swine influenza virus pre-infected dendritic cells. Vet Res 43(1):80

Myers SS, Gaffikin L, Golden CD, Ostfeld RS, Redford KH, Ricketts TH, Turner WR, Osofsky SA (2013) Human health impacts of ecosystem alteration. Proc Natl Acad Sci 110(47):18753–18760

Ngom EHM, Ndione J-A, Ba Y, Konate L, Faye O, Diallo M, Dia I (2013) Spatio-temporal analysis of host preferences and feeding patterns of malaria vectors in the sylvo-pastoral area of Senegal: impact of landscape classes. Parasites Vectors 6:332

Norberg J, Cumming GS (2008) Complexity theory for a sustainable future. Columbia University Press, New York

Oatley TB, Prys-Jones RP (1986) A comparative analysis of movements of Southern African waterfowl (Anatidae) based on ringing recoveries. S Afr J Wildl Res 16:1–6

Okanga S, Cumming GS, Hockey PA, Peters JL (2013) Landscape structure influences avian malaria ecology in the Western Cape, South Africa. Landscape Ecol 28(10):2019–2028

Okes NC, Hockey PA, Cumming GS (2008) Habitat use and life history as predictors of bird responses to habitat change. Conserv Biol 22(1):151–162

Ostfeld RS, Glass GE, Keesing F (2005) Spatial epidemiology: an emerging (or re-emerging) discipline. Trends Ecol Evol 20(6):328–336

Ostrom E (2009) A general framework for analyzing sustainability of social–ecological systems. Science 352:419–422

Owen M, Black JM (1990) Waterfowl ecology. Chapman and Hall, New York

Patz JA, Daszak P, Tabor GM, Aguirre AA, Pearl M, Epstein J, Wolfe ND, Kilpatrick AM, Foufopoulos J, Molyneux D, Bradley DJ, M. o. t. W. G. o. L. U. C. a. D. Emergence (2004) Unhealthy landscapes: policy recommendations on land use change and infectious disease emergence. Environ Health Perspect 112(10):1092–1098

Paul MC, Gilbert M, Desvaux S, Andriamanivo HR, Peyre M, Nguyen Viet K, Thanapongtharm W, Chevalier V (2014) Agro-environmental determinants of avian influenza circulation: a multisite study in Thailand, Vietnam and Madagascar. PLoS ONE 9(7):e101958

Pavlovsky E (1966) Natural nidality of transmissible diseases with special reference to the landscape epidemiology of zooanthroponoses. University of Illinois Press, Urbana

Pearce N, Merletti F (2006) Complexity, simplicity, and epidemiology. Int J Epidemiol 35(3):515–519

Perkins LE, Swayne DE (2002) Pathogenicity of a Hong Kong-origin H5N1 highly pathogenic avian influenza virus for emus, geese, ducks, and pigeons. Avian Dis 46(1):53–63

Perrings C, Castillo-Chavez C, Chowell G, Daszak P, Fenichel EP, Finnoff D, Horan RD, Kilpatrick AM, Kinzig AP, Kuminoff NV (2014) Merging economics and

epidemiology to improve the prediction and management of infectious disease. EcoHealth. doi:10.1007/s10393-014-0963-6

Petrie SA, Rogers KH (1997a) Activity budget of breeding white-faced whistling ducks *Dendrocygna viduata* on stock-ponds in semi-arid South Africa, and a comparison with north-temperate waterfowl. S Afr J Wildl Res 27(3–4):79–85

Petrie SA, Rogers KH (1997b) Ecology, nutrient reserve dynamics and movements of white-faced ducks in South Africa. Department of Environmental Affairs and Tourism, South Africa, Pretoria

Pickett STA, Jones C, Kolasa J (2007) Ecological understanding: the nature of theory and the theory of nature. Academic, New York

Pingali PL (2012) Green Revolution: impacts, limits, and the path ahead. Proc Natl Acad Sci 109(31):12302–12308

Pittman M, Laddomada A (2007) Legislation for the control of Avian Influenza in the European Union. Zoonoses Public Health 55:29–36

Plowright RK, Sokolow SH, Gorman ME, Daszak P, Foley JE (2008) Causal inference in disease ecology: investigating ecological drivers of disease emergence. Front Ecol Environ 6(8):420–429

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316

Polis GA, Power ME, Huxel GR (eds) (2004) Food webs at the landscape level. University of Chicago Press, Chicago

Pretty J, Toulmin C, Williams S (2011) Sustainable intensification in African agriculture. Int J Agric Sustain 9(1):5–24

RAHC (2013) Regional Animal Health Center (RAHC) for Southern Africa. RAHC. http://www.rr-africa.oie.int/en/RR/en_rahc_crsa_sa.html. Accessed 27 Feb 2015

Reisen WK (2010) Landscape epidemiology of vector-borne diseases. Annu Rev Entomol 55:461–483

Robinson SJ, Samuel MD, Rolley RE, Shelton P (2013) Using landscape epidemiological models to understand the distribution of chronic wasting disease in the Midwestern USA. Landscape Ecol 28(10):1923–1935

Roche B, Lebarbenchon C, Gauthier-Clerc M, Chang CM, Thomas F, Renaud F, van der Werf S, Guegan JF (2009) Water-borne transmission drives avian influenza dynamics in wild birds: the case of the 2005–2006 epidemics in the Camargue area. Infect Genet Evol 9(5):800–805

Rohani P, Breban R, Stallknecht DE, Drake JM (2009) Environmental transmission of low pathogenicity avian influenza viruses and its implications for pathogen invasion. Proc Natl Acad Sci USA 106(25):10365–10369

Rushton J, Viscarra R, Guerne Bleich E, McLeod A (2005) Impact of avian influenza outbreaks in the poultry sectors of five South East Asian countries (Cambodia, Indonesia, Lao PDR, Thailand, Viet Nam) outbreak costs, responses and potential long term control. World's Poult Sci J 61:491–514

Seckler D, Amarasinghe U, Molden DJ, de Silva R, Barker R (1998) World water demand and supply, 1990 to 2025: scenarios and issues. In: Research Report 19. IWMI, Colombo

Si Y, Wang T, Skidmore A, De Boer W (2010) Environmental factors influencing the spread of the highly pathogenic

avian influenza H5N1 virus in wild birds in Europe. Ecol Soc 15:26

Slenning BD (2010) Global climate change and implications for disease emergence. Vet Pathol 47(1):28–33

Smith G, Dunipace M (2011) How backyard poultry flocks influence the effort required to curtail avian influenza epidemics in commercial poultry flocks. Epidemics 3:71–75

Söderquist P, Gunnarsson G, Elmberg J (2013) Longevity and migration distance differ between wild and hand-reared mallards *Anas platyrhynchos* in Northern Europe. Eur J Wildl Res 59:159–166

Songserm T, Jam-on R, Sae-Heng N, Meemak N, Hulse-Post DJ, Sturm-Ramirez KM, Webster RG (2006) Domestic ducks and H5N1 influenza epidemic, Thailand. Emerg Infect Dis 12(4):575–581

Tamisier A, Grillas P (1994) A review of habitat changes in the Camargue: an assessment of the effects of the loss of biological diversity on the wintering waterfowl community. Biol Conserv 70:39–47

Telfer S, Lambin X, Birtles R, Beldomenico P, Burthe S, Paterson S, Begon M (2010) Species interactions in a parasite community drive infection risk in a wildlife population. Science 330:243

Thomas M, Bouma A, Ekker H, Fonken A, Stegeman J, Nielen M (2005) Risk factors for the introduction of high pathogenicity Avian Influenza virus into poultry farms during the epidemic in the Netherlands in 2003. Prev Vet Med 69(1):1–11

Tiensin T, Nielen M, Songserm T, Kalpravidh W, Chaitaweesub P, Amonsin A., Chotiprasatintara S, Chaisingh A, Damrongwatanapokin S, Wongkasemjit S, Antarasena C, Songkitti K, Chanachai K, Thanapongtham W, Stegeman A (2007) Geographic and temporal distribution of highly pathogenic avian influenza A Virus (H5N1) in Thailand, 2004–2005: an overview. Avian Dis 50:182–188

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D (2001) Forecasting agriculturally driven global environmental change. Science 292(5515):281–284

Tong S, Zhu X, Li Y, Shi M, Zhang J, Bourjeois M, Yang H, Chen X, Recuenco S, Gomez J, Chen LM, Johnson A, Tao Y, Dreyfus C, Yu W, McBride R, Carney PJ, Gilbert AT, Chang J, Guo Z, Davis CT, Paulson JC, Stevens J, Rupprecht CE, Holmes EC, Wilson IA, Donis RO (2013) New World bats harbour diverse influenza A viruses. PLoS Pathog 9(10):e1003567

Tran PM, Waller L (2013) Effects of landscape fragmentation and climate on Lyme disease incidence in the northeastern United States. EcoHealth 10(4):394–404

Tyson PD (1986) Climatic change and variability in Southern Africa. Oxford University Press, Capetown

Unwin MT (2011) The atlas of birds: diversity, behavior, and conservation. Princeton University Press, Princeton

Van Dalen KK, Franklin AB, Mooers NL, Sullivan HJ, Shriner SA (2010) Shedding light on avian influenza H4N6 infection in mallards: modes of transmission and implications for surveillance. PLoS ONE 5(9):e12851

van Dijk JGB, Hoye BJ, Verhagen JH, Nolet BA, Fouchier RAM, Klaassen M (2014) Juveniles and migrants as drivers for seasonal epizootics of avian influenza virus. J Anim Ecol 83:266–275

Vandegrift KJ, Sokolow SH, Daszak P, Kilpatrick AM (2010) Ecology of avian influenza viruses in a changing world. Ann NY Acad Sci 1195(1):113–128

Vittecoq M, Thomas F, Jourdain E, Moutou F, Renaud F, Gauthier-Clerc M (2014) Risks of emerging infectious diseases: evolving threats in a changing area, the Mediterranean Basin. Transbound Emerg Dis 61(1):17–27

Viviroli D, Archer D, Buytaert W, Fowler H, Greenwood G, Hamlet A, Huang Y, Koboltschnig G, Litaor M, Lopez-Moreno J (2011) Climate change and mountain water resources: overview and recommendations for research, management and policy. Hydrol Earth Syst Sci 15(2):471–504

Walsh MG (2013) The relevance of forest fragmentation on the incidence of human babesiosis: investigating the landscape epidemiology of an emerging tick-borne disease. Vector-Borne Zoonotic Dis 13:250–255

Wardrop NA, Kuo C-C, Wang H-C, Clements ACA, Lee P-F, Atkinson PM (2013) Bayesian spatial modelling and the significance of agricultural land use to scrub typhus infection in Taiwan. Geospatial Health 8(1):229–239

Weber TP, Stilianakis NI (2008) Inactivation of influenza A viruses in the environment and modes of transmission: a critical review. J Infect 57(5):361–373

Webster RG (2004) Wet markets—a continuing source of severe acute respiratory syndrome and influenza? Lancet 363(9404):234–236

Wilcox BR, Knutsen GA, Berdeen J, Goekjian V, Poulson R, Goyal S, Sreevatsan S, Cardona C, Berghaus RD, Swayne DE, Yabsley MJ, Stallknecht DE (2011) Influenza-A viruses in ducks in northwestern Minnesota: fine scale spatial and temporal variation in prevalence and subtype diversity. PLoS ONE 6(9):e24010

Williams RAJ, Peterson AT (2009) Ecology and geography of avian influenza (HPAI H5N1) transmission in the Middle East and northeastern Africa. Int J Health Geogr 8:47

Windhorst H-W (2007) Changing patterns of poultry production in the European Union. In: Commission of the European Communities (ed) Development of new integrated strategies for prevention, control and monitoring of epizootic poultry diseases. Commission of the European Communities

Yatsunenko T, Rey FE, Manary MJ, Trehan I, Dominguez-Bello MG, Contreras M, Magris M, Hidalgo G, Baldassano RN, Anokhin AP (2012) Human gut microbiome viewed across age and geography. Nature 486(7402):222–227

Zinsstag J, Schelling E, Waltner-Toews D, Tanner M (2011) From "one medicine" to "one health" and systemic approaches to health and well-being. Prev Vet Med 101:148–156