Pathogens of domestic and free-ranging ungulates: global climate change in temperate to boreal latitudes across North America

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Summary

In North America broad-based research networks explore the interaction of vertebrates, their characteristic arrays of pathogens and emergent disease. A diversity of programmes address the impact of environmental change on animal health, zoonoses, and human health, but as yet no comprehensive framework or strategy has emerged to develop and implement policy and planning. In a regime of climate change and ecological perturbation, the need to document and understand the health, agricultural, societal and economic impact of pathogens and emerging infectious disease is urgent. An integrated and proactive planning process linking national and international resources can lead to informed predictions about the impact of environmental change and can identify pathways for potential management and mitigation. An effective and comprehensive programme will have components for establishing priorities, developing primary data for faunal structure and biodiversity, a capacity for monitoring and surveillance (including scanning and targeted activities), and linkage to historical and contemporary baselines (against which to assess change) established through archival biological collections. Field and laboratory studies are also necessary to determine developmental thresholds, tolerances and tipping points for many pathogens to establish a context for recognising current constraints and future perturbation, and to explore factors that promote emergence for a variety of pathogens, vectors and pest species. Predictive modelling and risk assessment utilising a range of scenarios for climate change is a final step in this multidisciplinary process.

Keywords

Biodiversity assessment – Climate change – Emerging disease – Livestock – North America – Pathogen – Prediction – Survey – Ungulate.

Introduction

'Environmental changes and ecological disturbances, due to both natural phenomena and human intervention, have exerted and can be expected to continue to exert a marked influence on the emergence and proliferation of … parasitic diseases' (81).

Recognised and predicted impacts of environmental perturbation and climate change, including the cascading effects within complex host–pathogen systems which may drive the emergence of disease, have been receiving increasing attention across North America and in the wider global community (20, 26, 37, 47, 59, 80, 81). Zoonoses, and the distribution of potential infectious agents and disease in people are the focus of current interests (3, 10, 16, 28, 31, 76, 95). Although field-based and laboratory investigations have begun to explore the potential impacts of climate change on the interactions among ungulate hosts and some of their pathogens, much of this work has involved wildlife in natural ecosystems (55, 63); apparently, concerns about climate change and infectious disease have not yet been translated into research and regulatory programmes addressing pathogens in domestic ungulates, such as cattle, sheep, and farmed cervids, which serve as primary food resources. There is an urgent need for a more comprehensive understanding of future perturbation in these host–pathogen systems.

Climate change represents one of a number of factors that influence the distribution and emergence of pathogens and disease (1, 14, 21, 61, 76, 81, 85), but the pervasive impact of rapid climate change on the structure and function of terrestrial and aquatic ecosystems is considered to be paramount (13, 16, 22, 28, 69, 86). Climate change is expected to alter the scope and context of a diversity of pathogens and their significance for livestock, agriculture and human health. This suggests that a proactive and prediction-based programme could contribute significantly to the principally response-based infrastructure of animal health in North America and globally (96).

The concept that infectious agents are pervasive and exert a substantial impact on livestock systems has been clearly articulated (35, 87). Concurrently, the potential for interactions among domestic and wild ungulates across ecotones at the interface of managed and natural systems is under increasing scrutiny (18, 19, 73). Emergent pathogens represent a considerable threat to agricultural systems and domestic stock through primary mechanisms that are often linked to the breakdown of ecological barriers between continents and regions (including temporal and seasonally defined barriers) (4, 14, 21, 25, 39). Climate change and attendant ecological perturbation are now predicted to be a major driver in the introduction, dissemination and emergence of pathogens through altered geographic distributions and host associations (8, 10, 20, 47, 76). This paper explores issues related to the predicted and recognised impact of climate change on host–pathogen systems in domestic livestock (cattle, sheep, goats, farmed cervids) and free-ranging ungulates across North America. Current empirical evidence for a linkage between climate change and emerging disease in wild and domestic ungulates is addressed. Programmes designed to explore the interactions of pathogens must involve integrated approaches linking domestic stock, wildlife species and people in order to fully identify and understand the impacts of climate change.

Pathogens and ungulate systems

Climate change may modify host and geographic associations for macroparasites (helminths), microparasites (prions, viruses, bacteria, and protozoans), invertebrate vectors and pest species (primarily arthropods) (Table I). Broad-scale baseline information for particular ruminant species or geographic regions has been established through a number of reviews for macroparasites and vectors (2, 17, 42, 65) and microparasites (23, 24, 57, 58, 77). In North America, this has been supplemented by surveys of pathogens or disease conditions in livestock and wild ungulates that are listed by and reportable by various national and international bodies, such as:

– the United States Department of Agriculture Animal and Plant Health Inspection Service (APHIS: http://www.aphis.usda.gov)

– the United States Department of the Interior and National Biological Information Infrastructure (NBII: http://wildlife disease.nbii.gov/)

– the Canadian Food Inspection Agency (CFIA: http://www.inspection.gc.ca/english/animal/heasan/disemala/guidee.shtml)

– the World Organisation for Animal Health (OIE: http://www.oie.int/eng/maladies/en_classification).

Fine-scale knowledge about regional and local distribution remains elusive, and details about population structure for pathogens are mostly unavailable; for both domestic and wildlife species such information is often confidential and cannot be accessed. Temporal and spatial information on fine scales will become increasingly important in defining population-level parameters that may influence the host and geographic distribution of specific pathogens and emergence of disease. Some information, however, is available, e.g. for some macroparasites and arthropod vectors there is pertinent biological data about limiting factors on pathogen distribution (relative to parameters of

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Table I
Diversity of macroparasites, microparasites and invertebrate vectors, significant for livestock and wild ungulates in North America, with an estimation of the potential influence of climate change

Vector	Potential influence of climate change
Primary macroparasites (helminths)	
Digenean trematodes	
Fasciolidae (liver flukes): *Fasciola hepatica* and *Fascioloides magna* (domesticated and wild ungulates) indirect transmission through gastropod intermediates and ingestion of infective stages on aquatic vegetation	Expected to undergo range expansion or retraction (relative to currently recognised areas of endemism) coincidental with changing distribution and tolerances of gastropod intermediate hosts required for transmission (83). Range expansion by wild cervid hosts may also influence distribution with northward range shifts. Amplification of populations is possible through accelerated rates of development for larval stages, which are sensitive to temperature and humidity (70)
Dicrocoelidae, *Dicrocoelium dendriticum* (domesticated and wild ungulates) indirect transmission	
Filarioid nematodes	
Onchocercidae (tissue nematodes): *Elaeophora* spp., *Onchocerca* spp., *Setaria* spp. and *Wehrdikmansia* (primarily wild ungulates, also cattle and sheep) indirect transmission via dipteran vectors (Culicidae)	Expected outbreaks of disease in wild ungulates may be linked to amplification of populations of larval parasites, increasing abundance, and extended seasonal activity of dipteran intermediate hosts associated with warming trends (64)
Strongylate nematodes with direct transmission	
	Specific tolerances and developmental thresholds are expected to influence the potential for changing distributions for a diversity of gastrointestinal and some pulmonary nematodes. Some groups are predicted to be influenced by northward expansion (Haemonchines and Cooperiines; *Dictyocaulus*) linked to relaxation of current constraints due to moisture and low temperature. The potential for geographic colonisation and host switching is likely to increase coincidental with shifting distributions for primary ungulate hosts and development of northern agricultural practices; anthelmintic resistance may make measures for adequate control less effective
Trichostrongylina (gastrointestinal parasites): Trichostrongylidae-Cooperiinae: *Cooperia*; Haemonchinae: *Ashworthius, Haemonchus, Mecistocirrus*; Ostertagiinae: *Marshallagia, Mazamastrongylus, Orloffia, Ostertagia, Teladorsagia, Spiculopteragia*; Trichostrongylinae: *Trichostrongylus*; Molineidae-Nematodirinae: *Nematodirus, Nematodirella*; (domestic and wild ungulates, with some partitioning relative to parasite species diversity in bovids, caprines and cervids) (35, 42)	Distributions are strongly controlled by climatological patterns and weather linked to temperature and moisture (67, 68)
Dictyocaulidae (lungworms): *Dictyocaulus* spp. (domestic and wild ungulates)	Increasing temperature and availability of moisture may allow geographic colonisation of regions in central North America (35)
Strongylate nematodes with indirect life-cycles	
Protostrongylidae (lungworms and muscleworms): *Elaphostrongylus, Muellerius, Orthostrongylus, Parelaphostrongylus, Protostrongylus, Varestrongylus, Umingmakstrongylus* (wild and domestic caprines and cervids)	Expected outbreaks of disease in wild and domestic ungulates may be linked to amplification of populations of larval parasites and altered developmental rates and generation time in gastropod intermediate hosts associated with warming trends (36, 55, 63, 65). Disease will most likely be manifested as verminous pneumonia associated with larval and/or adult parasites in the pulmonary system. Modified geographic ranges and development of ecotones for ungulate species may also drive host and geographic colonisation (44)
Primary microparasites	
Prions, transmissible spongiform encephalopathies [a, b]	May not be directly influenced by climate change but lack of specific knowledge about environmental tolerances and patterns of transmission hinders any predictions (72). Apparent 'specificity' may limit the potential for exchange of prions among domesticated and wild ungulates associated with chronic wasting disease, scrapie, or bovine spongiform encephalopathy (93). Host factors including changes in population density and range shifts driven by climate may lead to interactions between infected and susceptible or naïve ungulates

Table I (cont.)
Diversity of macroparasites, microparasites and invertebrate vectors, significant for livestock and wild ungulates in North America, with an estimation of the potential influence of climate change

Vector	Potential influence of climate change
Viral pathogens	
Herpesviridae: malignant catarrhal fever [a, b] (cattle, bison, deer), direct transmission	
Adenoviridae: haemorrhagic disease (deer), direct transmission	
Poxviridae: parapoxvirus (wild and domestic caprines, bovids, antilocaprids and cervids), direct transmission	Probably will be directly influenced by climate change through changing rates of development (in vectors), persistence in the environment and patterns of transmission. Intrinsic or host-determined factors particularly expansion of geographic ranges, and development of new ecotones and contact zones for wild and domestic ungulate species could promote dissemination into new hosts and geographic regions. Arboviruses have a greater probability for changing dynamics of infection and disease linked to altered distributions and temporal/seasonal patterns of dipteran vectors and through the influence of temperature on transmission (34)
Reoviridae: bluetongue and epizootic haemorrhagic disease [a, b] (cattle, sheep, bison, and wild and domesticated cervids), vector-borne by biting gnats or sandflies (*Culicoides* spp.) and some ixodid ticks	
Flaviviridae: bovine viral diarrhoea [a, b] (cattle, bison, wild and domesticated cervids), direct transmission	
Arboviruses [a, b]: Western equine encephalomyelitis, Eastern equine encephalomyelitis, West Nile virus	
Bacterial pathogens	
Bacillus anthracis [a, b]: anthrax (domestic and wild ungulates), direct transmission and soil contamination	
Brucella abortus [a, b] and *Brucella* spp.: brucellosis (cattle, sheep, wild and domesticated cervids, bovids), direct transmission (12)	Expected to be potentially influenced by changing patterns of distribution for primary ungulate hosts and by interactions between wild and domestic ungulates; emergence of disease may be exacerbated by translocations and re-introductions of wild ungulates or through expansion of agriculture (17, 71). Horizontal gene transfer among pathogens and emergence of disease may be driven by development and modification of contact zones; this process can occur solely among free-ranging hosts or among free-ranging and domestic ungulates (56). Persistence may be related to differential changes in surface water and/or desiccation and drought related to tolerances and requirements for survival in the environment for specific pathogens. Extreme weather events involving shifts in humidity and temperature may trigger outbreaks of disease (97). Drought conditions may increase animal exposure to highly resistant *Bacillus anthracis* spores in the soil. Extreme flooding events may disseminate *Escherichia coli* in the environment
Escherichia coli [a, b]: (domestic and wild ungulates), direct transmission, soil, water, food contamination	
Francisella tularensis [b]: tularemia (domestic and wild ungulates), transmission by arthropod vectors (Tabanidae; ixodid ticks)	
Leptospira spp. [b]: leptospirosis (domestic and wild ungulates), direct transmission associated with contamination of mud and water (5)	
Mycobacterium paratuberculosis [a, b]: Johne's disease (cattle, sheep, wild and domesticated cervids and bovids), direct transmission	
Mycobacterium tuberculosis and *Mycobacterium* spp. [a, b]: tuberculosis (cattle, wild and domesticated cervids, bovids), direct transmission	
Pasteurella spp.: pneumonia (domestic and wild ungulates), direct transmission often associated with high humidity and temperature	
Rickettsia and Spirochaetes: *Bartonella* spp., *Borellia* spp., *Ehrlichia* spp., indirect transmission associated with ixodid tick vectors	
Salmonella spp. [a, b]: (domestic livestock), direct transmission	
Yersinia pseudotuberculosis: yersiniosis (farmed cervids, free-ranging cervids, bovids)	
Enteric protozoan pathogens	
Apicomplexa: *Cryptosporidium* spp., *Eimeria* spp., *Isospora* spp. (cattle, sheep, wild ungulates) (24)	Expected to be potentially influenced by changing patterns of distribution for primary ungulate hosts and may be influenced by interactions between wild and domestic ungulates. Extreme rainfall events and alteration in patterns of runoff may influence the occurrence and emergence of these pathogens (81)
Sarcomastigophora: *Giardia* spp. (cattle, sheep, wild ungulates) (77)	
Tissue-inhabiting protozoan pathogens	
Apicomplexa: *Besnoitia, Neospora caninum, Toxoplasma gondii, Sarcocystis* spp. (wild and domestic ungulates) (23, 66)	May be influenced by climate change through altered distributions of host species and modified trophic (predator-prey) interactions
Blood-inhabiting protozoan pathogens	
Piroplasms [b]: *Babesia* spp., *Theileria* spp., *Anaplasma* spp. (wild and domestic ungulates) (58)	Expected to be influenced by changing patterns of distribution for arthropod vectors

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Table I (cont.)
Diversity of macroparasites, microparasites and invertebrate vectors, significant for livestock and wild ungulates in North America, with an estimation of the potential influence of climate change

Vector	Potential influence of climate change
Arthropod vectors and ectoparasites	
Acarina-Ticks: Ixodidae: species of *Ixodes, Amblyomma*, and *Dermacentor* Argasidae: species of *Ornithodorus* and *Otobius*	Are expected to be substantially influenced (on a continuum from increasing abundance to local extirpation) linked to environmental parameters and changing patterns of temperature, precipitation and humidity. The greatest potential impact is linked to alteration in geographic distribution and seasonality in transmission of viral, bacterial, rickettsial and protozoan pathogens associated with ixodid and argasid ticks. Many of these pathogens have been confirmed as zoonotic, but may not have direct consequences for livestock (2, 10, 34)

(a) Listed pathogen under the National Health Surveillance System (NAHSS). See: United States Department of Agriculture, Animal and Plant Health Inspection Service (APHIS) – http://www.aphis.usda.gov
(b) Listed pathogen under the World Organisation for Animal Health (OIE); not an inclusive listing. See: OIE – http://www.oie.int/eng/maladies/en_classification2007.htm?e1d7

temperature and moisture). Collectively, these data can be used to develop a general framework for pathogens and their significance, which can be used to estimate how these systems will respond and be modified by global climate change and environmental perturbation (Table I). Although not comprehensive, this information provides a useful starting point for addressing challenges to future livestock systems and the linkage between agricultural/managed and natural environments in North America.

Scenarios for climate change in North America

The influence of environmental change driven by climate warming is already apparent in North America where changes in assemblages, in the epidemiology of macroparasites and ungulates (44, 55, 63), and in the distribution of important arthropod vectors, such as ticks, has been documented or predicted based on models (9, 10, 76). Climate simulations for regional change relative to patterns of temperature and precipitation are under development for North America (29) based on standard scenarios for the severity and duration of global warming (11, 27, 52, 74). Current projections identify mean increases in global temperature of 1.5°C to 5.8°C over the next century, with increasing variation and severity of droughts, extreme rainfall and temperature events, and changing patterns of hydrology (3, 13, 28, 79, 84, 86). Direct and indirect impacts of ecological perturbation on complex host–pathogen systems and the factors that serve as determinants of disease have been predicted and are expected to demonstrate regional to local variation, but there is a lack of definitive data which could be used as the basis of informed projections across temporal and spatial scales (59). Perturbation will involve changes at ecotones

on the boundaries of major biomes, altered phenology, new patterns of migration, shifts in the geographic ranges of hosts, and direct influence of temperature and humidity on the distribution of pathogens (28, 47, 86).

Anticipating and predicting change

Substantial evidence for the pervasive impact of climate change on the distribution and life history of both vertebrates and invertebrates and the structure of associated communities and biomes (including pathogens) is rapidly accumulating (34, 49, 51, 69, 78, 86). Climate change is anticipated to have a substantial influence on the spatial and temporal distribution of pathogens and the emergence of disease conditions among species of domestic and wild ungulates in North America. Primary responses in complex host–pathogen systems may be numerical (changes in density, prevalence and abundance for both hosts and parasites), functional (changes in ecological structure, geographic distribution, phenology, or host associations), and evolutionary (microevolutionary, often through local adaptation) (8, 34, 47) (Table II).

Responses exhibited by individual populations, species or particular assemblages of pathogens to climate change, however, are likely to be idiosyncratic. They will be determined by an interaction of the pathogen's capacity to track environments, habitats and hosts (spatial or niche tracking) and the potential for adaptation under directional selection pressure (where tolerances and thresholds for either development or survival are exceeded the pathogen will become extinct) (48, 76, 82). Not all pathogens will be influenced by climate change in a similar manner. For example, direct transmission for prions, and non-vector-borne viruses, as well as some bacteria and protozoans,

Table II

Predicted responses to climate change (temperature, precipitation, humidity) within complex host–pathogen systems involving macroparasites, microparasites and invertebrate vectors (adapted from 34, 47, 50, 59)

Vectors and predicted response to climate change

Macroparasites (helminths)

Changing dynamics for development and transmission

Temperature and humidity mediated increases (or decreases) in rates of development and survival for free-living stages, or those in intermediate hosts

Reduction in generation time, e.g., shifts from multi-year to single-year cycles, or from single to multiple within year

Extension of season for parasite growth and development, broadened seasonal windows for transmission

Amplification of parasite populations over time through accelerated development, increased rates of transmission, survival and availability

Influence of extreme weather events on distribution (flooding, droughts, patterns of soil humidity, severity and number of freeze-thaw cycles)

Extreme events for high temperature and humidity driving explosive emergence of disease

Changing patterns for host and geographic ranges

Shifting patterns of geographic range including altitudinal or latitudinal (expansion or retraction)

Alterations in host range for parasites through geographic and host colonization, ecotone effects, with successful establishment in naive host species and populations

Modification in phenology (timing) for habitat use through alteration of migration and migratory corridors (wild ungulates),

relative changes in temporal and spatial overlap

Modification of ecotones and contact zones including northward or southward expansion for hosts, parasites and pathogens

Concentration of hosts around water resources during droughts, or other forms of habitat fragmentation that can influence density for host populations

Extinction of local or regional populations where specific tolerances or thresholds are exceeded

Effects of competition among parasites

Changing evolutionary dynamics and adaptation

Local adaptation of parasites through selection for optimal patterns of development, thresholds and tolerances

Geographic mosaics or ephemeral patterns of local adaptation as a driver for emergence

Cumulative and synergistic effects as determinants of faunal distribution

Breakdown in mechanisms for ecological isolation promoting faunal interchange and cascading changes in ecosystems

Variable and cumulative synergy affecting the structure of entire parasite-host assemblages

Local to regional extirpation or extinction driven by cascading ecosystem collapse influencing trophic pathways and environmental structure

Microparasites (protozoans, bacteria, rickettsias, viruses)

Changing patterns of development and distribution

Decreased incubation period of pathogen at higher temperatures, particularly for arboviruses

Differential shifts in rates of replication at higher temperatures for arboviruses and bacteria; latitudinal effects suggest higher rates in Boreal–Arctic zones, and lower

rates in Temperate–Subtropical zones

Shifts (extension or reduction) in seasonal windows and dynamics of transmission

Host-mediated shifts in distribution and geographic colonisation linked either to definitive hosts or to vectors

Potential for horizontal gene transfer for specific pathogens in zones of contact for ungulate hosts

Extreme events of temperature, humidity, precipitation and flooding as drivers of emergence

Arthropod vectors/molluscan intermediate hosts

Changing patterns or differential survival (increases or decreases) for vectors relative to temperature, humidity, altitude and latitude

Changes in susceptibility by some vectors to specific pathogens, and alteration of incubation periods

Changes in rate of growth for vector populations

Changes in feeding rates, behavior and patterns of host contact

Changes in seasonality for vector populations

Shifting patterns of precipitation may influence the distribution of arthropods or molluscan vectors

Concurrent shifts in northern and southern boundaries for distributions of specific vector species

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may not be immediately temperature-dependant, although daily, and seasonal fluctuations may influence long-term survival, persistence and availability of infective stages in the environment (31).

Where the distribution of pathogens is largely controlled by spatial factors linked to either definitive hosts or arthropod vectors and their capacity for geographic expansion, a cascading influence linked to climate may be

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predicted. Extrinsic factors (here defined as direct effects related to temperature and other features of the environment, including rainfall and extreme events) and intrinsic factors (indirect or secondary effects determined by actions or distributions of host and vector species, independent of temperature and environment) are expected to be interactive and synergistic (34). Intrinsic factors may be determined by host and geographic distribution, ecotone-effects, and the potential for breakdown in mechanisms for ecological isolation or limitation promoting colonisation of new hosts or regions (8, 19, 39, 61).

Additional distinctions characterise responses related to extrinsic or intrinsic factors. The responses driven by extrinsic factors anticipated for some pathogens will be related to amplification of populations over time through changes in developmental rates, thresholds, tolerances, generation time and seasonal effects (34, 47, 62). For these pathogens, emergence '*in situ*' may occur, with or without substantial geographic expansion or acquisition of new hosts, and contribute directly to development of disease conditions. Intrinsic factors may drive responses emanating from the altered associations and expanding ranges of arthropod vectors or arthropod and molluscan intermediate hosts (10, 34, 76) and from environmental perturbation and a changing ecological context for definitive hosts (8, 44, 61). Additional effects may also be apparent if population amplification and increasing infection pressure by pathogens coincide with development of broader host ranges and concomitant increases (or decreases) in host population density. Such effects may increase interactions between wild ungulates and domestic livestock at the interface of natural and agricultural systems (73). Hierarchical and multifactorial responses are expected based on the interaction of hosts, pathogens and environment and the interplay of intrinsic and extrinsic drivers on a continuum specific to each complex system (34).

Predictions rely on understanding the distribution of biodiversity in complex systems and the underlying historical, evolutionary and ecological determinants of geographic and host associations for parasites and other pathogens (6, 7, 8). The dynamics of historical climates can serve as an analogue for the effects of accelerated change anticipated in North America and other regions (43, 47). Events on both ecological and evolutionary timescales must be factored into a broader understanding of the drivers of dynamic change that can result in the emergence of disease in these complex systems (6, 7, 8, 95).

Considerations for some macroparasites

Faunas in North America are composed in part of endemic elements or species with distributions and associations

extending over the past several million years and with strong connections to Eurasia (41, 46) (Fig. 1a). These contrast with often recently introduced faunas, primarily in domestic livestock, that have evolved and radiated elsewhere, and which arrived in North America coincidental with European contact after the 1500s (39, 42, 45); elements of this fauna continue to be introduced and established by contemporary processes (Fig. 1b). Exotic or introduced assemblages further have dual origins and encompass groups of parasites that originally radiated in boreal and temperate latitudes of Eurasia (e.g. some *Ostertagia, Teladorsagia*, and *Nematodirus*) or diversified among ungulates in Africa prior to colonisation of domestic stock (e.g. *Haemonchus* and *Cooperia*) (45, 46).

A complex mosaic structure for endemic and introduced nematode faunas in ruminants, and other elements of the livestock pathogen fauna, has particular importance under a regime of dynamic climate warming (Fig. 1). The unique historical constraints, life history patterns and developmental tolerances and thresholds (88) of the disparate species and species-assemblages of endemic and introduced parasites suggest that they may respond in fundamentally different ways to the altered patterns of temperature and precipitation linked to global climate change (45, 47). For example, economically important parasites in sheep and cattle include both the northern-adapted faunas (ostertagiine, nematodirine, dictyocaulid and protostrongylid nematodes) and the tropically adapted faunas with their origins in Africa (haemonchines and cooperines) (41, 45). The effect of interaction between climate and climate zones, but more particularly of the weather, on the distribution of these nematodes has long been recognised by veterinary practitioners and livestock producers (32, 33, 38, 67, 68, 75, 92, 94).

Tropical parasites appear to be constrained by generally cool and dry climates at boreal to subarctic latitudes in North America. Temperature increases, shifting isotherms and more abundant precipitation are expected to contribute to the northward expansion of introduced species and species of tropical origin in North America (41, 45) (Fig. 1b); concurrently, *Mecistocirrus* and *Ashworthius* are expected to undergo distributional shifts northward from Central America. The establishment of *Haemonchus* among domestic sheep in Sweden may represent such a range shift, although maintenance of the parasites in this situation appears related to selection for populations of nematodes that undergo extended periods of developmental arrest in host populations (91). Alternatively, some northern-adapted fauna, such as species of *Ostertagia, Teladorsagia, Marshallagia, Orloffia* and *Spiculopteragia* may undergo population amplification due to changing developmental rates and modified geographic ranges, mediated by expanding distribution of domestic and wild ruminant hosts (42); in addition, expansion of agriculture and animal husbandry into the
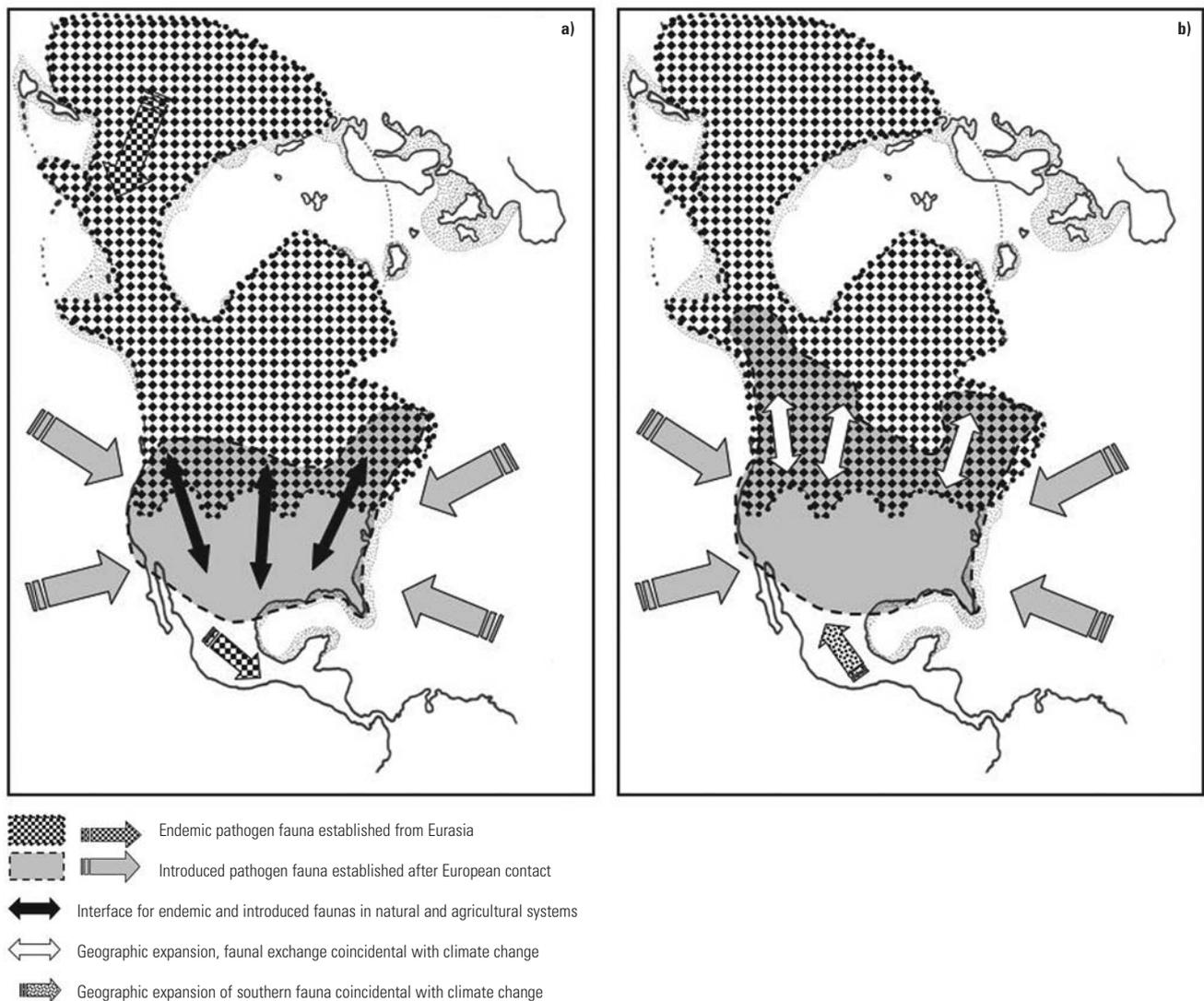
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Endemic pathogen fauna established from Eurasia

Introduced pathogen fauna established after European contact

Interface for endemic and introduced faunas in natural and agricultural systems

Geographic expansion, faunal exchange coincidental with climate change

Geographic expansion of southern fauna coincidental with climate change

Fig. 1
A simplified model and schematic representation of the origins, mosaic structure, and potential patterns of the changing geographic distributions of an assemblage of macroparasites among ungulates in North America

(a) Historical origins of endemic fauna are related to geographic colonisation of North America with hosts and parasites from Eurasia. This endemic fauna in wild caprines and cervids (e.g. Ostertagiinae, Nematodirinae, Protostrongylidae, Dictyocaulidae, Onchocercidae) has been strongly influenced by climatic fluctuations over the past three million years

(b) Development of the contemporary macroparasite fauna in ungulates occurred in the time frame extending from European contact in the 1500s to the present. A faunal mosaic developed with the introduction and establishment of exotic parasites (species of *Haemonchus* and *Cooperia*; some ostertagiines and nematodirines) in domestic stock (cattle, sheep, cervids), a process that continues today. Climate change with altered patterns of precipitation and humidity is predicted to drive perturbation in these systems. Processes linked to expansion will modify existing ecotones, lead to new interfaces, and increase the potential for geographic and host colonisation. Northward expansion of the component of the fauna currently limited by temperature and humidity is predicted. Emergence of disease may be a consequence of range shifts, but may also result from *in situ* processes even in the absence of geographic expansion of hosts. Range contraction and extirpation of some assemblages, at local to regional scales, may be a cascading effect of climate change

northern latitudes could result in translocation and dissemination of pathogens. Instances of reciprocal expansion and establishment of southern or northern components of these faunas could further be influenced by competitive effects among different genera and species of nematodes.

Emergent disease can result when climate change creates a new ecological context for host–parasite assemblages, a situation that is exacerbated by the developing and broadening resistance to most classes of anthelmintics among these nematodes (15). Thus, geographic and host colonisation may coincide with the decreasing effectiveness

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of standard means of parasite control based on traditional methods of management and the use of anthelmintics. Drug-resistant parasites could conceivably be swamped through geneflow among conspecific nematode populations occurring in proximity or in zones of contact between domestic livestock and wild ruminants. Alternatively, potential effects of spillover of populations of nematodes from livestock to wild ungulates could lead to broader dissemination of genes for drug resistance.

In the Central Canadian Arctic, detailed studies have identified links between climate warming and ecological change, phenological shifts in development and seasonal transmission, and population amplification of macroparasites in ungulate hosts. Warming trends have also been associated with changing dynamics of transmission and geographic distribution of elaphostrongyline (*Parelaphostrongylus odocoilei* and *P. andersoni*), mulleriine (*Umingmakstrongylus pallikuukensis*) and protostrongyline (*Protostrongylus stilesi*) nematodes in wild sheep, muskoxen and caribou (44, 47, 53, 55, 61, 62, 63) (Fig. 2). Field and laboratory experiments revealed specific tolerances and thresholds, and a direct relationship between temperature and the
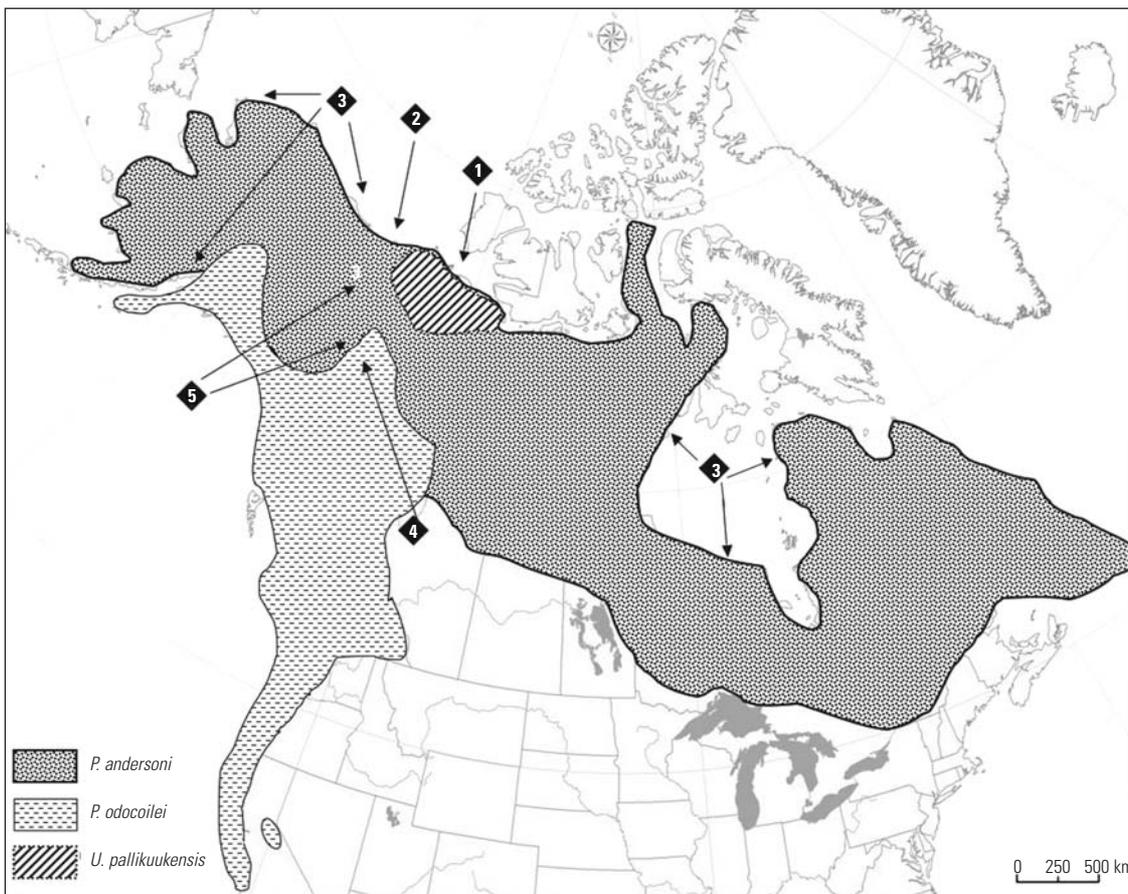

Fig. 2
Contemporary geographic distributions for some protostrongylid nematodes in northern ungulates for which links between parasite development, transmission dynamics and climate change have been demonstrated
(1) *Umingmakstrongylus pallikuukensis* is strongly influenced by long-term temperature trends. *In situ* processes influence developmental rates and generation time drives transmission and increases infection pressure
(2) Contact between reciprocally naïve populations of muskoxen at the Mackenzie River ecotone may facilitate host colonisation by *Umingmakstrongylus* and *Protostrongylus stilesi* (distribution not shown)
(3) Ephemeral emergence of *Parelaphostrongylus andersoni* and disease in barrenground caribou could result from short-term extremes of summer temperature
(4) As with other protostrongylids, increasing parasite loads and pathogenicity for *Parelaphostrongylus odocoilei* in wild sheep are predicted
(5) Additionally, for this elaphostrongyline, increasing temperatures are expected to release constraints on larval development, resulting in geographic expansion into the Richardson Mountains and exposure of currently naïve host populations. In general, for all northern protostrongylids, the intensity and duration of warming at high latitudes will influence patterns of distribution. Latitudinal gradients for development of larval stages related to thresholds would be predicted to shift northward over time; increasing sympatry for hosts and parasites, and synergistic pathogenicity would also be predicted within this assemblage

development of larval *U. pallikuukensis* and *P. odocoilei* in gastropod intermediate hosts; a model for rates of larval development was validated and applied to warming scenarios (50, 59). Based on projections from these models, a long-term and cumulative warming trend has led to significant amplification of populations of *Umingmakstrongylus* in endemic areas, because a reduction in generation times and broadened seasonal windows for transmission have contributed to heightened intensity of infection for individual hosts (47, 62, 63). Significantly for this lungworm in muskoxen, a tipping point was apparently attained in the late 1980s, leading to a shift from a multi-year to a single-year cycle of development and transmission. Additionally, it is predicted that long-term climate warming will release *P. odocoilei* from current environmental constraints. When combined with a breakdown in ecological isolation this could facilitate northward range expansion and colonisation of naïve populations of wild sheep (53, 55). In contrast, periods of temperature anomalies in the Northwest Territories and Alaska are thought to be the drivers of isolated mortality events caused by verminous pneumonia, apparently induced by larval *P. andersoni* or other protostrongylids in transit through the lungs of caribou definitive hosts (47). In similar circumstances in Fennoscandia, seasonally defined but extreme short-term high-temperature events were implicated in the expansion of nematode populations (*Setaria tundra*, with dipteran vectors and *Elaphostrongylus rangiferi* with molluscan intermediate hosts), leading to the emergence of disease and mortality in reindeer (36, 64).

Dynamics of transmission and severity of infection by digenean trematodes, particularly *Fasciola hepatica* and *Fascioloides magna*, are strongly influenced by climatological factors of temperature, precipitation and humidity (70, 83). For these fasciolids, increasing seasonal temperatures and precipitation may lead to expansion and amplification of parasite populations beyond the typically recognised enzootic regions in North America (83). Microhabitat conditions have a major influence on heterogenous geographic ranges for flukes, and such patchiness is likely to be further enhanced by the extremes of temperature, precipitation and humidity linked to climate change.

In most respects, a fine-scale understanding of the effect of temperature and precipitation on the developmental thresholds and tolerances of free-living and parasitic stages in molluscan intermediate hosts is still required (55, 63, 65). We also lack comprehensive knowledge of regional and local parasite diversity (species and populations) and of how gastrointestinal and other nematodes are distributed spatially and temporally, with respect to domestic and wild ruminants (42). Addressing this gap in knowledge contributes to developing our understanding of the current and future dynamics that will influence these complex assemblages of hosts and parasites.

Considerations for some microparasites

Microparasites in host populations and in the environment will respond in a variety of ways to climate warming and to associated patterns of precipitation (31, 81) (Table II). Where and how pathogens are sequestered in the environment will be a critical determinant for responses to variation in temperature (maximums, minimums, extremes, seasonal fluctuations, freeze–thaw cycles) precipitation, humidity (relative degrees of desiccation, patterns of hydrology) and exposure to direct sunlight (31). Environmental tolerances of exogenous stages and the capacity for survival of specific organisms will determine the direct or indirect influence of factors attributable to climate change. Relatively resistant exogenous stages transmitted through terrestrial or water-borne routes characterise many protozoans (*Giardia, Cryptosporidium, Eimeria*; less often oocysts of *Toxoplasma gondii* and *Neospora caninum*) and microsporidian fungi. For these organisms, distributions would be influenced by extreme events of flooding; alternatively, drought conditions may strongly limit the extent and severity of infections and disease (23, 24, 77). Blood-inhabiting protozoans such as *Babesia* spp. may be affected by climate change through changes in the distribution of their arthropod vectors (2, 34, 57).

Considerations for some arthropod vectors

Changing dynamics for complex host–vector–pathogen systems may be difficult to detect during the initial onset of environmental perturbation linked to climate warming (59). Modification of the geographic distribution (shifts from south to north or along westward trajectories) has been demonstrated for ixodid ticks associated with the transmission of Lyme disease in North America, and models predict substantial latitudinal and longitudinal expansion over the coming century, coinciding with warming (9, 10, 76). The seasonal dynamics and environmental constraints for ixodid and argasid ticks that are primary vectors for bacterial and rickettsial pathogens suggest that substantial shifts in latitudinal distribution could occur for entire host–pathogen assemblages (2, 34). Recent expansion of bluetongue into Northern Europe may be an example of how global movements of livestock can provide the mechanism for introduction and climate warming and adaptation allows for the establishment of local arthropod vectors (30). The impact of climate change may be compounded by, or synergistic with, globalisation of trade and travel, modification of suburban landscapes, habitat fragmentation, and reduced habitat quality, all of which can influence both domestic and wild ungulates (59, 81).

Emergent generalities
for pathogens and climate change

Range expansion and host switching among complex assemblages of ungulates and pathogens are predicted as

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climate change eliminates ecological barriers and constraints for pathogen transmission and redraws maps for host ranges and the timing of seasonal migrations. Range shifts are expected (expansion and contraction), ecotones will develop and change, and the potential for host and geographic colonisation will be heightened. Ecological perturbation emanating from climate change emphasises the necessity to document events at the interface of natural and agricultural systems. Wildlife pathogens, or diseases originating in wildlife, are emerging as a considerable threat to human health worldwide (18, 95). A pervasive association between host colonisation and emergence of disease is being recognised as one major outcome of climate warming (6, 7, 8, 26, 42). The potential for emergence of disease, however, will also result from *in situ* processes, even in the absence of geographic expansion of ungulate hosts.

Effects of climate change may be cumulative and played out over decades, or may result from isolated but extreme events. These processes are expected to be interactive. Long-term cumulative processes may be the drivers for changing dynamics between hosts and pathogens (e.g. generation time, developmental rates, amplification, shifts in seasonally defined transmission) and create the background for subtle effects that will be challenging to demonstrate in the absence of extensive baselines (55, 61, 63). In these instances, incremental and gradual increases in temperature may drive thresholds for developmental rates and tipping points, influencing transmission dynamics and the broad interface of the distribution of hosts and pathogens (63). In contrast, extreme weather events as an outcome of climate warming are predicted to result in a geographic mosaic of ephemeral and explosive emergence of disease resulting in mortality and morbidity events at regional and local scale (for example 36, 64). A mosaic structure for emergence arises against a broader background of the distribution of a disease agent when local factors are convergent (e.g. anomalies of high temperature and humidity, susceptible hosts) and conducive for the rapid amplification and selection within pathogen populations (89); such mosaics are also consistent with the axiom that the distribution of a pathogen is wider than the disease that it may cause (4). Morbidity and mortality events may be separated spatially and temporally from periods of anomalous temperature and humidity due to the lag times associated with the development of some macroparasites in their definitive hosts. Signals for both cumulative and ephemeral patterns have already been clearly demonstrated for high latitude systems in North America and Europe. These observations emphasise the generalities for processes of emergence for both animal and human pathogens and serve as a universal framework to understand, anticipate and forecast change in complex systems on global, regional and local scales.

Tools and programmes to assess the impact of climate change

Exploring or demonstrating the relationship of climate change to emergent disease conditions encompasses a number of integrated steps (34, 47, 53, 59):

– survey and surveillance activities to provide definitive specimens and baseline data which feed into archival museum collections to establish the distribution, ecology, epidemiology and effects of potential pathogens

– laboratory and field investigations to identify clear signals linking climate factors (temperature, precipitation and humidity) and pathogen characteristics (developmental rates, tolerances, and dynamics of transmission)

– development of evidence for regional climate change to identify potential responses and risks associated with complex biological systems

– integration of biotic and abiotic parameters and scenarios for environmental change to predict spatial and temporal effects on complex systems, particularly alteration in geographic patterns and host associations for pathogens (10, 76)

– development of broad-based networks to track the distribution of hosts and pathogens involving populations at fine spatial and temporal scales to detect and monitor the epidemiological and health consequences of climate change. Included here would be development of monitoring on transects to assess latitudinal and altitudinal changes over time and continued accumulation of archival collections documenting diversity and population structure for pathogens against which to assess change (10).

Effective baselines are required against which to assess perturbation over time and to understand the impact of climate and environmental change on complex systems of hosts and pathogens across North America. Geographically extensive and site-intensive surveys in conjunction with historical, phylogenetic and phylogeographic information are the foundations for elucidating diversity (faunal structure) and the temporal and spatial distribution of species and populations of pathogens (6). An effective and comprehensive programme will have components for the following:

– establishing priorities

– developing primary data for faunal structure and biodiversity

– a capacity for monitoring and surveillance (including scanning and targeted surveillance and monitoring in the sense of Salman *et al.* [87])

– linkage to historical and contemporary baselines established through archival biological collections (43, 47).

Tracking host, pathogen and geographic associations in space and time is dependent on the availability of archival collections (6, 43). In a cumulative process these biological collections of specimens are long-term baselines and also contribute to deeper historical studies exploring determinants on a continuum of evolutionary and ecological time. Archives are the essential and critical integrative tools linking synoptic and strategic collections from surveillance with informatics, phylogenies, history, biogeography, ecology and population structure in comprehensive frameworks. Such frameworks help us understand biodiversity and serve as the foundation for informed predictions about changing distributions and associations of hosts and pathogens (6, 40). Simply stated, in the absence of collections there can be no basis for definitive identification of pathogens, nor can there be any detailed understanding about ecological context or distribution of disease (6, 7, 40, 43).

Concurrently, experimental studies on targeted pathogens in the field and in the laboratory can identify the limits for environmental tolerances and the temperature-related controls and thresholds for the development of free-living stages in the environment or parasitic stages in intermediate hosts. Collectively, these factors help us to predict the effects of climate warming on pathogens and emerging disease in both domestic livestock and free-ranging ungulates. An exemplar for such integrated approaches is illustrated in the research programmes dealing with protostrongylid muscleworms and lungworms in northern ungulates (44, 47, 53, 51, 55, 60, 62, 63).

Field and laboratory studies are unified to establish the current and future drivers (or constraints) of emergence for pathogens and vectors. Predictive modelling utilising a range of scenarios for climate change is the final step in this multidisciplinary process. Models are validated and tested through increasingly robust methods for surveillance, detection and monitoring. The mitigating effects of adaptation are further incorporated in developing a synoptic understanding of responses in these complex systems (10, 47, 63, 76, 82).

Not all pathogens are equal and fiscal resources continue to be limited, so targeted activities relative to specific and recognised pathogens seem appropriate. Concurrently, we need accurate, broad-based and rapid diagnostic capabilities that can recognise new pathogens and which can complement geographically extensive and site-intensive sampling efforts (47, 54, 60). Needs for such surveillance capacity are heightened in situations where environmental perturbation and the subsequent development of new ecotones represents one cascading effect of climate warming (19). With increasing globalisation of trade and travel, North America must invest resources in developing an animal health and veterinary infrastructure beyond its borders in order to predict and mitigate the risks of global emergence and spread of diseases with significance for animal and public health. A critical component of this infrastructure must be targeted support for basic systematics research and diverse biological collections (6, 39).

A clear framework to prioritise surveillance of pathogens and disease should consider the following:

– expected sensitivity to climate change

– economic significance

– public health consequences

– pathogenicity

– animal welfare

– trade issues related to foreign animal diseases.

Surveillance for known pathogens of serious economic significance among livestock (i.e. reportable or listed pathogens) is an obvious priority. Flexibility is warranted, however, in regard to emergent or resurgent disease which may be caused by seemingly innocuous and/or newly recognised pathogens (7). Surveillance and monitoring alone cannot anticipate the dynamic changes in a future of climate warming, such as the establishment of new geographic associations and exposure of previously naïve hosts to new arrays of pathogens. In order to effectively address the potential for emerging infectious disease, we need comprehensive definitions of pathogen biodiversity for both domestic livestock and wild ungulates, an understanding of drivers for emergence, and robust predictive models (7, 8). Such an integrative approach would include the articulation of fine-scale information about patterns of host association and the geographic distribution of pathogens and the use of new tools and applications for molecular epidemiology and prospecting (47, 54, 60).

In North America at the present time there is a considerable network of independent investigations addressing aspects of host–pathogen systems, zoonoses, human health, and animal health. Although research is being increasingly conducted on aspects of climate and emergent disease (10, 31, 34, 63, 76, 96), most efforts have been to some degree disarticulated and relate to specific programmatic responses and targeted host–pathogen systems. As yet, no comprehensive framework or strategy has emerged to develop and implement policy and

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planning. Current and powerful networks for monitoring and surveillance of livestock pathogens in North America and elsewhere could be co-opted and modified to take into account the diversity of potential organisms that may respond to climate change. The urgency to document and understand the health, agricultural, societal and economic impact of pathogens and emerging infectious disease in a regime of climate change calls for informed predictions about the impact of environmental perturbation and identification of pathways for potential management and mitigation (16, 28, 87, 90, 96).

Acknowledgements

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Les agents pathogènes affectant les ongulés vivant en captivité ou en liberté et les effets du changement climatique global sous les latitudes tempérées et boréales de l'Amérique du Nord

E.P. Hoberg, L. Polley, E.J. Jenkins & S.J. Kutz

Résumé
En Amérique du Nord, plusieurs réseaux pluridisciplinaires de recherche ont pour objet d'étudier l'interaction entre les vertébrés, leur cortège d'agents pathogènes et l'émergence de maladies. En outre, des programmes s'occupent d'évaluer l'impact du changement environnemental sur la santé animale, les zoonoses et la santé publique, mais pour l'instant il n'existe pas de cadre légal ou stratégique intégré permettant de planifier et de mettre en œuvre des politiques dans ce domaine. Dans le contexte actuel de changement climatique et de perturbation écologique, il est devenu urgent d'observer et de comprendre l'impact sanitaire, agricole, sociétal et économique des agents pathogènes et des maladies infectieuses émergentes. Un processus de planification intégré et proactif associant des ressources nationales et internationales est nécessaire pour prédire l'impact du changement environnemental en connaissance de cause et pour concevoir les mesures de gestion et d'atténuation appropriées. Un programme efficace et complet doit se doter des composantes nécessaires pour fixer les priorités, recueillir des informations de base sur la structure de la faune et la biodiversité, assurer le suivi et la surveillance (dépistage et activités ciblées), et utiliser les informations historiques et actuelles (afin d'évaluer les changements) recueillies au moyen d'archives de données biologiques. Des études de terrain et de laboratoire doivent également permettre de déterminer les seuils de croissance, les tolérances et les points de basculement de nombreux agents pathogènes, d'établir une grille permettant de déceler les pressions actuelles et les perturbations à venir, et d'étudier les facteurs qui favorisent l'émergence d'un grand nombre d'agents pathogènes, de vecteurs et d'espèces nuisibles. La modélisation prédictive et l'évaluation des risques à partir d'une série de scénarios du changement climatique constituent les dernières étapes de ce processus pluridisciplinaire.

Mots-clés
Agent pathogène – Amérique du Nord – Animal d'élevage – Changement climatique – Étude – Évaluation de la biodiversité – Maladie émergente – Ongulé – Prédiction.

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Consecuencias del cambio climático mundial en los patógenos de ungulados criados en fincas o en libertad en las regiones templadas y boreales de América del Norte

E.P. Hoberg, L. Polley, E.J. Jenkins & S.J. Kutz

Resumen

América del Norte cuenta con amplias redes de investigación sobre las interacciones de los vertebrados, así como los agentes patógenos y las enfermedades emergentes que los afectan. Existen numerosos programas dedicados a las repercusiones del cambio climático en la sanidad animal, las zoonosis y la salud pública, pero hasta la fecha no se ha preparado un marco o estrategia completos para formular, aplicar y planificar políticas. Vistos el cambio climático y las alteraciones ecológicas, las consecuencias sanitarias, agropecuarias, sociales y económicas de los agentes patógenos y las enfermedades emergentes deben documentarse y comprenderse urgentemente. La existencia de una planificación integrada y previsora, que tome en consideración los recursos nacionales e internacionales, puede posibilitar el pronóstico de los efectos del cambio del medio ambiente con conocimiento de causa y la determinación de metodologías para su posible gestión y reducción. Un programa eficaz y exhaustivo comprenderá componentes para determinar las prioridades, reunir los principales datos sobre la estructura y la biodiversidad de la fauna, capacidades para la observación y la vigilancia (incluyendo actividades de barrido y para casos específicos), así como la referencia a observaciones anteriores y actuales incluidas en archivos de datos biológicos para medir los cambios. También es necesario realizar estudios de campo y de laboratorio para determinar los umbrales de desarrollo, las tolerancias y las evoluciones irreversibles de muchos patógenos a fin de establecer una metodología que permita determinar las dificultades actuales y las alteraciones futuras, así como estudiar los factores que favorecen la emergencia de distintas especies de patógenos, vectores y plagas. Los últimos componentes de esta metodología multidisciplinaria serán la creación de modelos de pronóstico y la evaluación de riesgos basada en distintas hipótesis sobre el cambio climático.

Palabras clave

Agente patógeno – América del Norte – Cambio climático – Encuesta – Enfermedad emergente – Evaluación de la biodiversidad – Ganado – Pronóstico – Ungulado.

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