



Deforestation, hunting and the ecology of microbial emergence

Understanding how novel microbes enter into the human population is perhaps the fundamental goal of the study of emerging infectious diseases (EID). The frequency at which microbes will emerge is determined by the diversity of microbes present in the environment, the level of contact between a potential host and this microbial diversity and the susceptibility of the novel host to infection. While a range of microbial media exist, including soils, plants and animals, the greatest emergence risks come through contact with media, such as wild vertebrates, that share susceptibility characteristics with humans and live in regions of high microbial diversity. Lowland tropical forests provide a rich environment for emergence due to their combination of high vertebrate and microbial biodiversity. Human activities that occur in lowland tropical forests, such as ecotourism, logging, and the hunting of wild vertebrates have the potential to increase the frequency of microbial emergence. Of these and other activities considered, hunting and the processing of bushmeat, particularly from nonhuman primates, involve the greatest level of risk for the transmission of microbes. While human hunting in lowland tropical forests poses a serious threat for microbial emergence, it is by no means alone among contemporary human behaviors in doing so, sharing risk characteristics with activities as diverse as lab microbiology, wildlife veterinary work, and modern food production practices.

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Infectious agents represent a significant risk to humans, their domestic crops and animals, and the planet's wildlife^[1-4]. The past century was punctuated by the emergence of a variety of infectious diseases. Perhaps most notable of the completely novel diseases emerging into the human population during this period was HIV-1, which will have a serious demographic impact on human populations^[5]. While recently emerged and reemerging pathogens has attracted substantial attention during the past decade, an understanding of the factors which influence microbial emergence remains elusive. Understanding the processes by which humans, or other organisms, acquire new diseases has practical implications for maintaining the health of communities as well as fundamental implications for understanding the functioning of ecosystems.

Historically, approaches to the study of infectious agents have focused largely on the impact of these agents on morbidity and mortality, or on the development of medicines to treat them.

These approaches have yielded significant progress in human and animal medicine. Nevertheless, these approaches have not generally placed infectious agents in the context of ecosystems or examined the general factors contributing to the emergence of such microbes. An ecological framework for examining emerging infectious diseases has a number of potential benefits. Such a framework will help to determine the impact of environmental factors on the changing prevalence of infectious diseases. It may also provide insights into the impact of human activities on the emergence of new disease. More generally, an ecological approach is likely to contribute to the well sought after goal of a predictive science of emerging infectious diseases.

The problems of defining an 'emerging infectious disease' have been discussed considerably elsewhere. One set of emerging diseases are those that are completely novel, or thought never to have gained a foothold within a given species or population before. The goal of this paper is to examine factors which influence human acquisition of completely novel microbes. We approach this problem from three directions. The first examines the underlying diversity of potentially emerging microbes. The second explores the impact of human activities on contact with this microbial diversity. The final direction investigates the influence of environmental change on the frequency of human contact. To demonstrate how such phenomena might be approached empirically, we present a case study of hunting and deforestation in Cameroon. Among the conclusions drawn from this study is that certain synergies, for example between logging activities, hunting of nonhuman primates, and international travel are likely to increase the frequency at which novel microbes successfully enter into the global human population.

Microbial media and the lottery of emergence

Humans and other animal communities participate in a range of mutualistic, symbiotic, and parasitic interactions with microbes ranging from small RNA viruses to large multicellular worms. These microbial interactions are often dynamic, and hosts constantly begin interactions with novel microbes and lose contact with previously acquired microbes. While previous research has not examined these phenomena in detail, factors exist which can influence the array of microbes in a vertebrate commu-

nity. Possibly influential factors include: local biological diversity and its components, including host diet and nutrition, host social factors such as gregariousness, and host interactions with other vertebrate and non-vertebrates species.

Two vital events in the relationship between animal hosts and microbes are *microbial emergence*, or the novel introduction of a microbe into an animal community, and *microbial extinction*, or the elimination of a microbe from an animal community. Both microbial emergence and microbial extinction can occur on a community-level, species-level, ecosystem-level or even global-level. While microbial extinction can have important positive or negative consequences for the host species, this review will focus on the determinants of microbial emergence.

Successful microbial emergence is directly related to the rate of *microbial emergence events*, or the number of times that individuals in a previously uninfected species are exposed and infected to a potentially emerging agent. In turn, successful emergence events will be directly related to at least three variables:

- 1 regional microbial diversity,
- 2 susceptibility of the novel host,
- 3 and the rate and intimacy of microbial contact

In addition to these variables, successful emergence will also depend on the existence of suitable opportunities for secondary transmission in the novel host. Changes in any of these variables can affect the probability that a microbe will successfully enter into a novel host population.

The lottery of emergence. The emergence of novel microbes occurs with some frequency in all animals. Nevertheless, the vast majority of exposure events with a given novel microbe will not lead to successful infections, still fewer will lead to secondary infections and even fewer will lead to secondary infections at a rate capable of being maintained in the novel community. Of those successful microbes which do enter into a new animal community, many are likely to be benign and some may even be beneficial. Nevertheless, a small number of novel exposure events will lead to a successful infection with significant negative consequences for the health of the host. While the majority of microbial emergence events may be of minimal significance, their potentially devastating nature makes them high risk events from the perspective of human or animal health.

Microbial diversity. While the study of biodiversity is still in its infancy, it is known that environments vary substantially in their biological diversity. For example, it is well accepted that lowland tropical forests hold a greater diversity of plant and animal life than other terrestrial ecosystems^[6]. As with plants and animals, environments vary with respect to microbial diversity. Most current research on variation in microbial diversity comes from studies of soil microbes of interest to geobiologists^[7]. General attempts to measure microbial biodiversity have been severely limited by the high numbers of unculturable microbes. While there have been some promising attempts to measure microbial diversity

through molecular techniques during the past few years^[8] these have been mostly directed at *within-host* organ systems^[9] and not at a larger ecological context. While little is known about the factors which influence the ecological distribution of microbes of medical relevance, it may be safely presumed that the diversity of medically relevant microbes does vary across environments.

One approach to examining the diversity of microbes of medical relevance is to consider the emergence potential of individual *microbial media*. In this sense, 'media' refers to any living or nonliving entity that maintains microbes which may potentially enter into a novel host population. Microbes

from a range of environmental, organismal, and artificial media have the ability to infect humans (Table 1). While no formal analyses have been conducted to date, some general patterns in the diversity of human pathogens in terrestrial media do seem to exist. The vast majority of known mosquito-borne pathogens are RNA viruses. Pathogens from environmental reservoirs of soil, wood, and decaying vegetation are primarily fungal. The few known pathogens associated with artificial media, such as metal and plastic implants are bacterial. The diversity of water, arthropod, and vertebrate-associated microbes seems perhaps more variable, and include a variety of parasites, viruses, bacteria and fungal sources. There have been few attempts to explain the distribution of medical microbial diversity, one exception is the suggestion that genomic characteristics of RNA viruses, such as high mutation and recombination rates have allowed them to more effectively negotiate the *host-space* between two highly dissimilar organisms^[10].

While carefully planned empirical results will ultimately be necessary to assess the variation in medically relevant microbes across microbial media, there are some general expectations which may act as null hypotheses in this search. It would be expected that microbial diversity should be greatest in contexts which display the greatest diversity of media. For example, soil-associated microbes are likely to be most diverse in regions with diverse soil-types. Plant-associated microbes are likely to be most diverse in regions with high levels of botanical diversity. The same would be likely to apply to arthropod and vertebrate-associated microbes.

Host susceptibility. While humans perceive a realistic threat of microbial emergence, the probability that a given microbe will end up infecting humans is exceedingly small. Given the incredibly large number of microbes on the planet and the very small number which end up infecting humans, contingency and other filtering effects play a very important role in determining which microbes become human diseases. Are there any ways for a microbe to improve the odds in this global microbial lottery?

Some microbes may win the emergence lottery through the luck of adaptation to an environmental medium similar to a human organ system. This is an example of exaptation, which occurs when an adaptation or set of adaptations in one context pre-

disposes an organism to success in a second unrelated context^[11]. For example, humans are only incidental hosts for *Legionellae* the bacteria that cause legionnaire's disease. The adaptation of legionella to moist environments has endowed it with the ability to grow successfully in the environment of the human respiratory system. This reasoning suggests one possible search strategy for potentially emerging microbes, namely to examine media which mimic the conditions in human organ systems. While some environmental media may accurately simulate human organ systems, surely the environment that best simulates the conditions in human organ systems is the organ systems of other mammals and vertebrates.

Microbes infect a range of multicellular organisms, including plants, fungi, and animals. The particular suite of adaptations present in any given microbe will allow it to successfully function in a particular medium. The closer the existing medium is to a potentially new medium, the more likely it will be that the traits allowing success in the previous medium would also translate in success in the novel medium. Holding all else equal, a microbe infecting one species would have a higher probability of successful infection in a closely related species than in a completely unrelated host species. For example, a microbe infecting a vertebrate would have a higher probability of successful infection in humans than a microbe infecting an invertebrate or plant. And microbes infecting invertebrates or plants would have a higher probability of successful infection in humans than microbes based solely in environmental media, like water or soil. This principle, which we have termed the *Taxonomic Transmission Rule* (TTR), states that the probability of successful cross-species infection increases with decreased genetic distance between hosts. This rule should apply equally to the emergence of microbes in any host. The TTR can be seen as a surrogate for susceptibility. Holding all else equal, the two closely related hosts should be susceptible to a larger number of the similar microbes than two more distantly related hosts.

Based on the TTR, we can expect that cross-species transmission between humans and vertebrates should be responsible for a range of newly acquired pathogens. There is good empirical evidence to support this prediction. A range of pathogens are thought to emerge from vertebrate hosts.

Table 1 Examples of human microbial infections originating from terrestrial microbial media

medium	disease	microbe	type of microbe	behavioral risks associated with infection*
arthropod	Rocky Mountain spotted fever	Rickettsia rickettsii	Rickettsia	outdoor activities
decaying vegetation	aspergillosis	aspergillus sp.	fungus	none, widespread
metals	implant infection	Staph aureus	gram-negative rod	Implantation of titanium prosthetic device (43)
plastics	implant infection	staph epidermidis	gram-negative rod	implantation of plastic polymer prosthetic device (44)
soil	melioidosis	Burkholderia pseudomallei	gram-negative rod	farming and other soil-oriented occupations
vertebrate, carnivore	rabies	rabies virus	RNA virus, family Rhabdoviridae	veterinary work
vertebrate, primate	simian B disease	Cercopithecine herpesvirus I	DNA virus, family Herpesviridae	veterinary work and possibly coconut-picking with macaques (in South/SE Asia)
vertebrate, rodent	hantavirus pulmonary syndrome	multiple hantaviruses	RNA virus, family Bunyaviridae	rodent exposure, possibly including small mammal research
vertebrates, ungulate	orf virus disease	orf virus	DNA virus, family Poxviridae	work with livestock as veterinarian, shepherd or in abattoir. hunting of wild ungulates
water, fresh	legionnaire's disease	Legionella sp.	gram-negative bacillus	none known, possible risk associated with work in an air-conditioned building

*Infectious disease laboratory workers are at risk for any agent studied, and are not listed individually

Microbes that have recently emerged from vertebrate hosts include: Ebola, influenza, HIV, and BSE. Nonhuman primates, in particular, play a special role in such transmission. Due to inherited similarities in physiology and disease susceptibility, nonhuman primates and humans share susceptibility to the majority of infecting microbes. In addition to acting as potential reservoirs or sources for microbial emergence, wild primate populations also hold valuable clues to the origins and evolution of important pathogens and can serve as sentinels for surveillance of emerging pathogens^[12]. For these reasons, it is likely that the hunting and processing of nonhuman primates can lead to substantially greater emergence risks than the hunting of other mammalian or non-mammalian species.

Cross-species transmission of this type, provides an important opportunity for the introduction of completely novel pathogens. In addition, cross-species transmission can provide the opportunity for horizontal transfer of genetic information between spatially separated microbial populations. Cross-species transmission, even when it does not lead to ‘success’ for the transmitted microbe, provides the opportunity for recombination between newly acquired pathogens and previously present pathogens. For example, one novel hypothesis for continued emergence of novel HIV genetic diversity is that human adapted HIV-1 is provided novel genetic diversity through the recombination of HIV-1 and SIV, perhaps in human hunters of nonhuman primates. While the general importance of recombination for disease emergence is unknown, there is evidence that horizontal transfer plays an important role in the origin of novel bacterial species^[13], and therefore it should be considered a potentially important source of microbial emergence.

Microbial contact. The taxonomic transmission rule is not always the last word in microbial emergence. Even microbes which may not be easily transmitted between two species can be transmitted in situations of sufficient contact intensity. This can be easily demonstrated by a quick glance through the large number of studies describing laboratory infection experiments conducted during the 20th century. By increasing inoculum, the number of exposure events, or altering the mode of entry, it is possible to experimentally increase the probability of a successful infection. In the same way, human behavior or ecological scenarios which increases the

intimacy or frequency of contact can increase the probability of a successful emergence event.

One example of the impact of microbial contact is the subset of infectious diseases shared by humans and hematophagous arthropods. In general, the number of microbes shared by humans and insects is low. Nevertheless, the number of microbes shared between humans and certain hematophagous, or blood consuming arthropods, such as mosquitoes can be very high indeed. The probability of transmission between arthropods and humans is limited by differences in susceptibility, so how can we explain the large number of microbes shared between humans and mosquitoes? One explanation is the radically increased contact facilitated by mosquito prey-seeking behavior. While substantial debate continues to exist over the arthropod or vertebrate origins of a range of vector-borne diseases, it can be certain that whether of vertebrate or arthropod origins, these microbes were initially capable of infecting only one of the two ecologically linked host. Following long-term ecological connection between vertebrate and arthropod, selection pressures favored traits which provided for exploitation of the novel niche. This may be understood as a function of the frequency of contact.

Emergence risk behaviors

Some vertebrate species must have a very low frequency of microbial emergence. A species that has minimal contact with other species and is restricted to a limited ecological niche which houses low microbial biodiversity would be subjected to relatively few microbial emergence events. Contemporary human populations represent the other end of this continuum. Today’s human societies are in many ways the ideal recipe for microbial emergence. They are characterized by high populations densities, substantial geographic mobility, close contact with large numbers of other humans and a range of other organisms in many different habitats housing substantial microbial diversity. In addition, contemporary human societies include a range of particular activities such as xenotransplantation and feed production which may also facilitate microbial emergence. These characteristics make contemporary human populations more vulnerable to disease emergence than our human ancestors or most other species.

Table 2 Microbial contact risks associated with human activities occurring in lowland tropical forests

emergence risk behaviors	examples of microbes transmitted at interface ^{**}	vertebrate contact risks associated with					protective measures taken
		body fluids	bites or Saliva	organ tissues	feces or urine	vectors (indirect)	
hunting	monkeypox ^[28] , ebola ^[27]	A	A	A	A	A	unknown
wildlife necropsy	ebola ^[29] , listeriosis	A	A	A	A	A	yes
butchering or other meat processing	anthrax , ebola ^[27]	A	A	A	A		unknown
keeping pets	herpes B virus ^[45] , salmonella ^[46]	S	A		A	A	unknown
logging / road-building	cutaneous leishmaniasis ^[47]		S		S	S	unknown
ecotourism/ research	measles ^{*[48]} , loa loa ^[49] , cutaneous leishmaniasis ^[50]		S		S	S	minimal
wood collection	chromomycosis		S		S	S	unknown

A=always involved; S=sometimes involved; *=microbe transmitted from human to wildlife; &=transmitted to chimpanzees from unknown prey item; **arboviral infections associated with sylvatic forest cycles, such as dengue and yellow fever may be transmitted at all of these interfaces

The role of host behaviors in the alteration of infectious disease prevalence is well known. Modifying human behavior either on an individual or social scale, while often difficult in practice, can be an effective tool for altering disease transmission. While the impact of behavior on transmission of microbes has been extensively examined, almost nothing is known about the impact of human behaviors on the initial acquisition of novel microbes. Nevertheless, host behaviors play an important role in microbial emergence. At least three classes of host behavior can impact microbial emergence:

- 1 behaviors which bring hosts into contact with a broader range of microbial diversity
- 2 behaviors which increase the contact with microbial media and particularly those media with similar susceptibility
- 3 behaviors which increase the spread of newly acquired microbes.

A range of behaviors falls into these classes. Diverse human activities which include keeping pets, international travel, ecotourism, veterinary research,

hunting, medical practices, archaeology, animal husbandry, vaccination, and even space exploration share some of these properties. When combined with regions of high microbial biodiversity, such as lowland forests, such behaviors often result in disease transmission (Table 2).

Human mobility also plays an important role in exposure to novel microbes. While a range of terrestrial mammals have moved long distances through geological time periods, contemporary humans and their commensals are unique among mammals in the speed and range of their migrations. Humans occupy most geographic locations on the planet, and even humans in remote regions remain connected through travel to the rest of the species. Human travel has increased to the point where global movement can occur quickly enough to overcome previous limitations on the spread of microbes with a very short incubation period^[14]. Migrations can occur in response to environmental factors, such as drought, or to human political factors, such as forced relocations or military movements. As popu-

lations migrate, they come into contact with new populations of microbes, increasing the probability that potentially successful emergence events will occur. This has been demonstrated at least in the case of some grass species in which geographical range is the best predictor of pathogen species richness^[15]. In certain conditions positive feedback may occur. Acquisition of certain microbes, like HIV, may contribute to immune system deficiencies which can increase susceptibility to a still larger range of microbes.

The contemporary human behavioral repertoire also includes a range of complex behaviors that involve very intimate contact both among humans and with other species. Modern human medicine includes transfusion of blood and transplantation of organs from one individual to another. Both of these activities have contributed to the transmission of known microbes. More recently transplantation medicine has experimented with the transplantation of nonhuman organs, or xenotransplantation. Due to the intimacy of tissue contact involved in all transplantation, and the need for immunosuppressive drugs, xenotransplantation may provide a particularly acute risk for cross-species transmission of microbes.

Even vaccination, with its nearly universally acknowledged benefits, may increase the risk of disease transmission, particularly when precautions become lax. A recent analysis of the distribution of Hepatitis C virus suggests that antischistosomal vaccination led to widespread infection^[16]. Vaccine-mediated transmission may also play a role in cross-species transmission and the emergence of novel disease. A recent book and a series of reviews and discussions have focused attention on the oral polio vaccine (OPV) hypothesis for HIV origins^[17]. This hypothesis suggests that nonhuman primate cell cultures used to cultivate attenuated vaccine strains of polio may have resulted in the inadvertent contamination of vaccine lots and subsequent introduction of HIV-1 and HIV-2 into the human population. The hypothesis is not without precedent; millions of Americans have been infected with SV40, a nonhuman primate virus, that was introduced through contamination of oral polio vaccine strains. Recent evidence suggests that these primary SV40 infections may even have led to secondary infections seen in individuals too young to have received contaminated vaccine, although the route of transmis-

sion, which may have been transplantation, remains unknown^[18]. While the OPV hypothesis for HIV origins is less parsimonious than other current explanations for HIV origins, the events involved in Central African human oral polio vaccine experimentation were, at the very least, a 'close call' as Robin Weiss puts it^[19].

Emergence risks associated with contemporary industrial activities are not limited to medical practices. Other activities that involve large-scale manipulation of biological materials may present similar risks. The agricultural process of animal feed and human food production, for example, involves the accumulation and distribution of animal tissues. In fact, the combination of these activities is thought to have resulted in two linked prion transmission events^[20]. The first involved the use of sheep brains in cow feed production. This is thought to have led to the transmission of a prion disease, perhaps scrapie, to cows. Subsequent consumption of cow products is thought to have led to a second transmission event to humans resulting in the current increase in BSE seen among people. While BSE has the focus of current policy-makers, other notable microbes, such as *E. coli* 01457^[21] contaminate tissues throughout the industrial processing and distribution of cow products.

While the rest of this paper focuses on human hunting in the lowland tropical forest, the review of other emergence risk behaviors in this section serves to demonstrate the range of potential emergence risk behaviors. Sometimes medical applications can bring microbial biodiversity from lowland tropical forests to distant locations, as demonstrated through SV40 infection. In addition, the intensity of contact facilitated by contemporary agricultural practices can lead to emergence from familiar media, such as the cow, with presumably limited microbial diversity, through radical alterations in interspecies contact patterns. So while human hunting in lowland tropical forests poses a serious threat for microbial emergence, it is by no means alone among contemporary human behaviors in doing so.

The Hunting-Logging Emergence Synergy

The hunting of wild vertebrates by humans is a biologically ancient and universal phenomena, and the lowland tropical forest regions of Africa, Asia, and the Americas are no exception. Human land-use patterns, and in particular logging activities, play

an important role in the frequency and intensity of hunting in lowland forest regions. The practices of the logging industry differ substantially from region to region. Logging patterns in Southeast Asian forests, for example, generally involve clear-cutting. Clear-cutting leads to a rapid decrease in all biological diversity and may result in desertification or vast monocultures, as in the oil-palm plantations which are rapidly replacing the rich tropical lowland forests of Borneo. The general ecological devastation of this pattern of deforestation has been discussed elsewhere and the costs of the disappearance of biological diversity are profound. Deforestation of this type creates its own emergence risks. Vast monocultures of oil palm like the vast human 'monocultures' discussed in the previous section, are highly susceptible to plant disease emergence. While the structure of deforestation activities in Southeast Asian tropical forests and South American tropical forests play an important role in disease emergence, this section focuses on the impact of logging practices and hunting in Central African tropical forests. At present Central African logging is characterized by a more selective logging regime, due, in part, to the high costs associated with timber transport. While the discussion is aimed specifically at Central Africa, much of this discussion will also have relevance to deforestation and the changing human behaviors in South American and Southeast Asian contexts.

Hunting Emergence Risks. Both subsistence and commercial hunting using cable snares, and more recently firearms are widespread activities throughout the forests of Central Africa. Particularly when strong economic forces drive the bushmeat trade, the effects of hunting on animal populations can be severe^[22-24]. Because of the conservation impact of hunting on endangered and vulnerable species, the process has received substantial review^[25]. Hunting behavior generally tends to focus around villages or new human settlements in logging camps or along road-sides. Muchaal and Ngandjui^[26] have examined hunting in a village in the Dja reserve and demonstrated that both the level and impact of hunting decreases as a function of distance from the village (Figure 1). These results have importance both for wildlife conservation as well as for assessing the risks of emergence associated with hunting, which will be the focus of this section.

Neither hunting nor the bushmeat trade is, in fact, a unified phenomenon. Each consists of a range of activities spread from the consumer to the hunter. As discussed in Box 1, a number of economic and other forces play a role in influencing the exact behaviors which make up these activities. Hunting itself involves tracking, capturing, handling, sometimes basic field butchering, and transportation of the carcass. Butchering involves opening, cutting, dressing, and preparation of the carcass. Still further participants are involved in transportation, sale, purchase and consumption of meat. Different activities associated with the bushmeat trade will

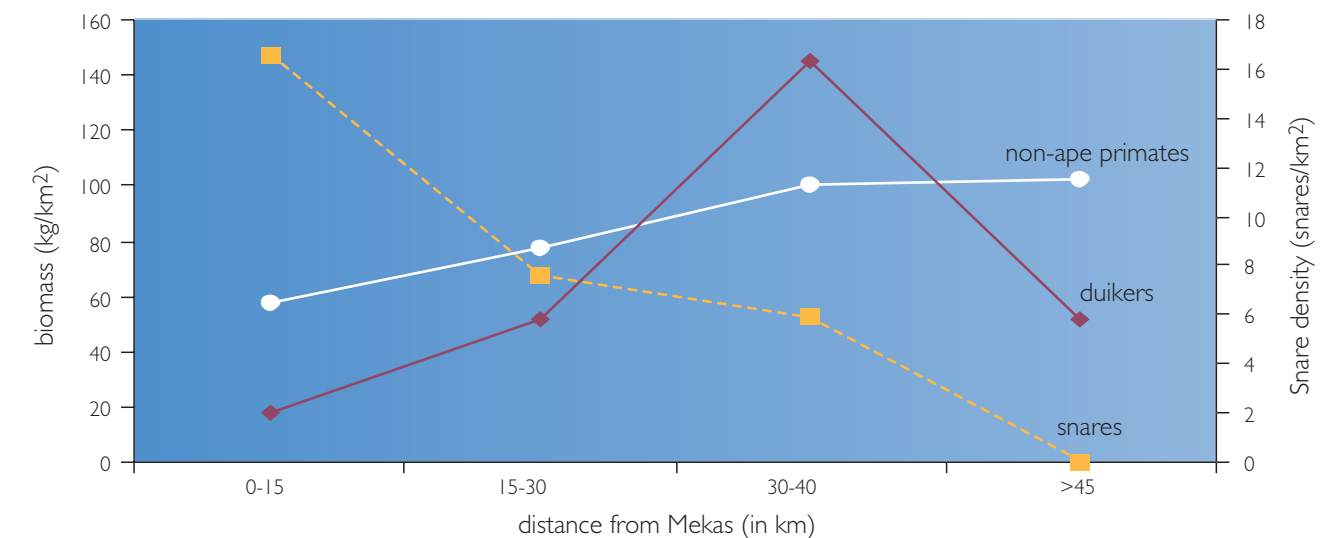


Figure 1 The density of snares and biomass of non-ape primates and duikers as a function of distance from Mekas, a hunting village on the Western boundary of the Dja Biosphere Reserve in Cameroon, adapted from Muchaal & Ngandjui^[26].

Box 1 The Anthropology of Bushmeat

The process by which a wild, forest-dwelling animal ends up in somebody's cooking-pot involves a range of behaviors and actions. While human and their ancestors have hunted for at least the last 5-7 million years, these behaviors are not static and hunting in contemporary human communities has changed over time as the historical circumstances have changed. Recent anthropological research has begun to examine indigenous theories of infectious disease^[40], but no data currently exists on local perceptions of health or other risks associated with hunting and consumption of bushmeat. Humans as well as other animals^[41] are known to employ behavioral adaptations to avoid exposure to infections, yet the type of protective strategies that hunters might employ and the effectiveness of such strategies remain unknown.

An anthropology of bushmeat would discover not only exactly what people do when they hunt; it would follow the process all the way to the village, the market, the kitchen, and onto the table. These practices are articulated along lines of gender and ethnicity. An understanding of the micro-level behaviors associated with butchering the animal and preparing it as food will be essential for the epidemiological work on risk emergence. A cultural context would also assist in understanding the patterns of behavior and preparing for possible future attempts to change them. What roles do men

and women play during the process, and have these roles changed over time? Do traditional rules exist as to who gets which parts of a kill? Do certain animals get consumed in the village, while other species are sent to the bushmeat markets? If the bushmeat is sold, who gets the money? Are there ritual components to hunting; does it have any sort of religious or spiritual meaning for the participants, in addition to its obvious nutritional and economic benefits?

Understanding human hunting behavior^[3] also means situating these behaviors in an economic context, in particular the role of markets. Markets are organized social institutions in which goods and services are exchanged. The process of exchange involves information flows between buyers and sellers. It also involves the transportation of goods and resources required to render services from suppliers to customers^[42].

The social science of bushmeat is not merely an intellectual exercise. In order to change behavior it is important not only to understand the nutritional and cash value of bushmeat, but also to understand the local meaning of bushmeat hunting and how best to modify behaviors. If further studies demonstrate the health risks associated with bushmeat consumption, it will be important to attempt to change this behavior. If so, detailed ethnographic studies will provide the basis for behavioral change.

involve different levels of contact and different levels of risk for microbial emergence. Hunting, for example, also involves contact with potentially infected vectors while distant consumption may not. As discussed earlier, contact with vertebrates and the microbial diversity of tropical forests contributes to an increased risk of emergence. In addition there may be particular high risks associated with the hunting of nonhuman primates, and even greater risks in hunting certain species such as chimpanzees which share nearly identical infectious disease susceptibility and, as active hunters themselves, are near the top of the *microbial food chain*.

The risks associated with hunting, both inside and outside of the tropics are well known. Exposure to a dead and presumably infected chimpanzee, led to Ebola infections both in those collecting and preparing meat and perhaps in individuals only involved in meat consumption^[27]. The hunting

of a red colobus monkey has been implicated in a localized epidemic of monkeypox, an orthopoxvirus similar to smallpox, which continued for four generations of human-to-human contact^[28]. Increased risks of this sort are not limited to the tropical forests, hunters in the U.S.A. for example are exposed to Orf Virus Disease and a variety of vector-borne diseases, like Lyme disease. Some non-hunting behaviors, such as wildlife necropsy involve an almost identical set of exposure risks, although some of these risks may be mediated by increased protective measures against disease transmission. The analogous risks of necropsy can be seen in the Ebola infection contracted by a Swiss behavioral researcher who performed a necropsy on a chimpanzee in the Tai forest^[29]. From a microbial perspective there is essentially no difference between transmission through necropsy and transmission through hunting.

Emergence risks associated with predation are not limited to humans. Other animals exhibiting predatory behaviors will also be subjected to increased risk of cross-species transmission of disease. One example is the increased risk for feline plague among cats that hunt rodents^[30]. Another is the recent epidemiological study of Ebola among wild chimpanzees. The primary risk factor for contracting Ebola among wild chimpanzees was hunting behavior, which showed a stronger association with infection than behaviors like "touching dead bodies"^[31]. Chimpanzees are regular hunters of monkeys and other forest vertebrates. Chimpanzee hunting involves consumption of raw meat as well as basic butchering with hands and mouth (NW unpublished data) and involves substantial risk for cross-species transmission. The potential cross-species transmission among nonhuman primates or among vertebrates generally has not been sufficiently included in models of the evolution of diseases like HIV. For example evidence of apparent cospeciation between chimpanzees and viruses could also result from cospeciation of a virus in another nonhuman primate prey species that varies geographically in a similar way to chimpanzees.

Logging roads, hunting, and microbial emergence.

The widespread practice of hunting among chimpanzees and bonobos, our closest living relatives, suggests that hunting and meat consumption have been a part of the diet of our ancestors for at least 5-7 million years. Clearly, then, close human contact with vertebrate and microbial diversity in lowland tropical forests is a biologically ancient phenomena. Ancient hunting behavior would include similar or greater risks for cross-species transmission. It is estimated that cooking is less than 1.9 million years old^[32]. While cooking is primarily thought of as an adaptation to increase available food sources, the microbial significance of hunting is great and cooking must certainly decrease the infectious disease risks of hunting wild animals. So if hunting is an ancient phenomenon, why would today's hunting patterns lead to a different scenario of microbial emergence than hunting at any point in the past? One answer is the change in land-use and migration patterns.

A variety of ecological changes are thought to impact the emergence of infectious diseases. Diseases which depend on environmental media are the most likely to be affected. For example, water asso-

ciated or transmitted diseases, such as cholera will be greatly affected by flooding. Diseases transmitted by vectors will be affected, in sometimes complex way, by changes in human land-use patterns. Changes in forest land-use patterns are also likely to impact the emergence of infectious diseases.

Deforestation has a range of general and specific geographical consequences relevant to microbial emergence. Because lowland tropical forests are rich in biodiversity, deforestation generally decreases both biomass and biodiversity. While the determinants of microbial biodiversity are not well understood, deforestation may be generally expected to decrease microbial biodiversity. This might, at first thought seem to be likely to lead to a decrease in the probability of novel microbial acquisition through a decrease in the density and diversity of both the microbes and or vertebrate hosts present in forested systems. Certainly in some instances deforestation must have just this effect, for example in the clear-cutting common in Southeast Asian tropical forests that results in endless fields of monoculture, such as oil palm. These and other newly desertified environments will presumably be associated with a decrease in the frequency of novel acquisition of certain diseases. Nevertheless, many other microbes that already exist in humans and their domestics will remain threats and in some cases clear-cutting deforestation may exacerbate their prevalence, although this is beyond the scope of this paper.

Current deforestation in Central African forests does not usually involve short-term clear-cutting. Because of the relatively high costs of extraction and transportation, logging in these environments generally involves extraction of particular high value timber species which are profitable. While this type of 'selective' extraction is still a threat to biodiversity, it is widely believed to have a higher probability of sustaining natural diversity than the clear-cutting widely practiced in Southeast Asia. Selective logging generally involves construction of road and transport of workers into relatively pristine forest regions. This process has a number of cultural and ecological correlates.

The general ecological impact of roads has been examined^[33]. Roads have a number of ecological effects including: diversity loss during road construction, mortality of wildlife through roadkill, road avoidance due to traffic noise, edge effects,

Box 2 Emerging Infections in Cameroon (EICAM)

The ecological diversity present in Cameroon and the range of new and changing land-use patterns make it perhaps the ideal setting to examine the impact of ecological changes, including road-building and hunting, on novel disease transmission. This opportunity is the basis of a Johns Hopkins University collaboration with the Cameroon Ministry of Health and Ministry of Defense to explore Emerging Infectious Diseases in Cameroon (EICAM). Cameroon's forests, ranging from incredibly wet evergreen forest in the rain shadow of Mount Cameroon to the semi-arid Guinea Savanna Woodlands of northern Cameroon, exhibit most of the variation in vegetation types found in Africa. Cameroon is also one of the few places in the world where tropical montane forest systems are found. Cameroon maintains considerable diversity of plants and animals, including an impressive array of so-called 'charismatic mega-fauna' such as elephants, western lowland gorillas, leopards,

lions, forest buffalo, bongo antelope, and chimpanzees, and has the only remaining population of black rhinos in West Africa. The richness of the biodiversity in its forests is exceptional among African countries^[35]. The diversity of plant and animals species is higher in the humid forest zone of Cameroon than elsewhere in the country. Of the 250 mammalian species in Cameroon, 162 exist in the humid forest (65%), with 132 of these species only found in this habitat. Clearly the biodiversity reserves of the moist humid forests of Cameroon are of high intrinsic value. Estimates of forest cover in Cameroon depend somewhat on the classification scheme and methodology. Forest cover of all types in Cameroon in 1995 was estimated by^[36] at 195 980 km² or 42% of total land area. Moist tropical forests with closed canopies were estimated by FAO to be 179 200 km² in 1980. While a variety of estimates of deforestation exist, it appears as if Cameroon experiences

a loss in dense moist forest cover of between 800 km² and 1 000 km² per year^[35].

The IITA Forest Margins Study Site. The International Institute of Tropical Agriculture has established a 15,000 km² study area called the 'benchmark area' to investigate the impact of deforestation on agricultural practices and land-use patterns. A dramatic decrease in primary forest cover can be seen along a south-north trajectory in the benchmark area. In order to characterize land-use in the project study site, an extensive geographic information system (GIS) including satellite data has been constructed.

Four near-real-time SPOT HRV satellite images were processed along a continuous swath in March 1995 in southern Cameroon^[37]. Differences in forest cover between the village sites can be seen clearly in the village land-use satellite maps in Figure 3. A difference in the road network is also apparent within this gradient with only 0.4% roads in the Southern sector of the benchmark and 1.4% roads in the Northern.

The Bushmeat Trade in Southern Cameroon. One of the most important nontimber forest product activities within the moist forest zone of Cameroon is the poaching of bushmeat by market hunters. Reductions in the cost of transportation and communications in Cameroon particularly since the mid 1980s have greatly increased the size of several markets. Among the important infrastructure projects was the construction of the Yaoundé-Douala trunk road in the mid 1980s funded by the World Bank and then the extension of this road to the border of the timber-rich East Province in 1992 funded by the European Union. These developments significantly reduced the cost of extracting timber in the remote East Province and led to the situation where today Cameroon is the leading exporter of tropical timbers in Africa.

Hunting increases in these regions in direct proportion to logging activities. When the logging companies open up new areas, snare and firearm hunters follow in their tracks^[35]. Logging camps in the region provide a cash market for fresh bushmeat and their trucks are often used as a means of transporting smoked bushmeat to the urban markets of Yaounde and Douala where demand is high. The densities of large primates (gorillas and chimpanzees) in the East Province are among the highest in all of Africa^[38]. As discussed earlier, the hunting of these ape species likely results in a higher risk of exposure than the hunting of other species.

Driving the bushmeat trade in Cameroon is the large and growing urban demand in conjunction with the opening up of logging concessions in the East Province. The market among households for sauce preparation in Yaounde alone is estimated at approximately \$4 million annually (IITA unpublished data). However in contrast to the conventional view that bushmeat is a luxury good consumed mainly by the rich, a recently conducted consumption study reveals that it also plays an important dietary role among poor households. Across income classes, the poorest two quintiles spent 16% and 17% of their meat budgets on bushmeat versus 7% for the richest quintile and 9% overall (IITA unpublished data). There were differences in the form of bushmeat consumed with the poor more likely to purchase smoked bushmeat rather than the more expensive fresh product. The conclusion is that in spite of its illegality, smoked bushmeat is an important protein source for the urban poor.

Furthermore, urban demand makes hunting a source of income for rural households. A survey of 225 households in 15 villages (five from each "block") of the benchmark was conducted in 1994. Among the information gathered was data on whether the household had generated any income from bushmeat sales. More than half the households in the Ebolowa block (52.7%) reported sales, versus 41.2% in the Mbalmayo block and only 9.8% in the Yaounde block ($p < 0.01$)^[39]. In another study, households in the 6 pilot research villages where IITA conducts on-farm research were asked about their reliance on forest resources for generating cash revenues (defined to include hunting, fishing and gathering of nontimber forest products). The results reveal significantly less reliance in households of the Yaounde block. Interestingly, there is more reported reliance among households in the Mbalmayo block than in the Ebolowa block ($p=0.056$) although the amount of forest resources in the Ebolowa block is higher. Among the likely factors contributing to this difference, are the better-developed market institutions of the Mbalmayo block, which increase economic incentives for these products. These data provide predictions for the extent of novel microbial exposure in the different study villages. The study of these phenomena requires diverse expertise on deforestation, microbes, wildlife, and human land-use patterns, yet holds the potential to identify techniques to decrease the risk of human acquisition of novel diseases.

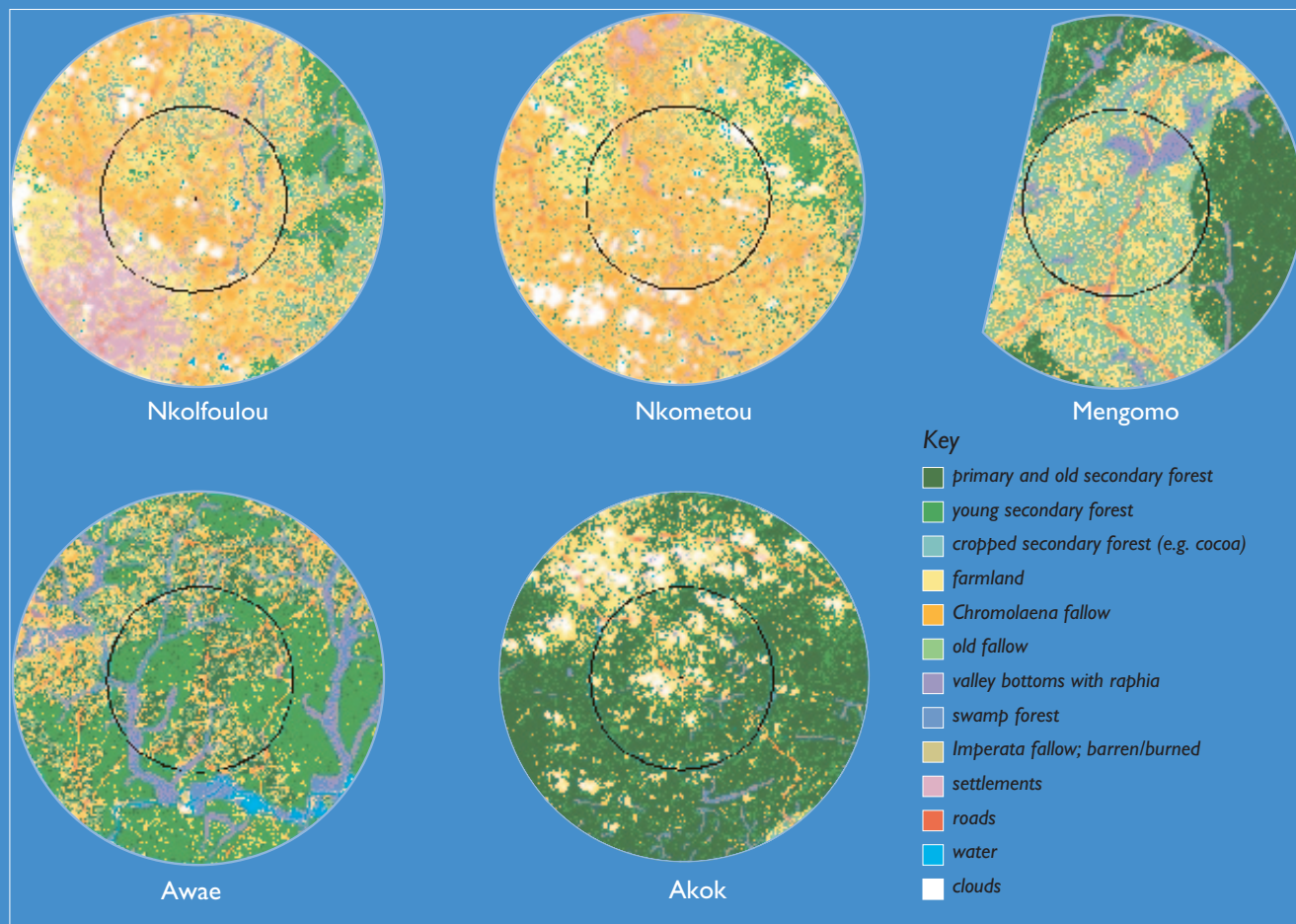


Figure 3 Land-use in a 5km and 10km radius around research villages in the IITA Humid Forest Benchmark Region, Cameroon. Derived from SPOT HRV image, March 1995^[37].

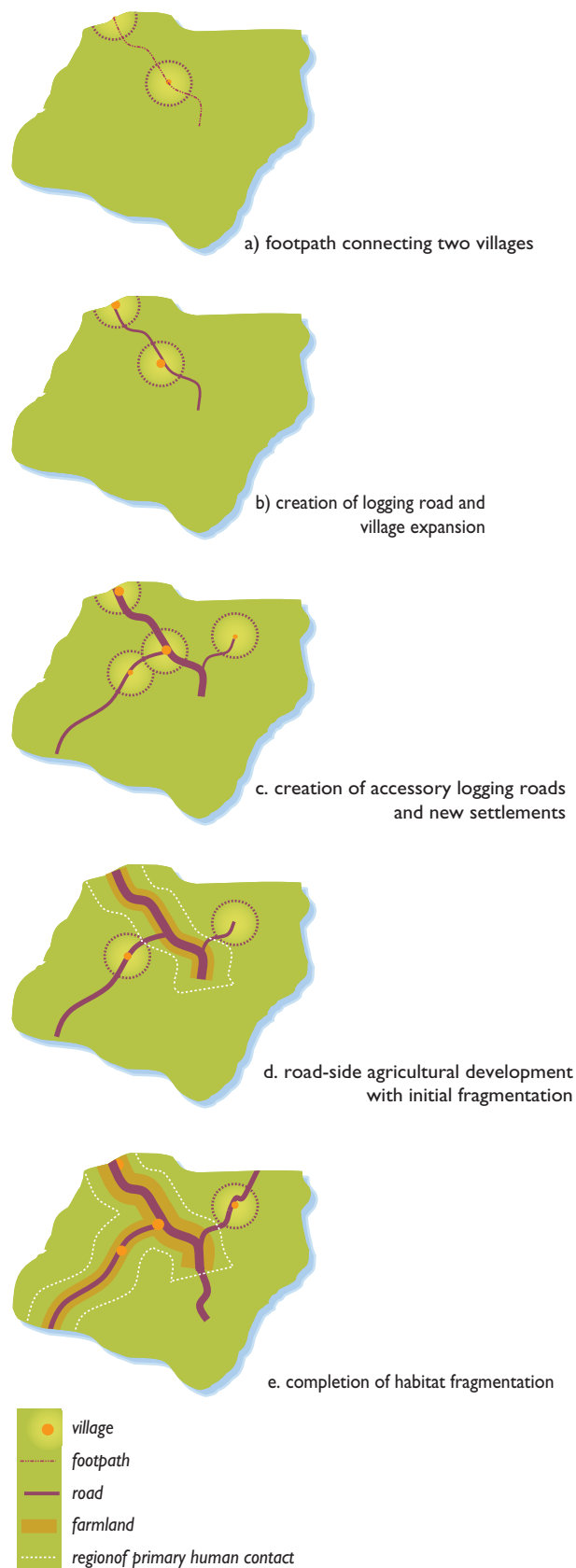


Figure 2 Idealized maps showing the impact of roads on habitat fragmentation and the range of human contact with forested microbial diversity

habitat fragmentation, and changes in water flow. These effects can be substantial. Forman & Alexander^[33] estimate that one million vertebrates per day are killed on roads in the United States alone. In many Central African countries, roads provide increased contact between remote human populations who live at low density and urban human populations living in large cities with immediate access to international travel. These new forms of cultural contact can play a potentially important role in the emergence of disease, giving generally localized emergence events the potential for rapid global spread.

Since in many areas, Central African logging is still selective and a range of forest environments remain, it is possible that wildlife can be sustained in some of these regions. Nevertheless, this does not appear to be the case. Instead, logging road access and logging vehicle transportation provides a link between urban demands for bushmeat and regions which are high in bushmeat. This has been examined by Wilkie et al. who found that the particular combination leads to an increase in the frequency of human hunting behaviors^[34]. Remote roads and transport provided by logging trucks, coupled with the demands of growing cities create a substantial demand for bushmeat and contribute to an increase in hunting behavior.

The process of road-building that accompanies logging practices also serves to increase the process of habitat fragmentation. One consequence of human movement to road-sides and habitat fragmentation is an increase in contact between forested regions and human populations (see Figure 2). Historically, hunting activities radiated in a circular fashion from isolated villages, with decreasing impact at the periphery of the hunting range (as shown in Figure 1). Roads provide an increased number of points at which hunting activities can commence. Road-side transport means that hunters can lay traps and hunt at the same distance from roads. This changes the pattern of human contact from a circular pattern to a banded pattern surrounding developed roads. This increases the area in which hunting can be conducted with economic returns. In essence the existence of roads and logging transport increases the functional interface between human populations and vertebrate diversity in forested regions, and provides the cultural incentives necessary to drive the trade.

So despite the fact that deforestation may eventually lead to a decrease in microbial diversity, the processes of deforestation are often likely to act to increase the frequency of microbial contact through increased access provided by logging roads. In Central Africa, the existence of new roads and access to regions that have not been intensively hunted increases hunting behavior. The hunting and butchering of prey items facilitates initial contact with a range of microbial organisms due to contact with diverse body tissues. The inclusion of phylogenetically similar prey items, such as nonhuman primates, increases the probability that hunters will be susceptible to infection by novel microbes that they come into contact with. Secondary transmission of novel microbes between human populations is facilitated by logging road networks and decreased travel time to cities and airports. Overall, deforestation, particularly in this context, is likely to lead to a substantial increase in the frequency of microbial emergence.

Conclusions

While a major portion of this paper has described the risks associated with hunting, it is also our goal to emphasize the variety of other behaviors that increase the frequency of microbial emergence. The scientific and conservation communities may be quick to point the finger at a distant hunter as the source of modern plagues. Nevertheless, a hunter, a careless lab scientist, and a globe-trotting chimpanzee owner would all share characteristics opening the portal for microbial entry into human populations.

Of course, this does not mean that protections against hunting-mediated emergence are not necessary. The number of contact events between Central African hunters and their prey items greatly outnumbers the contact events between scientists and novel microbes in labs or the relatively small number of primate or other high-risk pet owners. Appropriate research must be conducted to examine the level of risks for hunters to a variety of microbes. In addition, anthropological work must be conducted with hunters if there is any hope that viable solutions and alternatives to minimize disease risks might follow.

A major goal of the study of emerging infectious diseases is to develop predictions which can point the way to potentially emerging microbes. This

paper has suggested a few predictions based on the ecology of microbes and potentially novel hosts. First, microbes are likely to emerge from the interface of high microbial biodiversity and interconnected human populations. Second, microbes are likely to emerge from microbial media which are nearly identical to human organ systems, with risks increasing for vertebrates who are closely related to humans. Third, microbes are likely to emerge from scenarios involving a high frequency of contact or a high intimacy of contact between microbial media and humans.

These ecologically based forecasts can work together with other predictions based on the evolution of microbes. Burke has proposed three criteria of microbes which will increase the probability of emergence^[10]. These include: 1) proven ability to lead to human pandemics; 2) proven ability to lead to pandemics in nonhuman animal populations; and 3) proven high mutation rates and ability to recombine with other similar or dissimilar microbes. Ecologically and evolutionarily derived criteria can be combined to improve the success of search efforts. For example, one program could search for viruses with proven ability to recombine in ecological settings which involve extensive contact between humans and closely related vertebrates. These studies can play an important role in shifting the study of emerging infectious diseases toward a predictive science. Ultimately, an understanding of the mechanisms which influence microbial emergence has the potential to contribute to efforts to predict and control the reemergence of existing pathogens as well as the emergence of future unknown microbes.

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