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The Relationship Between Land Use Change and Disease Prevalence

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Title: The relationship between land use change and disease prevalence

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One Sentence Summary:

Land use changes alter disease prevalence by increasing contact points between hosts and humans and by effecting wildlife species compositions.

Abstract:

Zoonotic disease outbreaks are becoming more novel and are increasing in frequency. This increase can be partially attributed to land use changes including deforestation, urbanization, and cultivation. Land use change alters disease prevalence by causing an increase in contact rates between disease hosts and humans. Land use changes also alter species compositions in the area to contain more competent disease hosts. Each pathogen can react to these changes in different ways. The specific reactions that each pathogen has to land use changes should be further researched so proper mitigation steps can be taken. Once the effects of land use change are fully understood then land conversion can occur in a manner that prevents increases in disease prevalence.

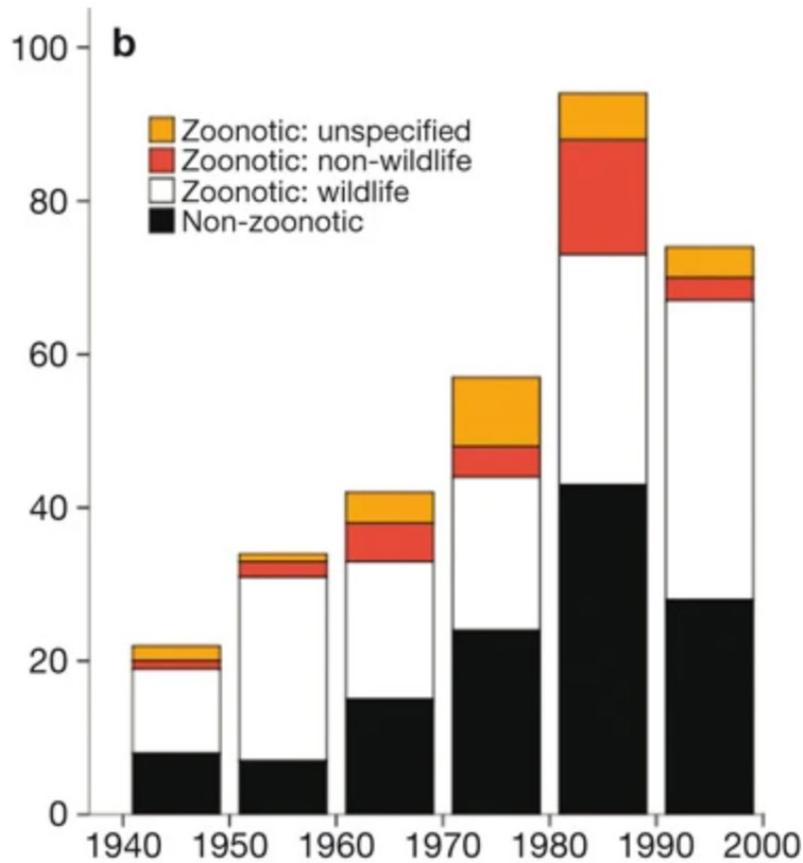
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Main Text:

Disease outbreaks have been increasing worldwide. From 1980 to 2013 the total number of outbreaks and the richness of causal diseases have increased (1, 2). More specifically, zoonotic disease outbreaks are increasing in frequency and are becoming more novel in human populations than human specific diseases (1-3). From 1940 to 2004 60.3% of the 335 newly emerged diseases were caused by zoonotic pathogens. Out of these zoonotic pathogens, 71.8% had a wildlife origin (1). This increase can be seen in Figure 1 which shows the classification and number of emerging diseases from 1940 to 2000.

Figure 1. Classification and number of emerging diseases from 1940 to 2000



The number of outbreaks has been increasing over the last decades. Zoonotic diseases are emerging more than human specific diseases (2).

Land use changes, or land conversions, can have a profound impact on the transmission rates of zoonotic disease. Almost half of the zoonotic diseases that have emerged since 1940 have resulted from at least one type of land conversion (4). Types of land use changes include deforestation, urbanization, and cultivation. Deforestation is the removal of trees or plants to clear an area. Urbanization is the process of clearing out of an area of plants and wildlife to develop infrastructure to support a gradual increase in human occupancy (5). Cultivation is similar to urbanization but is more specific to creating space for agriculture or livestock. Cultivation can also include terraforming the land to support irrigation and crop placement (6). Each type of land use change can have unique effects on transmission rates of zoonotic diseases.

Land use changes are also frequently accompanied by losses of biodiversity (2, 7). There are two theories addressing how a loss of biodiversity effects zoonotic disease transmission rates. The most common theory is the dilution effect. This theory argues that a high biodiversity dilutes zoonotic diseases in a variety of low competent hosts (4, 7-10). The competing theory is the amplification theory which argues that a high biodiversity creates a variety of hosts that could be reservoirs for new zoonotic pathogens (3). Land use changes give rise to both theories depending on the habitat, the wildlife, and the pathogen involved (11, 12).

The goal of this paper is to explore the effects that land use change can have on zoonotic disease transmission by causing changes in pathogen levels within the wildlife and in animal and human behavior.

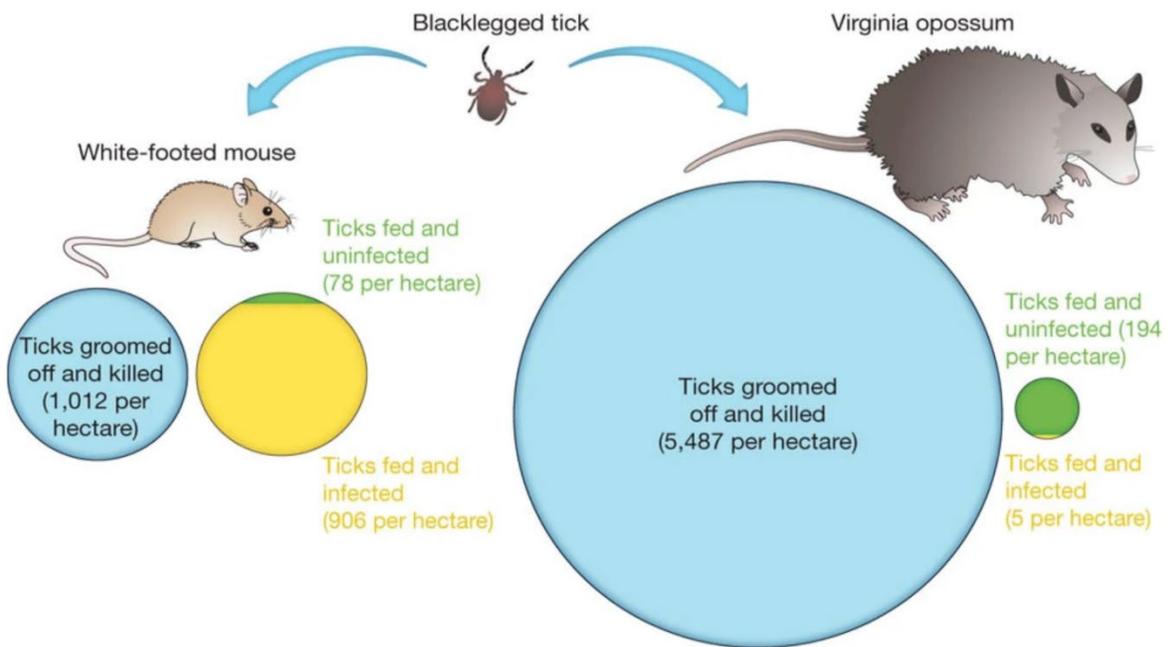
Biodiversity:

Biodiversity is the diversity of genes, species, and ecosystems in an area (4). As land use change occurs, biodiversity is lost (9, 13). A loss of biodiversity changes disease transmission

rates because pathogens rely on a multitude of hosts and vectors for their transmission cycles (4). There are two competing theories that attempt to address whether a loss of biodiversity leads to an increase or a decrease in pathogen emergence: the dilution effect and the amplification effect.

The dilution effect argues that a loss of biodiversity will cause an increase in disease transmission rates (8). The theory behind this effect is that a large biodiversity will include low competent and dead-end hosts that will not be able to spread the pathogen, therefore diluting the disease across a variety of species (4, 7, 9, 10, 12). When biodiversity drops, these low competent and dead-end hosts are the first species to be lost and are survived by more competent hosts (4, 12, 13). The difference in survival rates could be caused by specific traits that link increased hardiness to environmental changes with increased resilience to higher levels of pathogen (12).

Figure 2. How the white footed mouse leads to an increased vector population



As the white-footed mouse population increases, there are more infected ticks in the area than when there are more Virginia opossums are present. This leads to an increase in Lyme disease transmission (4).

The dilution effect is seen most often for rodent, bat, and bird-borne diseases in response to land use changes (12). When looking at Lyme disease in eastern North America the most competent host for the immature tick vectors and the disease itself is the white-footed mouse. The white-footed mouse is a resilient species that remains when biodiversity drops. In comparison, the Virginia opossum is one of the first species to be lost and is a poor host of Lyme disease that feeds on ticks. As the biodiversity drops, the species that could limit transmission, the possum, is lost and the species that amplifies transmission, the mouse, increases in population. The change in species composition as biodiversity drops will cause an increase in disease transmission rates as depicted in Figure 2 (4). This phenomenon has also been seen with West Nile encephalitis, hantavirus pulmonary syndrome, bartonellosis hosts, and a variety of parasites (4, 9, 10). A list of diseases that increase transmission rates in response to decreasing biodiversity can be seen in Table 1.

Table 1. Diseases that demonstrate the dilution effect

Disease	Mechanism
Amphibian limb malformation	B
Bacteriophage of <i>Pseudomonas syringae</i>	B
Coral diseases	A
Fungal disease of <i>Daphnia</i>	B
Hantavirus disease	A, B
Helminthic parasite of fish	A*
Lyme disease	A, B
Malaria	A
<i>Puccinia</i> rust infection of ryegrass	A*
Schistosomiasis	B
Trematode diseases of snails and birds	B
West Nile fever	A*, B*

The above table lists diseases that demonstrate the dilution effect. Mechanism A is host/vector abundance and mechanism B is host/vector/parasite behavior. Asterisks indicate that the mechanism was suggested, not stated (4).

The amplification effect argues that a loss of biodiversity reduces potential hosts and limits the number of novel diseases that will emerge (2-4, 10). This effect is mainly looked at in the tropics which have a high density of quickly mutating pathogens, vectors, and hosts (14). The

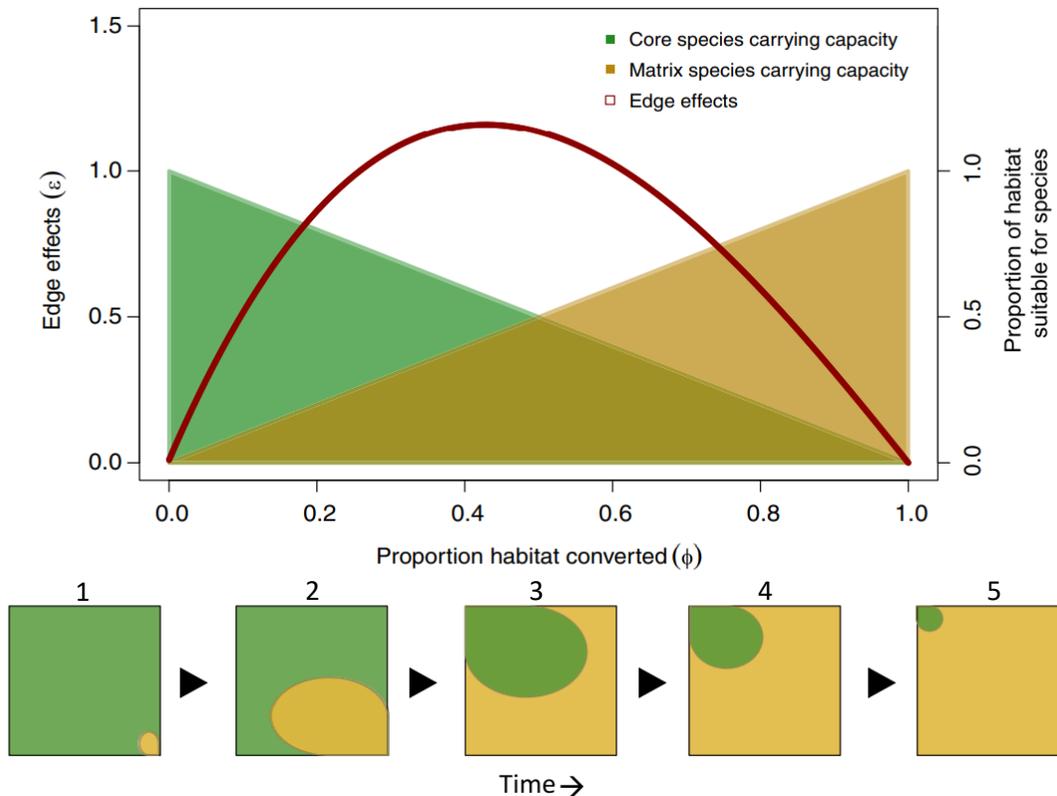
amplification effect is also expected to be seen for density dependent pathogens as the transmission rates depend on the density of the population of hosts. One example of this effect is the emergence of chytridiomycosis in frogs (10). There is a lower prevalence of the density-dependent fungal pathogen in small habitat patches of frogs than in large habitats. The more species that were present in the habitat, the higher levels of pathogen in the habitat (10).

Neither the dilution nor amplification effect is absolute. The specific effects that the loss of biodiversity will have on disease transmission rates will depend on a multitude of factors including but not limited to the habitat type, the species involved, and the pathogen itself (11, 12).

Land Use Changes:

To understand how land use change can affect disease transmission, it is important to first understand the relationship between core, matrix, and edge habitats. The core habitat is occupied by wildlife and is untouched natural habitat. The matrix habitat is the area occupied by humans and domesticated animals. The edge habitat is the boundary between core and matrix (16, 17). The edge habitat has a density that blends into both the core and the matrix habitats. Edge habitat is an area of increased contact between matrix and core species (16). This increase in contact points can lead to an increase in transmission. When forests were fragmented in New York, there was an increase in contact between developed, matrix, and non-developed, core, habitats. There was a strong independent association observed between forest fragmentation and an increase in giardiasis cases when the area was investigated from 2000 to 2010. The increase in cases was caused by the increased edge densities between the core forest land and the matrix developed or agricultural land (15).

Figure 3. Relationship between core, matrix, and edge densities



This figure demonstrates that as land use change increases, the core habitat decreases. The decrease in core habitat in turn decreases the core species carrying capacity of the habitat. The opposite effect can be seen with the matrix habitat as more land is converted. The red arch depicts the edge effects. At the extremes of land use change, the effects of edge density are diminished. At intermediate levels of land conversion, there is a high amount of edge effects. This change can also be seen in the squares below the graph which shows the conversion of land (16).

Figure 3 depicts the relationship between the three habitat types and how conversion from core to matrix affects the edge density and consequently disease transmission rates. As land is converted the core habitat decreases, and the matrix habitat increases. At the extremes of land conversion there are limited edge effects due to the large area of one habitat type. This is shown in squares 1 and 5 of Figure 3. The intermediate levels of land conversion cause high edge effects because there is more area shared between the two habitats as seen in squares 2, 3, and 4 in Figure 3. The high edge effects have the greatest chance of creating a disease outbreak since transmission is sustained between the core and matrix species (16). Lower edge effects tend to

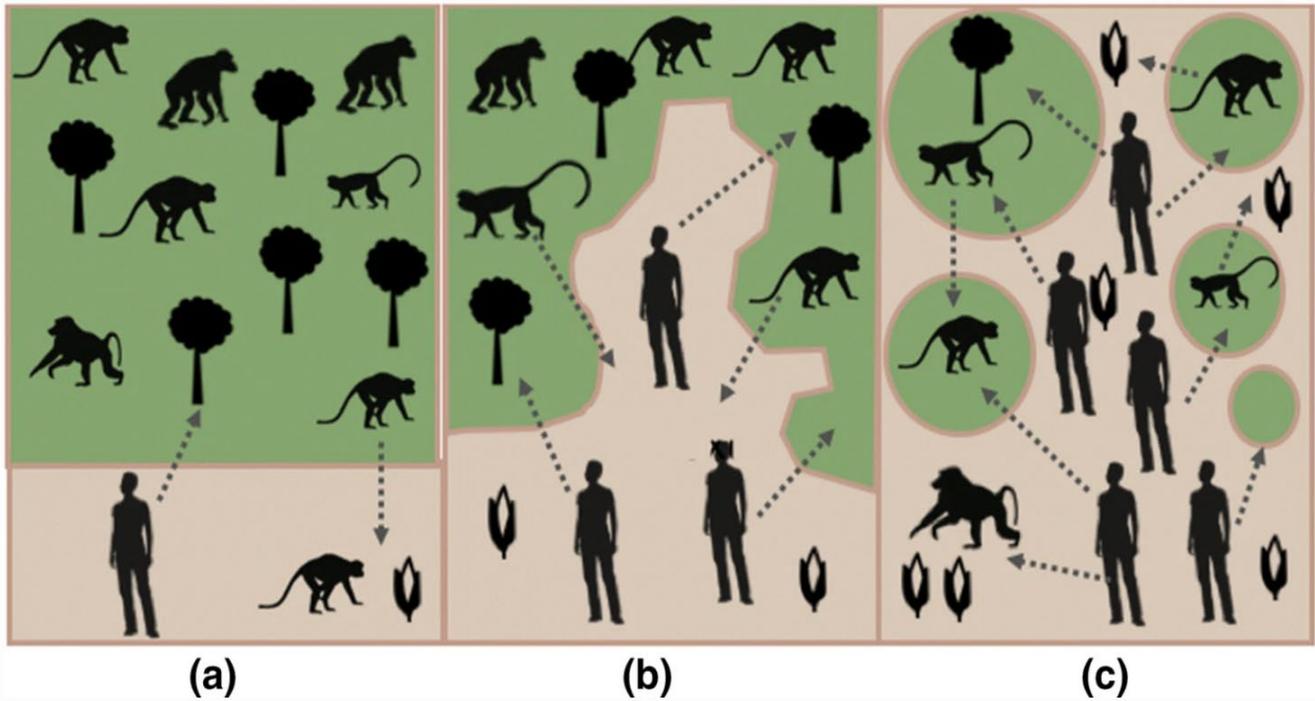
not lead to large outbreaks because the frequency of contact is lower. One exception to this, is when 80% to 90% of the land is converted. At this point, outbreaks are rare since the contact points are decreased from the lowered edge density, however when outbreaks do occur they are larger and more severe. These outbreaks are more severe because the larger matrix habitat can support a larger susceptible population (16).

The relationship between core, matrix, and edge habitats is an important factor to understand how different land conversions can lead to disease transmission. Each type of land conversion, including deforestation, urbanization, and cultivation, can exacerbate this relationship in different ways. In each of the following sections the specifics of each land use change will be explored and supported with case studies.

Deforestation:

Deforestation increases the chance that humans will come in contact with zoonotic diseases by directly impacting edge density. As core habitat is taken away, smaller pockets of core are made that are interconnected by matrix. This conversion creates a multitude of edge densities where there is increased contact between the matrix and core populations as seen in Figure 4. In Uganda it was found that habitat loss by the Kibale National Park created more contact points between humans and the primates living in the core habitat that remained (17). The increased contact was seen as wildlife entering the matrix to find food or passing through the matrix to reach a different core habitat. The increased contact was also seen as humans or domesticated animals going into the core for supplies, hunting, or exploration (17). These different routes of contact between humans and wildlife are common in edge densities.

Figure 4. How contact points are affected by changes in edge density

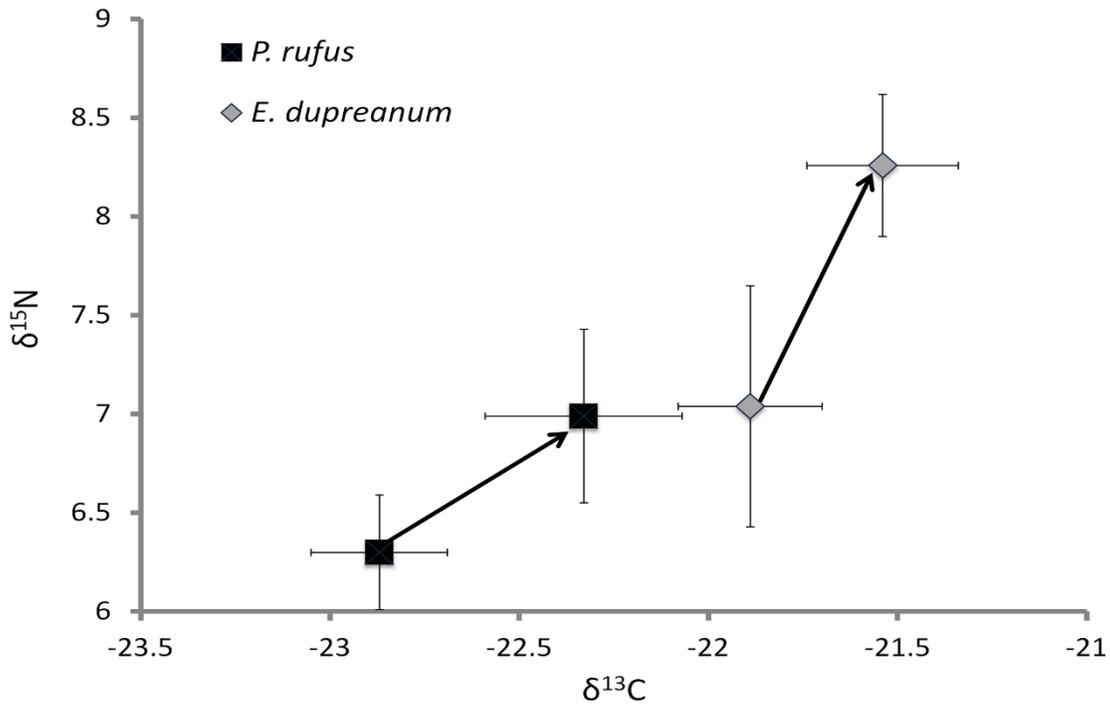


Depicts how deforestation and urbanization that extends into natural habitats of disease hosts can lead to increased point of contact between disease hosts and humans. This figure specifically depicts the interactions between humans and non-human primates (17).

One study on bats in Madagascar highlights in detail how deforestation can cause a change in behavior in core populations that leads to increased contact with humans. Bat species in Madagascar can spread filoviruses, Hendra virus, and henipavirus (18). In Madagascar more than 80% of the forest has been removed, with the remaining 20% being mostly fragmented and degraded. This has led to a change in habitat and behavior of the local bat species. The stable isotopes $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ within bat droppings can be used to analyze what the bat has been dieting on and to infer the preferred habitat of the different species. The $\delta^{15}\text{N}$ levels would increase if the bats were feeding on commercially grown fruits due to the higher nitrogen values in agricultural soils. The $\delta^{13}\text{C}$ levels can be used to analyze the seed dispersal habits and vertical stratification habits of the bats. If the bats feed at a higher stratification, then their $\delta^{13}\text{C}$ levels would drop. If the seeds are dispersed in a matrix site instead of a core forest, then the $\delta^{13}\text{C}$ levels would

increase. This study gathered data on three species of bats including *P. rufus*, *E. dupreanum*, and *R. madagascariensis*. The *R. madagascariensis* had a very low sample number of 7 individuals so the data on these bats is inconclusive. However, changes in habitat and diet were seen for *P. rufus* and *E. dupreanum*. It was found that *E. dupreanum* feeds more on commercially grown fruit and uses degraded habitat more than *P. rufus*. The authors assumed that this change in behavior could be caused by *P. rufus*, the larger of the two species, forcing *E. dupreanum* into the lower and worse habitats. This conclusion was supported by the fact that *P. rufus* prefers the higher canopies and by the fact that when *P. rufus* is in a degraded habitat without high canopies, it displaces *E. dupreanum* to an even more degraded habitat further into the matrix. This diet change is depicted in Figure 5 which shows the change in isotope levels when the two bats are caught in the same area (19). In these degraded habitats, despite the species displacement, it is possible that the two species of bats will be feeding off the same trees. When bats of different species visit the same trees, interspecies virus transmission can occur. The bats can feed off of the same fruits and share diseases through their infected saliva (20). The change in habitat preference along with the bats overlapping in feeding habits increases the potential for disease spillover from bats to humans as it increases the potential for contact between an infected bat and a susceptible human. The study of changing bat behavior in Madagascar is just one of many examples on how deforestation creates new opportunities for pathogens to spill over into humans and domesticated animals.

Figure 5. Dietary changes of *P. rufus* and *E. dupreanum* when caught together



When the two species of bats were caught together their diets shifted significantly. This shift is seen at the end of the arrows.

Another shared pathway of contact that increases with edge density is the sharing of disease through vector and parasite transport (16). Deforestation can lead to an increase in mosquito populations. Clearing out the trees and plants in an area increases the amount of sunlight the habitat receives and increases the chance for pools of water to form with an ideal pH. This creates an ideal breeding ground for mosquito larvae (7, 8, 13). The increased sunlight can also increase the temperature in the area. Higher temperatures can lead to a decrease in larvae maturation rates, an increase in adult mosquito life spans, and an increase in the vector capabilities of adult mosquitoes (6, 7, 21). The vector capabilities are increased because the higher temperatures lead to increased biting frequency and decreased pathogen maturation within the mosquitoes (6). These effects caused by deforestation that led to increased contact rates are the general trends seen for vector mosquitoes, but the effects can vary between species (6, 8).

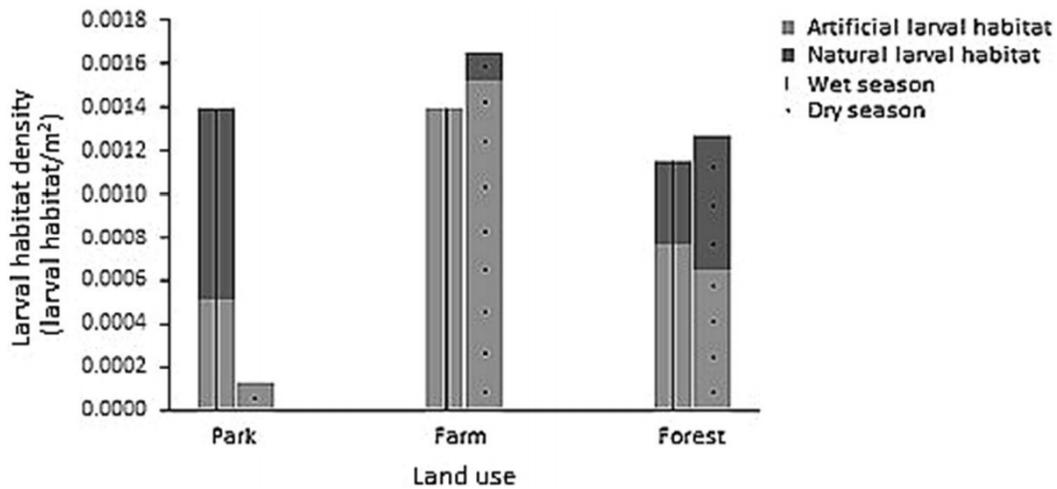
Deforestation can also affect the compositions of mosquito species. Vector mosquito species preferred the cleared out land while the non-vector mosquito species preferred the undisturbed forests (7, 8, 13). When deforestation led to humans interacting more in the Kruger National Park in South Africa, it was seen that the impacted bodies of water housed more mosquitoes and changed the composition of the mosquito population to support vector species like *Aedes aegypti* and *Culex* species over non-vector species (7, 22).

Deforestation causes an increase in disease transmission rates by creating more edge density and by changing species compositions. Often times deforestation is only the first step for land use changes. It can be followed by urbanization or cultivation which can both further alter transmission rates in their own way.

Urbanization:

Urbanization is the process of developing an area of land into a city while the human occupancy increases (5). The definition of “urban” can vary greatly across countries. High degrees of urbanization can lead to a decrease in disease transmission from better health care, nutritional access, clean water sources, increased education, and more (1, 23). However, highly urban areas can also create new breeding grounds for vector populations as seen in Figure 6 (23). In Malawi, small scale subsistence agriculture in more developed areas increased the abundance of vectors (23). The increased abundance is likely an effect from agriculture creating new microclimates for vector development. In the Amazon region it was found that these microclimates could be found in Ecuador and caused an increase in malaria transmission from the increase in vector populations (21).

Figure 6. Land use changes increase vector breeding grounds



There are more breeding grounds created in urbanized areas like the farm and the park than the forest. The one exception is that the park has less breeding grounds in the dry season. This difference could be seen because the forest sites were ones that included hiking trails and could have a high amount of available blood meals (5).

Lower degrees of urbanization that more closely resemble a rural environment than a well-developed one often see an increase in disease transmission (23). Developing countries exhibit rapid urban growth that is not well supported with health care or infrastructure, leading to increased disease transmission (8, 24, 25). In Central and South America, unplanned and uncontrolled urbanization created new larval habitats. Mosquitoes were able to breed in water containers, drains, and gutters with little to no competition or predation (5, 8). The new habitats led to a high mosquito density that created an increase in dengue virus transmission (8, 24, 26). In Blantyre, Malawi it was seen that less developed areas had a higher incidence of mosquitoes that are vectors for malaria. Houses farther from the city center, with thatched roofs, and open eaves had more mosquitoes than houses closer to the city center, with iron or tile roofs, and closed eaves (23). People in rural areas are more likely to be exposed to infected wildlife from their daily activities as well. Most contact points that led to seropositivity of bat-borne diseases

in rural Southern China occurred when raising poultry or having rodents or shrews in the house (27). The increased exposure in an urban environment can also be seen when well-developed cities experience unprecedented growth. In Asia after World War II there was a large migration into the city. The influx of people could not be supported by the infrastructure which meant many people had little sanitation, running water, or health care. This allowed dengue virus vectors to increase from the increase in available people to feed on which caused dengue virus to be a leading cause of morbidity in southeast Asia (8).

Rapid expansion of urbanization can also lead to an increase in contact points due to increased edge densities. For example, creating new roads through core habitat to connect growing places of urbanization can lead to pathogen spread (28). In rural Ecuador it was found that road development caused an increase in transmission of diarrheal disease due to increasing flooding. The increase in flooding lowered the water quality which allowed more pathogens to build up (28). The increase in edge densities from urbanization cause an increase in bushmeat hunting and wildlife trade that is encouraged by local markets (14). Bushmeat hunting can lead to a variety of diseases being spread to humans through increased bites and through contaminated meat (17). It is believed that bushmeat hunting is what caused HIV-1 spillover from primates to humans (17).

A study on bats in Australia can highlight how rapid urbanization can lead to a change in contact rates between bats and horses. Bats are known to be carriers of coronaviruses, filoviruses, henipaviruses, and more (29). In Australia, bats can deliver Hendra virus to horses. While it is extremely rare that the virus is then delivered to humans, having only had 7 reported cases from 1994 to 2013, it is still a risk (30). One study found that as urbanization in Australia continues, the bat niches were expanding into the agricultural areas. This habitat expansion led to

an increase in spillover from the bats to horses (31). The urbanization also caused the natural metapopulations of bats to split into smaller populations. This split meant less bats would be exposed to Hendra virus on a regular basis. On the surface, this seems like a good fact, however it causes a decrease in immunity across the bat population. Normally the virus is dispersed across the metapopulations of bats which causes the bats to develop an immunity to the virus. This immunity means each individual typically has a small viral titer which makes it harder to spill over into other susceptible species. When broken into smaller populations, the bats are not regularly exposed to the virus, so they do not have a strong immunity to it. A decreased immunity causes the exposed bats to get a higher viral titer which makes them more infectious. An increase in the bats infectious level in turn causes an increase in viral spillover to horses (31).

Urbanization causes an increase in disease transmission rates in humans by creating new vector habitats and by creating increased contact rates from changed wildlife and human behaviors. Land use changes caused by urbanization are ever expanding as the population increases and spreads to new territory. The land use change is also expanded because urbanization is often accompanied by land cultivation to support the growing population of humans.

Cultivation:

Land cultivation can lead to an increase in disease transmission by creating new breeding grounds and feeding reservoirs for vector populations. The new breeding grounds can be formed when creating irrigation or when terraforming the land. The new feeding reservoirs are created by increased livestock populations. Cultivation can also impact the local wildlife by altering their habits and compositions.

New vector breeding grounds can be created by irrigation and dams that are built to support cultivation. In Asia, the introduction of clean water increased the population of the vector for lymphatic filariasis whereas the creation of more stagnant puddles from the cleared out land increased the population of the vector for Japanese encephalitis (8). The increased vector population is not a universal trend across all vector species and habitats. In both Africa and Asia it was seen that land conversion to irrigation at first increased the spread of malaria, but eventually lowered transmission rates. It is unclear as to why this change occurred, but it could be from the better infrastructure created from the increase in crop production. The change could also have been caused by the irrigation eventually limiting vector populations (8).

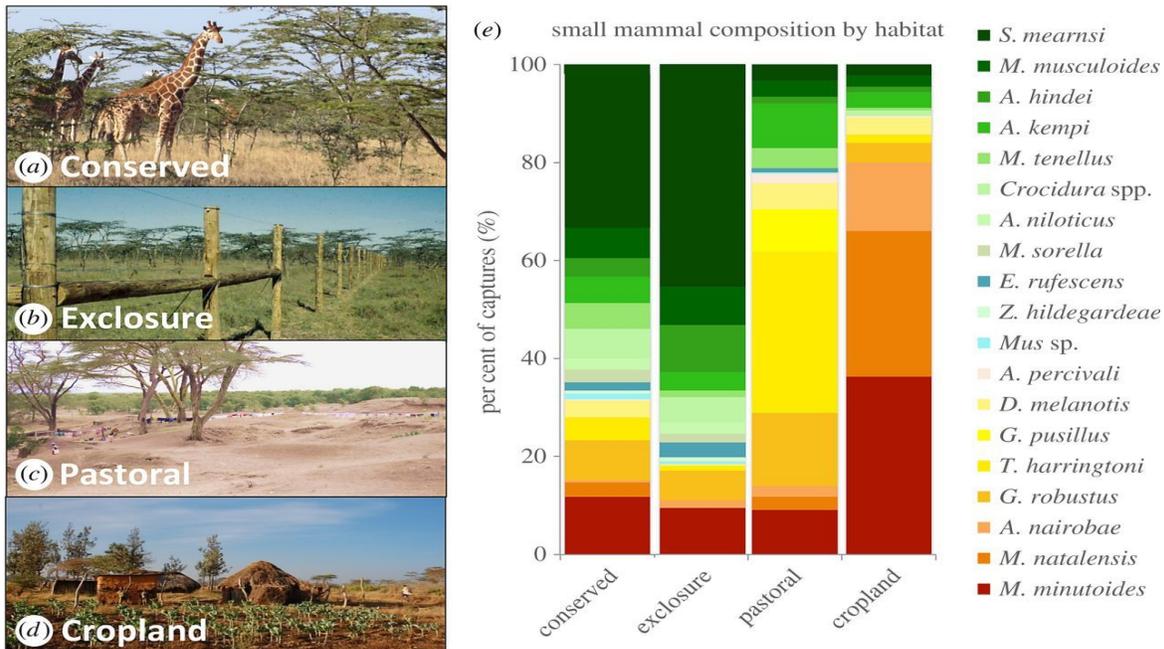
Terraforming the land to create agricultural landscapes can also impact vector breeding grounds. The south-western highlands of Uganda began draining and cultivating papyrus swamps in the early 1940's. Shortly after this in 1946 there was an outbreak of malaria (6). Typically, the highland areas are not susceptible to malaria outbreaks due to the cooler temperatures being inhospitable to mosquito larvae. This makes highland human populations more vulnerable to malarial outbreak than lowland populations since the highland population does not have any immunity to the disease (6). The uncharacteristic outbreak was caused by land terraforming in the cultivated swamps. When comparing the transmission parameters between communities near a natural swamp to those that are near a cultivated swamp, the latter had a consistently higher mosquito density after the wet season. The cultivated swamps had ditches formed between ridges for agricultural use in which mosquito larvae could be found. The difference in mosquito density between the two communities was not statistically significant, but it resulted in the communities near a cultivated swamp receiving an infectious bite at a seven fold increased rate (6).

Mosquito disease transmission rates can be affected by livestock populations as well.

Livestock production increases available blood for mosquitoes in a potentially competent reservoir that could maintain or amplify zoonotic pathogens (8, 13). Amplification of a zoonotic pathogen was seen in Asia where pig farming amplified Japanese encephalitis transmission. The pigs were able to mount high concentrations of the virus which increased the number of infected vectors in the area (8, 13).

Land cultivation can also affect mammalian disease hosts as seen in Figure 7. A study conducted in central Kenya found that cropland cultivation creates a change in the composition of rodent populations and tends to favor rodents that increase disease transmission rates (32). Areas where the large wildlife was lost had increases in small mammal populations like rodents. These increases were likely due to the loss of competition for food and a decrease in predation (32).

Figure 7. How species compositions change in response to land use changes



The species composition changes to support more host species than non-host species when land use changes occur. In the converted crop-land the *M. natalensis* population increases and it becomes a higher percentage of the overall species composition (32).

One major small mammal host is the mouse *M. natalensis*. This species of mouse is a common household and agricultural rodent that is a hyper reservoir for zoonotic disease including the plague (11, 32). It is one of the species that increases in response to land use change as shown in Figure 7. In East Africa, land cultivation has expanded by more than 70% in the last several decades (11). In Northern Tanzania it was found that a species of mouse, *M. natalensis*, that is highly competent for the plague, *Y. pestis*, was 20 times more abundant in agricultural sites than core habitats. The flea composition was also affected by the land cultivation. One of the two common vectors was only found in agricultural sites and the other common vector was five times more likely to be found in the agricultural site than in the conserved site (11). While there are still many avenues to be researched in this area, like the biting frequency of the two fleas, this data suggests that the cultivation of the land increased the transmission risk of the plague in this area by doubling the number of seropositive rodents in the area, creating a more competent vector community, and by having a largely susceptible human population in the cultivated matrix area (11). This case study is a direct example of how cultivating core habitats can change the composition of wildlife and in turn change disease transmission rates.

Conclusion:

Land use change is leading to an increase in disease prevalence. There are three main steps that must be taken to respond and mitigate the increase in disease outbreak: understanding, prediction, and prevention (33).

First it is important to fully understand the effects that are occurring. The key to understanding how pathogen transmission will change in response to land use changes is to have

a holistic approach. Research should be done that targets specific diseases and habitats to understand how the pathogens will respond to changing environments. The research should demonstrate which biodiversity theory the pathogen will follow, how the current hosts will respond to increasing edge densities, and whether species compositions will change. It is important to fully research and understand how the various factors are impacting each disease so we can learn to adapt to the changes occurring.

The next important step is prediction. It is unlikely that humans will be able to stop expanding into natural habitats. Using the research suggested above, it should be possible to predict how the land use changes will impact disease transmission. Predicting the suspected changes will allow populations to properly protect themselves by taking steps to avoid the interactions.

The final step is prevention. This step focuses on preventing the impacts of land use change by finding ways to sustainably clear, cultivate and urbanize land so that habitats are not degraded in the process. Restoration projects can also be incredibly important. Restoring natural habitats that were degraded and are no longer being used can help create new core landscapes for wildlife to occupy. Restoration can also help foster biodiversity which can be beneficial in controlling certain pathogens.

Following these three steps will require a combination of ecological and epidemiological practices along with increased funding and support. If completed successfully, the number of emerging zoonotic diseases should decrease.

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