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PREDICTING THE SPREAD OF WHITE-NOSE SYNDROME IN BATS:

A Strategy for Prioritizing Resources

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ABSTRACT

In 2006, cavers near Albany, New York first documented a few hibernating bats with a curious white fungus growing on their muzzles. Over the next seven winters, the aptly named white-nose syndrome (WNS) has decimated bat populations throughout the eastern United States, causing average declines of over 70%. The migration of WNS westward into regions with higher bat diversity and more extensive cave systems has potentially catastrophic consequences for species populations and the ecosystem services they provide. Predicting areas particularly susceptible to WNS as well as potential pathways for transmission of its fungal spores across the U.S. can inform targeted management practices. However, data on bat population sizes, locations, and dynamics is scarce. This analysis uses the limited data available to highlight areas of particular concern. Susceptibility to WNS infection at the county level was calculated using three variables: number of potential roost sites, bat species, and approximated cave temperature. Potential pathways of spore transmission were identified using susceptibility ratings and estimates of past dispersal distances. The results identify counties of interest in the Rocky Mountains and Pacific Northwest as well as a potential corridor facilitating transport of fungal spores into western states from Oklahoma and north Texas to eastern Colorado. Targeting these areas for future research and monitoring efforts could be an efficient use of limited resources and potentially curtail the impacts of this devastating epizootic.

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INTRODUCTION

In February 2006, cavers photographed a few bats in Howes Cave near Albany, New York with a curious white fuzz on their muzzles (Puechmaille *et al.* 2011a). Seven years later, over five million bats have died from the aptly named white-nose syndrome, prompting national response to this emerging epizootic (Statement of Gabriela Chavarria, Congressional Oversight Hearing, p. 7-8). White-nose syndrome is the first documented epizootic affecting bats (Foley *et al.* 2011), and is causing some of the fastest population decline rates observed in wild animal populations due to disease (Willis *et al.* 2011).

With rapid onset and high mortality, epizootics can complicate conservation efforts. Typically, the origins, dispersal mechanisms, and modes of killing in emergent diseases are poorly understood at the start of the outbreak, making it possible for epizootics to spread worldwide before scientists understand how to manage the disease and minimize its spread (Puechmaille *et al.* 2011a). As white-nose syndrome migrates westward into the population ranges of many new species, techniques to assess the threat white-nose poses to a given area are crucial to managing the spread of this disease. If the potential risk for white-nose syndrome is understood, resources can be directed to protect or quarantine areas with the highest risk, making the most efficient use of limited funds. Unfortunately, data on bat populations in North America is sparse at best. However, this limited information can be used to highlight areas of potential concern for targeted research and management practices.

WHITE-NOSE SYNDROME: AN OVERVIEW

Defining White-Nose Syndrome. White-nose syndrome (WNS) is a pathological infection caused by the newly described fungus *Geomyces destructans* (Puechmaille *et al.* 2011a). This cold-loving fungus invades the skin tissues of cave hibernating bats, causing the myriad of symptoms categorized as WNS (Cohn 2012). Bats affected by WNS suffer from frequent arousals from winter torpor, depleted fat reserves, and damaged wing membranes. Mortality from WNS is common (Puechmaille *et al.* 2011a).

The exact mechanism by which *Geomyces destructans* (Gd), and its associated WNS, causes death is unknown. Scientists suspect that the infection resulting from Gd disrupts physiological processes during hibernation (Reeder *et al.* 2012). The cycle of hibernation torpor and arousal is a natural process, but increased periods of arousal are well documented in bats suffering from WNS (Cryan *et al.* 2012). Arousal is a metabolically expensive process, as bats must significantly increase their metabolic rate to

warm their body temperature to a normal level (Reeder *et al.* 2012). Typically, total time spent in arousal is generally less than one percent of total hibernation time (Willis *et al.* 2011). Reeder *et al.* (2012) found an overall shorter torpor length in WNS bats and a positive correlation with infection severity and number of arousals. Bats that died via WNS had a significantly shortened average torpor, and correspondingly higher numbers of arousals. A normal number of arousals during hibernation will consume 80-90% of the bat's energy reserves (Reeder *et al.* 2012). As many cave-hibernating bats feed on arthropods, opportunities to replenish these energy stores during winter are scarce (Fenton 2012). Therefore, an increased number of arousals can quickly become unsustainable (Reeder *et al.* 2012). Further, bats with WNS are often seen roosting more closely to the entrances of hibernacula as winter progresses, perhaps relying on passive energy absorption from the sun to rewarm their bodies, rather than using their depleted energy reserves (Willis *et al.* 2011). Researchers believe the increase in arousals requires bats to use up their energy reserves before spring, leading to an acute cause of death of starvation (Fenton 2012).

Although fungal growth on the muzzle is the obvious symptom of WNS (Cryan *et al.* 2012), damage to the wing tissue may be a far more important consequence of Gd infection (Willis *et al.* 2011). Wings comprise four to eight times the exposed skin tissue of the rest of a bat's body and they play a key role in homeostasis and daily life. However, the wing tissue damage can be subtle, and thus could be underappreciated as a primary cause of death (Cryan *et al.* 2012).

Gd may affect several key functions of wing tissue, but increased water loss has gained the most traction as a significant impact. In general, bats are highly susceptible to water loss through both their wings and lungs. Healthy wings are essential for maintaining proper water balance and damaged wing tissue may be more vulnerable to increased water loss. Species seemingly more susceptible to WNS (*M. lucifugus*, *M. septentrionalis*, and *P. subflavus*) tend to roost tightly clustered in more humid environments suggesting that they may be more vulnerable to evaporative water loss than other species less impacted by WNS (*M. sodalis*, *M. leibii*, and *E. fuscus*). Unfortunately, the same behavioral modifications adapted to prevent water loss may also increase sensitivity to WNS (Cryan *et al.* 2012). Willis *et al.* (2011) confirmed that little brown bats (*M. lucifugus*), a species highly susceptible to WNS, exhibit higher evapotranspiration rates than Natterer's bats (*M. nattereri*), a species that appears to carry the fungus, but does not develop WNS, lending support to this theory. As dehydration is commonly listed as a contributing factor in WNS mortalities, scientists linked the increase in evaporative water loss

with increased arousals from torpor. WNS affected bats have been observed drinking water and eating snow during winter, suggesting that thirst could drive arousals from torpor (Cryan *et al.* 2012).

Other potential effects of Gd on wing tissue include interference with circulation, physical damage, interference with gas exchange, and loss of natural skin secretions. Circulation could be adversely impacted via two seemingly opposed mechanisms. First, the fungus could restrict blood flow to the wings, causing tissue damage via loss of oxygen. Second, bats naturally restrict blood flow to their wings during arousal to enhance metabolic warming of their core temperature. Damaged caused by Gd could allow unrestricted blood flow to the wings, causing rapid heat loss and therefore rapid energy expenditure. Physical damage to the wing tissue (loss of elasticity and tone, causing membranes to stick together and easily tear) could disrupt flight mechanics, decreasing wing control or stabilization. Bats may also rely on passive gas exchange through wing tissue during hibernation, as respiration drops significantly. A loss of this ability could trigger increased respiration and increased water loss through the lungs. Finally, Gd may eliminate natural secretions that moisturize and waterproof healthy wing tissue. These secretions could also protect the skin tissue from other microorganisms (Cryan *et al.* 2012).

Researchers also suspect that hibernation reduces the immunological response to Gd and that increased arousals from torpor is an attempt to increase immune system functioning to fight the fungus (Reeder *et al.* 2012). However, the sudden, extensive immune response upon arousal could induce a phenomenon known as immune reconstitution inflammatory syndrome (IRIS), first identified in human AIDS patients. IRIS can cause severe tissue damage, resulting in death (Meteyer, Barber & Mandl 2012).

Wing tissue damage and increased arousals from torpor are likely connected and interact to severely compromise bats affected with WNS. However, bats that survive the winter have the potential to heal damaged wing tissue during the summer months (Fuller *et al.* 2011). Much remains unknown about bats that survive exposure to WNS, including susceptibility to future infections, increased likelihood of mortality due to a subsequent infection, and functionality or regeneration of healed tissue.

Susceptibility to *Geomyces destructans* and WNS. Hibernating bats are ideal hosts for *Geomyces destructans*. Gd thrives at temperatures between 12.5 and 15.8⁰C, and cannot grow at all above 19.8⁰C (Verant *et al.* 2012). North American bats commonly roost in caves between 3 and 15⁰C (Foley *et al.* 2011). During hibernation, bats reduce their body temperature to near ambient air temperature levels to conserve energy and generally hibernate in humid environments to reduce evaporative water loss while in torpor (Willis *et al.* 2011). The reduced temperature of the bats combined with a moist

environment serves as excellent growing conditions for Gd. Further, hibernation suppresses immunological response, thereby enabling the fungus to spread unchecked (Cryan et al. 2010).

Mass mortality events do not always translate to reduced probability of long-term species survival. However, several life history traits unique to bats suggest that WNS may have significant impacts on species survival and recovery. Compared to other small mammals, bats are long-lived, (five to fifteen years) (Statement of Gabriela Chavarria, Congressional Oversight Hearing, p.7-8), but slow to reproduce, and generally have only one offspring per year (Fenton 2012). Many individuals fail to survive the first winter under the best circumstances and therefore never reproduce and pass their genes to the next generation. This combination of low fecundity and survival reduces the ability of populations to recover from the swift and extensive mortalities caused by WNS (Fenton 2012).

Although WNS is a potential threat to all temperate bat species, only cave hibernating species within the family Vespertilionidae are currently affected by the syndrome. This family includes 36% of all bat species worldwide (407 species) and has the greatest species richness in northern, temperate regions. No species outside this family range within the current extent of WNS, and therefore the potential impacts of this outbreak on other bat families is unknown (Puechmaille *et al.* 2011a).

Several characteristics common to Vespertilionid bats potentially enhance their exposure to Gd. Group formation and disbanding through seasonal social interaction increases the probability of spreading Gd between individuals. Both sexes roost together in winter hibernacula. However, they separate during the spring and summer, with males roosting alone or in small groups while females move into maternity colonies to raise offspring communally. As autumn approaches, males and females swarm together, mating prior to winter hibernation and enabling transfer of the fungus between colonies. Further, several species congregate at cave entrances before beginning hibernation, allowing transfer of the fungus between species (Foley *et al.* 2011).

Currently, seven cave hibernating species in the eastern United States have suffered mortalities attributed to WNS (USFWS 2012), with average population declines of 73% (Brooks 2011). Several of these species co-occur in the same hibernation sites, but with varying abundance and social behaviors (Langwig *et al.* 2012). Another two species carry the fungus, but have yet to develop the symptoms of WNS (Table 1) (Puechmaille *et al.* 2011a).

Scientific Name	Common Name
<i>Eptescius fuscus</i>	Big brown bat
<i>Myotis austroriparius</i>	Southeastern bat
<i>Myotis grisescens</i>	Gray bat (endangered)
<i>Myotis leibii</i>	Eastern small-footed bat
<i>Myotis lucifugus</i>	Little brown bat
<i>Myotis septentrionalis</i>	Northern long eared bat
<i>Myotis sodalis</i>	Indiana bat (endangered)
<i>Myotis velifer</i>	Cave bat
<i>Perimyotis subflavus</i>	Tri-colored bat

Table 1. Bat species diagnosed with WNS (red) and species testing positive for the Gd fungus (black).

Of the species currently affected by WNS, the little brown bat (*Myotis lucifugus*) has suffered the greatest losses. The little brown bat was once the most common species in the northeast United States, but many hibernacula have dropped upwards of 90% in size, prompting speculation of regional extinction within a decade (Cohn 2012). Northern long-eared bats (*Myotis septentrionalis*) are the second most affected species (Willis *et al.* 2011). Of particular concern is the impact WNS may have on populations of endangered species (Thogmartin *et al.* 2012), including the Indiana bat (*Myotis sodalis*) and gray bat (*Myotis grisescens*) (Foley *et al.* 2011). Populations of Indiana bat stabilized throughout the northeast between 1983 and 2005 and were even increasing throughout the Appalachians. However, based on surveys conducted in 2009, populations in the northeast are now decreasing and the growth of Appalachian populations has halted (Thogmartin *et al.* 2012).

The Extent and Transmission of *Geomyces destructans* and WNS. The first recorded cases of WNS occurred near Albany, New York in 2006. Subsequent surveys found Gd in all caves within a 130-kilometer radius of the initial site, with no occurrence beyond 200 kilometers (Puechmaille *et al.* 2011a). As of April 2013, WNS was found in twenty-two states and five Canadian provinces, having traveled north to Quebec, south to Alabama, and west to Missouri (USGS 2013) (Figure 1).

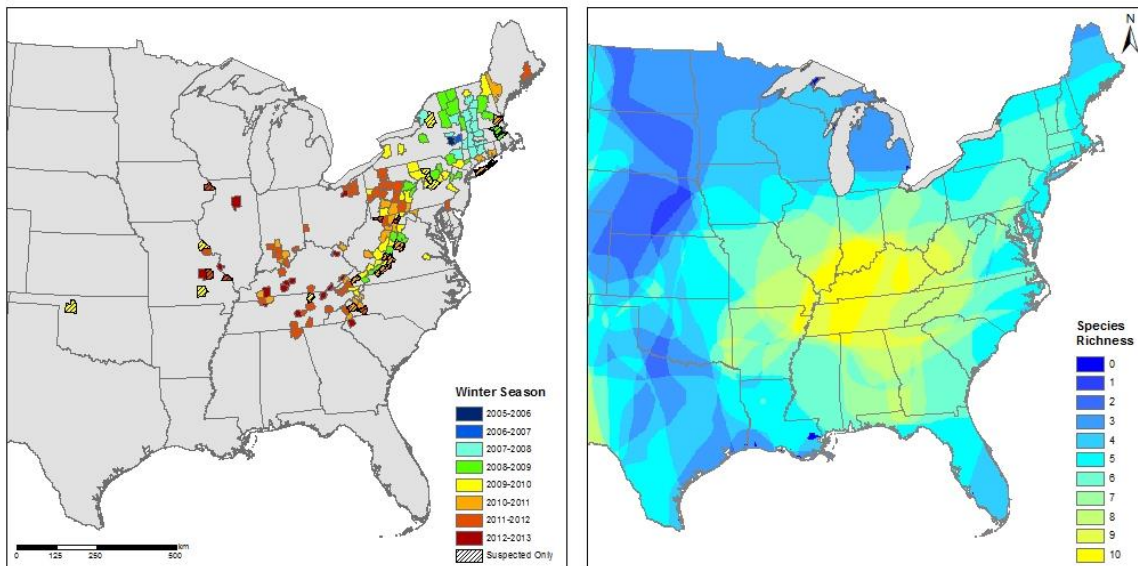


Figure 1: Spread of White-Nose Syndrome throughout the U.S. Solid colors denote counties with confirmed cases of WNS while lined counties have only suspected WNS cases (Canada not shown) (left). Species richness of cave hibernating bats in the eastern US (right).

* Georgia counties (confirmed in March 2013) not shown.
(Counties identified with WNS provided by Cal Butchkoski 2013.)

Although the exact means of transmission and spread are unknown, scientists suspect the fungus can be transferred via bat-to-bat contact and between bats and hibernacula substrate (Foley *et al.* 2011, Lorch *et al.* 2012). Humans are also a potential disease vector, transferring spores between caves (Statement of Justin Boyles, Congressional Oversight Hearing, p. 46). Direct bat-to-bat transmission is presently considered the most prevalent mode of transmission (Statement of Gabriela Chavarria, Congressional Oversight Hearing, p. 7). As discussed previously, bats can be gregarious species and transmission of Gd spores between individuals via simple daily contact, within summer maternity roosts, and within winter hibernacula is possible (Foley *et al.* 2011). Langwig *et al.* (2012) found higher mortality rates in species with larger pre-WNS populations as well as in highly social species that roost in tightly packed clusters, suggesting that transmission of Gd and WNS can be both density dependent and frequency dependent. Conversely, they found little evidence supporting either colony size or number of heterospecifics as a predictor of mortality from WNS. However, they caution this conclusion should be tested further (Langwig *et al.* 2012).

Because viable Gd spores have been found on the surfaces of hibernation sites, transmission between cave and bat is possible. Viable Gd colonies have been propagated from spores collected in late summer and from sites devoid of bat activity for at least one year prior to spore collection (Puechmaille *et al.* 2011b). Given these results, it is likely that Gd spores can survive without a host for extended periods and can infect new hosts upon the return of bats to infected hibernacula.

The Origins of *Geomyces destructans*. Once scientists identified Gd as the cause of WNS in the US, European scientists began closer examination of caves and bats throughout Europe. Reports of a white fungus on bats throughout Europe date back several decades, although the particular species had never been identified. Scientists discovered that Gd is associated with nine species of European bats in nine countries; however, Europe has never seen the mass mortality events associated with Gd in the US and the syndrome itself is only known from North American bat populations (Puechmaille *et al.* 2011b).

Several hypotheses have been proposed regarding the difference in impact of Gd in Europe versus North America. The most prominent hypothesis suggests that Gd is native to Europe and was accidentally transferred from Europe to the U.S. via a caver or a bat researcher. The rapid increase in mortality among North American species reflects the impact of a new pathogen on naïve populations (Puechmaille *et al.* 2011a). European bats possibly coevolved with Gd, and therefore populations are naturally more resistant (Cohn 2012) or a past outbreak of Gd in Europe could have left individuals with a higher tolerance of evaporative water loss or that tended to hibernate in drier environments (Willis *et*

al. 2011). That a fungus has been noted in Europe for several decades while no such evidence exists in the U.S. supports the hypothesis of accidental introduction of Gd from Europe (Puechmaille *et al.* 2011a). Further, the Gd strain found in North America has no genetic variability unlike the European strain, suggesting the fungus has been present longer in Europe than in North America. The North American strain is also less virulent than its European counterpart and could have evolved to be less deadly as its North American hosts die so readily (Raloff 2012).

Alternative hypotheses suggest that either Gd is a newly evolved pathogen of unknown origin or a new particularly virulent strain of a previously harmless fungus. However, if Gd originated via either of these methods, its distribution should be more widespread, rather than centered in an initial infection site (Puechmaille *et al.* 2011a). Lorch *et al.* (2012) demonstrated that the distribution of Gd is closely tied to areas with active WNS, supporting the notion that Gd is a new pathogen to North America, and not merely a new virulent strain of an existing pathogen. Scientists have also examined bats apparently killed by WNS for another possible agent, hypothesizing that Gd is not a primary cause but a secondary effect on immunocompromised individuals. However, no other biological agent or environmental contaminate (such as a toxin) has been identified (Puechmaille *et al.* 2011a). Further, Lorch *et al.* (2011) proved that exposure of little brown bats to Gd under experimental conditions causes white-nose syndrome. Thus, the prevailing theory is that Gd was accidentally introduced from Europe into naïve North American bat populations.

However, if Gd evolved in Europe, why was it never identified? I speculate that because Gd is not associated with mass mortality, no driving factor existed to identify the fungus seen on bats throughout the continent. Gd could also be less prevalent, because of the Mediterranean climate throughout much of Europe, with its truncated winters. The timing of bat surveys in Europe could also explain the lack of concern for Gd. Historically, surveys for bat populations in Europe occur between December and February. Gd begins to become visually apparent on individuals in January, with presence increasing in February and peaking in March. Therefore, the majority of surveys occur prior to an obvious fungal growth on a large number of individuals. Further, research on fungus identification in Europe has previously cultured specimens at 25-30°C, a much higher temperature than Gd can tolerate and thus the fungus never appeared in cultures (Puechmaille *et al.* 2011b).

Because many of Europe's bat species originated farther east in Asia, scientists now speculate that Gd may extend its presence into Russia and western or even Central Asia. Confirming the global extent of this fungus is now a top priority for researchers (Puechmaille *et al.* 2011b).

THE IMPORTANCE OF BATS

One-fifth of all mammal species worldwide are bats (Puechmaille *et al.* 2011a), with over 1,200 known species (Fenton 2012). They have existed for over 52 million years and fill a variety of niches, roosting in caves or trees by day, and feeding on insects, fruit, nectar, seeds, amphibians, mammals, and even blood at night. Humans have persecuted bats for centuries, associating them with demons, witchcraft, and other negative aspects of western culture. Habitat loss, habitat degradation, and hunting pressure have historically threatened the long-term survival of bat species. However, the development of WNS in North America adds significant pressure to this already persecuted group, and heightens conservation concerns (Kunz *et al.* 2011).

Beyond a worldly desire to preserve biodiversity, why should people care about protecting bats? These small mammals play critical roles in ecosystem balance and provide a great economic service in terms of agricultural pest control (Boyles *et al.* 2011; Brooks 2011; Fenton 2012; Reeder *et al.* 2012). The diversity of bats translates to a diversity of ecosystem services (Kunz *et al.* 2011). However, because the threat of WNS is currently restricted to insectivorous species, the role of bats in insect population control will be the focus here.

Approximately two-thirds of all bat species are either obligate or facultative insectivores, consuming moths, beetles, flies, cicadas, and hemipterans (true bugs). Conservative estimates (based on captive animals) suggest bats can consume on average 25% of their body mass in insects nightly. The varying conditions in the wild increase these estimates, particularly for lactating females who may eat between 70% (Brazilian free-tail bat) to over 100% (little brown bat) of their body weights each night. In North America, one little brown bat can consume between four and eight grams of insects nightly. With one million little brown bats lost to WNS, insect predation has been reduced by 660 to 1,320 metric tons in areas impacted by WNS (Boyles *et al.* 2011).

The contribution of bats to ecosystem stability and diversity via insect population control needs no further emphasis. However, insect population control extends beyond natural ecosystems and into human-dominated agricultural landscapes. Worldwide, herbivorous insects destroy 25-50% of all crops. Researchers estimate that one colony of 150 big brown bats in Indiana consumes 1.3 million insect pests annually (Boyles *et al.* 2011). Traditional response to agricultural pests has been through the application of pesticides, prompting the evolution of pesticide resistance within species. Even with the widespread use of pesticides, the percentage of U.S. crops lost to insects has doubled in the last sixty to seventy

years (Kunz *et al.* 2011). Naylor and Ehrlich (1997) estimate the total pest control services of all species between 54 billion and 1 trillion dollars. Estimating the contribution of bats to pest control is difficult. The overwhelming scarcity of information on foraging behavior and diet for many bat species presents significant challenges (Kunz *et al.* 2011). However, Boyles *et al.* (2011) extended estimates of bat pest suppression value in the cotton fields of Texas across the U.S., concluding the extinction of bats in North America would cost the agricultural industry between 3.7 and 53 billion dollars annually (average of 22.9 billion). This estimate includes the reduction in pesticide needed because of bat predation, but does not consider the negative trickle-down impact of increased pesticide use on ecosystems (which could be substantial). Scientists estimate that the agricultural industry could begin seeing the impacts of bat losses in four to five years (Nina Fascione, Congressional Oversight Hearing, p. 25).

While bats are commonly touted as being nature's mosquito control system, the scientific community lacks consensus on the importance of bat predation on these pests. Studies indicate that mosquitoes only make up a small portion of the diet of insectivorous bats and draw no inferences on the impacts of bats predation on mosquito populations (Reiskind & Wund 2009). However, Reiskind and Wund (2009) concluded that predation by northern long-eared bats (*Myotis septentrionalis*), one of the species most heavily impacted by WNS, significantly reduces the number of mosquito eggs laid under experimental conditions, and therefore the number of larvae. Whether this result holds true under natural conditions has yet to be determined. Given that mosquitoes are vectors of human diseases, such as West Nile, bats could play an important role in mitigating the frequency and transmission of these diseases through mosquito population control (Reiskind & Wund 2009). This possibility merits further research and the results could be used to drive public interest in bat conservation and the threat of white-nose syndrome.

Undoubtedly, bats are important regulators of insect populations, both in natural and agricultural ecosystems. The loss of bats could have catastrophic impacts on these systems, potentially costing the agricultural industry billions of dollars annually in increased pest control measures. Further, bats may also contribute to the mitigation of human diseases transmitted by insects, and therefore may provide an invaluable service to public health. Combined, these factors create a strong case for conservation of bats, including understanding and attempting to constrain the spread of white-nose syndrome.

ADDRESSING THE CRISIS

The scope of this epizootic triggered a national response from a coalition of over one hundred groups, including several federal agencies (USFWS, NPS, BLM, and NFS), state governments, and a myriad of other organizations. The U.S. Department of the Interior led the creation of a seven-prong National Plan (Statement of Gabriela Chavarria, Congressional Oversight Hearing, p. 8), requesting 11.1 million dollars in federal funding for the fiscal year 2012. The funding proposal stressed the potential impact of WNS on tourism, possible job creation, the cost to recover endangered species (an average of 15.9 million dollars per species, but has the potential to be much higher) and the need to increase use of agricultural pesticides (Statement of Nina Fascione, Congressional Oversight Hearing, p. 28-29).

One of the first responses to WNS was the creation of decontamination procedures to ensure Gd spores would not be transmitted between caves via people (Hallam & Federico 2012). However, a further step has proven much more controversial, cave closures. Some organizations have advocated closing caves to the public to prevent human introduction of the fungus into new caves (Statement of Nina Fascione, Congressional Oversight Hearing, p. 29). Most states with WNS positive sites are currently implementing cave closures to varying extents (Cohn 2012). Kentucky, in particular, had great success in requesting voluntary closures of private caves (Statement of Jon Gassett, Congressional Oversight Hearing, p. 21). The caving industry has been less than pleased with this development, as caving is a popular hobby for many people and serves as a source of income for organizations and towns alike. In a hearing before a U.S. House of Representatives subcommittee, the National Speleological Society stressed the need for targeted management, not blanket management. Their representative argued that cave closures are ineffective because the primary mode of transmission of Gd is bat-to-bat. Therefore, minimizing activity by people is unlikely to curb the spread of this disease and only serves to economically hamper areas reliant on caving tourism (Statement of Peter Youngbaer, Congressional Oversight Hearing, p. 31-33). While this argument has merit, human movements have the potential to facilitate transmission of this fungus far beyond the scope of natural transmission levels within a given timeframe. That Gd was probably introduced from Europe via a person speaks to the potentially devastating impacts of human facilitated transmission. Further, natural barriers, such as the Great Plains of the central United States may slow the westward spread of WNS into naïve populations; however, natural barriers cannot limit human facilitated introductions (Statement of Justin Boyles, Congressional Oversight Hearing, p. 46). Because the potential for human introductions to be significantly more

devastating than natural disease transmission mechanisms, many organizations and agencies feel cave closures are a necessary step in mitigating the spread of this epizootic.

Scientists have proposed a variety of other possibilities to address either the spread of WNS or mitigate its impacts on bat populations. However, many of these suggestions would be difficult at best to implement at the scale of this epizootic. Changing the conditions within hibernacula, such as increasing temperature or humidity, or providing food and water resources, could decrease the stress bats experience with increased arousals. Altering humidity in particular however, would be a tricky prospect as the moisture levels that drive optimal fungal growth are currently unknown (Hallam & Federico 2012). Providing additional food resources would mitigate the loss of fat reserves plaguing WNS bats, but bats may not recognize a novel food source encountered during hibernation periods or may not be physically able to process food. Treatment of individual bats has also been suggested, but no effective method of treatment has been developed; likewise, vaccinating bats against Gd has potential, but may not be successful (Foley *et al.* 2011).

Other scientists have proposed culling bat populations with WNS in an effort to stem transmission between colonies. However, culling wild populations is difficult and would have a very negative perception in the public's eyes. Culling could unintentionally result in local extinctions or remove individuals naturally resistant to Gd from the population (Foley *et al.* 2011). Hallam and McCracken (2011) concluded that culling would be ineffective because of the high rates of bat-to-bat contact and periodic movement of bats between roosts.

Another possibility is to treat the caves themselves with an antifungal agent. However, blanketing caves with a broad-spectrum antifungal agent is risky. From an ecosystem perspective, the application of such agents would most certainly affect, if not destroy, the unique microbiota and their associated ecosystems within caves (Foley *et al.* 2011). However, this method is also risky for humans. Humans are dealing with an increasing number of fungal diseases and the widespread application of generic fungicides could promote the evolution of drug resistant strains (Justin Blehert, Congressional Oversight Hearing, p. 48). Further, as the primary mode of transmission is suspected to be bat-to-bat, treating caves may not prove incredibly effective (Foley *et al.* 2011). Currently, without the development of a species specific fungicide, treating caves is probably more risky than would be helpful. A problem with all of these suggestions is scale. Implementing any of them at a scale likely to mitigate WNS across the country is simply not realistic. Despite all of these suggestions, cave closures, though controversial, are probably one of the easiest and widely implementable solutions currently available.

MOVING FORWARD

Much has been accomplished in the last seven years in understand this novel epizootic: the cause is known, strides are being made in understanding how it kills, its origin is known, methods of detection have been developed, and protocols to reduce human facilitated transport have been created. However, the potential impacts of WNS on bat populations escalates as the disease progresses westward into regions with both larger caves and higher species richness. Of the forty-five species of bats within the

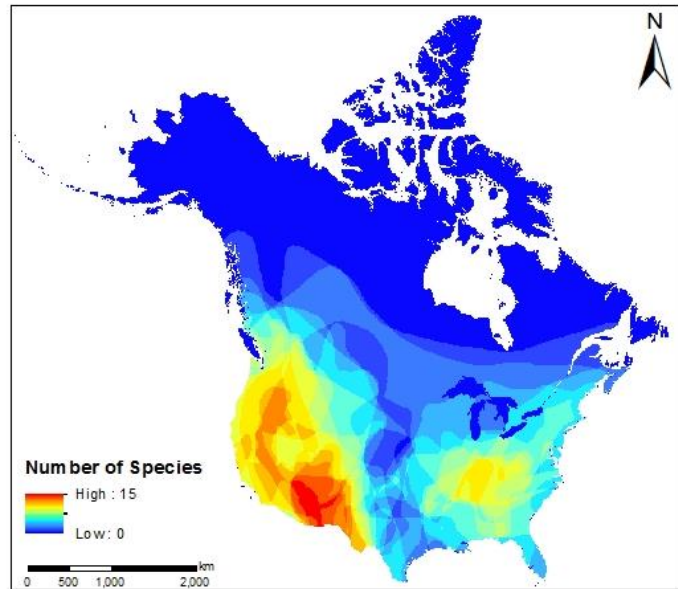


Figure 2: Species Richness. Species richness of cave-hibernating bats throughout North America

continental United States, twenty-five species are cave hibernating. The current extent of this epizootic now encompasses the majority of the remaining populations of two endangered species (gray bat and Virginia big-eared bat). The endangered Ozark big-eared bat may be at risk and USFWS is reviewing the status of the Eastern small-footed bat and the Northern long-eared bat to see if their population declines merit endangered species designation (Statement of Gabriela Chavarria, Congressional Oversight Hearing, p. 8). Looking westward, fifteen species only range throughout western states and the overall species richness is higher compared to eastern states (Figure 2). Natural barriers, such as the Great Plains region with its respectively fewer cave habitats (Statement of Justin Boyles, Congressional Oversight Hearing, p. 46), and varying environmental conditions (the warmer and shorter winters of southern states may reduce fatalities caused by WNS) have the potential to slow the westward progression of this disease (Cohn 2012). However, given the continental ranges of two species currently impacted by WNS (little brown and big brown bats), complete cessation of the disease's spread is unlikely. WNS has already killed an estimated 6.7 million bats in the eastern U.S. (Cohn 2012). When WNS spreads into western bat populations, the impact could be catastrophic. More research is needed on bat populations and experimental treatments for WNS and research efforts should be targeted in areas particularly susceptible to WNS infection or that will facilitate transmission of fungal spores into new populations.

PREDICTING THE SPREAD OF WHITE-NOSE SYNDROME

As WNS advances westward, identifying and protecting critical cave habitats could be a successful measure to curb the spread of this epizootic. Blanket management is largely an inefficient use of resources and therefore targeted management is a more realistic approach. Geospatial analysis techniques, such as threat mapping, can aid decision-making processes by using a selection of variables to highlight areas with the greatest risk of infection. Ideally, knowing locations of all roost sites and understanding the connectivity between caves (via species and relative abundances combined with dispersal) would enable the most accurate prediction of a site's susceptibility to WNS. Unfortunately, much information is unknown. Roosting sites are plentiful, being both caves and mines, and can occur on both public and private property. Exact numbers of bats roosting in each site is largely unknown, or even a confirmed number of species within each site. Connectivity between caves is even more problematic, as bat movements between roost sites are unknown. Humans add another level of complication. Although bat-to-bat transmission is the most common mode of spore transfer, humans can move spores well beyond the scope of natural dispersal in a limited timeframe. However, even limited information can highlight areas potentially susceptible to infection with *Geomyces destructans* and inform targeted management practices that can hopefully curtail this epizootic.

APPROACH

Assessing the threat of a particular area to WNS is feasible using a few key variables (physical, biological, and climatological) to approximate likelihood of exposure to, and thriving of, *Geomyces destructans*. Aggregating these factors at the county level determines the relative susceptibility of each county to infection of roost sites with Gd and an overview of the entire US can expose areas that could facilitate natural transmission of Gd spores westward into ranges of currently unaffected species. Overlaying accessibility by humans can highlight the relative likelihood of human introduction of spores into these critical areas. Extrapolating past rates of spread can estimate how quickly Gd spores will potentially infect key areas in the western United States. (All analysis was completed using ArcGIS 10.1 (ESRI).)

AVAILABLE DATA

- **Current WNS-Positive Sites:** Exact site locations are considered highly sensitive material and thus this analysis only incorporates the status by county (WNS positive or suspected), derived from publically available maps tracking the spread of WNS (Butchkoski 2013). Variables were either aggregated at the county level, or based on the county centroid for comparison. Importantly, only counties in the United States with confirmed WNS cases were used in this analysis and counties identified after 12 March 2013 are excluded.
- **Cave Number.** Dr. David Culver of American University provided a dataset of the number of known caves per county for the United States. This dataset is a compilation of sources, primarily from the National Speleological Society.
- **Species Distributions.** Ranges of all North American cave-hibernating bats species are freely available from Patterson *et al.* (2007).
- **Climate Data.** Interpolated rasters (1-km² resolution) of climate variables generated from climate station data are available for download (Hijmans *et al.* 2005).
- **Roads, Airports, and Urban Areas.** The National Atlas of the United States provides data on roads, airports, and urban areas throughout the U.S. for use in geospatial applications.

METHODS: SUSCEPTIBILITY VIA THREAT MAPPING

A combination of three variables describes the susceptibility of each county to infection with WNS: number of potential roost sites, number and characteristics of bat species, and approximated cave temperature. Each variable was scaled to a value of 1.0, and then weighted according to its accuracy, yielding a maximum susceptibility rating of 2.5.

- **Potential Roost Sites.** An increased number of roosting sites translates to an increased probability of a bat carrying Gd roosting in one of them. Therefore, counties with higher number of roosting sites, such as caves are at higher risk. Areas with high numbers of known roosting sites should be monitored more closely for exposure to Gd. Number of caves within a county ranged from zero to 1,928 (Jackson County, Alabama) (Figure 3, pg. 21). The data are heavily skewed to the right, with a median value of seven caves per county and a third quarter value of

26. To prevent the few counties with extreme values from negating the importance of counties with moderate number of caves, all counties with at least 100 caves were assigned a value of 1.0. The remaining counties were grouped into 10-count increments, reducing the value by 0.1 for every 10 count reduction in cave number (counties with 90-99 caves were assigned a value of 0.9, 80-89, 0.8, etc.). Counties with less than ten caves were assigned a value of 0.05. Counties with a count of zero were included within this category to account for the possibility of unknown caves.

- **Species Ratio.** Although no evidence has been found linking transmission probability with the number of different species present at a site, a higher number of species could translate to differing dispersals and therefore should increase the potential for a given hibernaculum to infect other areas. Therefore, this variable is calculated using the total number of species that potentially range within a county and weighted species known to be WNS positive or Gd carriers. The total number of species per county was divided by the highest number that range within a single county (15), and then a value of 1.0 was added for each species that is either WNS-positive or a known Gd carrier (a possible high score of 10.0). Because this variable is only meaningful in this context, the final values are a relative ratio, dividing the rating of each county by the value of the county with the highest rating (Figure 3, pg. 21).
- **Cave Temperature.** While microclimate conditions are unknown for most caves, surface conditions can be used as a proxy (Flory *et al.* 2012). Gd has been shown to have the highest growth rates between 12.5 and 15.8^oC in cultures (no growth above 19.8^oC) (Verant *et al.* 2012) and the average annual surface temperature of current WNS-positive counties ranges from 3.56-14.52^oC.

Data from WorldClim (Hijmans *et al.* 2005) was used to calculate the average annual surface temperature for each county (Figure 3, pg. 21). Counties with a mean surface temperature between 12.5 and 14.52^oC were assigned a value of 1.0 (range that incorporates both known WNS positive temperatures and highest potential growth rates). Counties with temperatures between 3.56 and 12.5^oC were assigned a value of 0.9 (within the range of current confirmed WNS positive sites) while those within the range of 14.52 and 15.8^oC were assigned a value of 0.8. (within maximum growth rate range). Counties outside these ranges were given incrementally decreasing values (Table 2).

Scientists historically assumed that a temperature within a cave is equivalent to the mean annual temperature at the surface; however, that probably only holds true for caves with low air circulation. Both the number of cave entrances (and therefore air circulation) and the presence of water within a cave (which could increase or decrease the expected cave temperature depending on the water temperature) can influence observed cave temperatures. Therefore, no general correlation exists between cave temperature and geographic location (Swezey & Garrity 2009). Because I have less confidence in the estimates of cave temperature, this variable was weighted at 50% when incorporating it into the final susceptibility calculation.

TEMPERATURE RANGE	ASSIGNED VALUE
-1.0-3.56	0.7
3.56-12.5	0.9
12.5-14.52	1.0
14.52-15.8	0.8
15.8-17.0	0.6
17.0-18.0	0.5
18.0-19.0	0.4
19.0-19.8	0.3
> 19.8	0

Table 2: Temperature Values. Assigned Values for Mean Annual Temperature.

METHODS: TEMPORAL PROGRESSION

Beyond understanding which areas are susceptible to WNS infection, understanding how quickly it could spread and via what pathways is also important to inform targeted management practices. Other studies have focused on estimating when a particular area will become infected with WNS (Mayer *et al.* 2012). However, tracking possible spore transmission through areas potentially less susceptible and into areas of higher susceptibility is also informative. Gd spores can survive higher temperature conditions than the range supporting fungal growth (Hallam & Federico 2012). Therefore, incorporating temperature restrictions is no longer appropriate in calculating pathways for transmission. This analysis was limited to those counties with a minimum susceptibility rating equivalent to that of current confirmed WNS sites using only the roost sites and species ratio variables to simulate a “worst case” scenario (a value of 0.633). The temporal expansion of spore transmission was based on the mean distance traveled between confirmed WNS positive sites in a single year (139 km). The counties within 139 km of current confirmed WNS-positive counties could possibly have spores transmitted into their bat populations sometime in the next year (before end of winter 2014). Counties within 139 kilometers of those counties could potentially be infected with Gd spores in 2014-2015. This iterative process assigned potential years of spore transmission to all counties of interest.

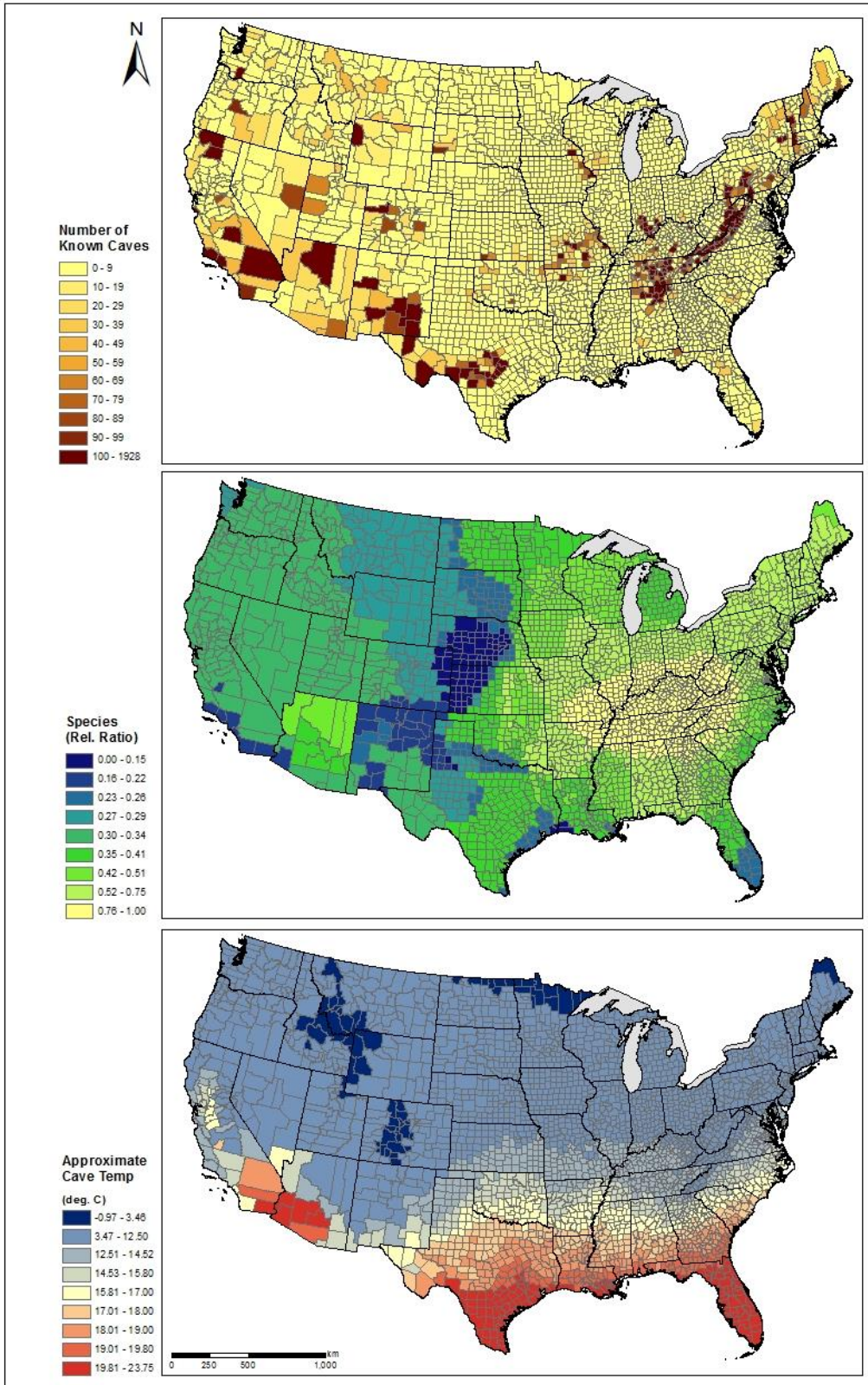


Figure 3. Variables Included in Susceptibility Calculation

Potential Roost Sites. Number of known caves per county.

Species Ratio. Maximum number of species per county, weighted if known to be WNS positive or a Gd carrier.

Estimated Cave Temperature. Counties colored medium to light blue are within known temperature ranges for Gd growth. Dark blue counties are potentially a little too cold while all other counties are possibly too warm.

METHODS: ACCESSIBILITY BY HUMANS

The goal of this analysis is to provide a visual guide to the relative accessibility of areas around the country. Contrary to the previous two analyses, this analysis was not aggregated at the county level; rather, a continuous grid describing the relative accessibility of each cell was created based on road density, proximity to airports, and proximity to urban areas (summarized in Table 3, Figure 4).

Road density was calculated using a 32.19-km (20 mile) radius based on major U.S. roads (defined as U.S. Interstates, U.S. Routes, and State Routes). Airports were divided into two classes based on the number of flights (and therefore the number of travelers): major airports with at least 10,000 flights per year and significant airports with at least 365 flights per year. For each cell, the total number of major and significant airports within a 160-km (100 mile) radius was calculated. A 100-mile radius was chosen because people are possibly willing to travel for several hours from an airport to reach a caving destination. Similarly, each cell was assigned an urban proximity value based on the number of urban cells (defined as having a population density of at least 10,000 people/mi²) within a 100-mile radius. Final cell values for each variable (road density, major airports, significant airports, and urban areas) were relativized against the cell with the highest value. The variable layers were summed, with road density, major airports, and urban areas weighted evenly but significant airports weighted at 25% to account for the lower number of travelers, creating a final accessibility grid.

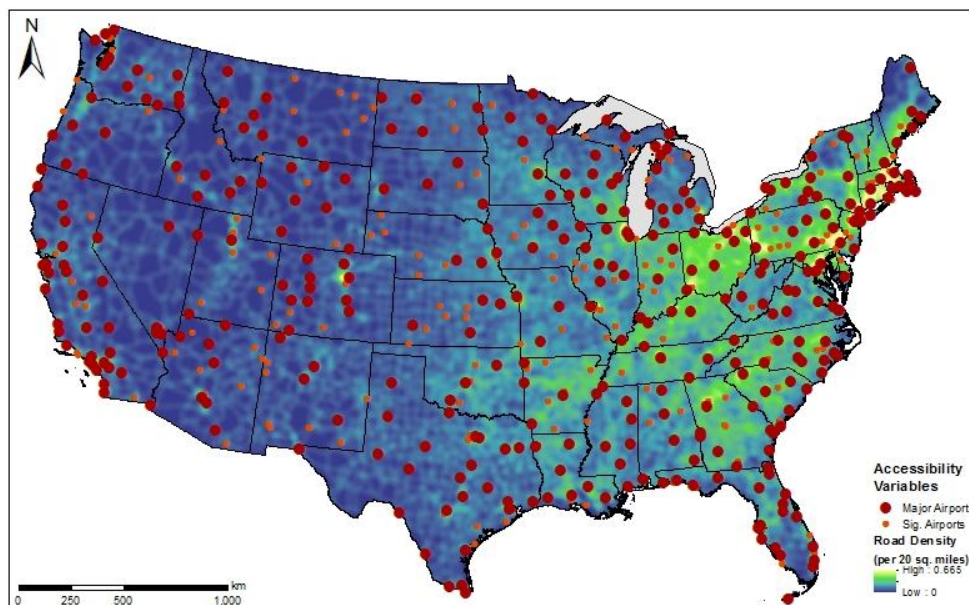


Figure 4: Variables Used in Accessibility Calculation. * Urban areas not shown.

VARIABLE	SPECIFICATIONS	SEARCH RADIUS	WEIGHT
Road Density	Major Roads: U.S. Interstates, U.S. Routes, State Routes	20 miles	1
Airports: Major	At least 10,000 flights per year	100 miles	1
Airports: Significant	At least 365 flights per year	100 miles	0.25
Urban Areas	Population density at least 10,000 people/sq. mile	100 miles	1

Table 3: Summary of Variables Used in Accessibility Calculation.

RESULTS: SUSCEPTILTY VIA THREAT MAPPING

General Results. Initial susceptibility ratings ranged from 0.19 to 2.50 (maximum possible). Generally, the areas with the highest susceptibility are in the Appalachian Mountain range, suggesting that perhaps the overall threat of white-nose syndrome is higher in the east than in the west. Several counties throughout the west rank in the top 10% most susceptible, but the overall susceptibility in the west appears much lower than the east (Figure 5). However, this result is likely misleading, as most of the species throughout the east have already proven susceptible to WNS or Gd and therefore rate higher in the species ratio calculation.

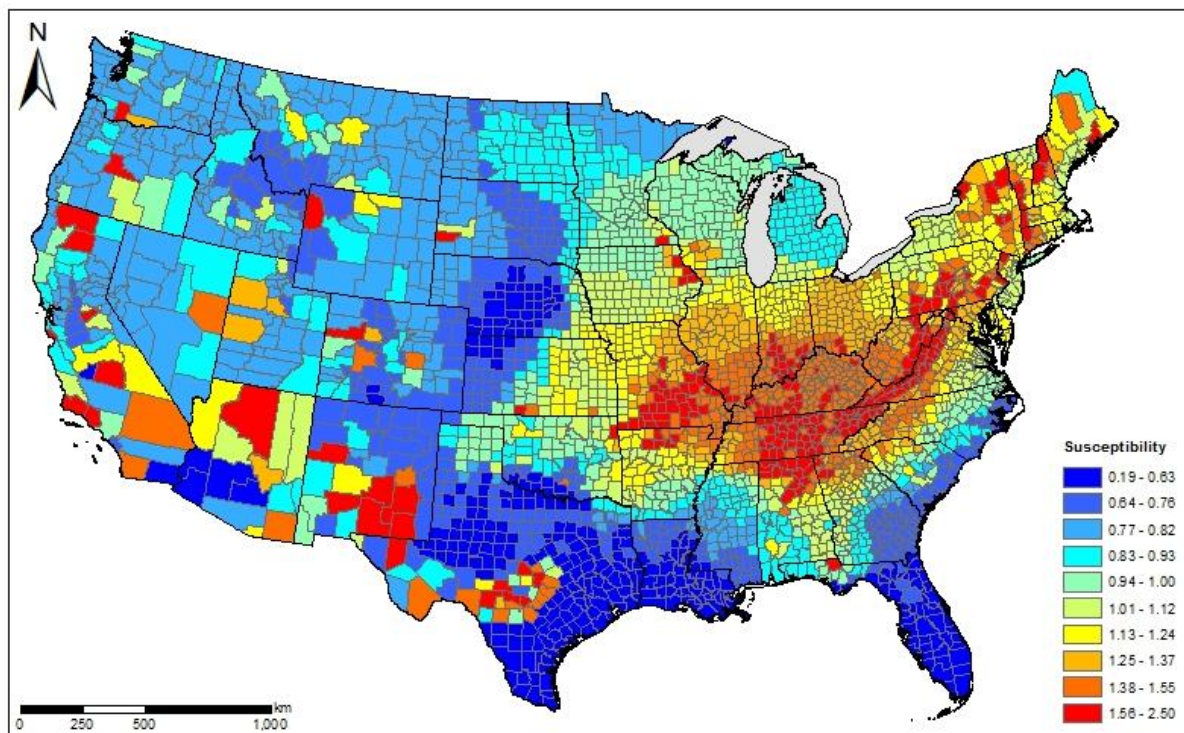


Figure 5: Initial Susceptibility to WNS Calculation. Each class represents 10% of the data. The most susceptible counties are the top 10%, colored red (rating 1.56–2.50).

Predicting the Past. The susceptibility ratings of those counties with confirmed WNS cases ranged from 1.05 to 2.5 (suspected counties ranged from 0.99 to 2.5). Of both confirmed and suspected, 88 of the 170 (52%) counties are in the top 10% most susceptible in the entire country. Most of the remaining WNS counties (42%) are in the top 40% most susceptible nationwide. The cluster of counties with the highest susceptibility is located in southern Indiana (susceptibility of 2.25-2.5). The general trend shows increasing susceptibility as WNS progressed south and west, which highlights the importance of where WNS was first introduced. This region (southeastern New York) and the surrounding area generally have a lower susceptibility rating (though still primarily in the top 30%). The initial two counties, however, have a susceptibility rating of 2.19, which is relatively high. Proximity is important to transmission and therefore the surrounding counties were possibly more likely to be infected simply because of their proximity to currently affected sites (Figure 6).

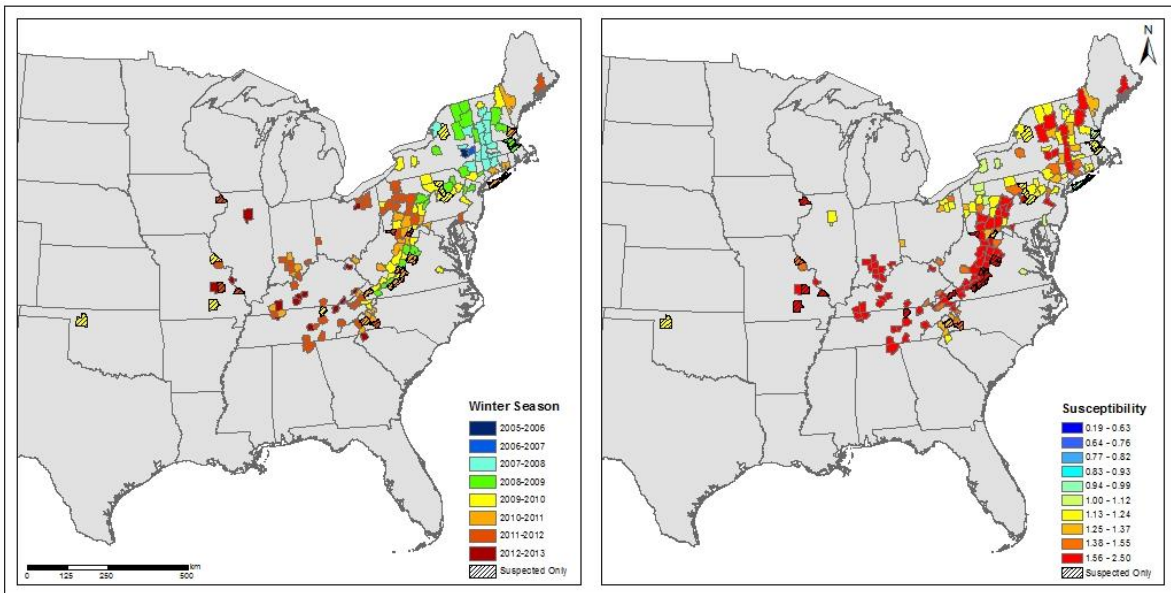


Figure 6: Comparison of Temporal Spread of WNS Against Calculated Susceptibility Rating. Susceptibility classes are based on quantiles, with each class representing 10% of the data.

Predicting the Future. The initial susceptibility calculation (Figure 5) suggests that eastern counties are far more susceptible to WNS and therefore the majority of the threat has passed. However, a significant portion of the calculation incorporates if a species is known to have WNS or carry Gd. Most of the eastern species fall into that category, but this information is largely unknown regarding species restricted to the western U.S. In order to more accurately predict the westward spread of WNS, the species ratio was recalculated, still using the total number of species, but only incorporating the WNS or

Gd status of those species with significant portions of their ranges in the western U.S. (*Myotis velifer*, *Myotis lucifugus*, and *Eptescius fuscus*) (Figure 7). The resulting susceptibility range was 0.35 to 2.43 with an overall increased level of susceptibility throughout the western states (Figure 8).

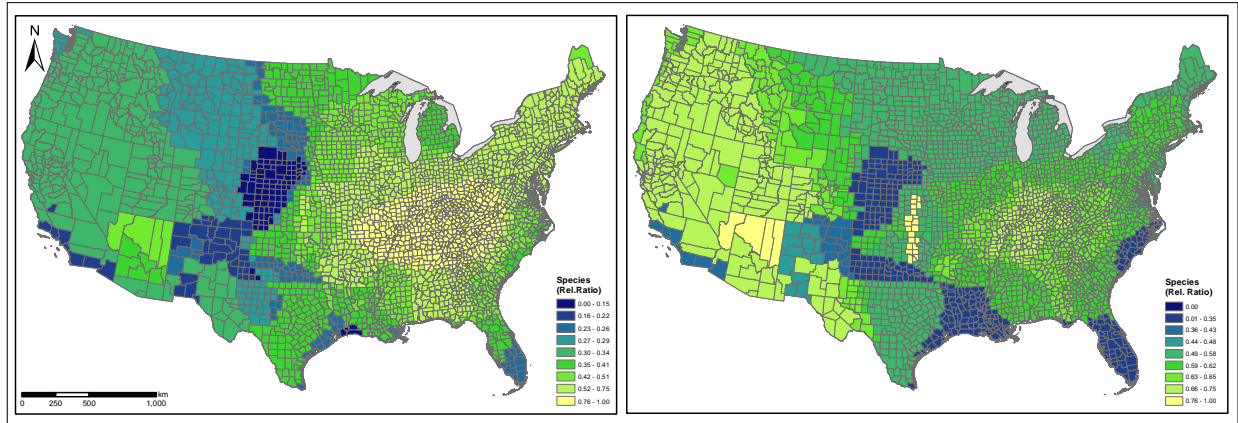


Figure 7: Comparison of Species Ratio Using All Weighted Species (left) and Reduced Weighted Species (right). The reduced species calculation only weights three species (as opposed to nine in the initial calculation).

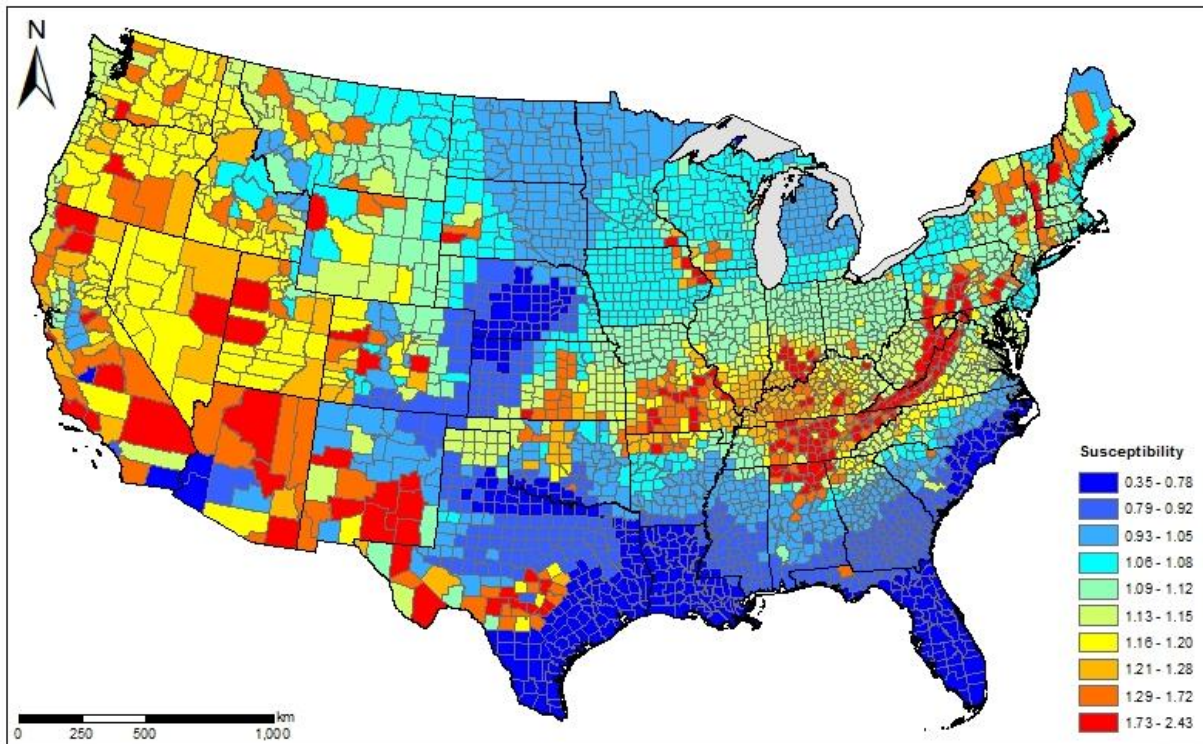


Figure 8. County Susceptibility Rating Using Fewer Species. Each class represents 10% of the data. The most susceptible counties are the top 10%, colored red (rating 1.73 – 2.43).

RESULTS: TEMPORAL PROGRESSION

Using the past mean distance traveled annually suggests that WNS could reach the west coast by 2027 (Figure 9). Importantly, this model does not suggest that all counties assigned a given year will be infected with spores. Rather, it suggests which year a given county could be infected based on the past rate of spread of WNS cases. The exact progression of the epizootic will heavily depend on which counties are infected in any given year. The most likely corridor to facilitate transport into western regions lies in western Oklahoma and north Texas to eastern Colorado (Figure 10), a jump that could occur between 2018-2020. Importantly, one county in western Oklahoma, Woodward, is the site of suspected WNS infection in 2009-2010. Although WNS was never confirmed in that site, if the fungus has persisted in that county, the transition westward into Colorado could happen much more quickly.

Using the mean distance traveled represents a moderate transmission scenario. However, WNS has traveled farther distances in a single year, up to 790 km. While transmission across the entire U.S. using this single measurement is unlikely, a much wider region could potentially act as a corridor between the eastern and western states, stretching from North Dakota to Texas (Figure 11). Thirty-three of the 54 most susceptible counties lie within this corridor

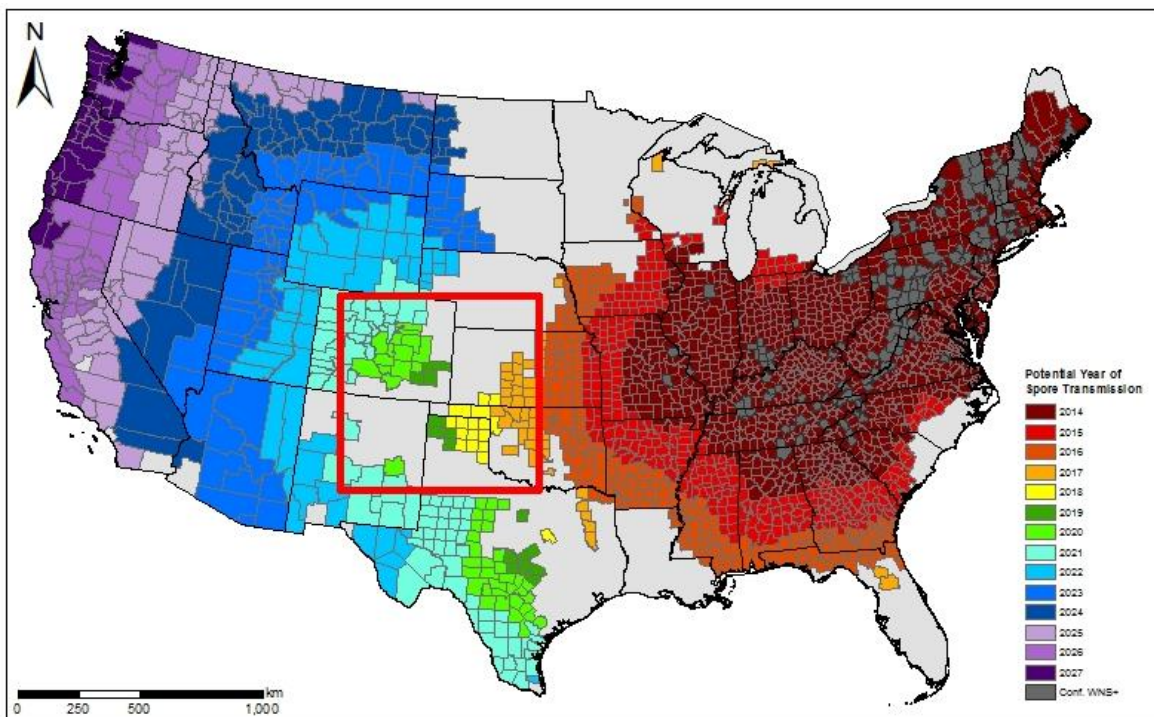


Figure 9: Temporal Progression. Potential initial infection years based on mean distance historically traveled. The red box shows the extent of Figure 10.

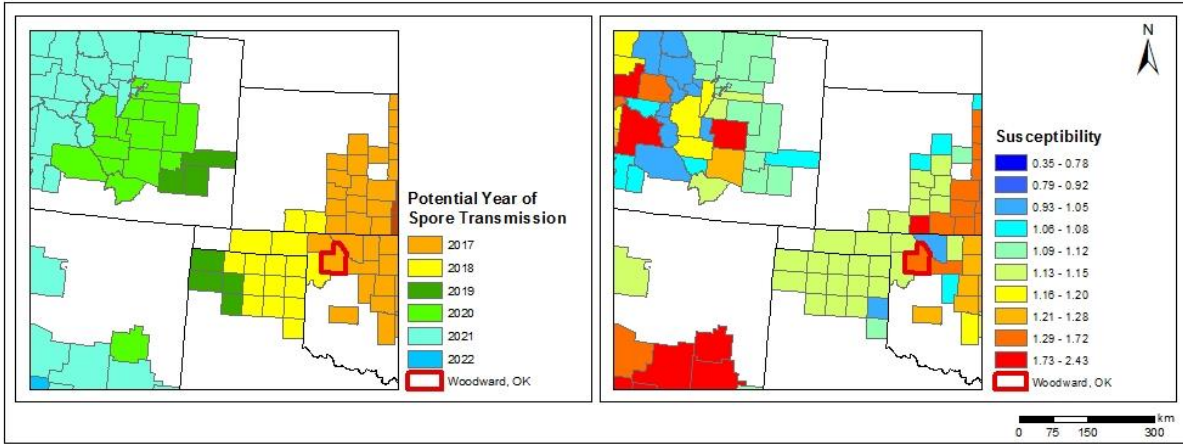


Figure 10: Corridor Predicted Using the Mean Distance Calculation. Woodward County, Oklahoma is highlighted in red (site of suspected WNS in 2009-2010). Many of the counties have relatively low susceptibility ratings; however, a few have significantly higher numbers (each class represents 10% of the data).

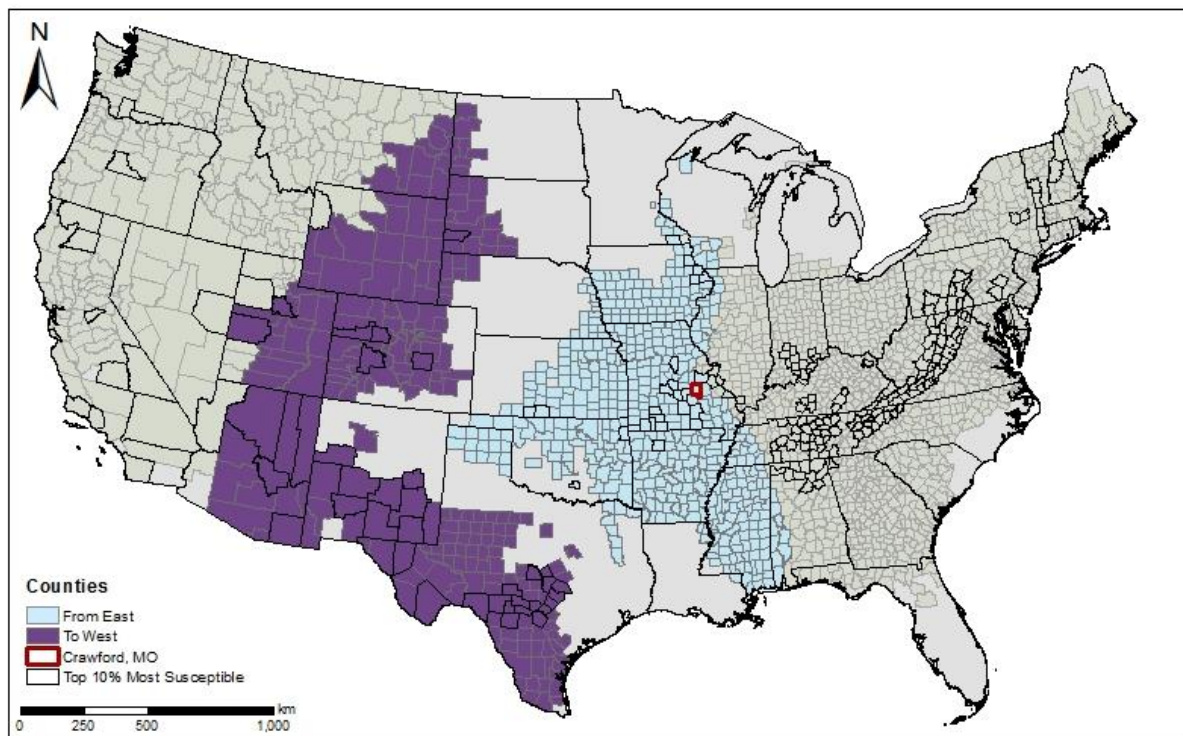


Figure 11. Potential "Jump" Corridor from Continuous Eastern Counties to Contiguous Western Counties. Each blue county is within 790 km of a purple county. Therefore, WNS could jump from east to west in a single year. Thirty-seven of the most susceptible counties lie in the western "jump" zone (purple). Crawford, Missouri is confirmed to have WNS, and therefore this jump could occur at any time.

AGGREGATED RESULTS: SUGGESTED AREAS FOR TARGETED MANAGEMENT

Based on potential susceptibility, several counties in the Rocky Mountains and Pacific Northwest plus the potential corridor between Oklahoma/north Texas and eastern Colorado should be targeted for increased research, both to gather baseline data and to monitor for Gd and WNS exposure (Figure 12, Table 4). These areas could also be managed using targeted cave closures, to eliminate the possibility of human introduction of Gd.

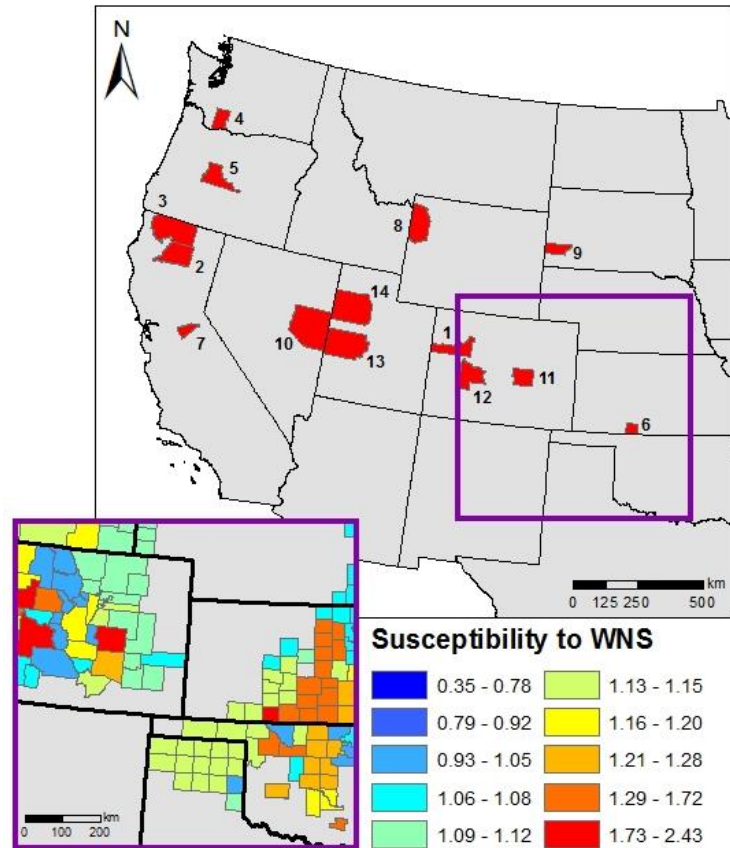


Figure 12: Areas to Target for Increased Monitoring. Counties throughout the Rocky Mountains and Pacific Northwest within the top 10% most susceptible counties (labeled by rank, Table 4)), and the potential corridor between contiguous eastern counties and contiguous western counties.

RANK	STATE	COUNTY	NUMBER OF CAVES	MEAN ANNUAL SURFACE TEMP	NUMBER OF SPECIES	SUSCEPTIBILITY	POSSIBLE YEAR OF SPORE INTRODUCTION
1	Colorado	Garfield	168	4.41	11	2.13	2021
2	California	Shasta	158	11.29	10	2.12	2026
3	California	Siskiyou	387	7.81	10	2.12	2026
4	Washington	Skamania	241	6.84	10	2.12	2027
5	Oregon	Deschutes	96	6.03	11	2.03	2026
6	Kansas	Comanche	94	13.88	6	2.00	2017
7	California	Calaveras	80	13.62	11	1.98	2026
8	Wyoming	Teton	135	-0.16	8	1.98	2023
9	South Dakota	Custer	94	7.57	6	1.95	2023
10	Nevada	White Pine	85	6.70	9	1.90	2024
11	Colorado	El Paso	86	7.83	7	1.87	2020
12	Colorado	Gunnison	83	0.92	10	1.82	2021
13	Utah	Millard	66	9.24	11	1.73	2023
14	Utah	Tooele	68	9.81	11	1.73	2023

Table 4: Counties of Concern. Characteristics of those individual counties within the top 10% most susceptible that should be targeted for increased monitoring, ranked by susceptibility.

RESULTS: ACCESSIBILITY BY HUMANS

Overall, accessibility by people is much higher in the eastern U.S. than the western U.S. Eastern states have a much higher density of roads, number of airports, and number of urban areas, with areas throughout the northeast highly accessible (Figure 13). Adjusting the scale to display only the accessibility of western states

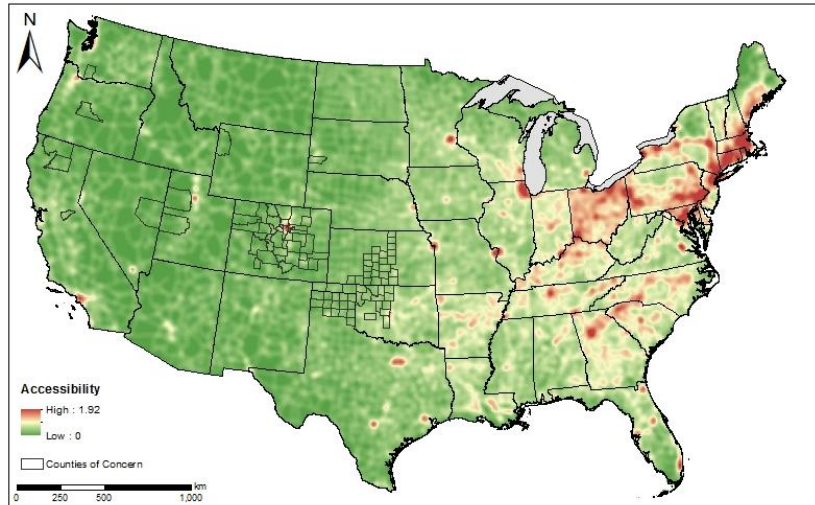


Figure 13: Accessibility by People Across the U.S. Calculated from road density, proximity to urban areas, and proximity to airports. Suggested counties for increased monitoring are outlined in gray.

highlights a few metropolitan areas near counties of interest, particularly Denver, which lies near three of the most susceptible western counties and is also near the potential corridor (Figure 14). Salt Lake City, Oklahoma City, and Portland also lie near areas of concern. Less noticeable, but important, the smaller city of Colorado Springs is within El Paso County, ranked eleventh in susceptibility within the counties suggested for increased monitoring.

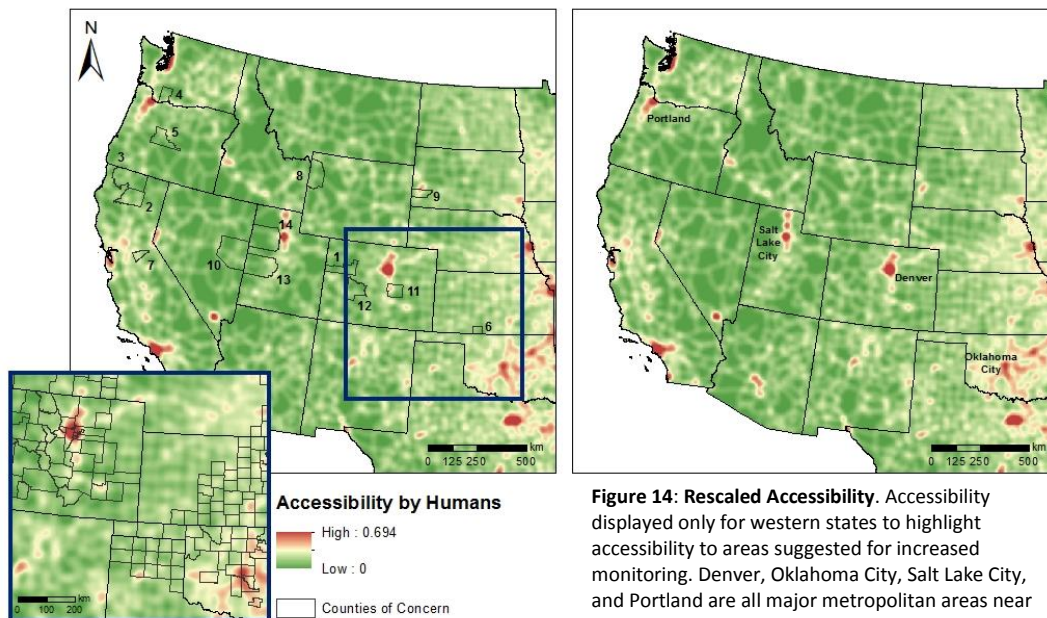


Figure 14: Rescaled Accessibility. Accessibility displayed only for western states to highlight accessibility to areas suggested for increased monitoring. Denver, Oklahoma City, Salt Lake City, and Portland are all major metropolitan areas near areas of interest.

DISCUSSION AND CONCLUSION

Predicting the future spread of white-nose syndrome can successfully highlight areas for targeted management practices, such as increased monitoring or cave closures. Pairing two straightforward techniques highlighted both the western counties most susceptible to infection with WNS and potential corridors for facilitation of *Gd* westward.

ACCURACY OF THE SUSCEPTIBILITY PREDICTION. Applying this threat mapping method to the entire U.S. highlighted its effectiveness in predicting where WNS has been confirmed or suspected. As WNS spread farther south and west, the model's accuracy increased. The reduced accuracy in the northeast suggests the importance of locale in the spread of WNS as *Geomyces destructans* was introduced into Albany, New York by chance. Had this fungus been introduced in Virginia, Kentucky, or Oregon, areas affected and spread could be very different. Also important, the values assigned to the temperature metric are based on the annual temperatures of confirmed WNS sites, enhancing the model's ability to accurately predict past sites. Removing the cave temperature variable from the calculation still yielded a reasonably accurate prediction, and thus defining the temperature variable using existing sites does not invalidate the model (Appendix 1).

Given that the model became more accurate as WNS spread, these results are probably reasonable for much of the U.S. The southwest, however, should be viewed with caution. Several of the counties with highest susceptibility are in this region, but the southwest has a high number of both bat species and known caves. Further, mean annual temperatures fall within the range of growth for *Gd* for several counties (Appendix 2). However, this region is subject to daily extreme temperature swings (Sheppard *et al.* 2002), likely influencing the mean annual temperature value. While average annual temperature is hardly a perfect proxy for cave temperature under the best conditions, I have even lower confidence that performs well in environments with such high daily variability.

ACCURACY OF TEMPORAL PROGRESSION. This prediction is based on a simple straight line metric to extrapolating previous distance traveled to predict future travel potential. However, a straight line metric is probably not the most accurate method. Traveling over vertical distances is likely to influence the rate WNS spreads westward over the Rocky Mountains. Previous models have shown that the

spread of WNS slows over these mountains (*Maher et al.* 2012) while this analysis does not incorporate elevation as a factor. This model also only used distances between confirmed WNS sites. Including suspected sites would change the measures used as distance metrics and therefore change the counties that could be infected annually (particularly as Woodward, Oklahoma is a suspected WNS site).

This analysis only highlights which counties could become infected with Gd spores based on this straight-line metric. Exactly which counties will be affected will be determined primarily by the movements of bats between roosts. Unfortunately, this variable is currently impossible to predict. Further, this analysis does not consider the potential of WNS to spread through Canada and south into the western U.S. Data on locations of caves in Canada is unavailable, and therefore it could not be included in this analysis. However, because winters are generally harsher in Canada than in the States, WNS affected bats tend to die more readily, limiting transmission between roosts (*Maher et al.* 2012). Human facilitated transmission could completely alter the temporal progression of Gd spores and WNS. Modeling accessibility provides some measure of the likelihood of human introduction of Gd spores. However, as only one person is needed to introduce Gd spores into a new area, the conclusions that can be drawn from this accessibility model are limited.

The results of this analysis are largely comparable to that of *Maher et al.* (2012), although that study suggests WNS will infect counties in Colorado by 2016, versus 2019 in this analysis. *Maher et al.* (2012) states WNS could reach the west coast by 2036, a slower progression than indicated by this analysis. However, that study also concludes that several of the most susceptible counties identified here (Shasta CA, Siskiyou CA, Skamania WA, and Deschutes OR) will be infected by 2031 (*Maher et al.* 2012). The results of this analysis for those counties are similar, suggesting spore introduction in 2026-2027.

IMPROVING THE ANALYSIS. This analysis heavily relies on approximated, publically available data. Total bat population size, colony size, conspecifics within a hibernaculum, and proportion of *M. lucifugus* within a hibernaculum have all been shown to influence Gd transmission rates (*Wilder et al.* 2011). Unfortunately, detailed information about bat populations is simply not known. Concentrating efforts on those areas suggested by the analysis may be an efficient use of resources to gather some of this information.

A lack of data led to the exclusion of other relevant variables: humidity and type of roost site. Humidity could be extremely important in predicting susceptibility to WNS because fungal cultures in general grow more readily in humid environments (*Wilder et al.* 2011) and it appears that species more

susceptible to WNS tend to roost in more humid areas (Cryan *et al.* 2010). Data on cave humidity is extremely scarce and therefore this factor cannot be included. As of 2009, most of the sites with WNS were caves rather than mines, but this result could merely reflect the preponderance of caves rather than mines within the current extent of WNS (Swezey & Garrity 2009). Wilder *et al.* (2011) found caves had a higher mortality rate than mines and hypothesized that result may be simply because caves have existed longer than mines. Mines may host more localized colonies with lower dispersal distances and rates. Further, the microclimates of mines may differ just enough from caves to influence the growth and development of Gd (Wilder *et al.* 2011). However, I was unable to obtain any information regarding the locations of mines and therefore this variable was excluded from the analysis.

THE IMPORTANCE OF CAVE CLOSURES. Although highly controversial, cave closures have the potential to eliminate the possibility of human introduction of Gd spores into new populations throughout the western U.S. While blanket cave closures are not likely to be tolerated, targeted cave closures may be more readily accepted. The areas highlighted in this analysis could be ideal locations for targeted cave closures as they are either highly susceptible to WNS or could facilitate transport of fungal spores from the eastern U.S. into the western U.S. Cave closures throughout many of the individual counties of concern (Table 3) would largely be easy to implement as much of the land in those counties is owned or managed by the Federal government. However, the potential corridor from Oklahoma and Texas into eastern Colorado has minimal Federal lands in Oklahoma and Texas counties as well as the eastern most counties in Colorado (Figure 15). Given the proximity of Denver and Oklahoma City, protecting this area from accidental transmission via humans could be extremely important and may require help from the public through voluntary cave closures on private lands.

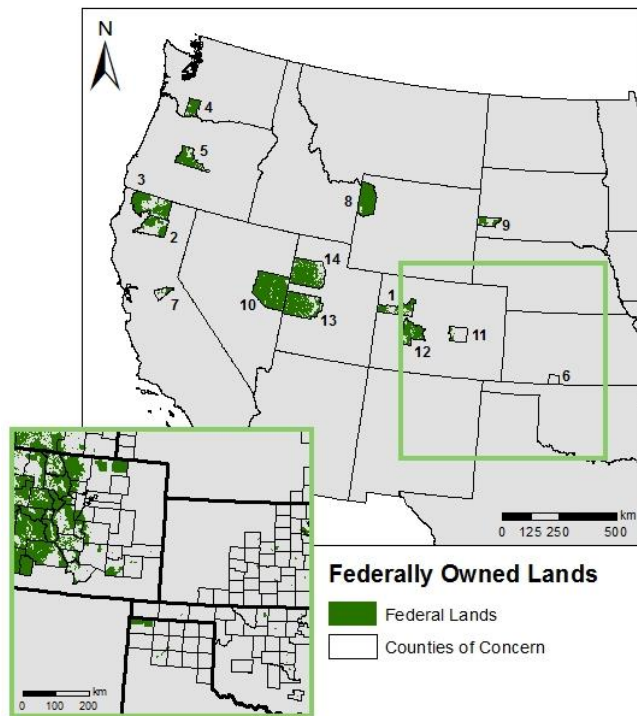


Figure 15: Federally Owned Lands in Areas of Interest.
Labels are ranks (Table 4, pg. 28).

CONCLUSIONS

Since 2006, white-nose syndrome has had devastating impacts across the eastern U.S. Predicting how and when a pathogen will spread can be crucial to effectively allocate resources for management. Certainly having more data on bat populations would improve predictions, but given limited time and resources, monitoring studies should be restricted to those areas prone to WNS infection or that will facilitate its movement into western populations. This study uses relatively little data to create reasonable results, highlighting several counties of concern in the western United States as well as a potential corridor of transfer into western states. Monitoring these areas and enacting targeted cave closures could be an efficient use of resources that could help manage the spread of this destructive pathogen. Most of the treatment suggestions for managing WNS cannot be implemented on a nationwide scale. However, it may be possible to implement some of them selectively into high-risk areas, such as those identified by this analysis, and curtail the impacts of this devastating pathogen.

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Current WNS Counties

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* Figure 1 (pg. 9) was recreated by C. Ihlo using ArcGIS10.1 using counties identified through C. Butchkoski (2013).

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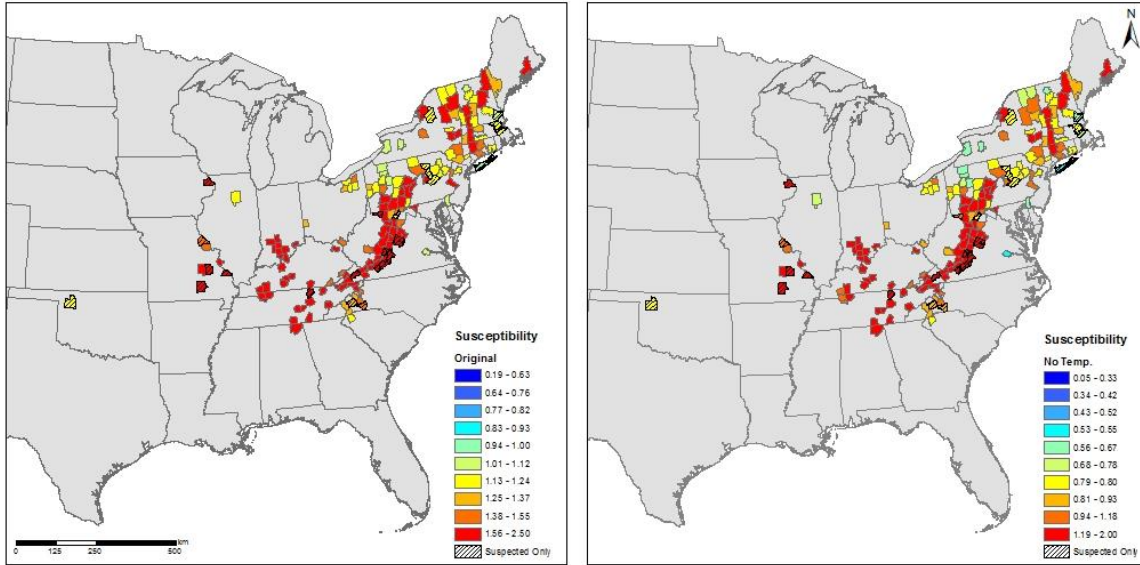
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APPENDIX 1:

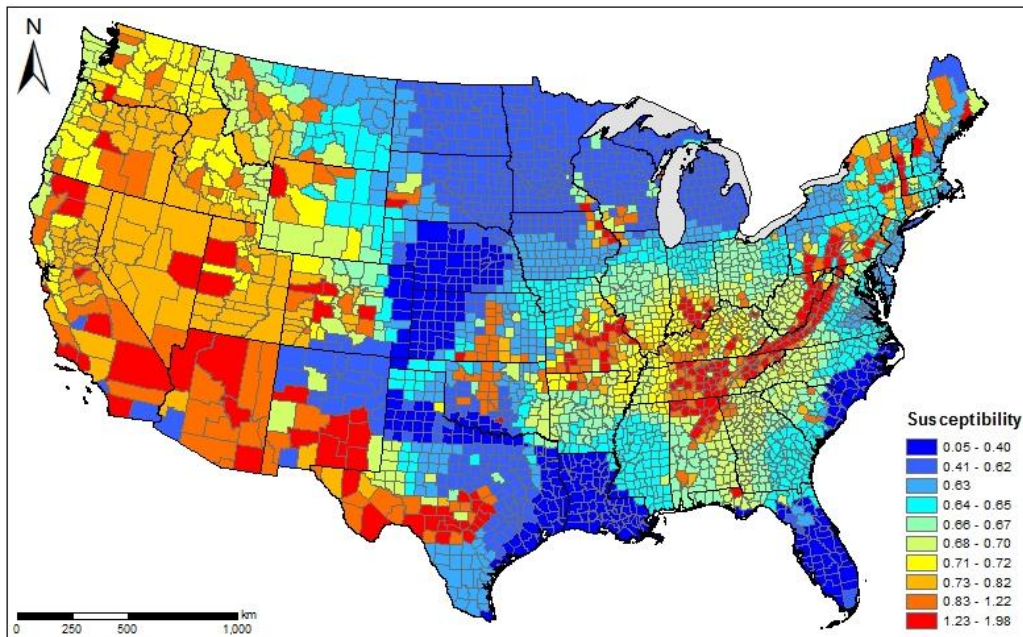
Susceptibility Calculation Excluding Cave Temperature Variable (Each class represents 10% of the data.)

PREDICTING THE PAST (Using All Weighted Species for Species Variable and No Cave Temp.)



PREDICTING THE FUTURE

(Using Reduced Weighted Species for Species Variable and No Cave Temp.)



APPENDIX 2:

Variable Values for Counties in the Southwest United States

(Counties in the top 10% most susceptible are highlighted in black.)

