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An Examination of White-Nose Syndrome Occurrence and Dispersal Patterns: Utilizing Global and Local Moran's I Analysis to Evaluate an Emerging Pathogen

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AN EXAMINATION OF WHITE-NOSE SYNDROME OCCURRENCE AND DISPERSAL PATTERNS: UTILIZING GLOBAL AND LOCAL MORAN'S I ANALYSIS TO EVALUATE AN EMERGING PATHOGEN

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Master of Science

By
Celia M. Davis

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AN EXAMINATION OF WHITE-NOSE SYNDROME OCCURRENCE AND DISPERSAL PATTERNS: UTILIZING GLOBAL AND LOCAL MORAN'S I ANALYSIS TO EVALUATE AN EMERGING PATHOGEN

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Celia M. Davis August 2012 38 Pages

Directed By: Dr. Jason Polk, Dr. Chris Groves, Dr. Jun Yan, and Dr. Rickard Toomey

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In this research, a novel approach that utilizes Moran's I statistical analyses to examine the spatio-temporal dispersal patterns of the White-Nose Syndrome currently affecting North American bat species is undertaken to further understand the disease transmission mechanism(s) of this emerging wildlife epidemic. White-Nose Syndrome has been responsible for in excess of five million bat deaths to date and has the potential to alter the ecological landscape significantly; however, due to a variety of factors, little research has been conducted into the patterns of infection on a national scale. Global and Local Moran's I analyses were performed on the spatial-temporal variable of month and location from the initial outbreak site in order to address the spread of the *Geomyces destructans* fungus that causes White-Nose Syndrome. A comprehensive dataset of outbreak confirmation sites has been compiled and statistical analysis using ArcGIS reveals a complex pattern of disease dispersion since initial discovery of the disease, and shows important policy and management implications, in particular the need for more standardized and rigorous data collection and reporting procedures.

Introduction

The small blue-green planet on which we live is a closed system and, within this closed system, each component part has its role to play in the continued functioning of the whole. The demands human beings place on the myriad interdependent eco-systems that surround and envelop us have far-reaching implications not only for our own survival, but for the almost infinite number of plant and animal species upon which we depend for the most basic of necessities. As global population growth continues unchecked, the rate at which finite natural resources are being consumed becomes an almost exponential equation, and anthropogenic consequences are the inevitable end-result. In light of this disturbing trend, it seems self-evident that any developments having the potential to disrupt or diminish existing agricultural production should be of great concern.

Worldwide population growth and an increasing standard of living in the United States place an unprecedented strain on available food resources for both domestic consumption and global export. The Food and Agriculture Organization of the United Nations estimates that in the past year alone the global economic crisis and continued population expansion will cause approximately 1.02 billion world citizens to be undernourished (FAO, 2009). American farmers and agri-business companies meet this increased demand in food production in a variety of ways, resulting in the use of higher yield genetically modified crops, increased pesticide usage, and alterations in crop-growing methods. A significant concern is that pesticide applications have long been linked to undesirable side-effects, such as contamination of the water table, along with severe short-term and long-term risks to humans directly exposed to the chemicals currently available for crop pest control. Along with the costs (both financial and human-health related) of extensive pesticide use, there is also a well-demonstrated tendency for natural pests to develop resistance to chemicals over ever-shorter periods of time. In light of these significant drawbacks to the use of chemicals in controlling the populations of crop-destroying pests, it is imperative to continue research into alternative schemes to reduce dependence on chemical pesticides.

The concept of “keystone” species is not novel, and the wide-spread attention drawn to serious population declines of the American honey bee and amphibian species in the latter half of the twentieth century indicates a dawning awareness on the part of the scientific community that the demands being placed on this closed system have consequences (Meteyer et al., 2000; Johnson, 2007). These consequences may not be readily apparent to the average world citizen; nevertheless, the decimation of seemingly peripheral species should serve as a warning that all is not well. In the same way other species as diverse as bees and frogs have sounded this warning, bats also function as bio-indicators for the environments surrounding their various species (Jones et al., 2009). As in most cases of this sort, the connections between human activities and broad-ranging declines amongst the flora and fauna surrounding person-kind are complex, nuanced, and multi-faceted.

Over time, nature has evolved a system of checks and balances between predator species and the insect populations that target the most prominent food crops grown domestically. In the case of corn, soybeans, wheat, and rice, a great number of bird and bat species have developed into extremely effective ‘bug killing machines.’ It is a well-documented fact that individual North American bats readily devour up to 2000 insects each night and crops without these nightly visits show over a 150% increase in pest load (Kalka et al., 2008). In addition to feasting on specific crop pests, bats are also believed responsible for significant control of mosquito populations in states like Texas and Florida, where millions of dollars are spent annually in efforts to control the spread of West Nile Disease (Cleveland et al., 2006). Given the financial and environmental impact of controlling insect populations by chemical means, it should be of particular concern when an emerging infectious disease decimates over 90% of affected bat populations and results in an even greater use of pesticides that eventually make their way downstream into the environment (Blehert et al., 2009).

The so-called “White-Nose Syndrome,” where bat populations affected by the *Geomyces destructans* fungus leave hibernation early and experience high mortality rates due to insufficient wintertime food resources, has become rampant along the eastern seaboard since its initial discovery in Albany, NY in 2006 (Blehert et al., 2009), and confirmation of the fungus itself being present occurred as far west as Missouri (Wibbelt et al., 2010) and Oklahoma, although there is no report of resulting mortality in those western-most states as of now.

Since its initial discovery in Howe’s Cave outside Albany, New York in the latter months of 2006 and subsequent confirmation in March of 2007, White-Nosed Syndrome (WNS) and its causative *Geomyces destructans* fungus have been responsible for decimating populations of *Myotis Lucifugus* (Little Brown bats) and *Myotis sodalis* (the already critically endangered Indiana bat). Based on census numbers from the United States Fish and Wildlife Service (FWS) and state-level agencies, the trend of mortality is apparent with greater than 90% declines in populations of both species at surveyed sites and predictive population models indicate regional extinction of *Myotis lucifigus* within shockingly short time frames (Frick et al., 2010). Despite intensive efforts underway in a variety of fields to understand the mechanisms and dispersal factors of WNS, researchers have yet to conclusively identify the pattern of the disease spread and are thus significantly handicapped in their attempts to predict where and when the next outbreaks will occur. This inability to pinpoint even approximate spread patterns leaves state and federal efforts lacking at being able to mitigate the devastating effects of this disease upon one of our most economically valuable wildlife groups.

The goal of this project is two-fold; firstly, to gather all existing WNS outbreak data by county level location and outbreak date at the level of month, and secondly, to utilize the statistical tools available within the ArcMap GIS software to perform an initial analysis of the disease dispersion patterns present as of April 2012 in an effort to better understand the mechanism(s) behind disease dispersion. Should outlier values be yielded by such a statistical analysis of confirmed WNS sites and their infection dates, it would be an indication that a host capable of acting as vector to the fungus over significant distances could be implicated in contributing to the disease dispersal.

Literature Review

The full economic impact of bat predation on pest insect populations is poorly documented; however, studies by Wickramasinghe et al. (2004), Cleveland et al. (2006), Kalka et al. (2008), and Boyles et al. (2011) indicate that the predatory role of bats on food pests is considerable. In the case of the Brazilian free-tailed bat, Cleveland et al. (2006) found that there was a 12% overall decrease in corn crop infestation by larval worm pests directly attributable to bat predation in south-central Texas. Although studies have not been conducted to confirm the effect across other parts of the country, this figure is likely to be similar in states that also have insectivorous bat populations whose range extends over agricultural areas. Given that insectivorous bat species function as a natural pest-control mechanism with not insignificant financial and environmental benefits, the loss of large portions of indigenous bat populations as seen in White-Nose Syndrome is especially troubling.

The first reports of this mysterious disease that resulted in high bat mortality were centered at Howe's Cave of Albany, New York, in the early spring of 2006 (Blehert et al., 2009) when recreational cavers noticed high numbers of dead bats immediately outside of the cave. Upon examination by local fish and wildlife employees, it became apparent that not only was the local population of little brown bats (*Myotis lucifugus)* experiencing mortality of greater than 90%, but that significantly abnormal behavior in flying and feeding patterns was observed in surviving individuals. Losses of greater than 90% were then discovered in nearby hibernacula during winter of 2006-2007 and the condition rapidly spread along the United States eastern seaboard. As of spring 2012, nine insectivorous bat species in nineteen states had experienced *Geomyces destructans* infection (USFWS, July 2012d) and research into the cause of WNS-associated mortality was well underway. Despite the identification of the *Geomyces destructans* fungus responsible for WNS (Lorch et al., 2011), and the physiological symptoms of the syndrome (Reichard and Kunz, 2009), the exact mechanism of the resulting fatality of infected individuals is still poorly understood. It is of particular interest that the presence of bats exhibiting White-Nose fungus symptoms has been well documented in a majority of European countries with no resulting mortality (Wibbelt et al., 2010). Equally noteworthy is the correlation existing research has found between body fat ratios and mortality rates (Geluso et al., 1976; Clark et al., 1983), since metabolic malfunction is one possible culprit behind White-Nose Syndrome deaths. Starvation after early awaking from hibernation has been implicated (Turbill and Geiser, 2008; Reichard and Kunz, 2009) and further research speculates that evaporative water loss leading to dehydration is the motivating force behind early awakening (Cryan et al., 2010; Willis et al., 2011).

Advances in computing power have allowed for increasingly rigorous investigations of Tobler’s First Law of Geography, which states, “Everything is related to everything else, but near things are more related than distant things” and this most fundamental statement of autocorrelation or the reality that, “any set of spatial data is likely to have characteristic distances or lengths at which is it correlated with itself” (Sullivan and Unwin, 2003; 180) and can now be readily applied to real world phenomena. Natural world occurrences, like those of White-Nose Syndrome, can be analyzed statistically to reveal patterns within the dataset that reflect autocorrelations and these patterns can be compared to a randomly generated matching dataset to establish the degree of non-randomness present in the phenomenon being examined.

One such analysis that examines spatial autocorrelation across a dataset is the Moran's I statistic which is typically applied to areal units that possess interval data characteristics and compares the relationship of observed data to that of randomly generated data in order to establish a measure of positive autocorrelation (clustered), negative autocorrelation (dispersed), or no autocorrelation (random) (O'Sullivan and Unwin, 2003; 197). Although useful for determining overall patterns of a particular dataset, the Global Moran's I statistic falls short when examining the relationships between sites of that dataset, and this shortcoming was addressed with the development of a Local Moran's I analysis that yields further information about where the patterns of autocorrelation exist within the occurrences of interest (Anselin, 1995). An important distinction between the analyses is that Local Moran's I is disaggregate and therefore examines the degree to which neighboring data points are similar or dissimilar.

Despite the significant volume of research that has been conducted around the physiological consequences of WNS, characterization of the fungus itself, and controlled examinations of transmission factors, less emphasis has been placed on understanding the patterns within the disease dispersal of existing sites. In part, the reluctance to undertake these sorts of analyses may be due to a perceived lack of tools to address the nature and scope of the epidemic. However, since the development of ArcGIS's sophisticated statistics software package and the inclusion of tests such as Global and Local Moran's I, Geary's Function, K Function, these statistics-driven analyses have been utilized by numerous researchers from very different fields of study to analyze similar phenomena and depict results in a concise, visually compelling manner.

In their research tracking shigellosis, McKee et al. (2000) employed a simple k-nearest neighbor calculation to explore infection patterns on a military base at Fort Bragg, North Carolina and established that the infection is indeed locally contagious. Prior to the shigellosis research, K-function analysis had also been effectively utilized by Morrison et al. (1998) in their work with tracking the spatial and chronological analysis of dengue cases in Florida, Puerto Rico, and this analysis also revealed a distinctive "hotspot" pattern. To address the shortcomings of k-nearest neighbor analysis, Local Moran's I analysis was used by Yeshiwondim et al. (2009) to further explicate spatial patterns of malaria incidents in Ethiopia and this increasingly rigorous analysis revealed that the CO-type (cluster/outlier type; referring to high-high, low-low, etc. data) "outliers" that result from Local Moran's I analysis do indeed offer a more nuanced, detailed examination of the phenomenon than that found by nearest neighbor statistics alone. Another study focused on Dengue fever in Northern Thailand by Nakhapakorna and Jirakojohnkoolb in 2006 used the more specific Local Moran's I and Geary's analysis available within the ArcMap platform to provide a detailed analysis of outlier regions within the epidemic study area. Again, this Local Moran's I analysis was utilized more recently in research by Sugumaran et al. (2009) that examined the spread and distribution of West Nile virus incidence in the United States to reveal areas in which neighboring counties showed significantly different values of viral outbreaks. West Nile Virus was also the focus of further research utilizing Local Moran's I analysis to examine spatial autocorrelations of hotspot activity over time (Carnes and Ogneva-Himmelberger, 2011).

In contrast to the dispersal patterns from auto-migration of zoonotic agents, communicable human-borne diseases have been shown to demonstrate a distinct pattern of dispersal that includes outlier values when analyzed statistically using Local Moran's I. In a study of meningococcal meningitis occurrences found in Niger, outlier values were found and illustrate how movement characteristic of human vectors and the respiratory and throat secretions accompanying such movements are reflected in the analysis output (Paireau et al., 2012).

The aforementioned studies illustrate an important distinction that should be made between the application of the Moran's I analysis on diseases like West Nile and meningitis, in which the single vector is known, and White-Nose Syndrome, in which multiple species with differing abilities to spread the causative fungus over distance are potentially acting in a vector capacity. Within the local statistical analysis, both a typical "hotspot" pattern as well as what can be considered an "outlier" pattern are reported and yield important information about the vectors responsible. Since the z-score results reported from Moran's I analysis are in essence the slope of a regression line derived from the scatter plot of the differences between data points and the CO-type reported is determined by which quadrant (e.g. "high-high", "low-low", "high-low", or "low-high") a particular relationship is found, these results contain telling information about the data. Because any CO-type outlier reported from the Local Moran's I statistical analysis represents an instance in which a single data point has a significantly different value from that of its neighbors, a pattern characterized by an outlier nature is indicative of a phenomenon in which a vector (most typically humans) carries the causative agent over greater distances than would be expected from the normal migration patterns of a wildlife vector given their normal range.

Thus, what could be clearly shown in the CO-type outlier results generated by Local Moran’s I statistical analysis, and particularly relevant to an understanding of White Nose Syndrome spread patterns, is what might be considered a “jump-gap” pattern indicating new infection of a site geographically (or in this case, temporally) distant from previous infection sites. Given the current lack of statistical analyses performed on potentially multi-vector diseases, this study shows promise in addressing a broader range of applications in epidemiological examinations.

Methods

To accomplish the first goal of gathering WNS outbreak data from the seventeen states affected by WNS as of March 29, 2012 into a single data set that was appropriate for importing into the ArcGIS platform, a time-intensive process of approaching individual researchers, research groups, private and university labs, conservation groups at the state and federal level, and members of the National Speleological Society to request all available data was necessary. Due to the various methods being used in existing studies for data collection purposes, the dataset used for this project was an amalgamation of data from multiple sources and the criteria used to determine what sites and dates were judged sufficiently rigorous to appear in the underlying dataset for this project deserve explication. The counties in the final dataset were provided by Cal Butchkoski of the Pennsylvania Game Commission and Carl Herzog of the New York Department of Conservation and were initially cross-checked against posted dates found from the USGS National Wildlife Health Center (NWHC) and work done by researchers at the United States Geologic Survey. An important detail to note, however, is that the dates of WNS confirmation in the NWHC dataset are frequently limited to seasons (i.e. “Winter, 2007) and thus are not particularly useful for analysis purposes.

From this initial dataset, monthly occurrence of first WNS confirmations were established from primary research sources and from the “suspicious mortality” listings of the NWHC for all data points when possible. Counties in which no published confirmation date could be used to establish month-level outbreak dates were assigned a month date that reflected the median date within the three month range provided by NWHC; for example, “Winter 2009” value was set to January 1, 2009 within the functional dataset used for analysis. Although this method is not without drawbacks, it was used consistently and notes were made within the attribute table to reflect points in which the monthly dates are approximated. The potential concern with using the aforementioned method to establish dates from the NWHC database was that it might artificially affect the results reported from a temporally sensitive analysis like the Local Moran's I (LMI) as it is being used in this context. To address this potential issue of date bias within the NWHC derived dates, an additional analysis was carried out on the dataset in which the confirmation date of *Geomyces destructans detection* was randomly altered by up to 3 months (either earlier or later by a computerized random algorithm) to reflect the seasonal reporting nature of these dates and the results of this analysis were compared to the unaltered analysis results. It is important to note that the data compiled for this research is comprised of sites in which the fungus itself has been confirmed rather than the appearance of WNS symptoms since there are sites such as Kentucky and Oklahoma which have confirmed fungus sightings without associated mortality or physiological symptoms of the disease.

A deficiency of the dataset that was a potential impediment to conducting an analysis of the WNS distribution pattern was that point data for most karst and cave areas, and thus hibernaculum areas, is not available for public use. A novel method was utilized in this analysis by using the compiled WNS confirmation month to establish interval data points within the attribute table upon which Moran's I global and local statistical and pattern analyses were based. Due to the nature of extensive cave systems, it is possible that county level data could be more representative of the distribution within a naturally occurring area and within ArcGIS analysis, it is possible to perform spatial autocorrelation statistical tests at this level. To avoid zero values and the inherent difficulties of mapping the results of mathematical analysis of these zero values, time zero (that of the first confirmed outbreak in Schoharie County, New York) was set to “1” and each successive outbreak month was then assigned a value relative to this first outbreak date. A clear understanding that the attribute being examined here is *time interval from initial outbreak* rather than the geographic location of the outbreak itself is crucial in any interpretation. The complete dataset on which final analyses were performed can be found in Appendix I. An additional note of importance is that the analyses carried out here were conducted only upon the sites listed and not on surrounding counties with no *Geomyces destructans confirmation.*

The assembled dataset as completed above was imported into ESRI’s ArcMap GIS and both Global and Local Moran’s I analysis was performed using the variable of time (in this case, months from initial outbreak) with inverse Euclidean distance parameters. The Local Moran’s I formula is shown below in Equation 1, which illustrates its utility in analyzing the deviation from global mean to establish the similarity of weighted neighbors that are reported as CO-type and associated degrees of significance.

$$I_i = \frac{x_i - \bar{X}}{S_i^2} \sum_{j=1, j \neq i}^{n} w_{i,j}(x_j - \bar{X})$$

Equation 1: Local Moran’s I

An additional factor in the decision to utilize Global and Local Moran’s I statistical analyses rather than similar statistical methods was the non-normative distribution of data points (Figure 1) within the completed dataset.

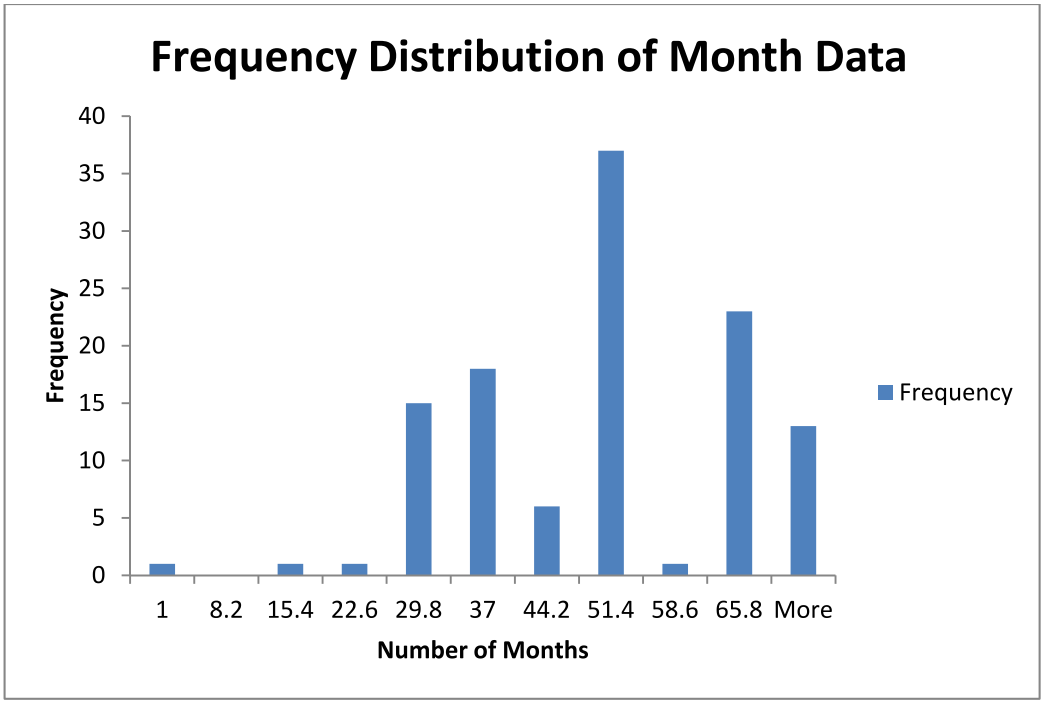
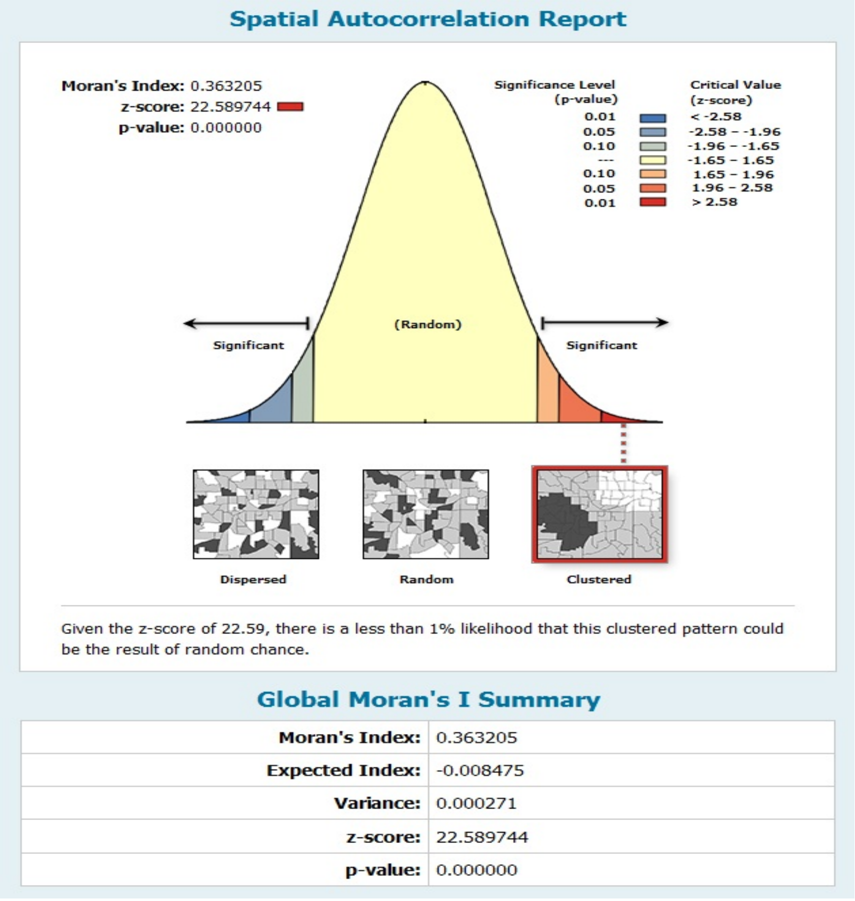


Figure 1: Frequency Distribution of Month Data was non-parametric, as is often found in these types of data related to spatio-temporal data points.

Although many analytical methods require the normal or “bell curve” distribution, this weakness is not shared by the Moran’s I test and is in fact a significant explanation as to why the LMI has been used extensively in a variety of epidemiology pattern-analyses. Since LMI is a measure of spatial autocorrelation analysis, the analysis results are dependent upon the relationship between data points rather than against the dataset as a whole, so it is uniquely suited for datasets such as this that are not demonstrably normal in distribution.

Results

One of the greatest advantages of graphically displaying the results of the Moran's I analyses conducted over the course of this study is that the underlying patterns make themselves readily apparent. Results from the Global Moran's I analysis demonstrate conclusively that there is indeed an overall clustered pattern upon examination of the entire dataset as shown below in Figure 2. The large z-score and extremely small p-value meaningfully show the clustered pattern to have a less than 0.01% chance of being due to random occurrence and strongly indicate that the real world phenomenon being examined does indeed have a spatiotemporally significant correlation. Put simply, the overall pattern of infection exhibits a significant grouping of similar values due primarily to the large number of sites found early on in the epidemic and this clustered effect is due to the occurrence of *Geomyces destructans* infection itself rather than random chance.



Spatial Autocorrelation Report

Moran's Index: 0.363205
z-score: 22.589744 🟥
p-value: 0.000000

Significance Level (p-value)		Critical Value (z-score)
0.01	🟦	< -2.58
0.05	🟦	-2.58 - -1.96
0.10	▨	-1.96 - -1.65
---	🟨	-1.65 - 1.65
0.10	🟧	1.65 - 1.96
0.05	🟧	1.96 - 2.58
0.01	🟥	> 2.58

Given the z-score of 22.59, there is a less than 1% likelihood that this clustered pattern could be the result of random chance.

Global Moran's I Summary

Moran's Index:	0.363205
Expected Index:	-0.008475
Variance:	0.000271
z-score:	22.589744
p-value:	0.000000

Figure 2: Spatial Autocorrelation Report, Global Moran's I demonstrating statistically significant degree of clustering.

Once the Global Moran's I analysis was completed and revealed a high degree of clustering within the dataset, the Local Moran's I analysis was performed to further examine the nature of individual relationships between data points. Figure 3 below shows the p-score results from LMI analysis and reveals areas of clusters with greater than 95% significance as determined by the p-test. The counties shown in red correspond to those counties having a greater than 99% significance relatedness, and the counties displayed in the pale green have between 95%-99% relatedness when contrasted against that expected of a complete spatially random dataset.

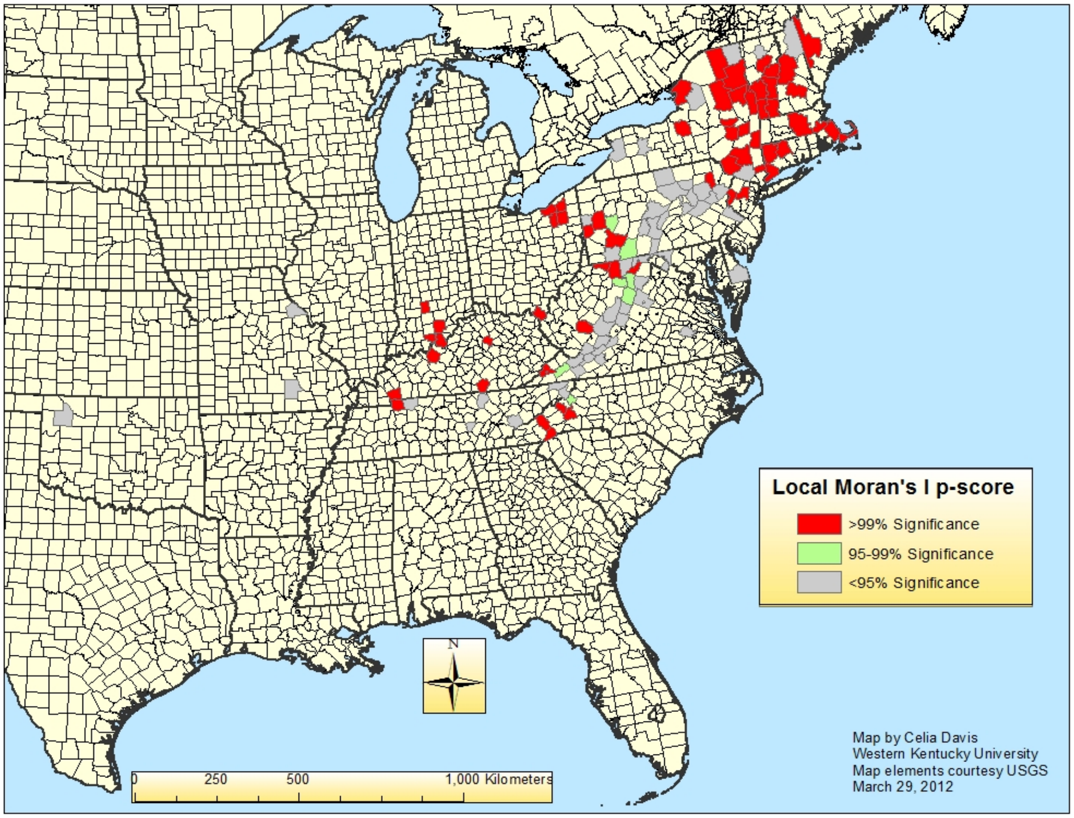
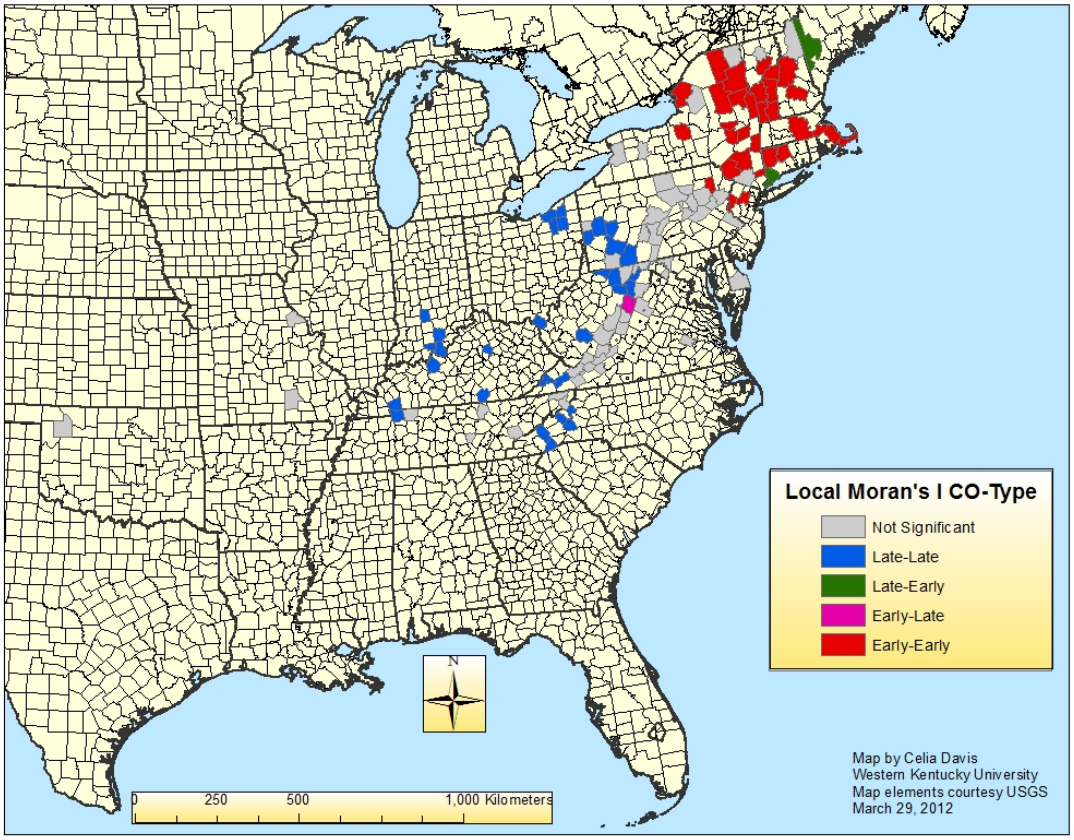


Figure 3: Local Moran’s I p-score demonstrating areas of significant clustering.

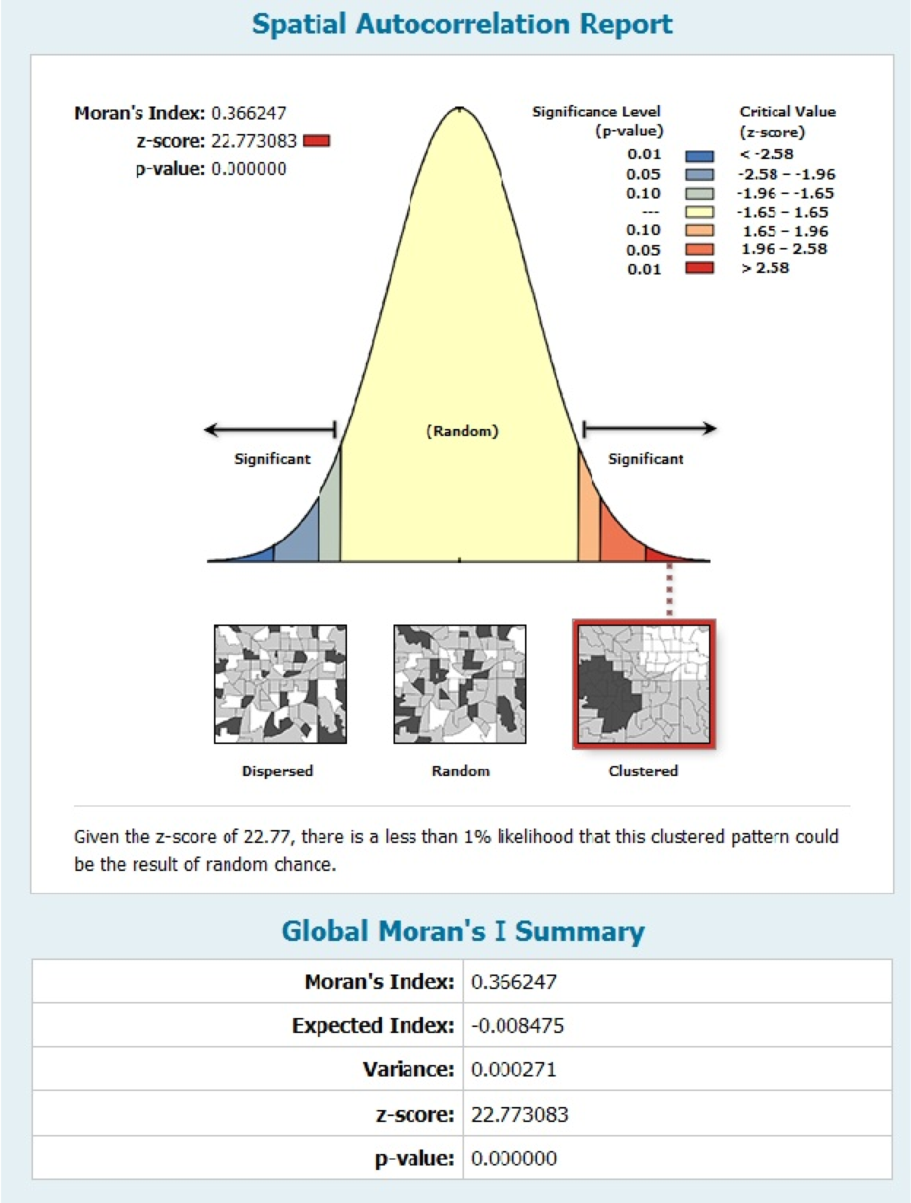
Notably, the areas of significance depicted in Figure 4 correspond to those areas shown to be clustered under the CO-type analysis reported from LMI conducted on the temporal assignments of WNS associated fungus confirmation, with those counties with “early-early” and “late-late” designations having >99% significance (Figure 4). In the context of this analysis, “early-early” is defined as a data point having low number of months after initial infection that is surrounded by neighbors of similar values and “late-late” is defined conversely. The presence of mixed relationships, “late-early” and “early-late” as shown in dark green and magenta, respectively, is significant based on the robustness of the analysis. The CO-Type results can be thought of as a measure of similarity to nearby sites, with "early-early" CO-Type signifying an early confirmation site that is effectively surrounded by other sites with similarly early confirmation dates.



Map by Celia Davis
Western Kentucky University
Map elements courtesy USGS
March 29, 2012

Figure 4: Local Moran's I CO-type reported for analysis of temporal distance from initial confirmation date showing Early-Late outlier (Pendleton County, WVA) and Late-Early outliers (Fairfield County, CT and Oxford County, ME).

As mentioned previously, in order to test the robustness of the dataset against date bias, an analysis with identical parameters to that of the original was performed upon the alternate dataset that varied each confirmation date within a range of three months and the results are depicted in Figures 5, 6, and 7. It is possible to understand from the observed results that the possible imprecision introduced into the dataset from the seasonal reporting at the NWHC does not alter the study findings in any statistically significant way.



Spatial Autocorrelation Report

Moran's Index: 0.366247
z-score: 22.773083 🟥
p-value: 0.000000

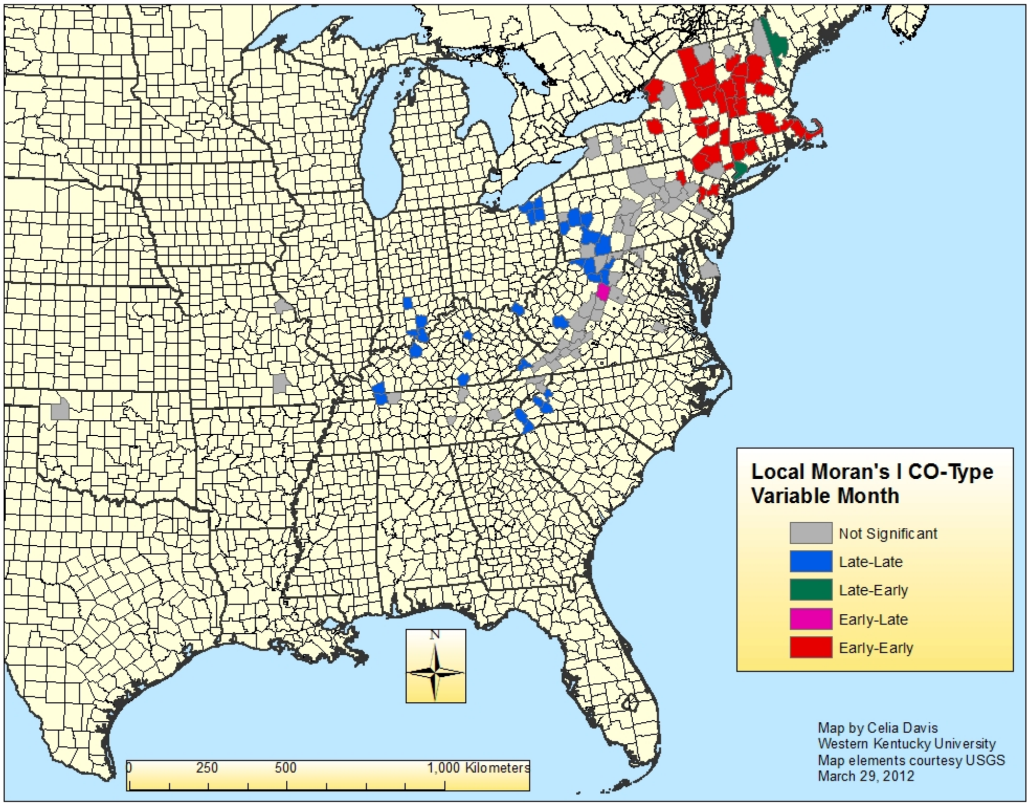
Significance Level (p-value)		Critical Value (z-score)
0.01	🟦	< -2.58
0.05	🟦	-2.58 - -1.96
0.10	🟩	-1.96 - -1.65
---	🟨	-1.65 - 1.65
0.10	🟧	1.65 - 1.96
0.05	🟧	1.96 - 2.58
0.01	🟥	> 2.58

Given the z-score of 22.77, there is a less than 1% likelihood that this clustered pattern could be the result of random chance.

Global Moran's I Summary

Moran's Index:	0.356247
Expected Index:	-0.008475
Variance:	0.000271
z-score:	22.773083
p-value:	0.000000

Figure 5: Spatial Autocorrelation Report, Global Moran's I Variable Date demonstrating statistically significant degree of clustering within variable month data.



Map by Celia Davis
Western Kentucky University
Map elements courtesy USGS
March 29, 2012

Figure 6: Local Moran's I CO-type, Variable Date reported for analysis of temporal distance from initial confirmation date showing Early-Late outlier (Pendleton County, WVA) and Late-Early outliers (Fairfield County, CT and Oxford County, ME).

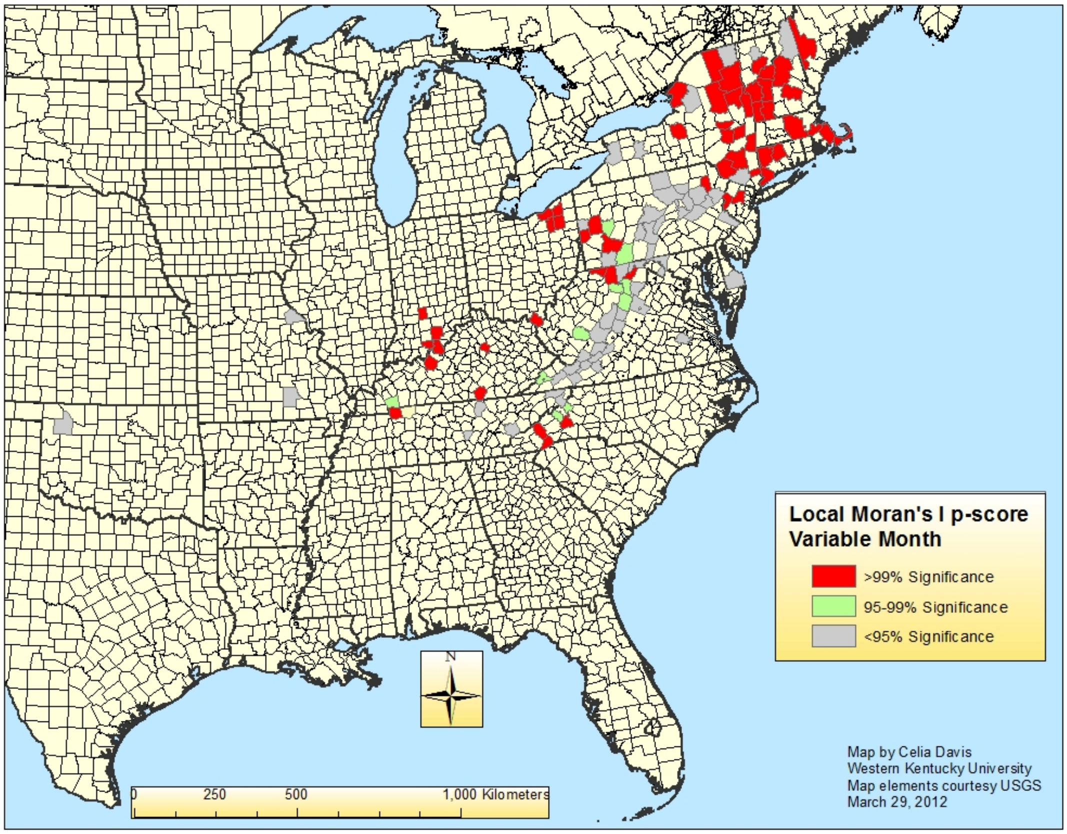


Figure 7: Local Moran’s I p-scores, Variable Date demonstrating areas of significant clustering.

Discussion

Once the labor intensive process of assembling the necessary data into a format conducive to analysis within the ArcGIS software platform was completed, it became clear that Moran's I global and local analysis yielded the most useful information in determining whether a pattern exists within the data itself (Global Moran's I, Figures 2 and 5) and, if such a pattern was present, what characterized the nature of that pattern (Local Moran's I, Figures 3, 4, 6, and 7). Although a statistically significant clustered pattern of WNS outbreak sites and dates is present, this is not unexpected due to the nature of typical disease outbreak and hotspot tendencies as illustrated by the West Nile virus, meningitis, and Dengue fever outbreaks discussed previously. Of more particular interest and relevance to the matter at hand is the precise nature of the pattern *within* the larger, global clustered pattern, and it is this question that the Local Moran's I (LMI) analysis is best suited to answer.

The most unique ability of Moran's I analysis in this context is the determination of the presence of so-called "outlier values," which would indicate a jump-gap transmission pattern despite the limitations of currently available data (the lack of cave specific latitude and longitude coordinates and thus "point" data). The aforementioned limitations of the dataset that make analysis by other methods inappropriate in this instance are not shared by LMI analysis and this makes it particularly useful in coming to an understanding of whether the *Geomyces destructans* fungus believed to be responsible for WNS follows the roughly linear spread pattern that would be expected from a bat-to-bat transmission mechanism (single vector with multiple reservoirs) like that shown by mosquito transmission of West Nile Virus (Sugumaran et al., 2009) or is instead being spread by human transmission from caver gear or clothing from site to site, which would be reflected by the presence of outliers within the dataset similar to those seen within the spread of meningitis as previously discussed (Paireau et al., 2012).

Considerable debate has ensued surrounding the nature of WNS dispersal, and because outliers within Local Moran's I analysis results occur when an individual data point is judged to be significantly different in value than its surrounding neighbor locations, the existence of numerous outliers could be interpreted as evidence of the "jump dispersal" pattern that might implicate human transmission by visitation to multiple caves after being in an infected cave as a culprit in the spread of the disease. Conversely, since only three CO-type outliers were found while performing the LMI analysis on the WNS mortality confirmation date dataset (Figure 4), the results of this study suggest that the dominant spread of WNS can be more likely attributed to direct contact transmission between affected individuals within the bat populations themselves rather than a human vector model of transmission. Because annual migration of the most severely affected bat species is limited to distances of 520 km or less for *Myotis sodalis* (Kurta and Murray 2002) and 48.5 km for *Myotis lucifugus* (Butchkoski 2010), the maximum annual transmission distance of *Geomyces destructans* by a bat carrier would be within that range based on the current transmission data. In contrast, human carriers could potentially travel well in excess of the above stated migration limits and thus "seed" a location with the fungus at much greater distances. If such a long-distance seeding were to occur by human carriers as a matter of routine transmission, the resulting White-Nose Syndrome mortality confirmation site would be revealed as an outlier with a value earlier than that of surrounding confirmed sites (or an “early-late” outlier within the LMI analysis as performed in this study).

The two “late-early” outliers found in Fairfield County, Connecticut and Oxford County, Maine (Figure 6) represent counties in which the *Geomyces destructans* fungus was detected at a statistically significant later date than those counties nearest the sites, and suggests that these counties may possess some topographical or ecological variation which prevented the spread of WNS into bat populations there at earlier dates. Alternatively, the surveying interval due to cave or mine access issues, or lack of surveying resources or personnel, could account for the difference in detection date; the fungus may have been present prior to reporting date but due to a delay in survey, was not discovered until later in the epidemic. Since the emphasis on most disease transmission research is the front edge of an epidemic, these “late-early” outliers are of potential interest in exploring what factors may have played a role in the transmission delay, however do little to explicate the underlying dispersal mechanism.

Of more concern and relevance to understanding the dispersal pattern of *Geomyces destructans* is the Pendleton County, West Virginia (WV) site (Figure 6) that is shown to be an “early-late” outlier by Local Moran’s I analysis. The presence of such an outlier could be interpreted as support for a “human as vector” model of disease transmission, and in fact, if analysis had revealed a pattern of such outliers, such a conclusion could be meaningfully drawn. However, closer examination of the dataset, particularly those counties surrounding Pendleton County, reveals that counties south of the site (Giles confirmed 2/2009, Bland confirmed 5/2009) showed earlier infection. The seven counties surrounding Pendleton County show considerable variation in reported dates (Figure 6- Pocohantas WV on 3/2010, Highland VA on 4/10, Rockingham VA on 8/2009, Tucker WV on 2/2011, Grant WV on 4/2011, Hardy WV on 3/2010, and Bath VA on 2/2009), and this constellation of occurrence dates suggests that the outlier status of Pendleton County, WV is perhaps a reflection of reporting artifacts and the much later reporting of Tucker and Grant counties in West Virginia is sufficiently later to alter the statistical analysis reporting of CO-type status even when weighed against the earlier dates of surrounding counties. Given the inherent financial, time, and access resource constraints placed on survey efforts in the mountains of West Virginia, it is possible that earlier appearances of the fungus were unrecorded.

When the analysis was performed again using a dataset that had been artificially altered to reflect a degree of three month variability in either the forward or backward temporal direction, the results did not differ in any statistically meaningful way from the original dataset, and again revealed a pattern with two clusters (early-early and late-late) along with the presence of outlier values for Pendleton County, WV, Fairfield County, CT, and Oxford County, Maine (Figures 5, 6, and 7). Performing the Moran's I analyses on a dataset in which the data points had been randomly altered by three months addressed a potential vulnerability of the analysis because of the possible variation in confirmation reporting dates due to the inherent difficulty in obtaining primary data; timing of cave surveys, difficulty in accessing hibernaculum sites, and seasonal limitations all have the effect of introducing a possible "timing artifact" bias into the results. It also addresses the possible issue of sensitivity of the analysis to be able to detect outliers within a larger reporting error. The variable month dataset and analysis results effectively demonstrate that the nature of the pattern found in this study is a reflection of the actual phenomenon being examined rather than a side-effect of the unavoidable data collection limitations. Had there been an alteration of outlier values in the CO-type reporting by such an alteration of the dataset, the veracity of such a statistical analysis could rightly be questioned. However, in this case, the affirmation by a high degree of similarity of reported values further emphasizes the robust nature of the analysis itself.

Ultimately, the results of this study, primarily the lack of multiple “early-late” outlier values as revealed by Local Moran’s I CO-type reporting and associated significance values (Figures 3 and 4), suggest that the dominant transmission pattern of White-Nose Syndrome in the United States is typical of that found in diseases characterized by direct transmission between individuals of affected bat species rather than that of a separate vector. One would expect that if humans were acting as a vector for *Geomyces destructans*, the dispersal pattern would resemble that of meningitis as discussed above and outlier values representing “jumps” in the dispersal would be present. This finding is contrary to much of what has been supposed about the dispersal of WNS and further emphasizes just how critical the creation of, and continued efforts to maintain, a comprehensive dataset of outbreak data is to appropriately address the issue at hand and arrive at policies that more effectively mitigate White-Nose Syndrome. As any research is limited to the quality of data upon which the analyses are performed, the discrepancy around the Pendleton, WV confirmation dates should serve as a strong reminder of how critically important the practice of standardized, rigorous data collection is to our understanding of the timing and occurrence of natural phenomena like infectious disease dispersal patterns. Additionally, because such robust data collection is made even more difficult with diminished resources, it should serve as a call for increased attention to communication and management at both the state and federal levels in order to more promptly develop monitoring and surveying plans, and mobilize “ground troops” for future outbreaks.

A more complete understanding of the dispersal patterns of White-Nose Syndrome, as revealed by careful statistical evaluation of the relationships between each confirmed site within the compiled dataset, is absolutely critical to the development of a scientifically valid, well-reasoned approach to addressing and possibly mitigating the devastating effects of WNS. Previously, such large-scale studies have not been conducted due in part to the lack of a comprehensive dataset and, now that the stated research goal of establishing such a dataset and determining its usefulness has been accomplished here, more scientifically rigorous evaluations of the dispersal patterns found within the epidemic can be built upon the results of this study. Of particular interest for future mitigation efforts could be the development of a dataset that compares *Geomyces destructans* infection dates against WNS associated mortality dates. Such a dataset would allow for the detailed examination of transmission and mortality expression rates and could potentially reveal crucial information about factors which influence disease development, however that data is not yet available and will take considerable cooperation and effort to develop into a meaningful investigative tool.

In addition to the chronological and temporal analysis of the disease spread itself, perhaps one of the most powerful aspects of applying ArcMap’s graphical capabilities to an examination of this disease spread pattern is that alternate variables, such as topography, prevailing wind patterns, and migration paths, can be incorporated into further analyses. Although it is impossible to predict at this stage which of these variables, if any, will prove to be significant upon further examination, the fact that the *Geomyces destructans* fungus is cold-loving and therefore potentially affected by factors such as annual temperature and geomorphology of the hibernaculum themselves strongly suggests that a correlation with these annual temperatures and dominant wind patterns should present itself when used as a co-variable against the spread pattern and resulting mortality. As of completion of this study, wide-ranging efforts are underway to establish robust baseline population numbers for affected bat species. These census efforts coupled with more sophisticated mortality counts could potentially allow further research into how the climatic and ecological factors mentioned above play a role in individual and population survivability.

Most current mitigation techniques have involved closing caves or mines, or limiting access by humans, along with evolving decontamination procedures (USFWS, 2012a,b). A better understanding of the fungus itself and its survivability in various environments from recent research also introduced continued discussion about how best to address WNS issues (Blehert 2011). However, many of the current efforts to curtail the spread of *Geomyces destructans* have been hampered by an incomplete understanding of the underlying patterns of dispersal, combined with the lack of a standardized method of disease discovery and reporting. Additionally, the policies in place at the federal and state government level regarding well-intentioned cave and mine closures may have had the unintentional effect of diminishing beneficial input from potential allies within the outside community. Given that eventual modeling efforts will be largely dependent on the robustness of site data (both spatial and temporal) and the large role played by nongovernmental visitors in establishing outbreak sites early in the disease, the decision to close all caves and mines on public land may have the end result of decreasing our ability to reasonably predict where and when future outbreaks will occur.

In order to effectively collect and compile a current dataset of ongoing outbreak sites, it will be necessary to establish a clearinghouse for suspected WNS sites at the federal level with a correspondingly rigorous protocol to determine data accuracy and what criteria by which to include new sites. For the purposes of this study, WNS associated mortality was not a prerequisite for inclusion in the dataset; however, the nature of the causative fungus and manifestation of WNS mortality itself is as of yet incompletely understood with some species exhibiting symptoms of WNS with no resulting mortality (USFWS, 2012b). As survey and census efforts intensify, more comprehensive data on sites infected with *Geomyces destructans* prior to mortality events may well lead to important discoveries regarding species susceptibility and survivability.

Perhaps of most urgent import to wildlife managers and conservation efforts is the ability to more effectively predict the areas which *Geomyces destructans* is most likely to infect and when it will affect those areas. The novel application of Moran’s I used in this research suggests that, not only would it be possible to create predictive geospatial models, but that *transmission time* itself can be used as a variable when constructing these predictive models. This study provides an example or the robustness of these techniques and their ability to play a crucial role in management activities associated with WNS and future outbreaks, while also illustrating the limitations of the analysis given the myriad data collection and reporting techniques used to date. This has significant implications not just for the disease being examined within the context of this study, but for the broader field of wildlife epidemiology as a whole.

APPENDIX
Geomyces destructans Confirmation Dates

STATE	COUNTY	FIPS	MonthYear	Months	Source
NY	Schoharie County	36095	1-Feb-06	1	Al Hicks/NY DOC
NY	Albany County	36001	1-Mar-07	14	Al Hicks/NY DOC
PA	Centre County	42027	1-May-07	16	USGS/NWHC
MA	Franklin County	25021	1-Jan-08	24	USGS/NWHC/NWHC
MA	Hampden County	25023	1-Jan-08	24	USGS/NWHC
NY	Ulster County	36111	29-Jan-08	24	Carl Herzog/NY DOC
VT	Bennington County	50003	1-Jan-08	24	USGS/NWHC
VT	Orange County	50017	1-Jan-08	24	USGS/NWHC
VT	Windham County	50025	1-Jan-08	24	USGS/NWHC
VT	Windsor County	50027	1-Jan-08	24	USGS/NWHC
NY	Montgomery County	36057	1-Feb-08	25	Carl Herzog/NY DOC
CT	Litchfield County	09005	1-Mar-08	26	USGS/NWHC
MA	Berkshire County	25001	1-Mar-08	26	Blehert, 2008
NY	Essex County	36031	1-Mar-08	26	Carl Herzog/NY DOC
NY	Jefferson County	36045	1-Mar-08	26	Carl Herzog/NY DOC
NY	Warren County	36113	1-Mar-08	26	Carl Herzog/NY DOC
NY	Columbia County	36021	1-Apr-08	27	Carl Herzog/NY DOC
NY	Sullivan County	36105	1-Apr-08	27	Carl Herzog/NY DOC
PA	Lackawanna County	42069	1-Nov-08	34	USGS/NWHC
NJ	Morris County	34027	1-Dec-08	35	USGS/NWHC
NJ	Warren County	34041	1-Dec-08	35	USGS/NWHC
PA	Mifflin County	42087	1-Dec-08	35	PA Game Commision
CT	Hartford County	09003	1-Jan-09	36	USGS/NWHC
NY	Onondaga County	36067	1-Jan-09	36	Carl Herzog/NY DOC
PA	Schuylkill County	42107	4-Jan-09	36	Cal Butchkoski
WV	Pendleton County	54071	1-Jan-09	36	WVDNR
MA	Middlesex County	25027	1-Feb-09	37	USGS/NWHC
MA	Norfolk County	25021	1-Feb-09	37	USGS/NWHC
NH	Grafton County	33009	1-Feb-09	37	USGS/NWHC
NH	Merrimack County	33013	1-Feb-09	37	USGS/NWHC
NY	Putnam County	36079	1-Feb-09	37	Carl Herzog/NY DOC
NY	Washington County	36115	12-Feb-09	37	Carl Herzog/NY DOC
VA	Bath County	51017	1-Feb-09	37	Sweezy
VA	Giles County	51071	1-Feb-09	37	USGS/NWHC
VT	Rutland County	50021	1-Feb-09	37	USGS/NWHC
VT	Washington County	50023	1-Feb-09	37	USGS/NWHC
NY	Hamilton County	36041	1-Mar-09	38	Carl Herzog/NY DOC
PA	Luzerne County	42079	1-Mar-09	38	PA Game Commission

NY	Franklin County	36033	1-Apr-09	39	Carl Herzog/NY DOC
VA	Bland County	51021	1-May-09	40	Sweezy
VA	Smyth County	51173	1-May-09	40	Sweezy
VA	Rockingham County	51165	1-Aug-09	43	Sweezy
NY	Lewis County	36049	16-Dec-09	47	Cal Butchkoski/Carl Herzog
PA	Bucks County	42017	1-Dec-09	47	USGS/NWHC
NY	Orange County	36071	15-Jan-10	48	Cal Butchkoski
PA	Carbon County	42025	1-Jan-10	48	USGS/NWHC
PA	Huntingdon County	42061	1-Jan-10	48	USGS/NWHC
PA	Lawrence County	42073	1-Jan-10	48	Cal Butchkoski
PA	Lycoming County	42081	1-Jan-10	48	USGS/NWHC
PA	Monroe County	42089	20-Jan-10	48	Cal Butchkoski
PA	Sullivan County	42113	16-Jan-10	48	Cal Butchkoski
NY	Erie County	36029	15-Feb-10	49	Cal Butchkoski
PA	Blair County	42013	1-Feb-10	49	USGS/NWHC
PA	Columbia County	42037	3-Feb-10	49	Cal Butchkoski
PA	Northumberland County	42097	16-Feb-10	49	Cal Butchkoski
PA	Tioga County	42117	23-Feb-10	49	Cal Butchkoski
TN	Carter County	47019	1-Feb-10	49	Sweezy
TN	Sullivan County	47163	1-Feb-10	49	Sweezy
VA	Tazewell County	51185	1-Feb-10	49	VA DOC
VT	Lamoille County	50015	1-Feb-10	49	USGS/NWHC
MD	Allegany County	24001	1-Mar-10	50	Sweezy
MD	Garrett County	24023	18-Mar-10	50	MD DNR
NH	Coos County	33007	1-Mar-10	50	Cal Butchkoski
NY	Clinton County	36019	1-Mar-10	50	Al Hicks/NY DOC
NY	Livingston County	36051	29-Mar-10	50	Cal Butchkoski
TN	Blount County	47009	1-Mar-10	50	Sweezy
TN	Montgomery County	47125	1-Mar-10	50	sweezy
TN	Van Buren County	47175	1-Mar-10	50	Sweezy
VA	Craig County	51045	1-Mar-10	50	Sweezy
WV	Greenbrier County	54025	1-Mar-10	50	Sweezy
WV	Hardy County	54031	1-Mar-10	50	Sweezy
WV	Mercer County	54055	1-Mar-10	50	Sweezy
WV	Monroe County	54063	1-Mar-10	50	Sweezy
WV	Pocahontas County	54075	1-Mar-10	50	Sweezy
DE	New Castle County	10005	1-Apr-10	51	Sweezy
MO	Pike County	29163	1-Apr-10	51	Cal Butchkoski
PA	Fayette County	42051	19-Apr-10	51	Cal Butchkoski
TN	Fentress County	47049	1-Apr-10	51	Sweezy

VA	Highland County	51091	1-Apr-10	51	Sweezy
WV	Jefferson County	54037	14-Apr-10	51	US FWS
MO	Shannon County	29203	2-May-10	52	Cal Butchkoski
OK	Woodward	40153	3-May-10	52	OK DWC
VA	Chesterfield County	51041	1-May-10	52	Cal Butchkoski
IN	Crawford County	18025	1-Jan-11	60	USGS/NWHC
IN	Washington County	18175	23-Jan-11	60	IN DNR
VA	Pulaski County	51155	1-Jan-11	60	VA DOC
VA	Russell County	51167	31-Jan-11	60	Cal Butchkoski
IN	Monroe County	18105	18-Feb-11	61	Cal Butchkoski
NC	Avery County	37011	1-Feb-11	61	NC Wildlife Resources
NC	Yancey County	37199	1-Feb-11	61	NC Wildlife Resources
VA	Wise County	51195	1-Feb-11	61	USGS/NWHC
WV	Tucker County	54093	14-Feb-11	61	Cal Butchkoski
CT	Fairfield County	09001	24-Mar-11	62	Cal Butchkoski
MD	Washington County	24043	1-Mar-11	62	MD DNR
OH	Lawrence County	39087	30-Mar-11	62	OH DNR
PA	Armstrong County	42005	17-Mar-11	62	Cal Butchkoski
PA	Butler County	42019	17-Mar-11	62	Cal Butchkoski
PA	Fulton County	42057	30-Mar-11	62	Cal Butchkoski
PA	Somerset County	42111	29-Mar-11	62	Cal Butchkoski
PA	Westmoreland County	42129	18-Mar-11	62	Cal Butchkoski
KY	Trigg	21221	13-Apr-11	63	KDFWR
ME	Oxford County	23017	1-Apr-11	63	USGS/NWHC
NC	McDowell County	37111	4-Apr-11	63	Cal Butchkoski
WV	Fayette County	54019	18-Apr-11	63	NPS
WV	Grant County	54023	15-Apr-11	63	WVDNR
NC	Transylvania	37175	1-Jun-11	65	Cal Butchkoski
OH	Summit County	39153	14-Jan-12	72	OH DNR
WV	Mineral County	54057	24-Jan-12	72	Cal Butchkoski
KY	Fayette County	21067	13-Jan-12	72	CDC
OH	Geauga County	39055	1-Jan-12	72	OH DNR
IN	Harrison County	18061	8-Feb-12	73	Cal Butchkoski
KY	Breckinridge County	21027	1-Feb-12	73	FWS
KY	Wayne County	21231	27-Feb-12	73	Cal Butchkoski
NC	Haywood County	37087	24-Feb-12	73	Cal Butchkoski
OH	Cuyahoga	39035	8-Feb-12	73	Cal Butchkoski
OH	Portage County	39133	16-Feb-12	73	Cal Butchkoski
PA	Beaver	42007	7-Feb-12	73	Cal Butchkoski
TN	Stewart County	47161	17-Feb-12	73	Cal Butchkoski
WV	Monongalia County	54061	21-Feb-12	73	Cal Butchkoski

WV	Preston County	54077	27-Feb-12	73	Cal Butchkoski

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