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Effects of Host Movement on Pathogen Population Structure and Epidemic Dynamics

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Effects of Host Movement on Pathogen Population Structure and Epidemic Dynamics

By

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B.S., Pennsylvania State University, 2007

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Abstract

Effects of Host Movement on Pathogen Population Structure and Epidemic Dynamics
By Brooke Bozick

This dissertation examines how host movement affects epidemic spread by characterizing spatial genetic patterns in pathogen populations. When hosts are highly mobile, measures of spatial distance should additionally incorporate the magnitude and frequency of movement between locations. Seasonal influenza A virus presents an ideal system with which to study the effects of mobility on viral dynamics due to extensive human transportation networks. To fully understand the processes of pathogen invasion and spread, a detailed understanding of the ecological and evolutionary factors that control distributional limits is necessary. I find that pathogens are not uniformly distributed across their hosts' ranges, and that pathogen evolutionary responses to conditions across the geographic range are modulated by both abiotic and biotic factors that differ across the landscape. An initial investigation of regional scale human mobility in the United States suggests that epidemics spread along predictable pathways defined by commuter volume. However, similar patterns are not detected for influenza epidemics in Europe. An analysis of the major European regional transportation networks reveals that both networks possess characteristics that facilitate long-distance transmission and international mixing of influenza. This analysis also uncovers important complexities associated with the spatial analysis of genetic sequence data, and a re-examination of US influenza epidemics leads to the conclusion that spatial structure based on mobility is not yet detectable in this system using the current genetic data. Finally, the effects of vaccination strategies targeted at different host age and social groups are evaluated using a stochastic metapopulation model simulating a city-suburb system. I find that targeting children provides the greatest benefits in terms of reducing incidence, but also show that vaccination of groups of employed adults provides similar reductions in incidence and additionally delays the speed and timing of inter-community spread when epidemics are severe and vaccine doses are limited. I conclude that the intricacies of epidemic spread make the detection of spatial genetic patterns based on movement networks difficult, but that the greater availability of high-resolution spatial genetic data will lead to a more detailed understanding of pathogen ecological and evolutionary dynamics.

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Dad: 31 years later, you finally have a doctor in the family. This is for you.

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Chapter 1

Introduction

In this dissertation, I examine how host movement influences pathogen transmission and spatial spread. By characterizing the underlying spatial genetic patterns in pathogen populations, I connect the evolutionary dynamics of pathogens with ecological processes driven by host-pathogen interactions. Patterns of population genetic diversity have been widely used to infer underlying ecological processes (Dobzhansky, 1970; Epperson, 2003; Ford, 1975). As many pathogens are completely reliant on their hosts for successful transmission, close concordance is often observed between pathogen genetic patterns and host behavior and population dynamics (Nadler, 1995; Nieberding and Olivieri, 2007; Rannala and Michalakis, 2003). For rapidly evolving viruses, ecological and evolutionary dynamics happen on similar time scales, allowing for the direct connection of evolutionary patterns with the ecological processes that generate them (Biek and Real, 2010; Grenfell et al., 2004; Real and Biek, 2007). As pathogens evolve at a rate much faster than that of their hosts, genetic data collected from pathogens has recently been used to understand host dynamics and distributions (Biek et al., 2006; Biek et al., 2007; Falush et al., 2003; Nieberding et al., 2004; Yanagihara et al., 2002).

1.1 Linking host movement to pathogen population structure

One such pattern-process combination is the structuring of genetic variation in pathogen populations by host movement and landscape barriers. Historically, a model approximating that of isolation by distance has served as the null hypothesis for expectations of how genetic diversity is structured (Epperson, 2003). Under this model,

the invasion of a completely naïve host population by a novel pathogen will cause pathogen genetic sequences collected further apart geographically to also appear more distant genetically. This phenomenon results when local transmission dominates a system and is widely observed in nature (Real et al., 2005a). Conversely, divergence from this observation allows for the estimation of the importance and magnitude of long-distance dispersal on transmission (Smith et al., 2005).

These null expectations will be violated in systems where hosts are highly mobile. In systems where long-distance movement is common, the null expectation should instead be that of a geographically well-mixed pathogen population. In such cases, alternative approaches to quantifying distance are necessary. One such framework involves considering not only the Euclidean distance between locations, but also the quantity of and frequency with which individuals are exchanged. This connectivity network is, in essence, a large-scale representation of a contact rate landscape. If long-distance movement occurs along well-defined pathways, a correlation between genetic distance and the magnitude of host movement should be apparent, rather than a cline in genetic similarity as geographic distance increases. Differential movement by hosts of different sexes, ages or social groups could theoretically allow for the identification of hosts that are important for transmission across various spatial scales by linking subgroup-specific movement to pathogen population structure.

1.2 Human movement and disease

Humans are clear examples of hosts that commonly move long distances in short periods of time. For humans, transport network availability presents a stronger barrier than the physical landscape in terms of allowing individuals to move between and interact with individuals in other locations. As a direct result, space is better defined as a

connectivity network; any underlying structure in human-associated pathogen genetic diversity should directly correspond to this network (Pybus et al., 2015).

The hierarchy of human mobility spans a wide range of spatial and temporal scales (Fig 1.1) (Stoddard et al., 2009). At the global scale, the transport of infected individuals over long-range mobility networks can seed epidemics of emerging or reemerging diseases (Khan et al., 2014; McLean et al., 2005; Semenza et al., 2014). Individuals traveling at this scale likely do so more infrequently, but longer trip durations provide opportunities for local transmission that can initiate outbreaks. Travel flows along these networks have been used to track past global pathways of disease spread (Bahl et al., 2011; Brockmann and Helbing, 2014) and to predict the most likely pathways that future pandemics will take (Gomes et al., 2014; Hufnagel et al., 2004). Although the magnitude of travel is well correlated with the timing of epidemic introduction, frequent long distance travelers contribute little to epidemiological dynamics once the epidemic is underway (Hollingsworth et al., 2007). At the local scale, detailed information on daily short-range movements and social contact networks has allowed for a more mechanistic understanding of how disease spreads through a community (Salathé et al., 2010; Vazquez-Prokopec et al., 2013). At this scale, individuals with high contact rates contribute disproportionally to disease spread (Stein, 2011). Recurrent local movements lead to increased exposure hazards for regular contacts, with the movement of children to and from school providing a prime example (Cauchemez et al., 2008). Regional mobility combines aspects of movement from both global and local scales, as it involves long-range transportation networks that may be used frequently and/or with high regularity to promote interactions among individuals from different communities. For example, the effects of regional movement on measles dynamics have been widely characterized in Africa, where seasonally-forced epidemics

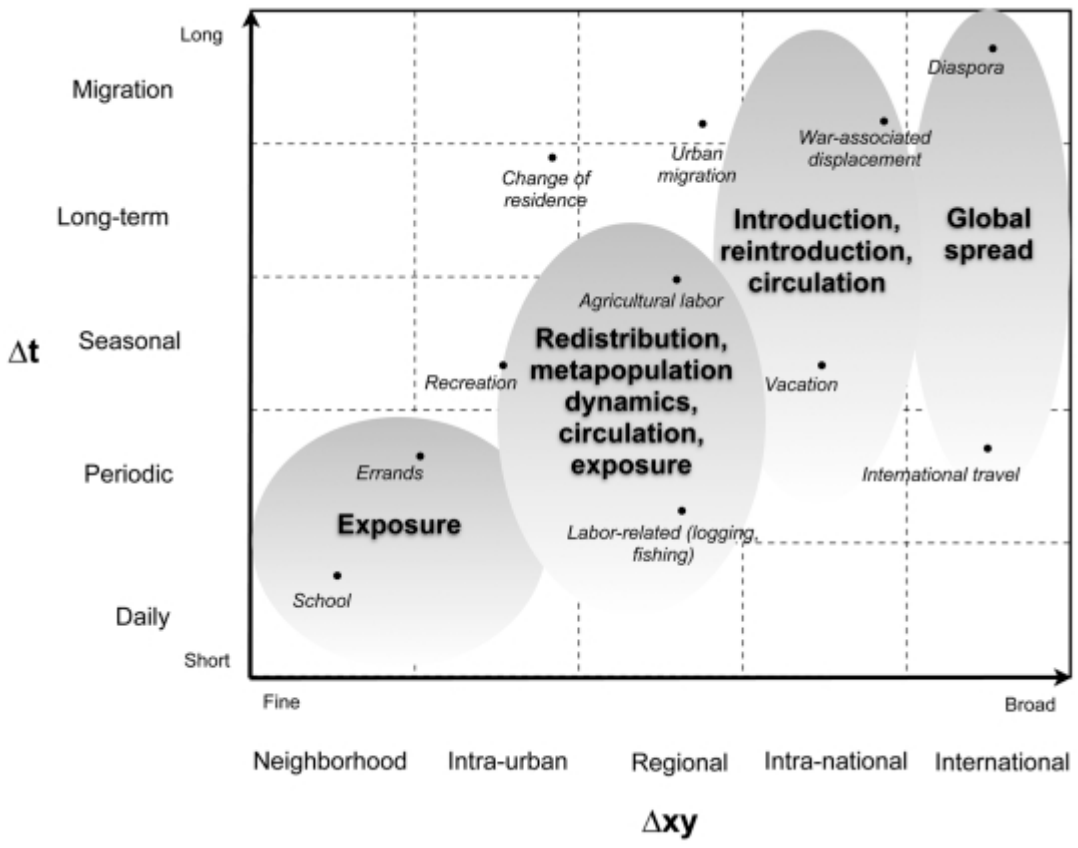

Figure 1.1. Temporal and Spatial Scales Over Which Human Movement Occurs and Implications for Pathogen Transmission. Human movement occurs across multiple scales ranging from the local daily trips of short duration (e.g. movement to and from school) to global journeys that can last for extended periods of time (e.g. seasonal migrations). *Reprinted from: Stoddard ST, Morrison AC, Vazquez-Prokopec GM, Paz Soldan V, Kochel TJ, Kitron U, et al. (2009) The Role of Human Movement in the Transmission of Vector-Borne Pathogens. PLoS Negl Trop Dis 3(7): e481*

are driven by human migrations between regional centers for agriculture (Bharti et al., 2011).

The effects of human mobility are pathogen-specific. Diseases with more complex life histories and life-cycle requirements depend not only on the movement of their human hosts, but also on the presence and movement of any other vectors or reservoirs that they require and/or the abiotic conditions necessary for transmission (Estrada-Pena et al., 2014; Halpin et al., 2007). For instance, the successful introduction of vector-

borne pathogens requires not only the presence of susceptible humans but also the availability of competent vectors.

1.3 Influenza A virus as a model system

Seasonal influenza A virus presents an ideal system with which to study the effects of host mobility on viral evolutionary and ecological dynamics. Influenza A is a directly-transmitted, negative sense, single-stranded RNA virus of the *Orthomyxoviridae* family. The ~13 kb genome is composed of 8 segments that code for 11 different proteins and that frequently reassort. The hemagglutinin (HA) and neuraminidase (NA) proteins are the major targets of the human immune system and are therefore most important antigenically (Bush et al., 1999; Wilson and Cox, 1990b). Eighteen HA types and 11 NA types have so far been identified, the combination of which is used to classify the virus subtype (Centers for Disease Control and Prevention, 2015b). Wild birds of the order *Anseriforme* and *Charadriforme* are the natural hosts of influenza A viruses (Webster et al., 1992), although other mammalian species including pigs and horses are susceptible to influenza infection as well (Nelson and Holmes, 2007).

Currently, only the H3N2 and H1N1 subtypes circulate regularly in the human population. Although both initially emerged from an animal reservoir, neither requires any additional species for replication or transmission. The emergence of new influenza subtypes in the human population is associated with reassortment events between human viruses and novel segments from viruses circulating in other avian or mammalian species as well as adaptation of avian viruses to human hosts (Kawaoka et al., 1989; Scholtissek et al., 1978a; Taubenberger et al., 2005). This process, termed 'antigenic shift', produces pandemics following the initial cross-species transmission event (e.g. 1918 Spanish flu, 1958 Asian flu and 1968 Hong Kong flu). In contrast, reassortant

lineages that have become established in the human population evolve through a process of mutation accumulation termed 'antigenic drift' in concert with reassortment between other co-circulating strains (Rambaut et al., 2008).

Influenza epidemics are strongly seasonal, with dramatic peaks occurring in the winter months in temperate regions and more modest peaks occurring in the tropics during the rainy season or circulating at low levels year round (Russell et al., 2008; Tamerius et al., 2013; Viboud et al., 2006a). The driver(s) of these seasonal patterns are still unclear, but have been attributed to seasonal indoor crowding among humans, reduced viral stability in warm temperatures, and/or reduced immune function due to host vitamin D deficiencies (Lofgren et al., 2007). Rapid lineage turnover evidenced by a ladder-like phylogeny is a hallmark of influenza A viruses (Fitch et al., 1997). This results from antigenic escape mutants that outcompete and replace existing lineages through a process known as genetic drift every 3-5 years (Smith et al., 2004). Due to these dynamics, epidemics must be newly seeded each season; there is no evidence for sustained local persistence between seasons in temperate regions (Nelson et al., 2007). As a consequence, annual epidemics can be considered as replicate manifestations of the same underlying invasion process, facilitating the comparison of epidemic dynamics and spatial patterns over multiple years. Although there is some evidence for cross-immunity between lineages of the same subtype, this effect is relatively small and annual updates to the vaccine are necessary to protect against that season's dominant strain (Blackburne et al., 2008; Shih et al., 2007; Wilson and Cox, 1990a). Despite the rapid evolution observed across seasons, influenza evolution during the course of a single season is generally thought to be neutral (Lavenu et al., 2006; Nelson et al., 2006).

The two currently circulating subtypes, H3N2 and H1N1, exhibit differing epidemiological dynamics. Since 1968, when it first entered the human population

during the “Hong Kong Flu” pandemic, H3N2 dominated most influenza seasons in the United States (US) (Holmes, 2009). During that period, H3N2 generally caused more severe epidemics characterized by larger peaks, greater morbidity and mortality, and faster spatial spread (Simonsen et al., 2005; Viboud et al., 2006b; Wolf et al., 2006). H1N1 circulated concurrently during this period, having most recently re-entered the human population in 1977 (Scholtissek et al., 1978b), but generally caused milder epidemics that were more genetically diverse. The mechanisms producing these differences in observed standing diversity have not yet been resolved, though hypotheses that highlight the effects of cross-immunity, epochal evolution and expansion load have been proposed (Ferguson et al., 2003; Koelle et al., 2006; Koelle and Rasmussen, 2015). In 2009, a new variant of H1N1 entered the human population after a triple reassortment event involving genes from human, swine and avian viruses (Dawood et al., 2009; Smith et al., 2009). In the northern hemisphere, the pandemic first peaked in the late spring and early summer of 2009, with a secondary peak occurring in the fall and winter of the 2009-2010 season (Centers for Disease Control and Prevention, 2016; Nelson et al., 2011). The pandemic strain did not have quite the impact that had originally been predicted (Viboud et al., 2010), but has since replaced the previously circulating H1N1 seasonal lineage (Blyth et al., 2010; Centers for Disease Control and Prevention, 2016).

Due to the regularity with which influenza epidemics occur and the large proportion of the human population that is annually infected, an abundance of publicly available genetic sequence data is available for this virus. In addition, much of these data are spatially referenced at scales that are relevant to transmission. Although multiple studies have investigated global patterns of influenza genetic diversity and spatial spread (Bahl et al., 2011; Balcan et al., 2009b; Lemey et al., 2014), and others have examined community-level drivers of transmission (Worby et al., 2015), far fewer studies have

examined epidemic dynamics at the regional scale. Those that have, have concluded that the virus is introduced into regions multiple times over the course of the season, that abundant genetic diversity is present across space and that spatial spread is so rapid that no genetic structure based on geography exists (Nelson et al., 2008; Nelson et al., 2006). This last conclusion is problematic for the design of effective control strategies, since it suggests that pathways of viral spread are unpredictable. In the following studies, I reexamine this finding and offer insights on policies that have the potential to aid in the control of influenza epidemics.

1.4 Dissertation Summary

In this dissertation, I explore the effects of human movement on pathogen population structure, using influenza A as a model system. I use phylogenetic techniques, spatial statistics and network analysis to detect underlying genetic patterns at the regional scale and utilize my findings to design and implement a novel vaccination strategy. To explore the processes of invasion and spatial spread, a detailed understanding of geographic range theory and the ecological and evolutionary factors that control distributional limits is necessary. In **Chapter 2**, I conduct a review of the literature to characterize the ecological and evolutionary factors than constrain the ranges of parasites and pathogens. These include abiotic factors (e.g. climate and host population structure) and biotic factors (e.g. interspecies interactions), as well as factors that control the organism's evolutionary response to these conditions. I conclude by outlining how an understanding of the spatial patterns observed throughout the geographic range can provide insights on the population dynamics of hosts and their pathogens.

While influenza A is considered a global pathogen, local extinctions in temperate areas during the summer months necessitate repeated invasions at the regional scale. In **Chapters 3 and 4**, I explore how regional human mobility structures influenza populations during these annual introductions. Although the study of transportation networks in the US performed in Chapter 3 initially suggests that influenza epidemics predictably spread along pathways defined by commuter movements, no underlying population structure is found when a similar analysis of influenza epidemics in Europe based on aviation and rail network connections is conducted in Chapter 4. A reexamination of the US influenza dataset correcting for strong differences in intra- and inter-state genetic distances and commuting patterns shows that the original observation of spatial structure was likely driven by these differences, rather than by the predictable decay of genetic similarity with decreasing travel volume. Additionally, an analysis of the European regional transportation networks and a comparison with those of the US reveals that the rail network, hypothesized to have a structuring influence on epidemics, shares several important characteristics with both the European and US aviation networks. This finding leads to the conclusion that both international transportation networks in Europe likely facilitate long-distance transmission and international mixing of influenza populations. The greater spatial organization of the US commuting network makes it a better candidate for imposing structure during epidemic spread, which may be detectable when more high-resolution spatial genetic data become available.

In **Chapter 5**, I evaluate whether targeted vaccination strategies can be used for the prevention and control of influenza epidemics. I construct a stochastic metapopulation model simulating a city-suburb system to test different vaccination schemes that incorporate host group and population-level characteristics. I compare the targeted vaccination of commuters, a host group thought to be important for inter-community transmission, with the targeted vaccination of children, an age group known

to drive transmission within communities. I find that targeting children provides the greatest overall benefits in terms of reducing incidence, but also show that vaccination of commuters and other groups of employed adults provides similar reductions in incidence and additionally delays the speed and timing of epidemic spread when outbreaks are severe.

In **Chapter 6**, I summarize my findings and conclude how human mobility affects influenza epidemics at the regional scale. I discuss the limitations of my work as well as avenues for future research. I also highlight the need for more detailed spatial genetic data to further expand on these findings.

Chapter 2

Integrating parasites and pathogens into the study of geographic range limits

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2.1 Introduction

Identifying factors that contribute to limiting species' distributions remains a central goal in ecology and evolution (Brown and Lomolino, 1998), as an understanding of how species' ranges are shaped can provide insight on the limits to natural selection. Populations at range edges where conditions are unfavorable should be under strong selection to adapt to the present environment, so factors that limit ranges also represent limits to adaptation. Identifying the abiotic and biotic factors that impose limits on natural selection will provide us with a greater understanding of the process of adaptation and of evolution itself. Although a diverse list of factors, including environmental variation, resource limitation, and evolutionary constraints have been invoked as general explanations for the formation of range limits, mounting evidence suggests that these factors vary between as well as within species over space and time.

A significant portion (30-70%) of the earth's biodiversity may be represented by parasites (de Meeûs and Renaud, 2002; Price, 1980). However, the vast majority of range limit studies have examined only free-living plants and animals. Parasites and pathogens are found on every continent, yet few are truly distributed worldwide. Even during pandemics, geographic range limits can be imposed by subspecies or by species-

specific geographic associations (Fig 2.1). Few studies have addressed the specific factors that set parasite range borders and have instead focused either on the impact of parasitism on host range (Antonovics, 2009) or on elucidating large-scale patterns in parasite distributions and diversity (Guernier et al., 2004; Louhi et al., 2010; Smith and Guegan, 2010; Thieltges et al., 2011). In this review we outline how geographic ranges are defined and then discuss major determinants of the geographic distributions of parasites. We additionally show how parasites provide novel systems with which to address ecological and evolutionary questions fundamental to understanding how range borders are formed.

2.2 Defining the geographic range

The spatial distribution of a species can be broadly defined as areas, accessible by dispersal, over which specific ecological conditions exist that permit population persistence (Soberón and Peterson, 2005). While abiotic conditions such as temperature, precipitation and humidity corresponding to a species' environmental tolerance range often delimit the fundamental niche at coarse spatial scales, local microclimates and biotic interactions further refine the subset of this expanse that a species can actually inhabit (Estrada-Pena et al., 2014). Given that dispersal allows access to these suitable locations, realized range limits should theoretically correspond with niche limits (Hargreaves et al., 2014). However, source-sink dynamics facilitated by dispersal allow species to inhabit areas that do not conform to their requirements (Hargreaves et al., 2014; Pulliam, 2000). Individuals emigrating from self-sufficient source populations can colonize sink habitats where survival is possible but where reproduction does not occur at a rate fast enough to exceed death and emigration. Phylogeographic analysis of the influenza A/H3N2 virus, for example, suggests that East-Southeast Asia may act as the source population from which global epidemics are

seeded and, despite annual outbreaks, temperate areas are merely sinks (Russell et al., 2008). Sinks should still be considered part of a parasite's geographic range, especially if relevant evolution that contributes to future spread or persistence occurs there, or if epidemics consistently reoccur in the sink (as opposed to isolated outbreaks that are not likely to be repeated). Additionally, species may be absent from suitable areas due to physical barriers, such as mountains or oceans, or historical and stochastic events.

A species' distribution can change due to expansions, contractions and/or shifts of range borders. Range expansions stem from adaptations to conditions at the margin or introductions to novel habitats, such as during pathogen translocations or cross-species transmission events. Range contraction or fragmentation results when conditions at the periphery become inhospitable, possibly through human-mediated pathogen control or due to declining host density. Range shifts occur when favorable conditions arise at one range edge and deteriorate at another, and have been observed for many species that act as vectors of disease (Mills et al., 2010). Expansions, contractions and shifts all have important consequences for population genetic diversity, generating specific patterns that can be used to infer underlying demographic processes (Templeton, 1998). A range at any point in time is therefore shaped by the interaction between the changing environment and the species' evolutionary response to these conditions.

2.3 Range limits

Range boundaries are created by ecological conditions that exceed the evolutionary capacity of a population (Table 1). Abiotic limiting factors consist of external processes that shape an organism's physical habitat while biotic factors refer to interactions mediated by the composition of the local community. For parasitic organisms, individual hosts act as habitat patches, so ecological factors that affect the

range of the host will in turn restrict the range of the parasite. Although the ranges of obligate parasites will be exclusively determined by host characteristics and within-host biotic interactions, parasites with free-living stages will be directly affected by external abiotic conditions. Evolutionary factors then modulate the response of the parasite to these ecological conditions. This evolutionary response is constrained by the amount of genetic variation available, as well as the organism's ability to make use of this variation under physiological constraints. The magnitude and direction of the evolutionary response is further dependent on the strength of the coevolutionary coupling between host and parasite, as well as on the extent of gene flow between connected populations that may experience differing selective pressures.

Historically, at the global scale, parasite ranges have been limited by biogeographic barriers such as oceans and landscape formations, over which their hosts could not cross. Until the discovery of the Americas by European explorers and the advent of the slave trade, many viruses including mumps, measles, smallpox, and yellow fever were confined to the Old World (Smith and Guegan, 2010). Globalization has vastly expanded the ranges of countless parasite species, as infected hosts are easily transported between continents through air and sea travel. The source of the recent and unintentional introduction of West Nile virus from the Old World to the Western Hemisphere probably occurred through air travel of an infected human or mosquito (Weiss and McMichael, 2004). Domestication of animal species for farming and their subsequent transportation has also contributed to parasite range expansion. For example, the endoparasite *Nematodirus battus*, an intestinal parasite of sheep, has been extensively transported around the world in the last 60 years, displacing other local species of *Nematodirus* (Hoberg and Brooks, 2008). However, in natural systems, the relationship between range size and host mobility is not always straightforward. Thieltges and colleagues (2011) investigated whether range size patterns in trematodes

differed between those utilizing birds or fish as definitive hosts and found no relationship, suggesting that at coarse spatial scales, biogeographic properties of the landscape may be more important in determining geographic range size than the local dispersal ability of the host.

The importance of different range limiting factors varies with scale (Estrada-Pena et al., 2014). A useful framework for defining distributions (Estrada-Pena et al., 2014) starts with dispersal; of all areas accessible to the pathogen, some will fall within the abiotic threshold of the pathogen as well as all essential host species. Within these defined areas, local environmental variation, as well as biotic interactions within the host community and across parasites species will determine the realized distributions over which parasite populations can persist. Additionally within-host dynamics constitute an even finer scale that must be considered, as the physiology, immunological defenses and genotypic profile of the host determine the outcome of host-parasite interactions upon infection. Although the presence of susceptible hosts is clearly of the utmost importance for pathogens, host and parasite ranges rarely correspond completely since parasites are often only associated with a subset of the host population. Many realized ranges are therefore only a subset of the potential range of a pathogen. Clearly, we must look beyond host characteristics; a more thorough investigation of the specific factors that impact pathogens is necessary to adequately describe parasite distributions.

2.4 Hosts as habitat

Trivially, by association, factors that limit the geographic range of hosts must also limit the geographic ranges of their parasites. Parasitic organisms are constrained to areas over which there are suitable ecological and demographic conditions to sustain all host species that are required for the life cycle, although environments in which primary

and spillover hosts interact must additionally be taken into account when mapping the distribution of a pathogenic disease (Halpin et al., 2007). Thus, generalist parasites, as well as those that are directly-transmitted, tend to have broader geographic ranges than those that are specialists or that require multiple hosts or external stages to complete their life-cycle (Smith and Guegan, 2010). Parasites that can utilize, but do not require, multiple host species should be least constrained in their geographic ranges. Rabies, a multi-host virus, has a nearly global distribution (Baer, 1975; Woolhouse et al., 2001). In a study comprising 341 flea species from five different global regions, Krasnov and colleagues (2005) confirmed a negative correlation between host specificity and geographic range size. As a corollary, invasions or deliberate introductions of host species into new areas can lead to a geographic range increase for their associated parasites, if these parasites can continue to complete their life cycle by utilizing other requisite hosts in the new location (Amundsen et al., 2013).

The extent to which parasites can evolve to utilize new host species is strongly dependent on parasite taxonomic group; even then, genomic conservation in viruses, some of the most rapidly evolving organisms known, could inhibit the ability of the organism to readily jump host species. Phylogenetic conservation of mechanisms involved in infection and replication is evidenced in the genus *Flavivirus*, where a strong phylogenetic signal in the ordering of tick-borne and mosquito-borne species suggests that the ability to replicate in a novel vector species evolved only once and has since remained highly conserved (Holmes, 2003). Cross-species transmission events appear to be much more likely among phylogenetically similar hosts (Streicker et al., 2010), perhaps because genes that control cell receptor recognition functions are highly conserved (Holmes, 2004). Additionally, correlations among fitness traits impose limits to adaptation by restricting the extent to which a trait can evolve without negatively affecting other traits. Fitness trade-offs may be especially limiting in vector-borne

viruses, which often must replicate in both vertebrates and invertebrates. In support, far lower rates of non-synonymous substitution have been detected in vector-borne viruses than in directly transmitted RNA viruses (Jenkins et al., 2002).

Just as habitats vary in their suitability, not all host individuals are susceptible to invasion by pathogens. Vaccination has virtually eliminated many once common viruses from developed countries by drastically decreasing the availability of susceptible hosts (Smith and Guegan, 2010). To date, humans have succeeded in eradicating the smallpox and rinderpest viruses (Smith and Guegan, 2010), and the ranges of many other pathogens have been successfully restricted through the development of vaccines and the implementation of control programs. Host diversity in innate immunity can prevent efficient transmission or replication in certain individuals. High diversity across genes of the major histocompatibility complex (MHC), which are involved in immune function in vertebrates, potentially stems from an evolutionary arms race with pathogens. Viral fitness decreases in hosts with unfamiliar MHC genotypes (Kubinak et al., 2012) and diversity in MHC genes has been linked to resistance of rabies virus in raccoons (Srithayakumar et al., 2011) and cytomegalovirus in mice (Adam et al., 2006). The abiotic environment can also play a role in mediating genotype-by-genotype interactions. With the exception of those macroparasites with free-living stages, parasites generally need only adapt to overcome host defenses while hosts must contend with both parasites and the surrounding environment. Resource availability and quality can affect the basic ability of a host to mount an immune response due to trade-offs in energy allocation. Therefore, spatial variation of resources can modulate host resistance, in turn affecting the local distribution of parasites (Boots, 2011).

For a pathogen to successfully invade, host populations must meet a critical community size (CCS), defined as the number of susceptible hosts necessary for pathogen persistence (Bartlett, 1957). Acute, highly transmissible viruses that rely on

density-dependent transmission require large host population sizes to establish endemically, so that the supply of susceptibles is constantly replenished. Measles represents a classic example, as the CCS has been estimated to be from 250,000-300,000 (Bartlett, 1960). A study of diseases carried by human tribes in the Amazon basin showed that persistent, low-morbidity viruses like herpes and Epstein-Barr were often endemic whereas acute, severe viruses like measles and mumps were rarely detected, potentially owing to human population sizes that seldom exceeded several hundred individuals (Black, 1975). In fact, in a study of 335 emerging infectious diseases of humans, human population size was found to be the single best predictor of disease emergence (Jones et al., 2008).

Further, high genetic diversity should render host populations more resistant to invasion (O'Brien and Evermann, 1988). Close associations between particular host and pathogen populations may prevent the pathogen from invading geographically distinct populations of the same host, especially if hosts are differentiated into unidentified cryptic species. Japanese Encephalitis Virus is found throughout Southeast Asia and the Pacific Islands yet has not been able to establish on the Australian mainland located merely 70 miles away, despite the presence of competent hosts, vectors, and amplifying hosts. Hemmerter and colleagues (Hemmerter et al., 2007) detected strong spatial genetic subdivision between populations of *Culex* mosquitoes in Northern Australia and identified several cryptic species, suggesting that the genetic diversity of vectors on the Australian mainland may prohibit the virus from establishing sustained transmission. The importance of genetic diversity in preventing infectious disease establishment has long been recognized in agriculture and guides some aspects of policy on patterns of intercropping in otherwise monocultures of economically important crops (Leonard, 1969).

Once a pathogen has successfully invaded, variations in the local abundance of individual hosts can restrict further spread. Commonly used models often assume an abundant center distribution, in which the population density of free-living species is highest at the core where conditions are presumed most favorable and decreases toward the margin as conditions decline (Brown, 1984). For parasites that rely on density-dependent transmission, variation in host density is analogous to variation in habitat connectivity; density declines decrease the probability of contact between infected and susceptible hosts. For example, urban to rural gradients in population density can limit the spread of human pathogens. Many directly transmitted, highly infectious viruses, such as measles and influenza, are primarily associated with urban centers (Fang et al., 2012; Grenfell et al., 2001; Viboud et al., 2006b), which act as foci for geographically widespread pathogens. Waves of infection traveling outward from urban areas to sparsely populated surrounding towns have been extensively documented for measles in the pre-vaccination era (Grenfell et al., 2001).

The traditional model of density-dependent pathogen spread predicts that parasites will still not occupy the full geographic range of their hosts, attaining maximum prevalence at the range core. In support, Antonovics et al. (2011), found that parasite-free zones existed at bumblebee range edges. Other studies, however, have provided conflicting results. Briers (2003) instead found a higher prevalence of trematodes in snail intermediate hosts at the margin. While inbreeding depression and low genetic diversity in isolated, low-density fringe populations can reduce immune activity in host individuals and make it easier for parasites to invade (De Castro and Bolker, 2005; O'Brien and Evermann, 1988), theoretical results show that sterilizing pathogens relying on frequency-dependent transmission are expected to be distributed throughout the entirety of their hosts' range and can even cause areas of low host density to emerge at the range core (Antonovics, 2009). Since host density and prevalence are uncoupled for

parasites that are transmitted in a frequency-dependent fashion, concordance between host and parasite range in these systems should be complete. Therefore, host abundance distributions alone are not adequate to map parasite ranges. Instead, range-wide data on population demography and genetic structure as well as biological interactions, parasite life history strategies and the physical landscape are necessary to draw accurate conclusions.

At larger spatial scales, range-wide structure and connectivity across multiple host populations can be nearly as important as host availability in establishing the range boundaries of parasites. Metapopulation models have shown that limited connectivity among host populations decreases the probability that marginal patches will receive infected hosts, thereby increasing global extinction probability (Fig 2.2) (Keeling et al., 2004). Isolated populations are unlikely to benefit from the 'rescue effect,' a process in which patches are continually colonized by infected hosts after stochastic population-wide extinctions occur. However, if population connectivity is too high, epidemic dynamics across multiple patches will become synchronized so that a single event can lead to the extinction of the pathogen across the entire metapopulation system. Intermediate levels of connectivity are, therefore, thought to be most favorable for long term pathogen persistence (Keeling et al., 2004). However, recent observations from a plant-pathogen system have challenged these long-standing predictions. Jousimo and colleagues (2014) found that well-connected host populations were less likely to be infected, positing that these populations instead benefited from the continual introduction of resistance alleles from surrounding populations.

Local coevolution between hosts and parasites is continually modulated by gene flow from surrounding populations. Host gene flow from parasite-free areas can swamp co-adaptation at high levels or provide genetic variation for resistance at low levels (Brockhurst et al., 2007). For example, gene flow from low-salinity refuges inhibits

adaptation of Delaware Bay oyster populations to the MSX parasite (Hofmann et al., 2009). In years when MSX is prevalent, the geographic range of the oyster population contracts, leaving surviving oysters in low-salinity refuges that are poor habitat for MSX; as these populations account for the majority of larvae spawned in subsequent years, there is no selection for resistance alleles. Models describing coevolution of parasites associated with spatially-structured hosts show that, if stabilizing selection favors geographic variation in optimal host phenotype, some sites can act as parasite sources while others can act as parasite sinks; high rates of host gene flow then disrupt local adaptation of parasite to host, resulting in declines in parasite abundance (Nuismer and Kirkpatrick, 2003). High rates of viral gene flow between populations can be beneficial if recombination or reassortment is common. For example, although low pathogenic avian influenza viruses sampled from North America and Eurasia are genetically distinct and reassortment events are rare, a greater proportion of reassortment viruses have been detected in areas where migratory flyways overlap (Ramey et al., 2010).

The geographic mosaic theory of coevolution (Thompson, 2005) predicts that coevolutionary hot and cold spots arise based on the spatial distribution of hosts, their parasites, and the direction and magnitude of gene flow. In a simulation study, Nuismer (2003) showed that it was critical to note whether parasitized areas occurred at the periphery or the core of the host range because this had significant effects on the extent to which host populations already under selection due to environmental pressures could effectively adapt to parasitism. A greater degree of overlap between host and parasite range resulted in greater maladaptation of parasite to host, providing an alternative explanation as to why parasite ranges may be limited to a subset of their hosts' range.

The composition and spatial arrangement of host populations often changes seasonally, causing range boundaries to fluctuate in their associated parasites. For example, human crowding in indoor spaces in the winter may facilitate the spread of

directly transmitted pathogens; this proposal has been put forward to explain the local extinction of influenza each summer in temperate regions (Nguyen-Van-Tam, 1998). This mechanism may also explain seasonal expansion of diseases in wildlife populations. Winter peaks in *Mycoplasma gallisepticum* prevalence among house finches have been attributed to aggregation of birds at man-made feeders in winter, which aids in the rapid spread of the pathogen throughout finch populations (Hosseini et al., 2004; Robb et al., 2008). Additionally, host dispersal often varies seasonally, increasing the chance for transmission into naïve populations during times when hosts are moving frequently and over long distances. In Ontario, biannual peaks in skunk rabies prevalence are associated with seasonal changes in contact rates which increase when mature animals breed in the spring and when juveniles disperse in the fall (Webster et al., 1974). The seasonal movement of mule deer influences transmission of chronic wasting disease. In the winter, movement between tightly knit population units is rare and transmission primarily occurs within groups; transmission between groups occurs mainly in the summer, leading to seasonal oscillations between patchy and widespread infection (Conner and Miller, 2004). Seasonal birth pulses can create a similar effect, as the introduction of new susceptibles through birth allows pathogens to invade naïve populations even though parasite prevalence may drop to low levels or go locally extinct between breeding seasons (Altizer et al., 2006). Additionally, gradients in the length and timing of the reproductive period in wildlife populations can create patchy distributions of disease in regions where infection is strongly seasonally forced, with spatial synchronization of epidemics occurring in populations with longer birthing periods (Duke-Sylvester et al., 2011).

2.5 External Environment

The dynamic nature of the external environment can lead to shifts, contractions, or expansions of the geographic range of competent hosts and vectors. Numerous studies have investigated the role of climate as a determinant of geographic range, since many species have specific temperature and humidity requirements that make colonization outside a specific climatic region impossible. Until recently, bluetongue virus occurred endemically in the tropics and sub-tropics, between approximately 40° North latitude and 35° South (Purse et al., 2005) which corresponds to the thermal tolerance of the local vector, the *Culicoides imicola* midge. Temporal variability in climatic conditions, such as temperature and rainfall, can also significantly affect host distributions (Stevens, 1989). Tropical organisms experience a much more restricted range of temperatures annually than do temperate or arctic species, potentially limiting their intrinsic ability to survive in regions where conditions change drastically from season to season. This is thought to be the underlying driver for the observation by Rapoport (Rapoport, 1975, 1982) that the latitudinal range of free-living species tends to decrease as latitude decreases. This in turn would constrict the geographic ranges of obligate parasites, unless the host range is sufficiently general as to include multiple climate-zone adapted species.

Climate can further influence ecological conditions that are necessary for reproduction and sustainable transmission of parasites themselves. Tick-borne encephalitis virus, primarily transmitted through co-feeding between nymphal and larval stage *Ixodid* ticks, occurs in focal patches scattered throughout Europe and Asia despite the broad distribution of its host, *Ixodid ricinus,* over much of the two continents (Hillyard, 1996). Co-feeding, the process by which saliva is shared between ticks attached in close proximity on the same host, only occurs where climatic conditions facilitate rapid declines in ground surface temperature between seasons, allowing for temporal

stage overlap between nymphs and larvae (Randolph et al., 2000). A large-scale study of the spatial distributions and diversity of 332 parasitic and infectious diseases found that temperature and annual variation in precipitation best explained the distributions of parasites with external stages, i.e. vector-borne and helminth diseases (Guernier et al., 2004).

Recent attention has focused on how global climate change will affect biodiversity by modifying current species' distributions (Anderson et al., 2009; Hickling et al., 2005; Parmesan et al., 1999; Rosenzweig et al., 2008; Warren et al., 2001). Importantly for pathogens, the ranges of many vector species appear to be expanding pole-ward (Hongoh et al., 2012; Van Den Hurk et al., 2010). Recent expansion of *C. imicola* from Africa into Northern Europe has been attributed to an increase in winter and nighttime mean temperatures and has resulted in bluetongue epidemics occurring further north than previously recorded (Calvete et al., 2006; Purse et al., 2005). Of direct benefit to parasites with free-living stages, climate change may accelerate parasite life cycles and increase transmission and virulence. Helminths that undergo development as free-living larvae are directly affected by soil temperature and humidity, and could therefore experience increased rates of development. Kutz and colleagues (Kutz et al., 2005) found that *Umingmakstrongylus pallikuukensis*, a nematode infecting muskoxen, can now complete its life cycle in one year rather than two due to warming in Arctic ecosystems. This has led to intensified infection pressure in muskoxen, and increases the potential for invasion of naïve populations previously residing outside the nematode's habitable zone. However, not all parasites are predicted to benefit from climate change. Future hot and dry conditions could hamper spore growth, reducing the risk of fungal infections (Harvell et al., 2002).

Warming temperatures may also modify host susceptibility to infection. Behavioral fevers, i.e. self-induced increases in mean body temperature, have been

shown to enable hosts to better fight infections. Ectotherms may therefore be at an advantage as ambient temperatures rise. For instance, summer decreases in the prevalence of *Entomophthora muscae* fungal infections in house flies were attributed to exposure to high temperatures in the early stages of infection (Watson et al., 1993). However, this is not a general rule. Drastic increases in pathogen loads of gorgonians leading to mass die-offs were correlated with increases in sea temperatures that severely stressed the organisms and hampered their ability to fight infection (Cerrano et al., 2000). Similarly, studies have shown that the amphibian immune response is negatively affected by increasing temperature variability (Raffel et al., 2006), linking climate change with chytrid-associated amphibian population declines (Rohr and Raffel, 2010). Clearly, the effects of climate change on geographic range will not be uniform across all parasite taxa and merit further study.

Modifications to the external environment can also be caused by anthropogenic activities. For example, local microclimates can be modified by deforestation. This could extend malaria risk to previously unsuitable areas, as increased temperature and relative humidity at deforested sites correlates with increased vectorial capacity of the major mosquito vector of *Plasmodium falciparum* malaria (Afrane et al., 2008). However, deforestation has also been correlated with a decrease in disease risk for humans (Valle and Clark, 2013), since the loss of biodiversity at disturbed sites can remove hosts necessary for the completion of parasite life cycles. These effects likely arise from scale-dependent consequences of host removal; zoonotic diseases tend not to circulate in urban areas, where the probability of humans and reservoir hosts coming into contact is low (Wood and Lafferty, 2013; Wood et al., 2014).

Dengue virus (DENV) provides a prime example of the effects of human intervention and behavior. Widespread use of the insecticide DDT in the 1940's nearly eradicated the invasive *Aedes aegypti* mosquito vector in the Americas (Spiegel et al.,

2005), considerably reducing the range of DENV (Gubler, 2004) and eliminating New World dengue fever epidemics between 1946 and 1963 (Wilson and Chen, 2002). *Aedes aegypti* re-expanded its range throughout the Americas when vector control programs were ceased, however a re-emergence of DENV was only recorded south of the United States. The discrepancy in geographic range between host and virus is explained in part by present socioeconomic and behavioral differences that affect transmission likelihood, which might weaken direct effects of climate on host and vector distributions (Reiter et al., 2003). Air conditioning, more widely available in the United States, allows people to keep windows and doors closed during the summer season of heightened mosquito activity. In contrast, lack of affordable air conditioning in Mexico means that windows and doors are often left open, allowing infectious mosquitoes to invade dwellings. Dengue prevalence has also been correlated with the practice of storing water in open containers outside of the household, which function as mosquito breeding sites. This practice is widespread in areas where the supply of clean water is unreliable, again linking viral presence to human behavior and socioeconomic status (Barrera et al., 2011; Barrera et al., 1993; Barrera et al., 1995).

2.6 Community interactions

Community composition and biological interactions such as competition, mutualisms, and apparent competition can create biotically enforced range limits. Community biodiversity can expand ranges if amplifying hosts are introduced that promote pathogen transmission. For example, following the introduction of a new subspecies of muskoxen to the Arctic coastal plain, a new geographic record was set for the eastern distributional range of the lungworm *Protostrongylus stilesi* in a geographically isolated population of its native sheep host; spillover of the lungworm from sheep to muskoxen was likely followed by spillback from muskoxen to sheep in

areas of range overlap, as the muskoxen occupy a continuous geographic area between the disparate sheep populations (Hoberg et al., 2002). Further, introductions of non-native species have upset food webs, introduced novel parasites and led to the reemergence of pathogens that were once controlled. For example, a trophic cascade resulting from the introduction of Nile perch to Lake Victoria for farming led to a drastic increase in schistosomiasis when populations of the natural cichlid fish predators of the intermediate snail-host were suppressed (Constantin De Magny et al., 2008). .

Parasites engage in competition for hosts, an interaction often mediated by the host immune system. While theory predicts that competition can cause the exclusion of a pathogen, empirical studies are difficult to perform. Using anecdotal and historical evidence, Lietman and colleagues (1997) modeled how the spread of tuberculosis bacteria could have eliminated leprosy in Western Europe. They found that tuberculosis would have been able to completely exclude leprosy if its basic reproductive rate was greater and if complete cross-protection existed. It is seldom the case that competition between related viruses can be observed directly; instead, a virus may not be able to invade a region due to cross-immunity resulting from a currently circulating virus. Yellow fever virus has never succeeded in establishing itself as an endemic parasite in Asia even though the required hosts are present and short transmission chains have been recorded. One hypothesis is that an immunological barrier exists due to a closely related, currently circulating virus (Holmes, 2009). In addition, abiotic conditions can mediate competitive interactions. The geographic distributions of two species of feather lice were shown to differ along a gradient in relative humidity across the US, with the geographic range of the inferior competitor set by competition and the range of superior competitor set by decreases in relative humidity in the zone of overlap (Malenke et al., 2011).

Mutualisms can render hosts resistant to infection. In *Drosophila* species, *Wolbachia* bacteria has been shown in the lab to confer resistance to several viruses

including Drosophila C virus, cricket paralysis virus, Nora virus and flock house virus by boosting basal level immunity (Hedges et al., 2008; Teixeira et al., 2008). It has also recently been demonstrated that *Wolbachia* promotes resistance to dengue virus, chikungunya virus and *Plasmodium* species in *Aedes aegypti* mosquitoes (Bian et al., 2010; Moreira et al., 2009). Although these species do not interact in nature, this mutualism could be used in the future to limit the range of these important human pathogens.

Alternatively, symbionts can facilitate host utilization and transmission. For example, the bacterium that causes cholera, *Vibrio cholera*, requires infection by a bacteriophage to infect and sustain transmission in humans (Constantin De Magny et al., 2008). Similarly, the distribution of some pathogens can be positively influenced by others. The rise of the HIV/AIDS virus has allowed for the recent reemergence and range expansion of several pathogens including herpes simplex virus, hepatitis C virus, human papilloma virus, *Mycobacterium tuberculosis*, *Plasmodium* species and *Schistosoma haematobium* through the subsequent global increase in immune-compromised individuals that are highly susceptible to these opportunistic diseases (Gibson et al., 2010).

Apparent competition through mutual predation can lead to local spatial differentiation in the ranges of prey species, with the width of the intersection zone controlled by the effectiveness of the predator (Holt and Barfield, 2009). Parasite ranges could be constrained if increased virulence in novel hosts delayed or prevented the establishment of persistent infection within the spillover host population (Reullier et al., 2006). The northward expansion of deer carrying the meningeal worm *Paralaphostrongylus tenuis* is thought to restrict the southern ranges of moose and caribou, two spillover hosts that suffer high mortality when infected (Anderson, 1972). Additionally, predators may be able to limit the range of a parasite species through

predation on the host species. Models show that, as wolves continue to expand their range southwards from Canada into the Midwestern US, selective predation on deer infected with chronic wasting disease could eliminate the prion disease from the deer population (Wild et al., 2011).

2.7 Using parasites to study range limits

Advances in genetic sequencing technology have allowed molecular ecology to move to the forefront of biological research, and studies of geographic ranges are now increasingly conducted using a molecular ecology framework (Biek and Real, 2010). However, using genetic information to study the ecology and evolution of complex organisms has several inherent difficulties. Substitution rates are often low, leading to negligible genetic variation and differentiation among populations. Detectable evolution occurs over hundreds of thousands of years, imparting a genetic signature of historical processes rather than recent events. In contrast, the ecological and evolutionary dynamics of parasites, especially viruses and bacteria, happen on similar time scales due to highly error-prone replication mechanisms and short generation times. Genetic variation in these organisms is abundant compared to their host organisms and their relatively small genomes make it easier to obtain and sequence their genetic data. For these reasons, parasites are uniquely suited for use in tracking host movement and demography, which can be an important tool for investigating the ecological and evolutionary mechanisms that cause range limits to form. Genetic data from insects, intestinal worms and ectoparasites have been employed to infer host population dynamics, though relatively few studies of this nature have been conducted using viruses.

2.8 Using parasites to understand host geographic range limits

Parasites species which are most suitable for host inference are highly host-specific, have direct life cycles, and do not possess a free-living phase (Nieberding and Olivieri, 2007). These characteristics imply high dependence on the host organism, so that host movements will be reflected in the parasite genealogy. However, the time scale over which host movement can be detected differs for parasites whose ranges are shaped by vicariance or dispersal; the ranges of parasites that co-diverge with their hosts should be most influenced by vicariance whereas the ranges of parasites that are horizontally transmitted are most likely to be shaped by dispersal (Holmes, 2004). Dispersal ability is intimately tied to transmission mode and infectivity, as those that are highly transmissible will be able to more efficiently spread among populations (Holmes, 2004). In viruses, this distinction closely parallels that between DNA and RNA viruses, as DNA viruses generally establish persistent infections while RNA viruses tend to be acute (Villarreal et al., 2000). The genetic structure of acute, horizontally transmitted parasites reflect host contact patterns over short time scales, often providing an estimate of host population structure at a finer resolution than the host phylogeny itself. This can aid in identifying recent dispersal barriers that may be critical for defining current and future distributions. Biek et al. (2006) showed that a host-specific feline retrovirus (FIV) accurately tracked population growth in its cougar host (*Puma concolor*) following a sharp decline only 80 years earlier. The authors hypothesized that the distinct spatial distribution of viral lineages corresponded to the pattern of previous host range fragmentation even though little genetic structure was detected in the cougar population.

Persistent viruses, microbes or parasites that co-diverge with their host organism are well suited for tracking ancient range fluctuations. For example, a helminth (*Heligmosomoides polygyrus)* phylogeny that closely corresponded to the phylogeny of its rodent host (*Apodemus sylvaticus)* further revealed strong subdivisions within the

three primary, geographically distinct host lineages, probably representing the separation of mouse populations that were not yet visible in the host phylogeny (Nieberding et al., 2004). Several parasitic organisms, including *Helicobactor pylori*, human papillomaviruses and polyomavirus JC (JCV) appear to be ideal candidates for inferring past human migration events (Falush et al., 2003; Holmes, 2004; Wirth et al., 2005). JCV, a persistent DNA virus, is thought to have been associated with humans since the appearance of modern forms in Africa (Yanagihara et al., 2002). Because its evolution rate is two orders of magnitude greater than that of humans (Hatwell and Sharp, 2000), JCV population structure has been used to document past range expansion events through inference of the direction of ancient migration patterns from the Old World to the Americas (Agostini et al., 1996) and from continental Asia throughout the Pacific islands (Yanagihara et al., 2002) and Japan (Yogo et al., 2004).

2.9 Studying geographic ranges of parasites

The abundant genetic diversity observed in viral populations makes them ideal organisms with which to empirically test theoretical predictions of the distribution of genetic variation in populations with dynamic range boundaries. The majority of work to date has focused on the invasion of naïve host populations by pathogenic organisms. One such theoretical model, the surfing mutation model, predicts that new mutations generated at the expanding edge of the range are propagated faster than mutations that occur at the center of the range (Edmonds et al., 2004; Klopfstein et al., 2006). The lineages that arise from these edge mutations establish spatially distinct founding populations that are genetically differentiated from neighboring populations. This pattern was observed during a major raccoon rabies epidemic and was still evident 30 years after the initial infection wave (Biek et al., 2007). Theoretical work has shown that range contractions and shifts also impact genetic diversity and that the shape and speed

of these processes can have important consequences on the structuring of genetic variation (Arenas et al., 2012). Understanding how these processes affect variation is essential for predicting the impacts of climate change on biodiversity and for developing conservation strategies that retain maximal genetic diversity within a species. Further work using viruses to identify patterns of variation in expanding populations as well as in those whose ranges are contracting or shifting will allow us to connect ecological and spatial processes to observed genetic patterns over short time scales.

2.10 Conclusions

The contemporary study of geographic ranges has evolved considerably since the birth of population biology in the 1960s. While early research focused on identifying specific environmental conditions that were not conducive to the survival of a particular species and employed straightforward models with many simplifying assumptions, current research has shifted towards identifying evolutionary limits to adaptation using genetic data and complex metapopulation models that can incorporate both environmental and evolutionary dynamics in a spatially-explicit context. Previous research focused primarily on understanding the determinants of range limits in plants and animals, neglecting those of parasites, which account for a substantial portion of Earth's biodiversity. While the geographic distribution of the host organism plays an integral part in defining a parasite's range, ecological factors including host abundance distributions and genetic structure must be taken into consideration. Although abiotic conditions are often central to defining the host geographic range, only a subset of parasites, those with free-living stages, ever experience these abiotic conditions; biotic factors are therefore much more important. Parasites and pathogens can provide insight on how microevolution and ecological processes shape their hosts' distributions and

provide a new source of information on how evolutionary processes shape patterns of variation over geographic space.

Several unanswered questions remain regarding the determinants of geographic range limits. First, it is clear that the relative importance of ecological versus evolutionary forces in shaping the geographic distributions of species has not yet been resolved. Although range boundaries seem to arise as a result of ecological conditions, evolutionary forces control their dynamics. We suggest that parasites can provide an informative means with which to better investigate this interaction, owing to their rapid rates of evolution and abundant genetic variation. As the evolutionary rates of hosts are far slower than that of their parasites and because host genetic data often proves more difficult to collect, using parasites to connect observed ecological patterns with genomic data will allow us to track evolution at range borders over short time scales.

Secondly, while the roles of many abiotic factors in establishing range limits for free-living organisms have been well characterized, the importance of biotic factors in setting range limits is an active area of research. Since most parasites complete their entire life-cycles within their host organisms, interactions between parasite and host are therefore the defining factor in establishing the range of many pathogens. At a broader scale, the importance of host community structure as well as interactions between parasite species needs exploration. Worldwide environmental change has led to extensive alterations of host communities and has resulted in massive declines in biodiversity. These ecosystem changes may favor the proliferation of generalist parasites over specialists, warranting further study into the differing interactions of each with their hosts. As parasites and pathogens continue to expand their ranges through global human movement, interactions between parasitic species will become increasingly important. Both the rapidly increasing number of immune-compromised individuals and the elimination of many once common pathogens have led to increases in previously rare

pathogen species. As a recent example, local outbreaks of monkey pox in the Congo have been attributed to waning immunity to pox viruses following the global eradication of smallpox (Heymann et al., 1998). Formerly rare pathogens are alarming future threats, and it is essential to understand the factors that control their current distribution and spread.

Finally, the impact of climate change on the range of organisms, both parasitic and free-living, is one of the most pressing issues in ecological research today. Under current debate is whether climate change will cause the expansion of parasite ranges, leading to an overall increase in global disease burden (Epstein, 2000; Martens, 1998; Martens et al., 1995), or whether parasite ranges will instead shift, for example by expanding at the temperate edge and contracting at the tropical edge (Lafferty, 2009). Under a shift scenario, the net number of humans affected by a disease could potentially remain constant or even decrease as the affected areas shift to present-day temperate zones or high altitude locales, although this prediction is highly dependent on the vulnerability and density of hosts in the areas of expansion (Pascual and Bouma, 2009; Rogers and Randolph, 2000). Although studies have identified some systems for which a shift is either already apparent or predicted to occur (Moore et al., 2012), other recent studies have suggested that expansion rates are exceeding rates of contraction at the trailing edge, for example, in high altitude environments where warming temperatures have allowed vector-borne diseases, such as malaria, to invade previously unsuitable highland areas without a concurrent contraction in already suitable lowland areas (Caminade et al., 2014; Siraj et al., 2014). Further, the overall impact of these new geographic distributions is unclear, especially for infectious diseases of humans. While parasites may expand or shift their ranges as climate changes, the socioeconomic status of these newly colonized areas will influence whether pathogen incursions can be mitigated by human intervention (Randolph, 2010; Sachs and Malaney, 2002). Studies

of wildlife diseases which are not controlled by human intervention may be able to shed light on this question, although multiple confounding factors that affect the ecophysiology of host pathogen interactions complicate the straightforwardness of the conclusions that can be drawn (Altizer et al., 2013). It is clear that the effect of climate change on infectious disease will not be uniform; therefore, the extent of the impact of climate change on disease distribution and burden remains an important area of research.

Long term climate change is predicted to have extensive negative effects on plant and animal biodiversity, in turn affecting the diversity of parasites found on the earth. Parasites could provide a key indicator of host population viability, as parasite ranges should respond faster to climate change than that of their hosts'. According to metabolic theory, rapid metabolic rates, decreased internal processes, decreased number of cells and short generation times will allow parasites to more quickly acclimate to temperature shifts and withstand greater temperature extremes than their hosts (Rohr et al., 2011). Parasite loss could therefore be used to indicate host population declines at specific locations within the range. However, climate change, as well as the increase in climate variability that is also predicted to occur, may alter host-parasite interactions. Thus, the effects of climate change on host immunity, host and parasite life-history traits and habitat suitability may be species-specific. Understanding the effects of increased warming as well as increased climate variability on parasite range is vital, especially since these effects will vary with the system under study. Though many questions still remain unanswered, coupling experimental approaches with theoretical models and taking advantage of new technology and novel systems will shed new light on these longstanding questions.

2.11 Tables

Range Limiting Factor	Adaptation to Parasites	Selected References
Ecological - Abiotic		
Barriers to dispersal	Physical barriers separating host populations; recent globalization often negates this for human pathogens	(Smith and Guegan, 2010; Weiss and McMichael, 2004)
Habitat availability	Susceptible hosts must be present	(Adam et al., 2006; Srithayakumar et al., 2011)
Habitat abundance	Host critical community size is necessary for pathogens to persist	(Bartlett, 1957, 1960)
Habitat structure	Fragmentation, isolation of host populations and declines in host density limit parasite transmission; pathogen persistence affected by host population connectivity	(Jousimo et al., 2014; Keeling et al., 2004)
Climate	Affects parasite survival ability, development rates, and transmission opportunities as well as host/vector distributions	(Guernier et al., 2004; Kutz et al., 2005; Lafferty, 2009; Randolph et al., 2000; Rohr et al., 2011)
Anthropogenic effects	Human mediated control of infectious disease (i.e. vaccination, behavior); landscape alterations modify local microclimates, host communities and their susceptibility to invasion by and persistence of pathogens	(Afrane et al., 2008; Reiter et al., 2003; Spiegel et al., 2005; Wood et al., 2014)
Ecological - Biotic		
Dispersal ability	Infectivity and transmissibility	(Holmes, 2004; Villarreal et al., 2000)
Community biodiversity	Invasive species, transmission amplification	(Constantin De Magny et al., 2008; Hoberg et al., 2002)
Competition	Interspecific competition between parasites leads to immunological barriers in hosts and competitive exclusion among parasites	(Grenfell et al., 2004; Lietman et al., 1997; Malenke et al., 2011)
Mutualisms	Aid in host resistance to infection; facilitate parasite utilization of new host species	(Constantin De Magny et al., 2008; Hedges et al., 2008; Moreira et al., 2009)
Apparent competition	Shared parasite limits range of most susceptible host and/or pathogen	(Anderson, 1972)
Predation	Predation on diseased hosts can limit geographic distribution of pathogen	(Case et al., 2005; Holt and Barfield, 2009; Wild et al., 2011)
Evolutionary		
Genetic conservation	Phylogenetic conservation of infection and replication mechanisms; cross-species transmission more likely between phylogenetically similar hosts	(Albà et al., 2001; Holmes, 2003; Lefeuvre et al., 2007; Martin et al., 2005; Streicker et al., 2010)
Genetic correlations	Fitness trade-offs for pathogens that must replicate in diverse host taxa	(Jenkins et al., 2002; Mizokami et al., 1997)
Coevolution	Local adaptation of host and parasite	(Hemmerter et al., 2007; Nuismer, 2006; O'Brien and Evermann, 1988; Thompson, 2005)
Gene flow	Host gene flow can disrupt local adaptation between host and parasite; beneficial if leads to recombination or reassortment in pathogen, or if allows for movement of resistance alleles	(Brockhurst et al., 2007; Hofmann et al., 2009; Jousimo et al., 2014; Nuismer and Kirkpatrick, 2003; Nuismer et al., 2003)

Table 2.1. Factors affecting species' geographic distributions and their application to parasites

2.12 Figures

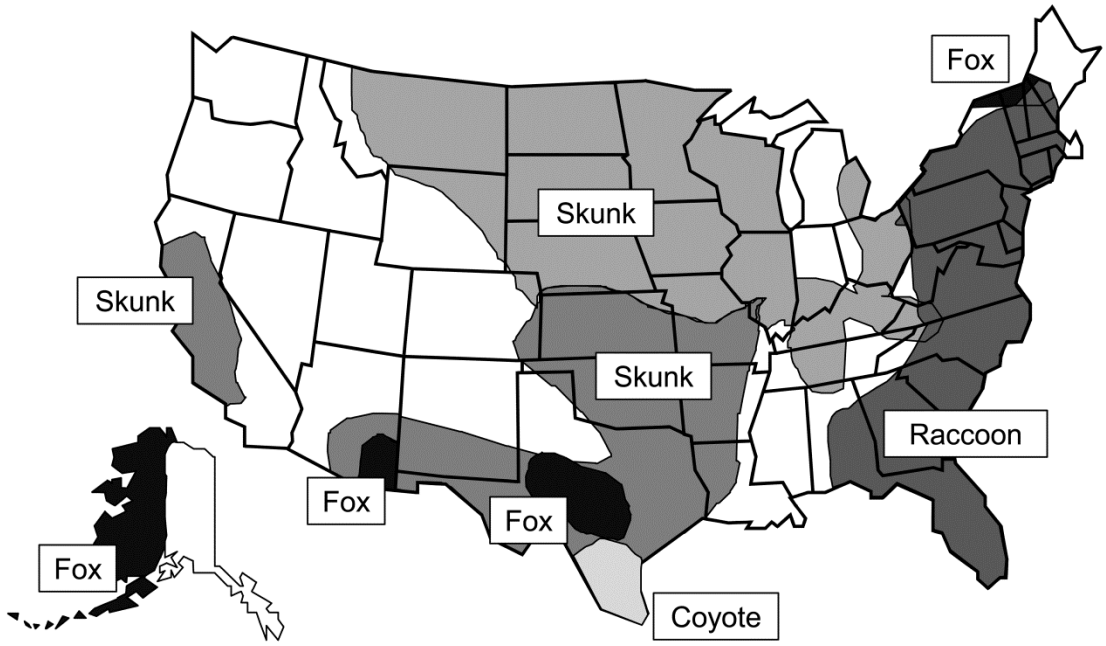

Figure 2.1. Geographic distribution of rabies virus in the United States. Shaded regions correspond to unique rabies virus variants circulating within specific carnivore host species'. (Real et al., 2005b)

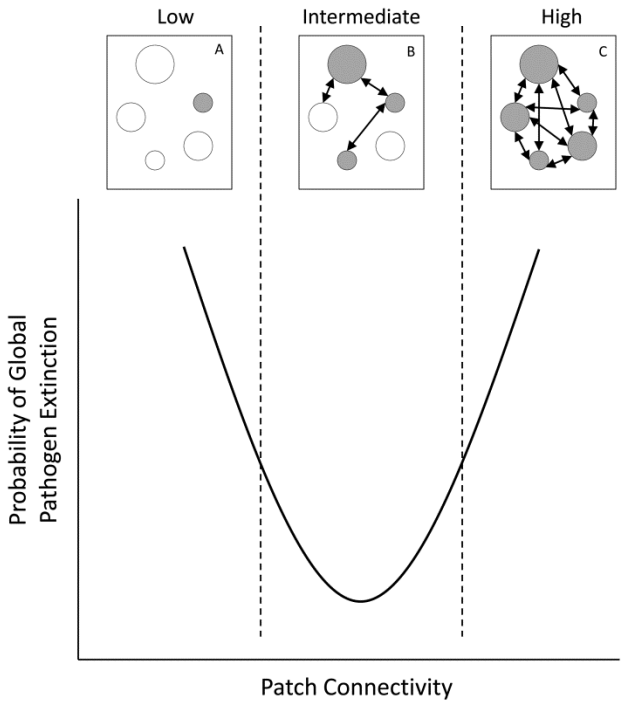

Figure 2.2. The effect of patch connectivity on global pathogen persistence within a metapopulation system. Shaded and open circles represent infected and uninfected patches, respectively. Both low and high levels of patch connectivity result in increased metapopulation-wide extinction probability for the pathogen, whereas intermediate patch connectivity promotes pathogen persistence. In systems with low patch connectivity (A), patches in which the pathogen has gone locally extinct do not receive infected colonizers to reseed the epidemic (rescue effect) whereas in systems with high patch connectivity (C), epidemic dynamics become highly synchronized such that a single event could lead to the extinction of the entire metapopulation. Intermediate patch connectivity (B) balances the benefits of the rescue effect with the negative effects of high synchronization of epidemic dynamics across patches.

Chapter 3

The Role of Human Transportation Networks in Mediating the Genetic Structure of Seasonal Influenza in the United States

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3.1 Introduction

When infectious agents invade naïve host populations and are propagated predominantly by local transmission, we expect to observe wave-like spread across geographic space (Biek et al., 2007; Real et al., 2005a; Walsh et al., 2005). Local transmission processes should concomitantly generate patterns of pathogen genetic variation approximating isolation-by-distance, where the geographic distance between locations and the genetic distance between pathogen variants is positively correlated (Epperson, 2003; Wright, 1943). However, for pathogens of humans and other hosts that frequently travel long distances or along pathways not determined by local geography (e.g. aviation networks), accounting for species-specific movement patterns provides an alternative method of defining distance which may better describe spatial spread. For example, diseases may transmit over a network, spreading first between well-connected populations through to poorly-connected populations. Populations that are geographically close to one another may not necessarily be well connected; distance in this model should instead be defined by the quantity of individuals moving between locations rather than their spatial proximity (Brockmann and Helbing, 2014; Colizza et al., 2006a, b; Gomes et al., 2014; Hufnagel et al., 2004; Rvachev and Longini, 1985; Tatem et al., 2006).

For human pathogens, transmission between distant populations has become increasingly common, as modern transportation now frequently allows individuals to move long distances over short periods of time (Jones et al., 2008; Smith and Guegan, 2010). Recent work has repeatedly shown that incorporating human mobility into epidemic models allows for more accurate predictions of the rate and timing of disease invasion and spread (Balcan et al., 2009a; Brockmann and Helbing, 2014). However, the impact of these various transportation networks on pathogen genetic structure is strongly dependent on spatial scale. Failure to detect similar patterns in structure across multiple spatial resolutions suggests that transmission processes are scale-dependent. For instance, although connectivity based on air travel volume between locations often correlates well with the trajectory of pathogen diffusion at the global scale (Brockmann and Helbing, 2014), at finer resolutions, this mobility network may instead facilitate random mixing among hosts. These contrasting outcomes are influenced by attributes of the mobility network, which can include its size and span in relation to the geographic scale of interest, the number of hosts that utilize it and the regularity of host movements along it, as well as by the epidemiological properties of the pathogen.

Seasonal influenza A, a virus which causes major morbidity and mortality worldwide (Simonsen, 1999), provides an ideal system with which to compare the effects of human movement networks on pathogen population structure across various spatial scales. Although evidence suggests that the H3N2 subtype of influenza A (H3N2) is genetically structured as a source-sink metapopulation at the global scale (Bahl et al., 2011; Russell et al., 2008), it is generally accepted that no structure is present at finer spatial scales (Nelson et al., 2008). This is problematic for the design of containment strategies, since it suggests that the seasonal spread influenza within countries is determined by stochastic processes and is therefore unpredictable. However, epidemiological reports and mortality statistics from influenza-like illness (ILI) data

have revealed that spatial patterns do exist, with greater synchronization in epidemic peak timing observed between cities that are geographically close and exchange many commuters (Viboud et al., 2006b).

Studies tracking the intra-continental spread of influenza have thus far utilized ILI and excess mortality data, which cannot differentiate between the two subtypes of influenza A (H3N2 and H1N1) that circulate each season. Of the two viruses, H3N2 causes the most morbidity and mortality and has been dominant in six of the past ten influenza seasons in the United States (US) (CDC). Its rapid evolution results in annual lineage replacement so that little genetic diversity is observed within seasons (Ferguson et al., 2003). In contrast, lower substitution rates are common for seasonal H1N1, and seasons dominated by this subtype are generally characterized by reduced mortality and morbidity and increased genetic diversity among co-circulating lineages as compared to H3N2 (Ferguson et al., 2003; Rambaut et al., 2008; Simonsen et al., 2011). It follows that these contrasting epidemiological dynamics could lead to subtype-specific population structure and that the patterns revealed previously using ILI data may be driven by a single subtype, but this hypothesis has not yet been formally tested.

We explored whether using alternative measures of distance can explain the population genetic structure of seasonal influenza A subtypes within the US. Since it has been shown that airline travel is important for the spread of influenza at the global scale (Lemey et al., 2014) and that both commuter and airline travel contribute to the epidemiological dynamics of influenza within the US (Brownstein et al., 2006; Viboud et al., 2006b) , we investigated the roles that these transportation networks play at the regional scale. We constructed models of the US aviation and commuter networks and quantified interstate connectedness based on the daily number of individuals exchanged. If transmission is dominated by the local spread of influenza across the commuter network rather than long distance spread over the aviation network, we expect that

sequences collected from pairs of states that are well-connected in terms of commuter flow will be more similar to each other than those collected from poorly-connected state pairs. To test this hypothesis, we obtained influenza sequences collected from 2003-2013 to compare associations of intra-seasonal pairwise genetic distances with geographic and network distance measures. Results indicate that population structure is indeed detectable, though this pattern is subtype specific.

3.2 Materials and Methods

Sequence Data

In total, 3,076 influenza A/H3N2, and 1,366 A/H1N1hemagglutinin sequences collected from 2003-2013 in the continental US were obtained from the National Center for Biotechnology Information Influenza Virus Resource for use in this analysis (Bao et al., 2008). Collection date was used to assign each sequence to a season, with seasons defined as occurring from Oct 1 to May 31. We restricted our analyses to seasons containing more than 90 sequences that were collected in at least 10 different states. This criterion was based on a natural break in the data, as seasons that did not fit this criterion tended to have fewer than 30 sequences that were restricted in their geographic distribution. This criterion was therefore necessary to achieve representative seasonal datasets in terms of sequence diversity and geographic coverage. For example, only 11 H3N2 sequences were available from the 2009-2010 season since the H1N1 subtype was dominant; this season was therefore excluded from all analyses of H3N2 data. Using this criterion, we were able to evaluate influenza population structure in nine seasons for H3N2 (2003-2004 to 2012-2013, excluding 2009-2010), and six seasons for H1N1 (2006-2007 to 2012-2013, excluding the 2009-2010 pandemic; see below). For each subtype, isolates came from all locations within the 48 continental states and the District of Columbia. The specific set of states represented varied seasonally and with each

subtype. GenBank accession numbers for all sequences used in this study, as well their location and collection dates are listed in Table S1.

Phylogenetic Analysis

Sequences were aligned using MUSCLE in Geneious (Biomatters) and the HA1 domain was extracted for use in all analyses (H3N2: 987 nt, H1N1: 1701 nt). Seasonal influenza is introduced into the US multiple times over the course of the season (Nelson et al., 2008). To account for these multiple introductions, phylogenetic trees were inferred separately for each season using a Bayesian framework in the program BEAST (Drummond et al., 2006; Drummond and Rambaut, 2007). To construct phylogenies, we used the SRD06 codon position model to accommodate different substitution rates for the first and second versus the third codon position, with the HKY85 substitution model applied over these two codon positions (Shapiro et al., 2006). For two seasons for which an extremely large number of sequences were available, H3N2 2007-2008 and H3N2 2012-2013, we down-sampled from states that contributed exceptionally large numbers of sequences. For the H3N2 2007-2008 season, the GTR+I+G model used, as convergence could not be achieved using the codon position model. Trees were constructed using a strict molecular clock, with an exponential growth tree prior and relatively uninformative priors on all phylogenetic parameters except for the substitution rate, for which we used a lognormal prior with mean = 0.0055 (sd=0.7) substitutions/site/year for H3N2 sequences (Nelson et al., 2006) and mean = 0.0018 substitutions/site/year (sd=0.4) for H1N1 sequences (Ferguson et al., 2003). MCMC chains were run until convergence was reached and a maximum clade credibility tree was annotated after removing the first 10% of the sampled trees as a burn-in. We defined clades as groups of at least 20 sequences stemming from a node with a posterior probability of $\geq$ 0.9. We corrected for independent introductions into the US by choosing

clades for which the entire HPD interval for the divergence time of the MRCA did not fall more than three months before the beginning of the flu season. This time limit was chosen as it was generally the most recent time period for which high posterior support could be obtained for clades.

For each clade analyzed, pairwise genetic distances were calculated as the proportion of sites that differed between each pair of sequences. To ensure that the choice of genetic distance metric did not affect our results, analyses were repeated using the evolutionary substitution models available in the R package APE (Paradis et al., 2004). The results remained the same regardless of the distance metric chosen, so we chose to present those results obtained using the raw pairwise distance measure. Pairwise spatial distances were calculated based on the great circle distance between state population centers.

The 2008-2009 and 2009-2010 seasons presented a special case for H1N1, as a new pandemic lineage emerged in the spring of 2009 that differed markedly from the currently and previously circulating H1N1 lineages. As epidemiological dynamics of influenza pandemics differ substantially from those of annual seasonal epidemics (Simonsen et al., 2011), sequences from the pandemic lineage in the 2008-2009 season, as well as the entire 2009-2010 season, were excluded from analyses. To distinguish between antigenically distinct pandemic isolates and the previously circulating H1N1 viruses, a phylogenetic tree was inferred for the 2008-2009 season using a neighbor-joining algorithm. Two clades were immediately obvious, each encompassing distinct time periods during the influenza season that corresponded well with the circulation times of the epidemic and pandemic lineages. Using the A/California/07/2009 strain of pandemic H1N1 (GenBank accession: FJ981613) as a reference, sequences were classified and excluded accordingly.

Transportation Network Models

Data on the origin, destination and passenger volume of airline routes within the continental US during October to March from 2003-2012 were obtained from the Office of Airline Information, Bureau of Transportation Statistics, Research and Innovative Technology Administration (BTS). Data were restricted to this time period to best represent human movement during the US influenza season, which occurs during the fall and winter and generally peaks anytime from late November to March (CDC, 2013). Passenger movement data for each airport were aggregated by state, so that each state was considered a node in each season-specific aviation network model. Data on intra-state passenger movement was excluded. Each seasonal aviation network model therefore contained 48 nodes (all continental US states), with directed edges weighted by the number of daily passengers traveling between each unique state pair during the influenza season. Because there are no airports located within the District of Columbia, sequences from this location were excluded for the aviation analysis. To ensure that this did not affect our results, we repeated the analysis with sequences from the District of Columbia coded as being from Maryland or from Virginia; no qualitative differences in the Mantel test results were observed. To facilitate summary comparisons with the commuter network model, a single aviation network model was also constructed based on the average number of passengers exchanged per day between states over all ten winter seasons

Data on the origin, destination and commuter volume between all US county pairs collected during the 2000 census were available from the US Census Bureau (Census, 2000). Commuter volume estimates were based on census participant responses when questioned on the county location worked in most often during the preceding week. As commuting data are intended as a proxy for long-distance influenza transmission occurring by means other than airline travel, commutes exceeding 150

miles (242 km) were excluded from the final commuter network (and accounted for only 0.07% of county to county movements). To assess the sensitivity of our results to this assumption, the analyses were repeated using the full commuter network, which included journeys of all distances. For all but one H3N2 clade, and two H1N1 clades tested, results were similar regardless of whether the full or reduced commuter network was used; we therefore only present the results using the reduced commuter matrix. Intra-state commutes were also excluded. Data on commuter movements between counties in neighboring states were aggregated by state so that the final commuter network model contained 49 nodes (all continental US states and the District of Columbia) with directed edges weighted by the number of daily commuters traveling between each unique state pair.

For each transportation network model, each node corresponds to a single state, and each edge represents the total daily number of either commuter or air travel passengers moving between those states. Edges were excluded from the network model if no individuals traveled between the two states on a daily basis. To compare the basic properties of the two different transportation networks, node degrees and graph density metrics were calculated. Node degree is defined as the total number of connections per node and graph density is calculated as the proportion of edges present in the graph out of the maximum number of edges possible.

To assess the validity of aggregating sequences by state, a community detection algorithm based on simulated annealing (Newman and Girvan, 2004; Reichardt and Bornholdt, 2006; Traag and Bruggeman, 2009) was run for both unweighted and weighted networks of county level commuter movements. We used the methods described by Thiemann and colleagues (Thiemann et al., 2010) to compute 1000 partitions of high modularity to determine the underlying community structure for each network. Communities in this context refer to groups of nodes which have stronger ties

internally than externally. The community structure of a network can be summarized by network modularity, Q, which measures the overall magnitude of difference between partitions (Newman and Girvan, 2004). The modularity value of a particular set of partitions is calculated by taking the difference between the fraction of total connections occurring within communities and the expected value of the fraction of total edges occurring within communities in a network of identical community partitions with randomized connections between nodes. Q is bounded between 0-1, with Q = 0 indicating that that the community subdivisions provide no more information than that of a random partitioning of nodes.

Associations between pairwise genetic distances and measures of geographic and network distance were assessed individually for each season through the use of Mantel's test (Legendre and Legendre, 1998). In order to conduct these tests, connection weights between states for each of the transportation networks were symmetrized by taking the sum of both connecting edges. Mantel tests were performed on both the raw connectivity distance matrices (constructed using the raw number of people traveling between states) and connectivity distance matrices constructed using the effective distance metric developed by Brockman et al. (Brockmann and Helbing, 2014). This metric is based on the proportion of individuals commuting between states in relation to the total number of commuter in the entire US. Results were similar regardless of the connectivity metric chosen; all results presented are those results obtained using raw connectivity. To account for multiple comparisons, a Bonferroni correction was applied to the results when multiple clades were tested from a single season. When multiple distance metrics (geographic, aviation or commuter distances) were significantly correlated with genetic distance for a single clade, partial Mantel tests were performed to account for these interactions. Partial Mantel tests allow for the comparison of two matrices while controlling for the effects of a third by regressing the two matrices of interest on the third

matrix, and performing a standard Mantel tests using these residuals. Results of the partial Mantel tests were used to identify the distance metric responsible for driving patterns of population structure.

3.3 Results

Transportation Networks

Comparison of the aviation and commuting networks within the continental US revealed significant differences in their basic properties, despite the similarity in data resolution (travelers/day) (Fig 3.1). The aviation network, composed of 48 nodes connected by 2,160 edges, is highly homogeneous in terms of the total number of connections per node (degree) and has a high graph density (density = 0.96), reflecting that most states are directly connected to most other states. In contrast, connection weights differed greatly across state pairs. During the influenza season, approximately 1.6 million people travel along the interstate aviation network per day. In contrast, the commuter network is composed of 49 nodes and only 312 edges. Decreased graph density (density = 0.13) in comparison to the aviation network reflects that the commuter network is highly spatially organized, with connections generally only occurring between neighboring states. Over 3.8 million people travel daily across the interstate ground-travel commuter network, and interstate connections in the east tend to be stronger than those in the west.

The community detection algorithm identified an average of 16 communities in the unweighted commuter network with an overall mean modularity of 0.55 (sd = 0.003) across the 1000 simulations (Fig 3.2A). In the weighted commuter network, an average of 135 communities were identified and mean modularity was 6.03×10^{-4} (sd = 1.33×10^{-5}) (Fig 3.2B). For both networks, communities tend to span multiple states.

Influenza A/H3N2

Phylogenetic trees were constructed for nine influenza seasons within the US from 2003-2004 to 2012-2013; seven of these seasons contained clades for which we were able to evaluate population structure (Fig S1-S7; see Appendix I). The number of sequences available per season varied from 147 in 2005-2006 to 1,276 in 2012-2013 and the number of states represented during a season varied from 29 in 2003-2004 to 49 in 2010-2011, 2011-2012, and 2012-2013 (Table S2). The most recent common ancestor for each season existed from 1-3 years before present. Clades fitting the criteria for inclusion (see Materials & Methods) were not available from the 2004-2005 or 2008-2009 seasons. Detailed information on each season and clade tested obtained through the phylogenetic analysis can be found in Table S3.

We detected a significant correlation between genetic distance and commuter distance for seven out of the 23 clades tested encompassing six out of seven seasons studied (Table 1). Mantel r correlation coefficients ranged from 0.09-0.38. We detected a significant correlation between genetic distance and geographic distance for five clades in four of the nine seasons (Mantel r: 0.13-0.32) and between genetic distance and aviation distance for two clades in two seasons (Mantel r: 0.31-0.42). Temporal distance between sequences, measured as the difference in number of days between collections, was never a significant predictor of population structure.

For many clades, more than one distance measurement was significantly associated with genetic distance. After performing partial Mantel tests to account for these interactions, we found that commuter distance remained significant for four clades in four different seasons. Geographic distance remained significant for three clades in three different seasons and air travel remained significant for two clades in two different seasons.

Influenza A/H1N1

Phylogenetic trees were constructed for six influenza seasons within the US from 2006-2007 to 2012-2013; five of these seasons contained clades for which we were able to evaluate population structure (Fig S8-S12; see Appendix I). Correlations between genetic distance and commuter travel were detected for a greater proportion of clades when the analyses were repeated for H1N1 at the regional scale (Table 2). The number of sequences available per season varied from 165 in 2007-2008 to 371 in 2010-2011 and the number of states represented during a season varied from 16 in 2008-2009 to 48 in 2010-2011 (Table S2). The MRCA for each season existed from 1-4 years before present (Table S4). Detailed information on each season and clade tested obtained through the phylogenetic analysis can be found in Table S4.

Significant associations between genetic distance and commuter network distance occurred in all five seasons (Mantel r: 0.17-0.38). Both aviation network distance and geographic distance were associated with genetic distance in two clades in one and two different seasons, respectively (aviation Mantel r: 0.26-0.32; geographic Mantel r: 0.44-0.56) and temporal distance appeared significant in one clade from the 2011-2012 season (Mantel r: 0.31). After performing partial Mantel tests for clades in which more than one distance measure was significant, the commuter network remained significantly associated with genetic distance in five clades over four different seasons. In the 2012-2013 season, both commuter distance and aviation distance were significantly associated with genetic distance, although partial Mantel tests showed that neither were significant when accounting for the other.

3.4 Discussion

We have shown here the first evidence, to our knowledge, that population structure for seasonal influenza A is detectable at the scale of the continental US.

Although all distance metrics were correlated with genetic distance for at least one clade, we find that the commuter network is more often associated with genetic distance than any other measure of spatial or network distance for the H1N1 subtype. Further, the association between genetic distance and the commuter network often remains significant after geographic distance is taken into account, demonstrating that the relative magnitude of host movement over space has a greater influence on the route of pathogen spread than the geographic proximity of sampling locations. In contrast, population structure was not detected in the majority of clades tested for H3N2, even though both geographic distance and commuter distance were, at times, correlated with genetic distance. This discrepancy suggests that epidemiological differences between H3N2 and H1N1 affect our ability to detect population structure of influenza within a season at this spatial scale.

Striking differences in the epidemiological dynamics of seasons dominated by H3N2 and H1N1 have been previously documented (Viboud et al., 2006b). The rapid bicoastal spread of H3N2 should obscure our ability to detect patterns based on geography or commuting if long distance transmission (through the aviation network, for example) quickly moves the virus between spatially distant localities. Models of the effect of R_o on the spread of influenza across the US and its implications for spatial synchrony have previously shown that ILI cases in cities across the entire US tend to peak around the same time when influenza spread is rapid (Viboud et al., 2006b). In contrast, seasons dominated by H1N1 tend to be milder and characterized by slower dispersal. The slower nationwide spread of H1N1 may facilitate the detection of population structure if H1N1 is allowed to diffuse over short-range connections once it is introduced into a new geographic area. Differences in the rate of spread between multiple clades from the same season could possibly account for our failure to consistently detect these patterns across all lineages. The degree of matching between

vaccine strains and circulating lineages could also potentially act to reduce transmission so that the commuter network would be able to exert a sufficiently strong influence in structuring the influenza population. However, there are multiple other factors that vary seasonally which could confound this relationship including, for example, vaccine efficacy, availability, population coverage, or age structure of vaccinated individuals. Models combining genetic and epidemiological data may be able to shed light on this proposed relationship but have only recently been utilized (Ferguson et al., 2003; Koelle et al., 2006; Koelle et al., 2010; Ratmann et al., 2012); adding a spatially explicit component to these models remains an area for future research (Bedford et al., 2012).

An investigation into the two circulating lineages of influenza B, a virus which causes milder disease than either subtype of influenza A (Atkinson et al., 2012), would provide an interesting point of comparison to our findings. As population structure based on commuter travel is more pronounced for A/H1N1, we might expect it to also be evident for influenza B. However, as influenza B primarily affects children (Atkinson et al., 2012), the role of commuters in transmission may be reduced such that structure is instead based on geographic distance. Interestingly, recent work on the epidemiology of influenza B in China showed that the Yamagata lineage tends to infect older age groups than the Victoria lineage [30]; examining these lineages separately may reveal differences in population structure patterns and/or modes of spread within the US. So far, little research to date has been done on the spreading patterns of influenza B and unfortunately, few sequences are publicly available on GenBank, as compared to either influenza A subtype.

Apart from biological explanations, uneven sampling may also be responsible for our inability to detect population structure in more seasons, or across all clades within a season. Differences in the number of sequences available for each season are a product of inconsistent sampling among states within a season and differential severity of the

influenza virus across seasons. For example, the number of testing facilities differs by state and the quantity of samples sequenced has historically been a function of individual laboratory capacity (APHL, 2012). Additionally, seasons that are characterized by more severe influenza subtypes or poor vaccine performance tend to yield more sequences (CDC, 2014) and influenza sequencing intensity tends to vary throughout the season. In order to determine the dominant strain circulating during a season, samples are more likely to be collected and tested during the beginning stages of the epidemic, especially when patients present with severe illness or other uncommon symptoms. Furthermore, seasons dominated by H3N2 generally result in higher rates of morbidity and mortality than those dominated by H1N1 or influenza B (Simonsen et al., 2005). Better virologic surveillance in less populous locations that are not travel hubs (i.e. in states outside of New York or Texas for example, which often contributed an excess of sequences per season) would enable us to better catalog influenza diversity outside of major cities and potentially increase our power to detect spatial patterns in this genetic data.

The correlations we detected are not as strong as those observed between these same distance metrics and epidemiological data (Viboud et al., 2006b). First, we caution against the interpretation of the Mantel r value as a standard correlation coefficient such as that calculated from a linear regression. Mantel r correlation coefficients are typically much lower than those reported for other statistical tests, owing to the comparison of distances between variables rather than their absolute values (Legendre and Fortin, 2010). Further, due to differences in the calculation of the sum of squares statistic, a standard R^2 cannot be derived from this value for use as a measure of the variation in the dependent variable explained by the predictor variable (Legendre and Fortin, 2010). However, the discrepancy in correlation strength may be due to differences in the underlying processes producing these associations. For example, epidemics in different locations could follow similar trajectories in terms of peak timing if one directly seeded

the other; however, this could also result if the epidemics were initiated at similar times due to similarities between states in population size or climate. In contrast, correlations between locations based on genetic distance should arise if epidemics in one location were directly seeded by the other, and not due to location-specific characteristics. In systems such as this, where long distance dispersal is prevalent, noise due to the circulation of multiple lineages in a single location likely obscures fine scale signatures of diffusion (Nelson et al., 2008). We have attempted to account for this noise by using phylogenetic methods to aggregate samples by clade so that only sequences derived from the same introduction, and therefore the same genetic lineage, are compared. However, uncertainty surrounding divergence dates always exists; that we are able to detect any correlation at all is surprising, as none have been found previously (Nelson et al., 2008).

At this spatial scale, the ability of the commuter network to exert a structuring influence on regional influenza populations is directly counteracted by the aviation network, which instead acts to create a randomly mixed viral population. These opposing effects stem from differences in the predictability of transmission processes within the two transportation networks. The commuter network is highly spatially organized, with 99% of commutes occurring over distances less than 150 miles (242 km). Individuals travel along the commuter network on a daily basis, repeating these movements for years at a time, increasing both the probability of transmission to coworkers and any others with whom an infected individual encounters regularly, as well as the annual consistency of these infection pathways. These movements along the network lead to a genotypic cline; viral sequences collected from nodes separated by less traveled paths appear less similar than those collected from node pairs that are well connected. In contrast, movement along the aviation network is less predictable. Although individuals traveling by air are likely to remain at their destination for several days, these trips are not likely to reoccur annually or even multiple times within a season, thus counteracting the

structuring effects of routine commuting. That we find any structure at all is an indication that daily travel to and from work is an important route of interstate spread for seasonal influenza. Although infection pathways can be linked to air travel at the global scale (Lemey et al., 2014), at the regional scale, air transportation likely functions to move the virus long distances into new areas that have not yet been invaded (Balcan et al., 2009a) where it then undergoes short-range dispersal by commuters.

In our characterization of the US commuting network, we were able to partition the US into communities of high modularity based on county-to-county connections. While partitioning these communities using daily total commuter flow estimates (weighted networks) resulted in weakly supported subdivisions that provided little information on about human mobility, analyzing county-to-county connections based on the presence or absence of commuter movements (unweighted networks) resulted in subdivisions of high modularity. These communities tended to span multiple states, lending further support to the hypothesis that interstate commuter travel is a viable means of influenza transmission. More importantly, states tended to be part of multiple communities, suggesting that aggregation of sequences by state may be somewhat arbitrary and that finer scale location data for sequences is needed. Our results are in good agreement with previous characterizations of US community structure (Thiemann et al., 2010), which have used currency movement as a proxy for human mobility. Since human movement tends to be limited to spatially compact groups of counties and repeated studies have shown that commuters are responsible for a significant portion of transmission, grouping sequences by commuting community rather than by state may provide a more accurate method of determining which sequences are most likely to be closely related (Lemey et al., 2014); comparing these sequences sets with network distance may then yield stronger and more consistent relationships between genetic distance and the commuter network. Further, these communities may in fact provide a

measure of the spatial extent over which commuting is responsible for the majority of transmission, with air travel operating to transfer influenza lineages between communities. Unfortunately, the spatial data associated with most publicly available sequences is currently limited to the US state of collection. Since commuting communities are defined by county-level associations, the availability of only state-level reporting hinders our ability to analyze the data at this alternative resolution. Clearly, there is a need for more informative spatial data to be made publicly available in order to facilitate analyses using more natural geographic groupings, rather than those arbitrarily imposed by political boundaries.

The results from our study complement recent findings that the aviation network plays an important role in the world-wide transmission of seasonal influenza. While the aviation network is undoubtedly of importance in structuring populations at the global scale, we find that, when population structure is detectable, it is the commuter network that is of greater importance at more regional scales. Host movement governs disease transmission patterns, and distinct modes of movement by discrete segments of the population can have varying levels of importance. While the magnitude of the correlations we detected was not overly strong, this may not be the case at finer geographic resolutions, such as within commuting communities or at the state-wide level, or at finer temporal resolutions, such as during the onset of an epidemic before any appreciable long distance transmission has occurred. While commuters living near state borders likely accounted for much of the interstate connectivity measured by our metric, at the intrastate scale, commuters moving between counties may comprise a larger segment of the population. However, local movement networks, such as that of children being transported to and from school, may prove more important in structuring influenza populations at this scale. Previous work has suggested that children are responsible for much of the transmission within communities (Medlock and Galvani,

2009). Future work is needed to further elucidate the scales at which different movement patterns contribute most to disease transmission.

3.5 Addendum

Since this study was published, additional analyses have been performed that suggest the patterns detected here may be explained by biological processes that do not require the predictable decay of genetic similarity as a function of connectivity based on passenger travel. In particular, the inclusion of multiple sequences collected from within the same state under the Mantel test framework can produce weak, negative correlations between genetic distance and distance measured by travel volume, if travel volume and sequence similarity are both much higher within states than between states. In this case, two clouds of points will be visible in the scatter plots created using the two distance matrices: a cloud of points representing pairwise comparisons between sequences collected from two different states, in which overall genetic diversity is higher but associated travel volumes are lower, and a cloud of points representing pairwise comparisons between sequences collected from within the same state, in which overall genetic diversity is lower and associated travel volumes are higher. The weak negative correlation between these two clouds of points does not indicate that travel volume predicts genetic relatedness outside of state borders, but can explain the significant associations presented in the study. Chapter 4 of this dissertation extends this analysis to consider the spread of influenza epidemics across Europe, taking into account the differences in genetic similarity of sequences collected from different spatial regions. As the conclusions reached in Chapter 4 differ from those presented a here, a re-analysis of the US influenza dataset is undertaken and a more thorough explanation of the data structure issue summarized here is given which provides and alternate and more likely explanation for the patterns detected in this study.

3.6 Tables

	Correlation with genetic distance based on:			
Season	**Temporal**	**Geographic**	**Aviation**	**Commuter**
2003–2004				
clade 1	0.01 (p = 0.43)	0.20 (p = 0.03)	0.29 (p = 0.04)	***0.38 (p = 0.0009)***
clade 2	0.12 (p = 0.14)	0.07 (p = 0.16)	-0.13 (p = 0.89)	0.09 (p = 0.15)
2005–2006				
clade 1	0.02 (p = 0.39)	-0.17 (p = 0.98)	-0.01 (p = 0.53)	-0.04 (p = 0.67)
clade 2	0.00 (p = 0.48)	0.04 (p = 0.33)	***0.31 (p = 0.02)****	***0.25 (p = 0.02)****
2006–2007				
clade 1	-0.01 (p = 0.51)	***0.22 (p = 0.009)****	-0.02 (p = 0.57)	***0.13 (p = 0.005)***
clade 2	0.11 (p = 0.06)	0.04 (p = 0.17)	0.01 (p = 0.45)	0.04 (p = 0.05)
2007–2008				
clade 1	-0.05 (p = 0.76)	-0.03 (p = 0.77)	0.12 (p = 0.07)	0.04 (p = 0.06)
clade 2	-0.15 (p = 0.88)	-0.08 (p = 0.74)	0.31 (p = 0.04)	-0.10 (p = 0.85)
clade 3	0.11 (p = 0.03)	-0.04 (p = 0.81)	0.06 (p = 0.21)	0.04 (p = 0.11)
clade 4	0.15 (p = 0.02)	***0.16 (p = 0.0007)****	0.06 (p = 0.23)	***0.09 (p = 0.0001)***
clade 5	-0.02 (p = 0.70)	0.00 (p = 0.50)	0.00 (p = 0.49)	0.01 (p = 0.25)
2010–2011				
clade 1	-0.26 (p = 0.96)	-0.06 (p = 0.64)	-0.33 (p = 0.96)	-0.10 (p = 0.91)
clade 2	0.00 (p = 0.49)	-0.11 (p = 0.84)	-0.11 (p = 0.84)	-0.05 (p = 0.72)
2011–2012				
clade 1	-0.15 (p = 0.94)	***0.14 (p = 0.0002)***	0.27 (p = 0.03)	0.14 (p = 0.02)
clade 2	-0.07 (p = 0.80)	0.07 (p = 0.17)	0.08 (p = 0.23)	0.06 (p = 0.15)
clade 3	0.11 (p = 0.09)	***0.16 (p = 0.005)***	0.10 (p = 0.14)	***0.22 (p = 0.0001)****
clade 4	0.19 (p = 0.13)	-0.15 (p = 0.84)	0.06 (p = 0.39)	0.03 (p = 0.40)
2012–2013				
clade 1	-0.06 (p = 0.65)	-0.13 (p = 0.76)	-0.10 (p = 0.69)	-0.15 (p = 0.91)
clade 2	-0.04 (p = 0.57)	0.13 (p = 0.28)	-0.16 (p = 0.77)	0.11 (p = 0.25)
clade 3	0.24 (p = 0.06)	-0.04 (p = 0.61)	-0.19 (p = 0.90)	0.05 (p = 0.23)
clade 4	0.01 (p = 0.44)	***0.33 (p = 0.005)***	***0.42 (p = 0.003)****	***0.32 (p = 0.006)***
clade 5	0.03 (p = 0.33)	0.10 (p = 0.10)	-0.10 (p = 0.82)	***0.15 (p = 0.001)***
clade 6	-0.15 (p = 0.94)	0.07 (p = 0.09)	-0.07 (p = 0.70)	0.01 (p = 0.42)

Significant p-values are based on a Bonferroni correction, computed to account for multiple clade comparisons within a single season. When more than one distance metric is correlated with genetic distance, asterisks denote those metrics that remained significant after partial Mantel tests were conducted (at the p = 0.05 level).

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Table 3.1. H3N2 Mantel Correlation Coefficients. Mantel r correlation coefficients measuring association between matrices of genetic, temporal, geographic, aviation network and commuter network distance for H3N2 sequences. Significant p-values are based on a Bonferroni correction, computed to account for multiple clade comparisons within a single season. When more than one distance metric is correlated with genetic distance, asterisks denote those metrics that remained significant after partial Mantel tests were conducted (at the p=0.05 level).

	Correlation with genetic distance based on:			
Season	**Temporal**	**Geographic**	**Aviation**	**Commuter**
2006–2007				
clade 1	0.11 (p = 0.19)	***0.56 (p = 0.0001)****	***0.32 (p = 0.005)***	***0.36 (p = 0.0003)***
clade 2	-0.09 (p = 0.76)	***0.44 (p = 0.001)****	-0.21 (p = 0.98)	***0.38 (p = 0.0001)****
clade 3	0.07 (p = 0.32)	0.13 (p = 0.12)	-0.17 (p = 0.86)	***0.20 (p = 0.002)***
2007–2008				
clade 1	-0.11 (p = 0.80)	0.07 (p = 0.23)	0.15 (p = 0.20)	***0.20 (p = 0.04)***
2010–2011				
clade 1	0.17 (p = 0.12)	0.28 (p = 0.03)	0.08 (p = 0.29)	***0.28 (p = 0.005)***
clade 2	-0.11 (p = 0.79)	-0.09 (p = 0.75)	-0.04 (p = 0.61)	0.03 (p = 0.30)
clade 3	0.00 (p = 0.49)	-0.16 (p = 0.99)	-0.12 (p = 0.92)	-0.04 (p = 0.83)
2011–2012				
clade 1	***0.31 (p = 0.0002)***	0.09 (p = 0.08)	0.04 (p = 0.35)	***0.17 (p = 0.007)***
clade 2	-0.08 (p = 0.93)	0.00 (p = 0.50)	0.01 (p = 0.46)	0.02 (p = 0.30)
2012–2013				
clade 1	-0.13 (p = 0.88)	0.04 (p = 0.37)	***0.26 (p = 0.04)**⁺*	***0.22 (p = 0.03)**⁺*

Significant p-values are based on a Bonferroni correction, computed to account for multiple clade comparisons within a single season. When more than one distance metric is correlated with genetic distance, asterisks denote those metrics that remained significant after partial Mantel tests were conducted (at the p = 0.05 level).

⁺ Neither metric remained significant after a partial mantel test was performed (at the p = 0.05 level).

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Table 3.2. H1N1 Mantel Correlation Coefficients. Mantel r correlation coefficients measuring association between matrices of genetic, temporal, geographic, aviation network and commuter network distance for H1N1 sequences. Significant p-values are based on a Bonferroni correction, computed to account for multiple clade comparisons within a single season. When more than one distance metric is correlated with genetic distance, asterisks denote those metrics that remained significant after partial Mantel tests were conducted (at the p=0.05 level).
+ Neither metric remained significant after a partial mantel test was performed (at the p=0.05 level).

3.7 Figures

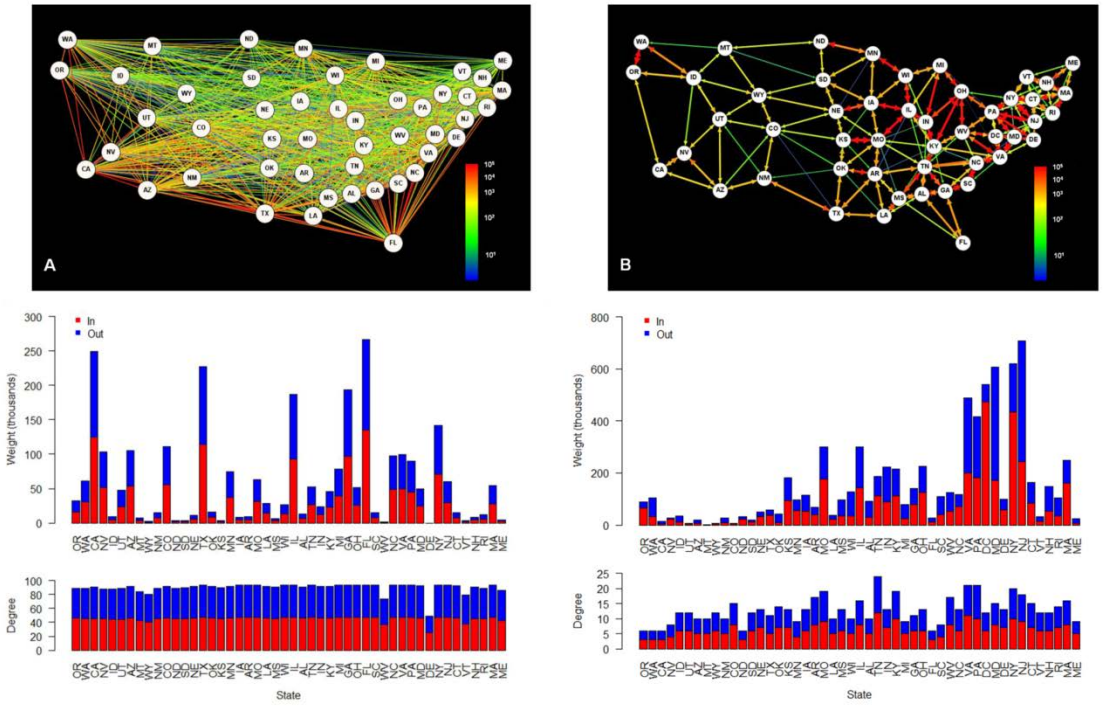

Figure 3.1. Aviation (A) and Commuter (B) Network Models for the Continental US. Edge colors represent the number of individuals traveling between each state pair per day. Bar plots directly below each network depict the weight (total number of individuals moving in and out of a state; top) and degree (total number of connections in and out of a state; bottom) for each of that network's nodes, ordered from left to right by the longitude of each state's population center. Out-degree/weight (number of people leaving a state per day) is colored blue and in-degree/weight (number of people arriving in a state per day) is colored red.

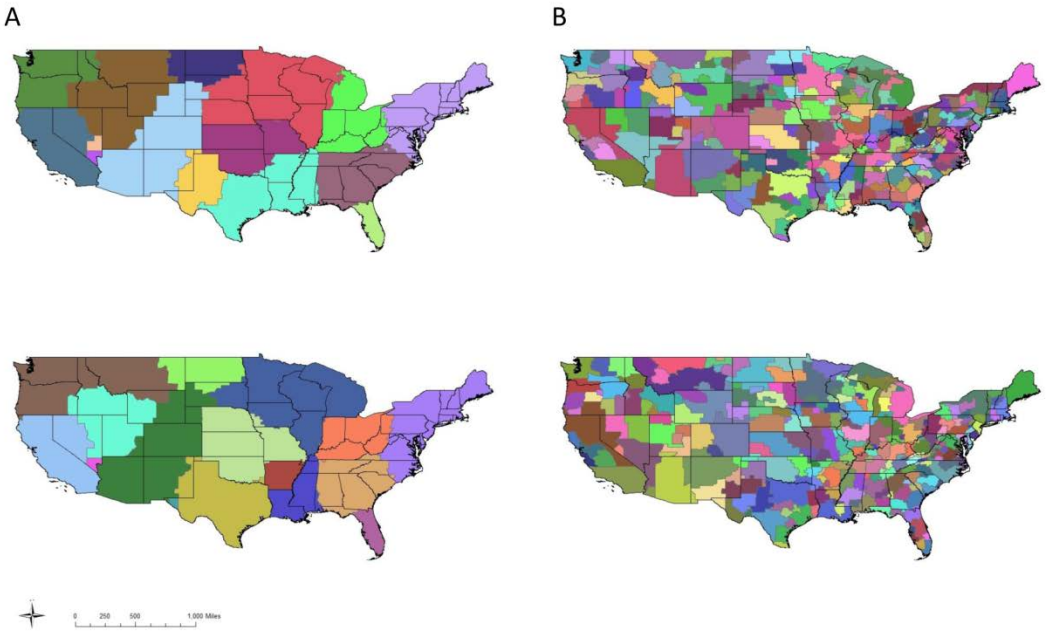

Figure 3.2. US Commuting Communities. Two realizations using the simulated annealing algorithm to partition the US into communities based on an A) unweighted network and B.) weighted network of county-to-county commuter flows. Modularity is similar across all realizations for a given network type, although exact community compositions differ. In all realizations, community boundaries do not neatly coincide with state borders.

Chapter 4

Regional transportation networks do not structure seasonal influenza A/H1N1 in Europe

4.1 Introduction

The relatively recent rise in global connectedness by long distance transportation networks has facilitated the emergence and worldwide spread of many infectious diseases (Colizza et al., 2007; Khan et al., 2014; Pybus et al., 2015; Semenza et al., 2014). Recent examples of this phenomenon include the 2007 SARS epidemic, which spread rapidly from its origin in Hong Kong to cause outbreaks in distant cities including Toronto, Canada (McLean et al., 2005), West Nile, which spread from the Old World to New York in 2009 and then across the Americas (Weiss and McMichael, 2004) and the recent Ebola epidemic, which caused widespread concern over the potential international exportation of the pathogen from West Africa (Gomes et al., 2014). The trajectories of these outbreaks clearly illustrate that the epidemiological distance between locations should not merely be measured in terms of geography, but also in terms of the volume of human movement (Brockmann and Helbing, 2014).

Influenza A virus is a prime example of a pathogen for which human movement networks provide a direct means of rapid long-distance spread. However, the functions of the various modes of transportation appear to be scale dependent. At the global scale, 2009 pandemic H1N1 epidemic arrival times across various countries are well correlated with an effective distance metric based on international airline passenger volume (Brockmann and Helbing, 2014). Furthermore, the genetic signatures of spatial spread also correspond to global airline connectivity for the seasonal H3N2 subtype (Lemey et al., 2014). At finer, regional scales, commuter movements are associated with viral spreading pathways. Within the United States (US), state-level commuter movements

tend to correlate with the timing of H3N2 epidemic peaks defined by influenza-like-illness and mortality data (Viboud et al., 2006b) as well as with genetic distance between H1N1 sequences (Bozick and Real, 2015).

Although commuting patterns act to structure seasonal influenza spread in the US, the generality of this pattern has not yet been tested. Specifically, countries and continents similar to the US in terms of population and land area rely more heavily on other forms of transportation for frequent long-distance movements (Eurostat, 2015, 2016). These transportation networks could similarly facilitate spread and potentially organize pathogen populations, depending on the underlying structure of the network. Europe in particular presents an interesting case comparison to the US, as it constitutes a collection of relatively contiguous interacting political units with open borders. Europeans similarly utilize airlines and personal cars for travel, but additionally use railway systems at a higher rate than in the US (Eurostat, 2015, 2016; International Union of Railways, 2014). Europe therefore provides an interesting opportunity to investigate whether alternate forms of ground transportation could be similarly associated with influenza spread.

We obtained seasonal influenza A/H1N1 sequences from across Europe over a four year time span to compare associations of intra-seasonal pairwise genetic distances with connectivity measures derived from rail and airline travel between European countries. Results show that rail travel does not appear to correlate with epidemic spread. Comparison of the structure of European rail and aviation networks reveal that the rail network shares several important characteristics with the aviation network that make it more likely to facilitate long-range transmission and random mixing of the influenza population. In addition, a re-examination of the population structure of influenza in the US reveals that, after accounting for scale-specific differences in

transmission and travel intensity, spatial structure is not detectable based on commuter mobility.

4.2 Materials and Methods

Sequence Data

In total, 1143 influenza A/H1N1 hemagglutinin sequences collected in Europe during four influenza seasons from 2007-2011 were obtained from the National Center for Biotechnology Information Influenza Virus Resource for use in the analysis (Bao et al., 2008). This temporal range was chosen to ensure that datasets were representative of both sequence diversity and geographic location; all seasons contained at least 100 sequences collected from at least 15 different countries, although the set of countries and the number of sequences available from each country varied from season to season. To avoid over-representation of countries due to sampling bias, we subsampled from countries that contributed exceptionally large numbers of sequences during a single season. Sequences were assigned to a season based on their collection date, with influenza seasons defined as occurring between Sept 1 and May 31. GenBank accession numbers for all sequences used in this study, as well as their location and collected dates are listed in Table S1.

Phylogenetic Analysis

Seasonal sequence alignments were constructed using MUSCLE in Geneious (Biomatters), and a portion of the HA1 domain was extracted for use in all analyses (>1000 nt). To account for multiple introductions of influenza into Europe that may have occurred over the course of a single season, we inferred separate phylogenetic trees for each season using a Bayesian framework in the program BEAST (Drummond et al., 2006; Drummond and Rambaut, 2007). Phylogenies were constructed using the SRD06

codon position model to accommodate different substitution rates for the first and second versus the third codon position (Shapiro et al., 2006), with the HKY85 substitution model applied over codons 1+2 combined, and codon 3 separately. Trees were constructed using a strict molecular clock, with an exponential growth tree prior and relatively uninformative priors on all phylogenetic parameters except for the substitution rate, for which we used a lognormal prior with mean = 0.0018 (sd = 0.7) substitutions/site/year based on estimates of seasonal A/H1N1 substitution rates (Ferguson et al., 2003). MCMC chains were run until convergence was achieved, and a maximum clade credibility tree was annotated after removing the first 10% of the sampled trees as burn-in. We defined clades as groups of at least 10 sequences stemming from a node with a posterior probability of $\geq$ 0.9. We corrected for independent introductions into Europe by choosing clades for which the entire highest posterior density interval for the divergence time of the most recent common ancestor did not fall more than three months before the beginning of the influenza season. This limit was generally the most recent time period for which high posterior support could be obtained for clades. Pairwise distances between sequences within clades were calculated as the proportion of sites that differed between each pair of sequences. In our previous study on influenza spread in the US, we found that using a substitution model to calculate pairwise differences did not qualitatively change the measurements in a way that would affect the outcome of the spatial analysis (Bozick and Real, 2015).

Transportation Network Models

Transportation data for the aviation and rail networks across 29 European countries were obtained from Eurostat (http://ec.europa.eu/eurostat/web/transport/data/database). For both modes of transport, the data were structured such that each reporting country provided counts of

the number of individuals traveling on routes that connected that country with all other partner countries. This data structure provided us with two estimates of passenger volume for each country-to-country connection. Aviation passenger volumes were available by quarter, so we restricted our analyses to transit that occurred from October to March (fourth and first quarters) to best represent human movement during the influenza season, which occurs in the winter in temperate regions (Finkelman et al., 2007; Tamerius et al., 2013; Viboud et al., 2004).

As not all countries reported each year, and not all passenger counts from reporting countries matched completely with the coupled estimates from their partner countries, we constructed composite aviation and rail networks using data from 2007-2010, the time period during which our influenza sequences had been collected. In these networks, each node represented a country and nodes were connected to each other by edges weighted by the volume of passengers transported between the two countries. We first constructed separate networks for each year of available data. In these networks, passenger volumes were symmetrized to create undirected networks by summing the number of incoming and outgoing people on each connection. Edge weights for the composite air and rail networks were then computed by averaging the reported passenger volumes from both countries over the four years of data. Edges were retained in the composite networks as long as one node had reported passenger flows between itself and the connected node during the four-year time span. These edge weights were compiled into separate adjacency matrices for the aviation and rail networks, which were then used for tests of association between genetic distance and network distances.

Networks that had previously been constructed based on US aviation and commuter data were used for all comparisons between Europe and the US. Details on the construction of the US transport networks can be found in Bozick & Real (2015).

Networks were compared using a variety of metrics. A node's degree is a measure of its connectedness and is defined as the total number of edges emanating from it. Node volume sums the weights of these edges, with weight defined as the number of passengers traveling on the connection. To determine whether particular nodes acted as hubs on the basis of their connectedness or on the volume of passengers they serviced, we calculated both unweighted and weighted hub indexes for each node (Kleinberg, 1999). The hub index is based on the principal eigenvector of the graph's adjacency matrix. In addition, betweenness centrality can also identify nodes that are important for overall network connectivity. Betweenness centrality is an index of the number of shortest paths that stem from a node. Network density is the ratio of edges present to the total possible number of edges in a fully connected network. Network diameter is a measure of the steps needed to traverse the network; is it calculated as the shortest path between the two most distant nodes in the system.

Communities refer to groups of nodes that have stronger ties internally than externally. Many different community detection algorithms exist; we chose to use the simulated annealing method, following the described by Thiemann et al. (Thiemann et al., 2010). Because this method involves a stochastic algorithm, we ran 100 simulations, recording the modularity of each partition. Modularity, Q, measures the overall magnitude of difference between partitions (Newman and Girvan, 2004) and is calculated by taking the difference between the fraction of total edges occurring within communities and the expected value of the fraction of total edges occurring within communities in a network of identical community partitions with randomized connections between nodes. Q is bounded between 0-1, with Q=0 indicating that the community subdivisions provide no more information than that of a random partitioning of nodes.

Spatial Statistics

Pairwise spatial distances between countries were calculated based on the great circle distance between geographic centroids as well as between population centroids (Hamerly, 2006)(Fig 4.1). No qualitative differences were observed between these two distance measures under the Mantel test, so results presented are those of the analysis performed using geographic centroid coordinates.

Mantel tests were used to test for correlations between pairwise genetic distance matrices and matrices composed of geographic distance, aviation network connectivity and rail network connectivity. All transportation metrics were log transformed before analyses were performed. To account for comparisons between sequences from the same location, we tested two data transformations that can produce the symmetric distance matrices required for the Mantel test. First, we found the centroid of the cluster of points corresponding to between-country comparisons and assigned this value to all within-country comparisons (Broquet et al., 2006). This transformation removes variability introduced by the within-country comparisons and resulted in an n x n dimensional distance matrix for each clade where n is equal to the number of sequences tested. Second, we aggregated sequences within a clade by country and calculated the mean genetic distance among all pairwise comparisons for each country-to-country connection. This transformation resulted in an n x n dimensional distance matrix for each clade where n is equal to the number of locations represented. A Bonferroni correction was applied to results when multiple clades from a single season were tested. To visually check for correlations between genetic diversity and travel volume, a regression of genetic diversity on edge weight was performed using pairwise genetic distances pooled across all seasons. To determine the effect that transportation networks have on genetic diversity, we calculated the nucleotide diversity among all sequences

collected from a single country, and then performed regressions of diversity against node degree and node volume for each transportation network. In these analyses, diversity values each corresponded to a single country for a single season.

4.3 Results

Transportation Networks

Similar to differences observed between air and ground transportation in the US, the European aviation and rail networks differed in their basic properties (Fig 4.2). The rail network was sparser than the aviation network, as not all countries were directly connected to all other countries by rail. This is evident in the lower density of the rail network (d = 0.45) as compared to the aviation network (d = 0.96). Node connectedness was lower and much more variable in the rail network (mean = 12.62, var = 51.31) than in the aviation network (mean = 26.9, var = 2.81) (Fig 4.2). Degree distribution plots further illustrated these differences (Fig 4.7); the uniformity of the degree distribution of the aviation network indicates that, in terms of unweighted connectivity, few countries acted as travel hubs. In contrast, we observed a wider range of degree values for the rail network, where the number of connections per node was generally lower and more variable. The unweighted hub index further suggested that connectivity among nodes is similar in the aviation network (Fig 4.4A), but showed that, in the rail network, countries geographically located on the outskirts of Europe tended to be less well connected than those more centrally located on the continent (Fig 4.4B).

The daily volume of air travel was 4.2 times that of the rail network (air ~ 821,000 passengers/day, rail ~ 194,000 passengers/day). Even if seasonal travel volume fluctuations were incorporated, the difference in magnitude between the two network volumes suggested that the aviation network was much more heavily utilized than the

rail network. Travel volume along connections in the rail network steeply declined as a function a function of geographic distance, up to distances of approximately 1500 miles (Fig 4.3). At distances greater than 1500 miles, rail connections between countries were still present, but travel volume along these connections was lower and appeared to be independent of the distance traveled. In contrast, air travel volume was entirely independent of the geographic distance between countries although the majority of air travel occurred at distances less than 2000 miles. The total volume of passengers associated with each node was highly variable in both networks, although a cluster of high volume nodes was apparent in Western Europe in both networks (Fig 4.2). Weighted hub indexes revealed that the United Kingdom acted as a travel hub both in the air and rail networks (Fig 4.4 C,D). We also identified high-volume edges by constructing sparse networks that only retained edges supporting passenger volumes larger than the mean (Fig 4.5). In the rail network, several high-volume edges connect the cluster of countries in northwestern Europe, with Germany providing a link between those countries and the countries of eastern and southern Europe. In this high-volume network, Germany's betweenness centrality, a measure of how centrally located a node is within a network, is notably higher (b = 88) that of the next highest country's betweenness centrality (Italy, b = 37).

The unweighted diameter of the rail network (d=5) was higher than that of the aviation network (d=2), indicating that the shortest path between the two most distant nodes in the system involved five steps in the rail network. However, this was due to the relative lack of connections between the Baltic States (Estonia, Latvia and Lithuania) and the rest of Europe. Removal of the Baltic countries from the network resulted in a rail network diameter of two, equal to that of the aviation network.

An analysis of community structure for the aviation and rail networks based on both unweighted and weighted edges using the simulated annealing method (Newman and Girvan, 2004; Reichardt and Bornholdt, 2006; Traag and Bruggeman, 2009) did not detect any high modularity partitions in either network. Modularity was below 0.12 in all community analyses.

We further investigated the basic properties of the European rail network to determine how similar its function was to the of the US commuting network. The US commuting network is made up of 49 nodes, is highly spatially organized and has a density of 0.13 (Fig 4.6). In comparing degree distributions among the two US and two European transportation networks, we found that the European railway network is structurally more similar to the US commuting network, both with larger proportions of lower connectivity nodes than either aviation network, but with generally more connections per node than the US network (Fig 4.7). However, the diameter of the US commuter network was 9, higher than that of the rail network, owing to 99% of commutes being less than 112km and the much larger geographic expanse that the US network encompasses. Taken together, this evidence suggested that rail network shares properties of both the US commuting network and the European aviation network. US and European aviation networks tended to behave similarly, as the US aviation network is also very dense (d = 0.96), its degree distribution is large and highly uniform and it moves approximately 1.8 million passengers per day (Bozick and Real, 2015).

Influenza A/H1N1

Phylogenetic trees were constructed for four different seasons in which influenza A/H1N1 circulated: 2007-2008, 2008-2009, 2009-2010 and 2010-2011 (Appendix II: Figs S1-S4). A new pandemic lineage of H1N1 emerged during the spring of the 2008-2009 season, causing a secondary epidemic peak over the summer. We built separate

phylogenetic trees for each H1N1 lineage the circulated that season, but found that no clades met our criteria for inclusion from the 2008-2009 seasonal strain. Therefore, all clades analyzed from this season belonged to the pandemic lineage. This lineage eventually replaced the existing seasonal H1N1 virus, so that all seasons following this were dominated by the pandemic lineage; however, the epidemic dynamics of this lineage eventually approached those resembling the seasonal lineages. In total, we were able to analyze nine clades over these four seasons. The number of sequences used per season varied from 518 in the 2009-2010 season to 111 in the 2007-2008 season, and the number of countries represented varied from 21 in 2007-2008 to 13 in 2010-2011 (Appendix II: Table S3; see Appendix II: Table S4 for a summary of all sequences used in the spatial analysis after clades were been identified and extracted from the original phylogenetic trees). Further details obtained through the phylogenetic analysis are listed in Appendix II: Table S5.

No significant associations between genetic distance and any other measure of distance were detected using either distance matrix formulation for any of the nine clades tested. To further investigate the lack of genetic structure detected, we compared sequence diversity with a variety of network metrics. We found that neither country connectivity (degree) nor travel volume were correlated with nucleotide diversity for either network (all $p > 0.05$). When the data were pooled across seasons, no significant correlations existed between international edge weight and nucleotide diversity for either transportation network (Fig 4.8). Upon further inspection, we found that mean nucleotide diversity was significantly greater between countries than within countries (student's t test, $t = -10.37$, $df = 191$, p-value < 0.001) and that rail travel was also significantly higher within countries than between countries (student's t test, $t = 6.73$, $df = 72$, p-value < 0.001).

This finding led us to reexamine the sequence data collected from the United States, as our previous analysis had suggested correlations between genetic distance and commuter volume in multiple clades from multiple seasons. However, this analysis was conducted using all pairwise comparisons between sequences within each clade and did not account for the possibility that sequences collected from the same state might be much more similar and that commuter travel within states might be might higher than between states. As with Europe, we found that when the data were pooled across all seasons, no significant correlation existed between interstate commuter travel volumes and mean pairwise nucleotide diversity for either the H3N2 or H1N1 subtype (Fig 4.10A; blue points/line). Genetic diversity was significantly lower ($t = -26.16$, $df = 208$, p-value < 0.001) and commuting volume was significantly higher ($t = 13.29$, $df = 175$, p-value <0.001) within states than between states (Fig 4.9), which resulted in a highly significant negative correlation when all comparisons were included (Fig 4.10A; black line). This correlation, however, was driven solely by the coupling of decreased intra-state genetic diversity with increased intra-state commuting volumes. This was not the case when the US aviation network was considered because intra-state air travel volume is highly variable (Fig 4.10B). We therefore conclude that the significant associations detected previously using the Mantel test were driven by collections of highly influential data points located at the extremes of the genetic and commuting distance space (i.e. highly similar or identical sequences collected from within the same state). Reexamination of the scatter plots from each US clade in which genetic distance appeared significantly correlated with commuter travel volume further showed that these points did indeed drive the significant association. These results were confirmed through the use of the Mantel test after transforming the data for each US clade using the previously described methods (all $p>0.05$). In addition, H3N2 genetic diversity was more variable than for H1N1 (Fig 4.9), which likely accounts for the reduced occurrence of significant

associations detected for the H3N2 comparisons under the Mantel tests. In this case, points corresponding to within-state comparisons would not be as clustered at extreme commuting values and therefore would not have had as great an impact on the overall result.

4.4 Discussion

We found that transportation network flows are not associated with the genetic distance between influenza sequences in Europe. This result is not particularly surprising, as we found that the rail transportation network in Europe shares some important characteristics with regional aviation networks (e.g. long range connections and higher node connectivity). Instead of acting to structure contacts within the population, the rail and aviation networks in this area instead most likely facilitate long-range transmission of pathogens by allowing infected hosts to move rapidly over vast geographic expanses. This process leads to an admixed population rather than a spatially structured pathogen population.

Similar to differences observed between air and ground transportation in the US, the European aviation and rail networks differed in their basic properties despite the fact that they were constructed from the same 29 countries. The rail network was sparser than the aviation network, as not all countries were directly connected to all other countries by rail. Country connectivity in the rail network was much more variable than in the aviation network, with geographically distant countries like those in Scandinavia tending to be less connected than those countries that were more central geographically. The total volume of air travel was 4.2 times that of the rail network, demonstrating that the aviation network is much more heavily used than the rail network. In contrast, over 3.6 million people per day traveled along the interstate US commuter network compared

to approximately 1.8 million passengers traveling per day on the US aviation network. Western European countries tended to experience much higher passenger volumes in both the aviation and rail networks, and we found that Germany acts as a link in terms of passenger flow between the cluster of countries in northwestern Europe and the countries of eastern and southern Europe.

Strong community structure was not detected in either the air or rail network. In contrast, we previously found that modularity of the US county-to-county commuting network was 0.55 (Bozick and Real, 2015), a value similar to estimates obtained by Thiemann et al. (Thiemann et al., 2010) using currency movements as a proxy for human movement. The high modularity of the US network is due to well-defined communities composed of geographically compact collections of counties. Although groups of well-connected nodes were visually apparent in the rail network (Western Europe, for example) connectivity between these countries and the rest of the network was high enough to negate any clustering effects. This likely contributed to the homogenization of the influenza population.

While the properties of the European and US aviation networks were similar, our analysis showed that the properties of the European rail network fell between that of the US commuting network, a low-density, highly spatially organized network, and the aviation network, a high-density network in which most nodes are connected to most other nodes. For the majority of the European rail network, one would only need to traverse two connections in order to reach the two countries farthest from each other in both the rail network and the aviation network. In contrast, one would need to traverse nine connections to reach the two most distantly connected states in the US commuting network. This disparity indicates that, despite the rail network being less dense than the aviation network, pathogens could reach almost any other country in Europe through as

little as two connections, confirming our hypothesis that the rail and aviation networks both promote long range mixing.

Our diversity analysis revealed that genetic distances between sequences collected from within the same country are significantly lower than genetic distances between sequences collected from different countries. If comparisons between samples collected from the same location are not accounted for, incorrect conclusions can be drawn from correlations observed under the Mantel test. Without this correction, a correlation will result merely from the comparison of within population sequence diversity to among population sequence diversity. Under these conditions, no predictable decay in genetic distance exists across locations, but a correlation will nonetheless be detected due to low variation among sequences from the same population. After re-analyzing the US influenza dataset using appropriate transformations and validating our results with a regression of diversity on edge volume, we believe that the correlations previously detected were due to this phenomenon and not to the effect of commuter mobility on influenza transmission. While commuters are thought to contribute to the regional spread of influenza (Viboud et al., 2006b), we cannot at this time definitively corroborate that observation with genetic data at the geographic scales considered and suggest that alternative techniques and more spatially detailed sequence data are necessary to further clarify the role of this host group in epidemic transmission.

It would be interesting to perform a more complete comparative analysis in which commuting networks in the US and Europe could be analyzed for correlations with genetic distance among sequences at a finer resolution that is more consistent with the spatial scale at which actual transmission occurs. At this time, data on the connectivity and volume of human movement due to car travel for the European continent is unavailable for international travel, making even broad comparisons

between Europe and the US difficult. Regardless, commuting networks probably, for the most part, do not extend beyond country borders. Although the European Union operates under an open border policy, it is unlikely that many people regularly work in a country other than the one in which they reside. Further, while sequence availability varied by country, the resolution of the spatial data associated with most of these sequences is not currently fine enough to undertake this analysis.

Although it is not an exact replica, Europe, as a large landmass composed of contiguous political units with open borders, provides a unique comparison to the US which can be further exploited when more detailed data become available. Our findings highlight the need to consider the specific characteristics of the study area and local population before generalizing the existence of previously detected patterns. Understanding the processes generating, or obscuring, the spatial genetic patterns in a particular location will aid in the development of more informed strategies for the surveillance and control of epidemics.

4.5 Figures

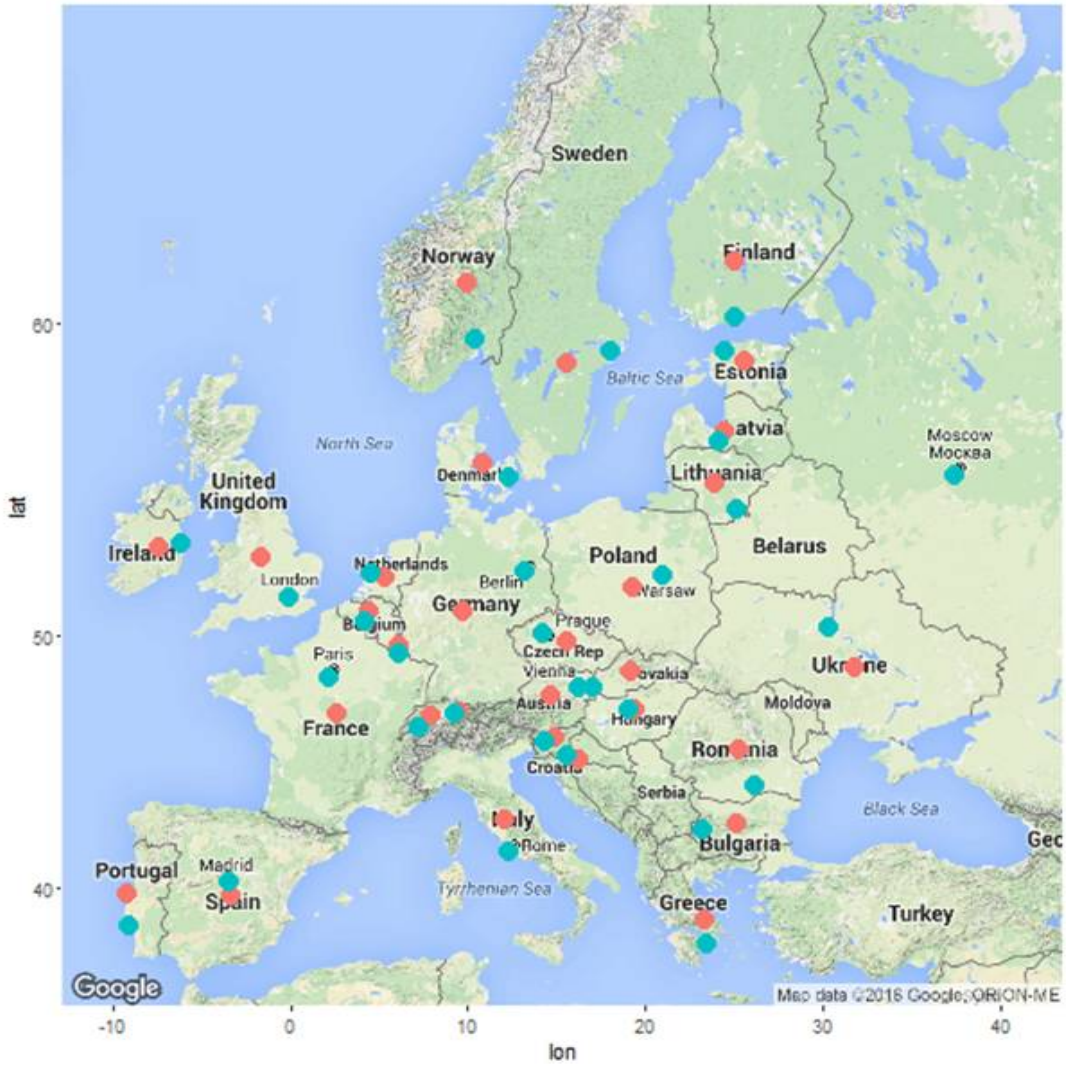

Figure 4.1. Geographic and Population Centroids of European Countries. Blue dots represent population centroids and red dots are geographic centroids.

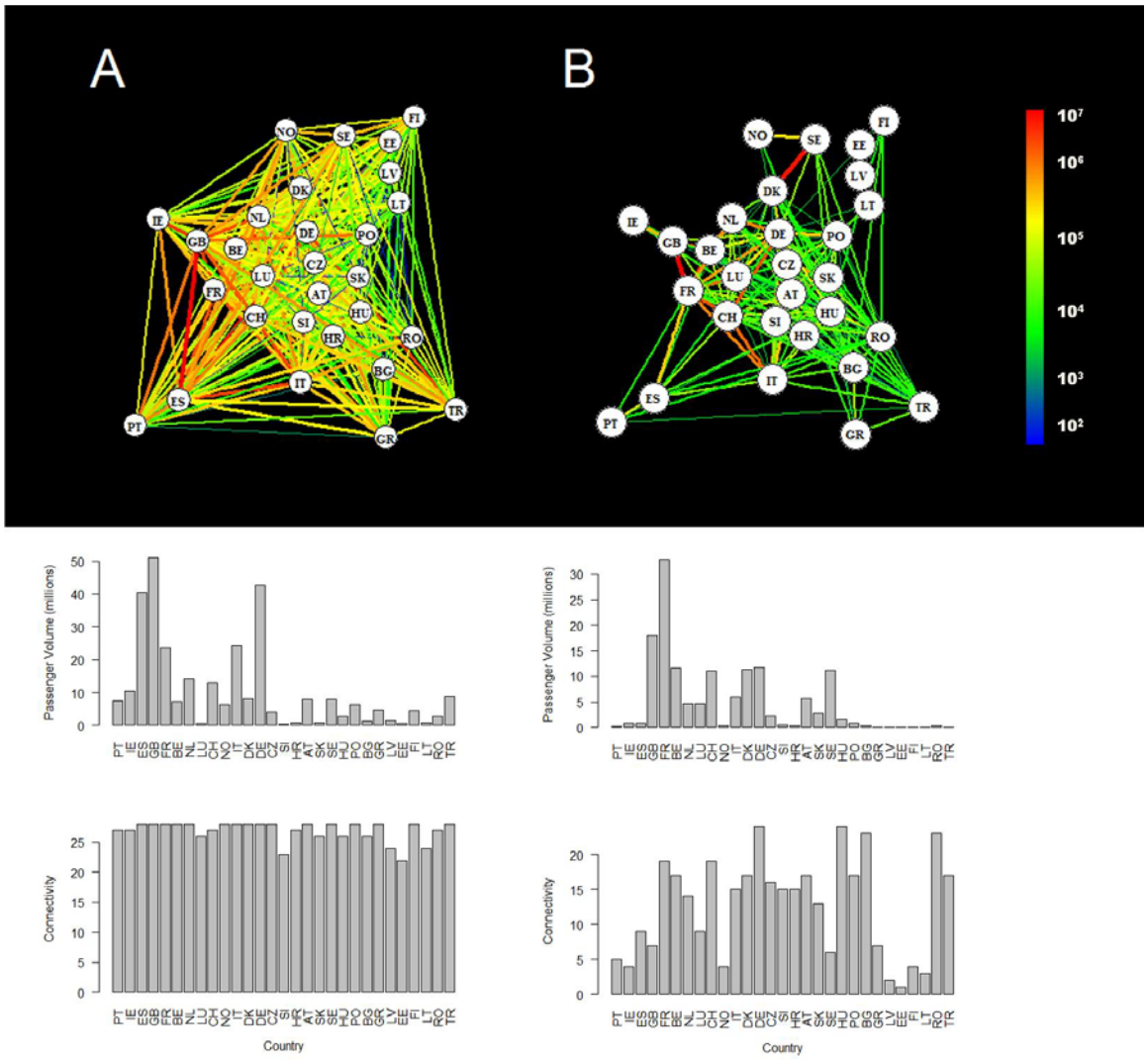

Figure 4.2. European Aviation (A) and Rail (B) Networks. Nodes are labeled by European country code (Table S2). Edge colors and widths indicate volume of travel on each connection (wider, red edges have highest travel volumes). Node degree (bottom bar plots) and volume (top bar plots) are plotted below each network according to longitude.

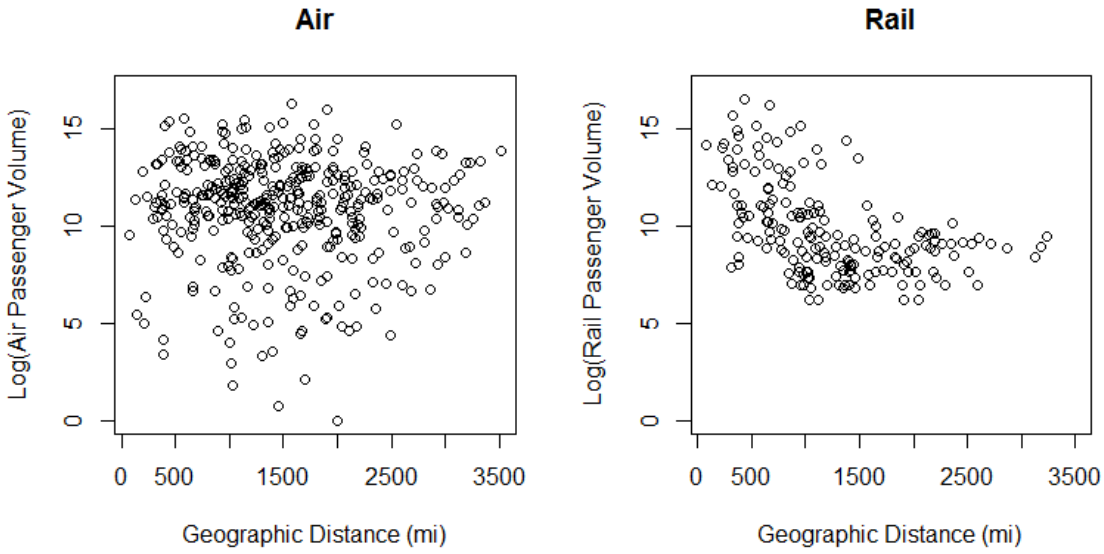

Figure 4.3. Association Between Travel Volume and Geographic Distance for the European Aviation and Rail Networks. While travel volume is independent of geographic distance in the aviation network, passenger flows along rail network connections decrease with increasing geograhpic distance up to approximately 1500 miles.

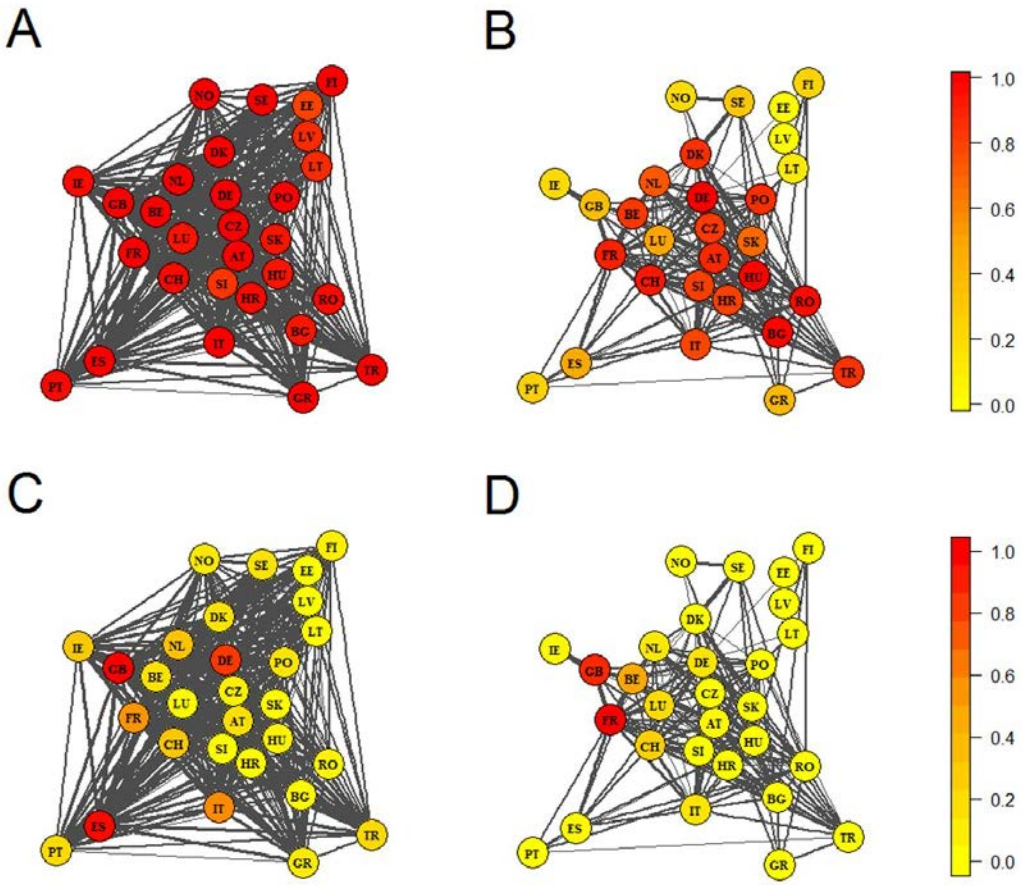

Figure 4.4. Unweighted and Weighted Hub Indexes. Hub indexes for the air (left) and rail (right) networks. Higher index values indicate greater connectivity (A & B) and travel volume supported (C & D).

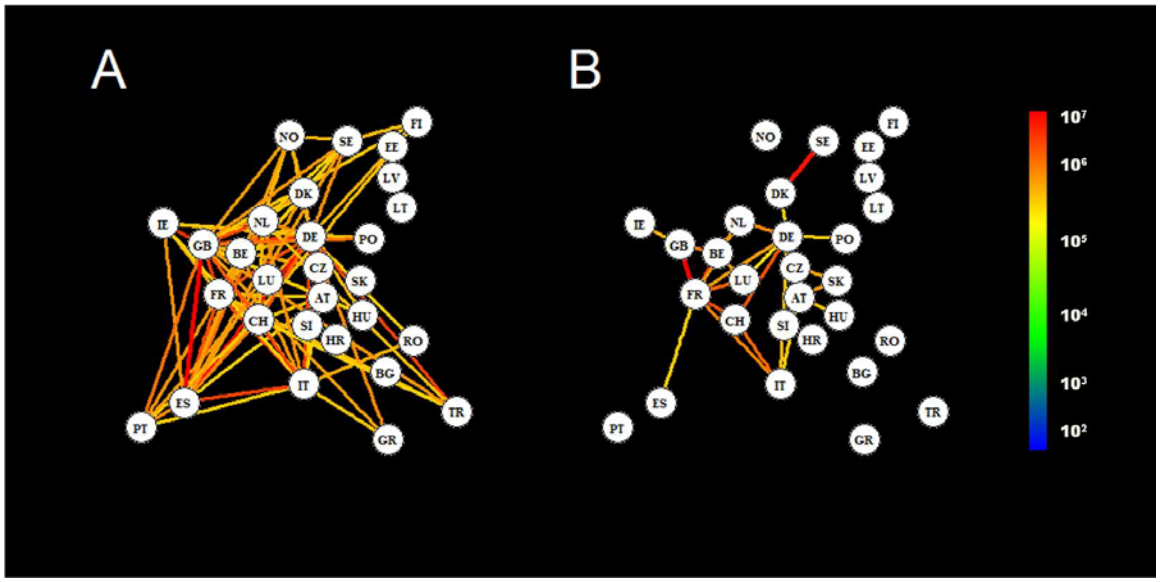

Figure 4.5. High Volume Edges. Air (A) and rail (B) networks retaining only edges with larger than average volume connections.

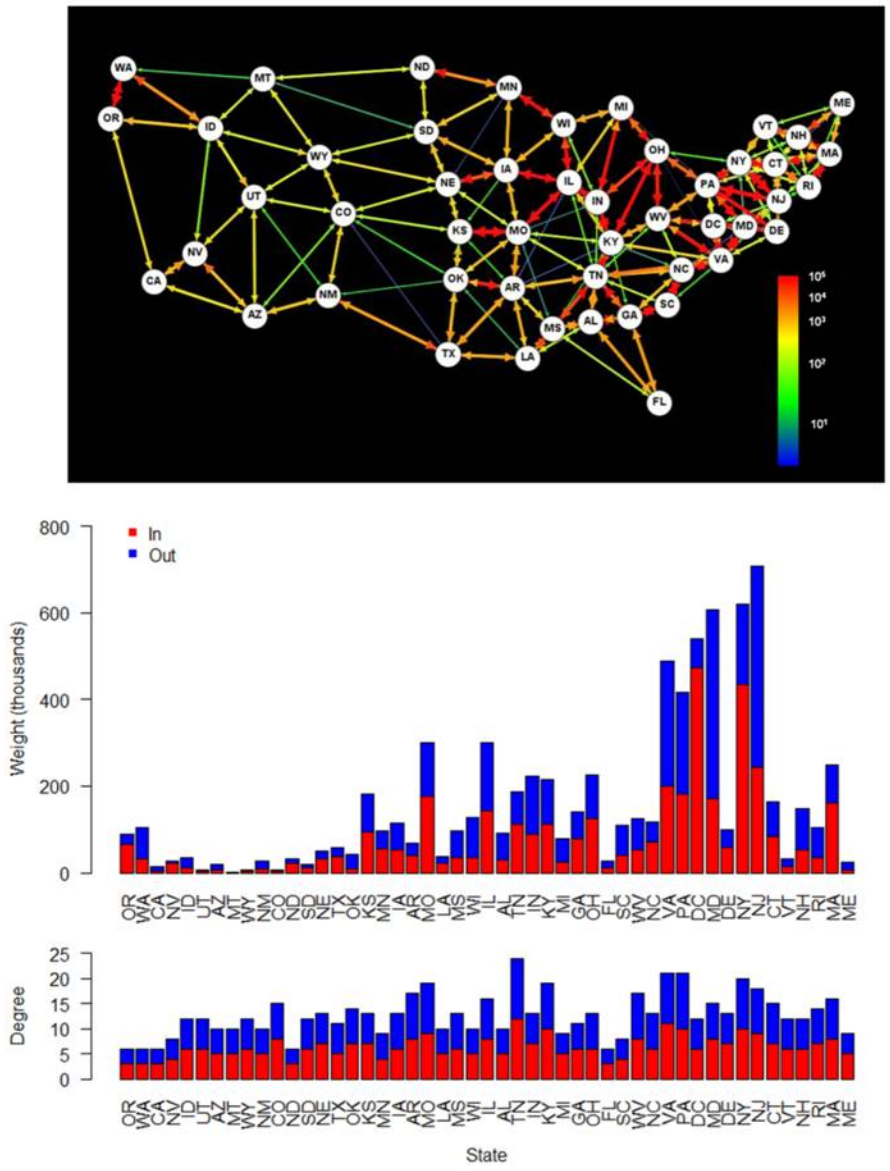

Figure 4.6. US Commuting Network. Edge colors and widths indicate volume of travel on each connection (wider, red edges have highest travel volumes). Node degree (bottom bar plot) and volume (top bar plot) are plotted according to longitude. Red bars indicate travel into the state and blue bars indicate travel out of the state. *Adapted from PLoS Pathogens, 11(60), Bozick & Real, The role of human transportation networks in mediating the genetic structure of seasonal influenza, e1004898, 2015.*

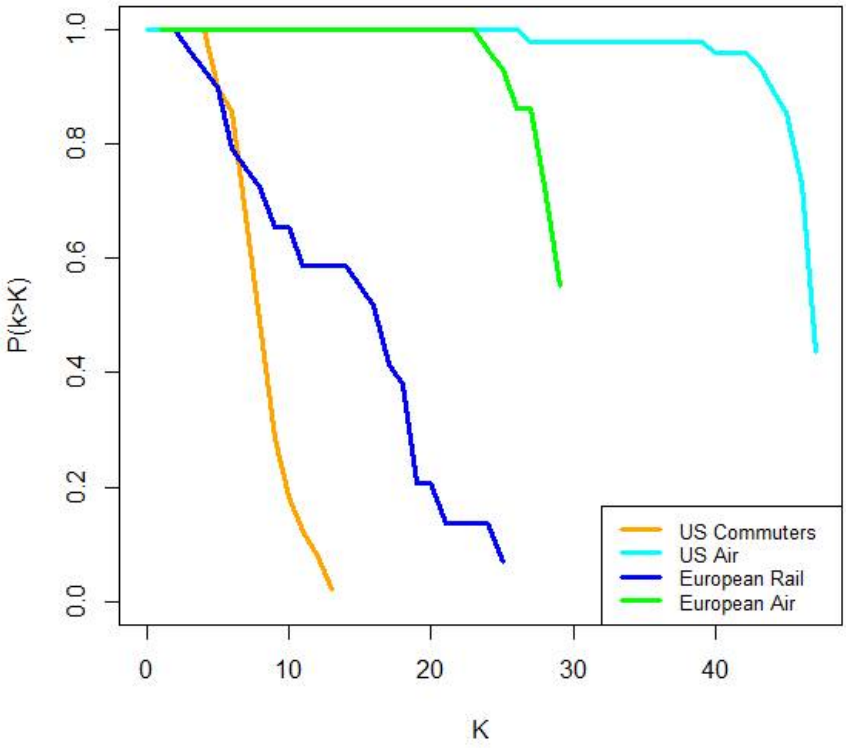

Figure 4.7. Degree Distribution Comparison of Air and Ground Transportation Networks. The distribution is based on the fraction of nodes (k) with a degree greater than or equal to K

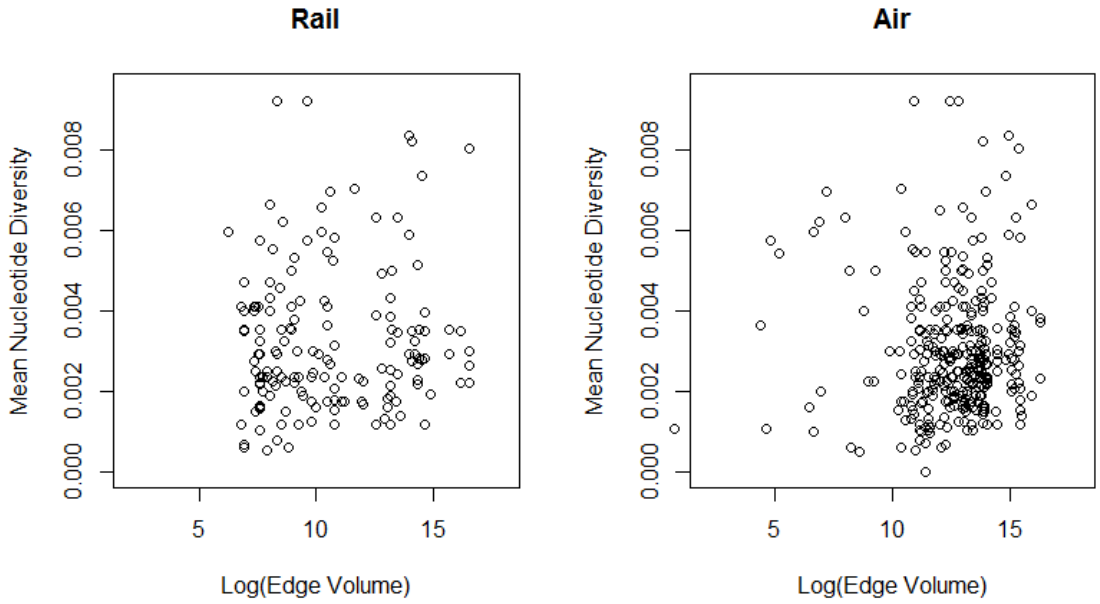

Figure 4.8. Regression of Nucleotide Diversity on Edge Volume: Europe. Dots represent edges connecting two distinct countries (international travel) during a single season in a single clade. No significant associations are present (rail: $p = 0.23$; air: $p = 0.62$).

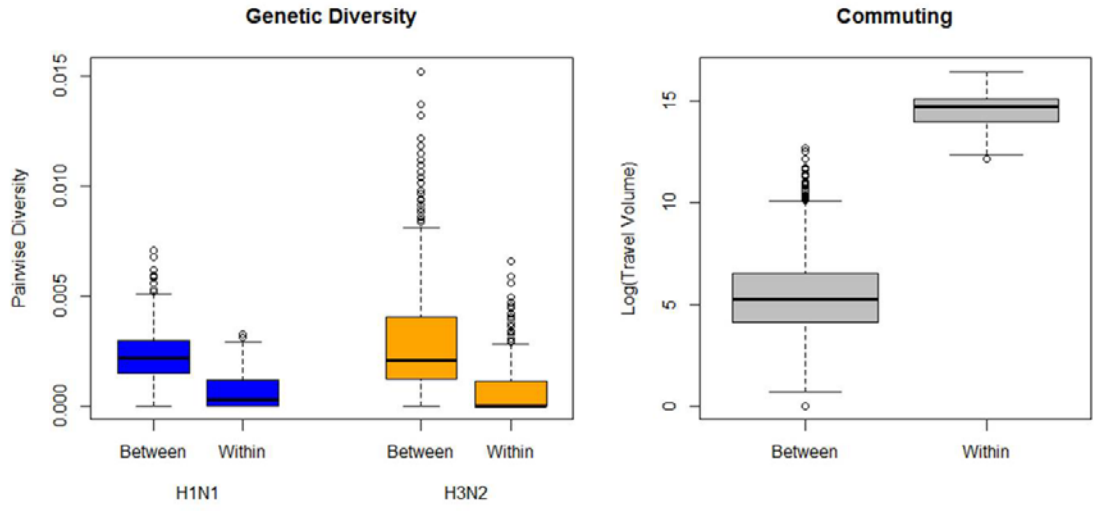

Figure 4.9. Genetic Diversity and Commuting Volume Within and Between US States for the H1N1 and H3N2 Subtypes. Genetic diversity is significantly higher between states for both subtypes whereas interstate commuting volume is significantly lower than intra-state commuting volume.

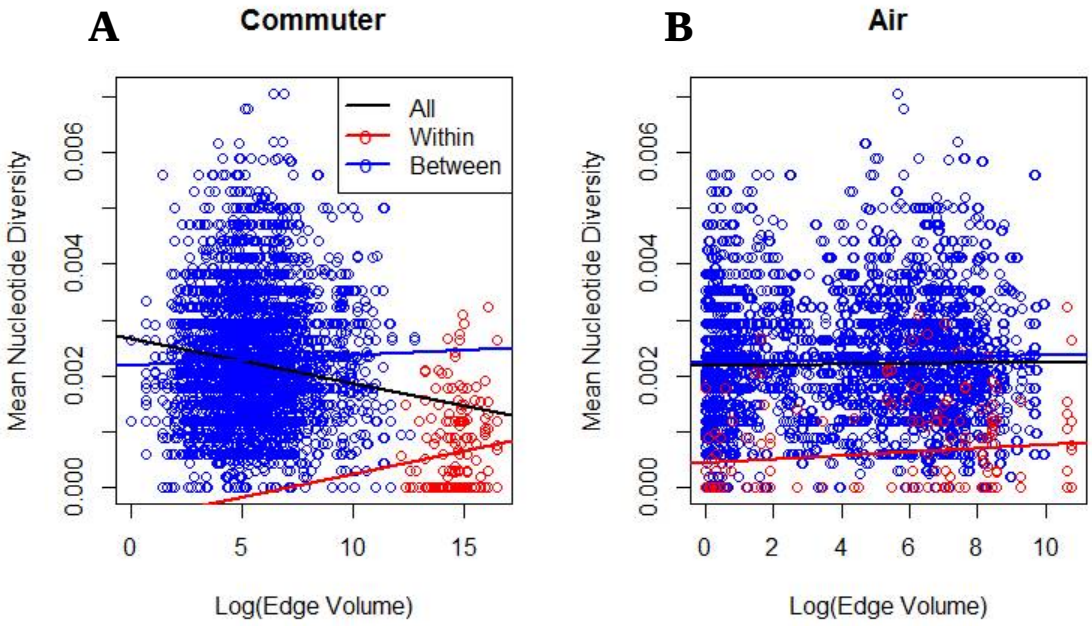

Figure 4.10. **Regression of H1N1 Nucleotide Diversity on Edge Volume: US.** Edge volumes correspond to commuter travel (A) and air travel (B). When examining the relationship between genetic distance and commuter travel volume (A), a highly significant correlation driven solely by the difference between the two clouds of points is observed when within-state sequence comparisons are included. These clouds of points are composed of comparisons between sequences collected from within the same location (red) and comparisons between sequences collected from two different locations (blue). Black line represents regression using all data (commuter: $R^2 = 0.04$, $p < 0.001$; air: $p = 0.3$); red and blue lines correspond to regressions considering either only intra-state comparisons (red) (commuter: $p = 0.18$; air: $p = 0.07$) or inter-state comparisons (blue) (commuter: $p = 0.05$; air: $p = 0.06$).

Chapter 5

Modeling the effects of commuter-targeted vaccination strategies on influenza epidemics

5.1 Introduction

Annual influenza epidemics result in an estimated 3-5 million global cases of severe illness each year, with 90% of deaths occurring in adults older than 65 years (Simonsen, 1999; 2016). The total annual economic burden of influenza in the United States has been estimated at $87.1 billion when direct medical and productivity costs as well as life-years lost are considered (Molinari et al., 2007). Widespread vaccination is currently our best line of defense against the virus, but the vaccine must be updated annually to track the rapid evolution of the influenza A virus (Rambaut et al., 2008). Therefore, new vaccines must be distributed each season.

Although the CDC currently recommends the seasonal influenza vaccination to all adults and children (Grohskopf et al., 2015), in times of shortages the recommendations instead prioritize older adults, the very young, individuals at high risk and health care workers (Centers for Disease Control and Prevention, 2015d). Current vaccination rates among age groups are approximately 70% for young children, 56% for school age children, 38% for adults and 67% for adults older than 65 years (Centers for Disease Control and Prevention, 2015a). Despite this, attack rates for influenza are estimated to be between 10-20%, although they can reach 30-50% in certain age and social groups (Chunara et al., 2015; Cox and Subbarao, 2000). A drawback of the current policy of prioritizing those at high risk for complications is that the influenza vaccines have the highest efficacy in younger, healthy individuals (Goodwin et al., 2006;

Osterholm et al., 2012). Current recommendations focus on reducing individual risk for high consequence groups rather than on reducing transmission in the population.

A large body of work suggests that vaccination of school age children can provide population-wide benefits, as previous data has shown that school age children are the major driver of influenza within communities, particularly within households (Longini et al., 1982; Worby et al., 2015). Children not only have extremely high contact rates with members of their own age groups, but also frequently contact members of other age groups (Mossong et al., 2007; Wallinga et al., 2006). Accordingly, attack rates tend to be highest for school-aged children. Targeted vaccination of children has been shown to reduce total population incidence both theoretically (Halloran et al., 2002; Longini et al., 1978; Longini et al., 2004; Medlock and Galvani, 2009; Patel et al., 2005; Weycker et al., 2005) and empirically (Monto et al., 1969; Piedra et al., 2005; Reichert et al., 2001). Despite the evidence, the US does not require routine vaccination of children for influenza.

Research on influenza transmission at the regional scale has suggested that commuters are important for inter-community spread. Influenza-like-illness data and mortality data have been utilized to demonstrate correlations between commuter movements and timing of influenza epidemic peaks (Viboud et al., 2006b). Further exploration of the importance of human mobility for pathogen transmission has shown that differences in city-specific commuting patterns are sufficient to cause variation in epidemic dynamics (Dalziel et al., 2013). Given this group's importance in transmitting influenza, it is pertinent to ask whether targeting employed adults, the most mobile segment of the population, provides population-wide benefits similar to those that result from targeting children, the segment of the population experiencing the highest contact rate.

To address the effects of targeting employed adults for vaccination, we built a fully stochastic metapopulation model to track host mobility and interactions between individuals from multiple ages and social groups. We tested multiple vaccination strategies aimed at these different age and social groups and assessed the effectiveness of each by comparing the time to metapopulation-wide infection and total incidence at the end of the epidemic. We confirm that vaccinating children is most successful in terms of reducing incidence, but find that vaccinating adults based on employment status and mobility also lowers total incidence while additionally delaying spatial epidemic spread.

5.2 Methods

Model Formulation

To assess the effect of targeted vaccination of mobile adults on epidemic dynamics, we constructed a fully stochastic metapopulation model that approximates the basic epidemiology of a directly-transmitted human pathogen. The model tracks epidemic progress across 11 interconnected populations with a total metapopulation size of one million individuals. We define each of these interconnected populations as a patch, and designate one patch as a city and the remaining 10 patches as suburbs. We assume that the population in the city accounts for half the total metapopulation size and distribute the remaining individuals evenly among the 10 suburbs.

Within patches, individuals are classified as children, employed adults, adults not in the workforce and elderly. The population is composed of 25% children, 50% employed adults, 10% adults not in the workforce and 15% elderly. This age and employment distribution approximates data from the US Census Bureau (United States Census Bureau). Contact rates among groups were calculated using previously published

estimates (Mossong et al., 2007), with contact rates among children being the highest and contact rates among the elderly being the lowest.

The model assumes SEIR-type infection dynamics in each patch. Since the model only simulates epidemic progress over the course of a season, we assume a finite population in which no births or deaths occur, and we assume that immunity is complete and long-lasting, such that it does not wane during the time period of the epidemic. The basic equations describing transitions between model compartments for a population group *x* in a single patch are as follows:

$$dS_x = -v_x S_x - \lambda_x^t S_x$$

$$dE_x = \lambda_x^t S_x - \theta E_x$$

$$dI_x = \theta E_x - \gamma I_x$$

$$dR_x = \gamma I_x + v_x S_x$$

where:

x = population group (children, adults in workforce, adults not in workforce, elderly)

v = vaccination rate

λ = force of infection

t = time of day

$1/\theta$ = latent period

$1/\gamma$ = infectious period

S, E, I and R give the number of susceptible (S), exposed (E), infected (I) and immune (R) individuals. We include both vaccinated individuals and individuals that

have recovered from infection in the immune class. Although we include a term for vaccination of susceptible individuals, we note that all vaccination in the simulations presented occurs before the start of the epidemic, and that the vaccination rate is zero during the course of the epidemic. While we present the equations here as a set of ODE's for clarity, transitions between classes in the model are implemented stochastically based on Gillespie's stochastic simulation algorithm (Gillespie, 1976, 1977).

For each group, the force of infection λ is given by a specific $\beta I/N$. Within this, β can be further decomposed into the product of the probability of transmission, a constant *b*, and the contact rate between population groups, $C_{x,y}$. The matrix C describes contact rates between three age groups (children, adults and elderly). These rates are adapted from data from Mossong et al. (2007), as well as previously published models of influenza transmission between age groups (Araz et al., 2012; Medlock and Galvani, 2009). To approximate an influenza-like pathogen, we assume a latent period of four days and an infectious period of five days, although published parameter estimates can vary widely depending on the subtype and whether the outbreak is that of a seasonal or pandemic strain (Elveback et al., 1976; Gojovic et al., 2009; Ratmann et al., 2012; Tuite et al., 2010). We use a transmission probability (*b)* that corresponds to a R_0 for the entire metapopulation of 2.3 (Dietz, 1993), which is in line with estimates of a major influenza pandemic (Coburn et al., 2009). However, we recognize that seasonal influenza epidemics in the US are generally characterized by an average R_o of 1.3 (Viboud et al., 2006b), which we aim to explore in future implementations of the model.

In order to simulate more realistic forms of population mixing, we vary the force of infection (λ) for each group based on the time of day (Keeling et al., 2010). Nighttime dynamics only include contacts between residents from the same patch; all groups within a given population interact with each other and infection occurs in a frequency-

dependent manner. Frequency-dependent transmission was used to reflect heterogeneities in host contact rates at coarse spatial scales. At the city-suburb level modeled here, contact rates across cities of different sizes are expected to remain relatively constant rather than scaling with density (Bjornstad et al., 2002; Keeling and Rohani, 2011).

As an example, consider only the infection dynamics in a single patch. At night, λ for group *x* only includes contacts between residents from the same patch and is calculated as:

$$\lambda_x^{night} = \sum_y \frac{\beta_{x,y} I_y}{N}$$

where N is the total number of residents in the patch, and the *x,y* subscript denotes the β calculated from the contact rate between group *x* and group *y*.

During the day, we assume that children, adults not in the workforce and elderly individuals that reside in the same patch interact in a similar fashion, but that employed adults only interact with other employed adults. Among children, adults not in the workforce and the elderly, the calculation of λ remains the same as above, except that the denominator N is modified to exclude employed adults that reside in the patch. Among employed adults, the daytime infection rate is based on contacts between infected and susceptible adults employed in the same patch. The force of infection for adults in the workforce that reside in patch *h* and work in patch *w* is therefore calculated as:

$$\lambda_{(h,w)}^{day} = \sum_j \beta_{A,A} I_{(j,w)} \frac{1}{\sum_k N_{(k,w)}}$$

where $\beta_{A,A}$ denotes transmission between adults. The denominator gives the total number of adults in the workforce that work in patch *w*, allowing us to model frequency-dependent transmission.

Commuting Network

Among employed adults, we define *non-commuters* as individuals that are employed in their home patch and *commuters* as individuals that are employed in a patch other than their home patch. We group all employed adults according to their work and home patch combinations and use a matrix to track inter-patch movements. The movement matrix is based on the metapopulation connectivity network, which we defined as a nearest-neighbor network (Fig 5.1). For all simulations, we assume that 50% of employed adults in each patch are non-commuters and that the commuters from each patch are distributed equally among all connected patches.

Vaccination

Simulations were run in which from 50,000-800,000 vaccine doses were available (in intervals of 50,000), corresponding to vaccination of from 5-80% of the entire metapopulation. In each simulation, epidemics were seeded by introducing 10 infected non-commuters into the city patch. We first simulated the random distribution of vaccines. Under this strategy, each patch was allotted vaccines in proportion to its total population size, and each age group in each patch was vaccinated according to its frequency. In all simulations, we assumed that 15% of every group refused vaccination, even if there were vaccine doses available. This assumption ensured that the epidemic had the opportunity to spread, since employed adults were the only group in this simple model that interacted with individuals from outside their home patch. With this assumption in place, all groups at least partially contributed to infection dynamics across all simulations.

This random distribution strategy was then compared to strategies in which vaccines were initially distributed to one of four target groups: all employed adults, commuters, non-commuters or children. To compare the effects of vaccination across the different targeted strategies, we adopted an approach in which we considered scenarios in which from 50,000-200,000 doses were available as "Limited Vaccination" and scenarios in which from 250,000-800,000 doses were available as "Excess Vaccination". In the limited vaccination scenarios, only the target group received vaccination (i.e. in these scenarios, fewer vaccine doses were available than the maximum possible number of individuals that could be vaccinated in each target group).

In the excess vaccination scenarios, vaccines were first distributed to the target group. When targeting children, commuters and non-commuters, which each made up 25% of the population, this meant that the maximum possible number of individuals in the target group could be vaccinated. The remaining vaccine doses were then distributed to other groups based on their frequency in the population. Employed adults, however, made up a larger proportion of the population (50%; commuters and non-commuters combined) than each of the other three target groups. To accurately compare this strategy with the other three, we ensured that, initially, the number of vaccines distributed to employed adults was equal to the maximum number of vaccines that could be distributed to children, commuters or non-commuters. The remaining vaccine doses were then randomly distributed to the rest of the population in the same manner described previously but, in this case, employed adults could continue to be vaccinated with these excess doses based on their remaining frequency in the population (i.e. without being targeted).

Outcome Metrics

One hundred simulations were run for each vaccination strategy. For all model runs, we quantified epidemic timing using three metrics: (1) the total time necessary for the epidemic to reach all patches, defined as the number of days between peaks in the first patch infected and the last patch infected, (2) time to dispersal, defined as the number of days between the peak in the seeding patch and the peak in the second patch to become infected, and (3) speed of spread, defined as the inverse of the mean time between epidemic peaks across patches excluding the seeding patch. We also recorded the total incidence at the end of the simulation as well as the incidence in each age group at the end of the simulation. We quantified the effectiveness of our intervention strategy by calculating the difference between the total number of possible infections (all individuals that did not receive a vaccination) and the total number of actual infections.

5.3 Results

Across all vaccination strategies, increasing vaccination in any of the four target groups (children, employed adults, commuters and non-commuters) decreased the total metapopulation incidence beyond what would be expected if everyone except those vaccinated had become infected (Fig 5.2).

Limited Vaccine Availability

When vaccination was limited and targeted at either commuters, non-commuters or employed adults, epidemics spread across the metapopulation slower than when vaccination was administered randomly or to children (Fig 5.3). The increase in spreading time was attributable to both an increase in the time necessary for the epidemic to initially disperse out of the introduction patch and a decrease in the speed of spread. At low levels, vaccinating children appeared to decrease the time necessary for

the epidemic to spread across the metapopulation. This effect was due to the synchronization of epidemic peaks across patches, which was not as pronounced under any of the other strategies. Vaccinating children when doses were limited resulted in more infections averted than any other strategy, although vaccination of commuters, non-commuters or working adults all only performed slightly worse (Fig 5.4). All targeted vaccination strategies led to more infections averted than random vaccination. Unsurprisingly, targeted vaccination led to the greatest decreases in incidence in the targeted group when incidence was partitioned by age (Fig 5.5). Furthermore, targeting children had little effect on adult incidence and targeting any class of employed adults had little effect on incidence in children. Although random vaccination produced the greatest decrease in incidence in the elderly, targeted vaccination of children produced a slightly greater reduction in incidence in the elderly than targeted vaccination of commuters, non-commuters or employed adults. No spatial differences in incidence were observed in the city or suburb patches under any vaccination strategy.

Excess Vaccines Available

Similar trends were observed when vaccine availability was not limited. Total spreading time and dispersal time increased and spreading speed decreased as more vaccines were deployed, an effect which was more pronounced when vaccinating commuters than non-commuters and employed adults (Fig 5.6). Initially targeting children for vaccination resulted in faster spreading speeds than all other strategies tested.

Initial targeted vaccination of children reduced metapopulation-wide incidence the most, the effects of which became more obvious when vaccination doses exceeded 500,000 (Fig 5.7). When more than 500,000 doses were available, random vaccination also led to more infections averted than targeting employed adults, commuters or non-

commuters, and the initial targeted vaccination of children led to greater decreases in incidence in the elderly than the other three targeted strategies (Fig 5.8). Vaccination of approximately 65% of the population was necessary to prevent most epidemics from occurring.

5.4 Discussion

In line with previous studies, we found that targeted vaccination aimed at children yielded the greatest benefit in terms of reducing total incidence. Targeted vaccination of employed adults, commuters and non-commuters resulted in marginally greater total incidences as compared to targeting children, but also delayed epidemic spreading time and speed. These delays could potentially increase the effectiveness of intervention strategies implemented during the course of the epidemic (Germann et al., 2006). The larger reductions in incidence observed when targeting children for vaccination rather than adult subgroups are explained by the underlying differences in contact rates among age groups. Children's contact rates are high both with other children and with individuals in other age groups; vaccinating the group responsible for transmitting the majority of infections therefore led to the greatest decrease in incidence.

Our model included several simplifying assumptions that limit its application to real world transmission processes, particularly for influenza epidemics. First, we quantified the success of each vaccination strategy in terms of incidence rather than mortality. Although estimates of mortality due to influenza and pneumonia correlate well with incidence (Cox and Subbarao, 2000; Simonsen, 1999; Viboud et al., 2006b), influenza-induced mortality varies drastically by age group. In particular, the elderly and the very young tend to suffer much higher mortality due to influenza than older children or healthy adults (Simonsen, 1999; Simonsen et al., 2005). While total incidence may

remain high, mortality in the elderly could be reduced by vaccinating other social groups with whom they interact (Medlock and Galvani, 2009). However, to accurately capture this effect, our model would need to additionally incorporate several important complexities. Specifically, we assumed that vaccine efficacy was 100%, that an individual's probability of transmission was constant regardless of the time since infection and that all infections resulted in symptomatic, infectious cases. In reality, annual influenza vaccine efficacy is probably lower than 70%, with efficacy dropping to as low as 20% in years when the vaccine does not match the dominant circulating strain (Osterholm et al., 2012). Vaccine efficacy further varies by age group; vaccination is less effective when administered to the elderly than to healthy adults (Goodwin et al., 2006). In addition, vaccination in many epidemic models is often assumed to reduce influenza symptoms and decrease infectiousness, even when it does not provide complete protection against infection (Chao et al., 2010; Medlock and Galvani, 2009; Weycker et al., 2005). Coupled with the reduced probability of transmission by asymptomatic individuals (Patrozou and Mermel, 2009), these complexities could significantly affect measured mortality rates, especially in the elderly and other vulnerable populations. This outcome would not have been apparent in our current model and should be explored in future studies.

Another simplifying assumption of our model was that commuters were the only group that interacted with individuals in patches outside their home patch. In reality, all groups likely interact with each other in many different spatial locations, although the relative magnitude of these interactions likely varies by age and with the spatial scale under observation. At the city-suburb scale that we aimed to replicate, children and adults certainly contact others outside of their home community, although inter-community interactions between employed adults probably occur more often and more regularly than do inter-community interactions among other groups. In addition to

incorporating the more complex vaccine-related parameters outlined previously, future implementations of the model should also include parameters accounting for the weaker but relevant interactions of other age groups with residents of other communities.

Although the body of literature demonstrating the benefits of vaccinating children against influenza is extensive, this policy has not been widely implemented. The CDC currently recommends vaccination for all healthy adults and children, but vaccination of these groups prior to the start of the 2014-2015 season had only reached around 40% each (Centers for Disease Control and Prevention, 2015c). Our results suggest a possible alternative strategy that, while marginally less effective that the optimum, could provide additional benefits in terms of epidemic timing and may be easier to implement if adults are more amenable to vaccination than children. Developing a more complex model that better approximates real-world metapopulation systems will help to further determine the conditions under which vaccination of mobile individuals could control influenza epidemics.

5.5 Figures

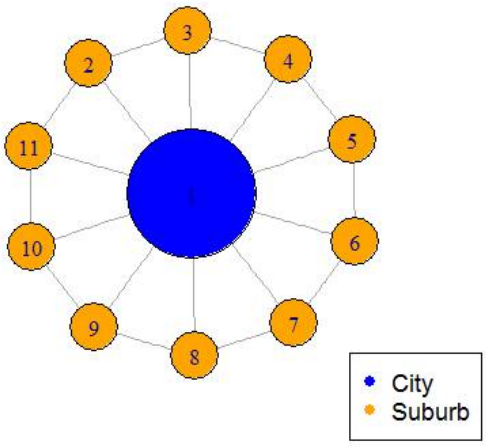

Figure 5.1. Nearest-Neighbor Commuting Network. The metapopulation is composed of one city population (blue) and 10 suburb populations (orange). Each suburb is connected to two neighboring suburb populations and the city population through commuting. The number of individuals that reside in the city accounts for 50% of the total metapopulation size.

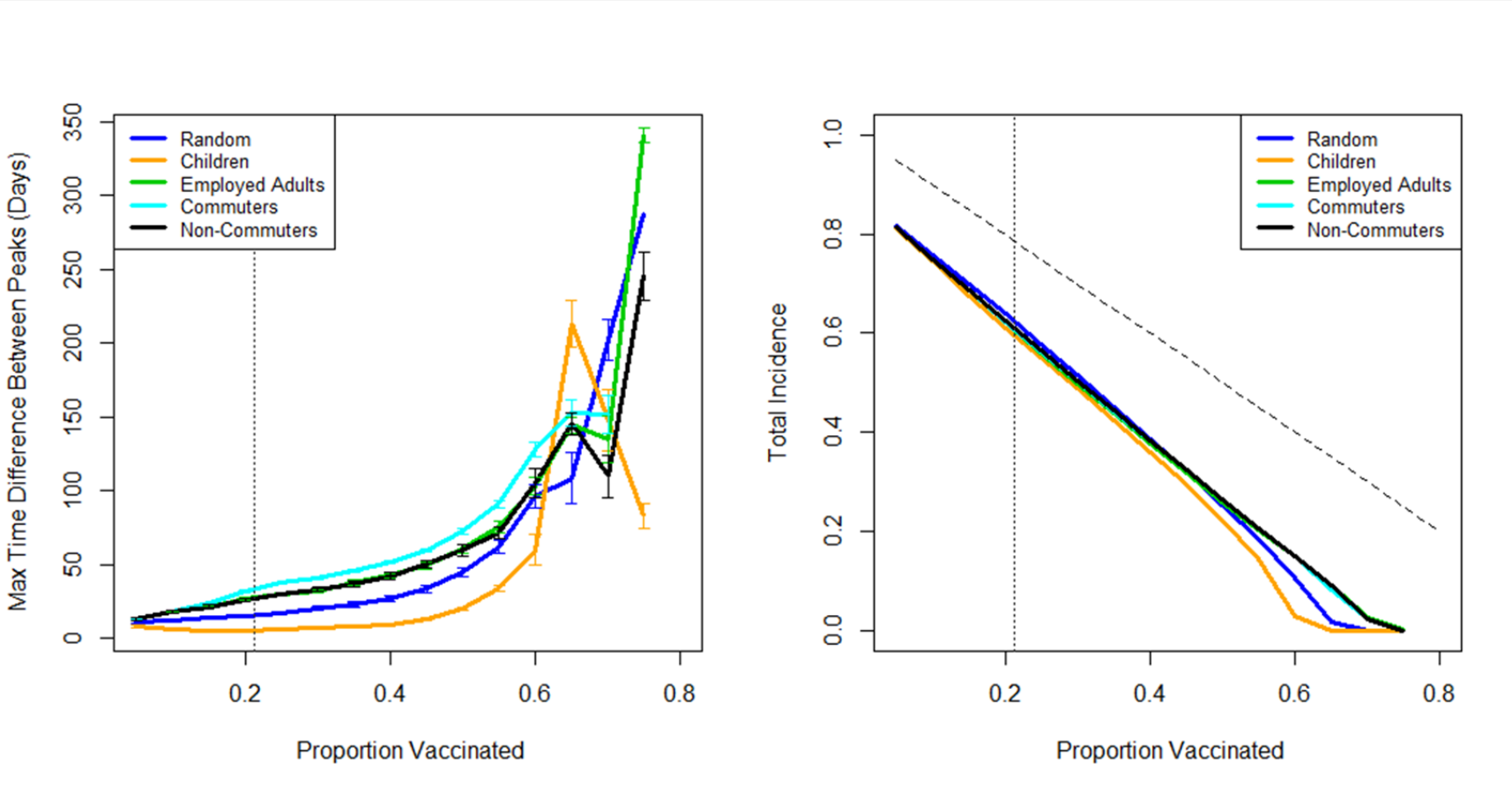

Figure 5.2. Epidemic Timing and Incidence in Response to Targeted Vaccination. Changes in timing (left), incidence (right) in response to targeted vaccination of children, employed adults, commuters or non-commuters compared with the random distribution of vaccines across all age groups. The vertical dotted line at indicates the point at which excess vaccine doses are available and individuals outside the target group may be vaccinated.

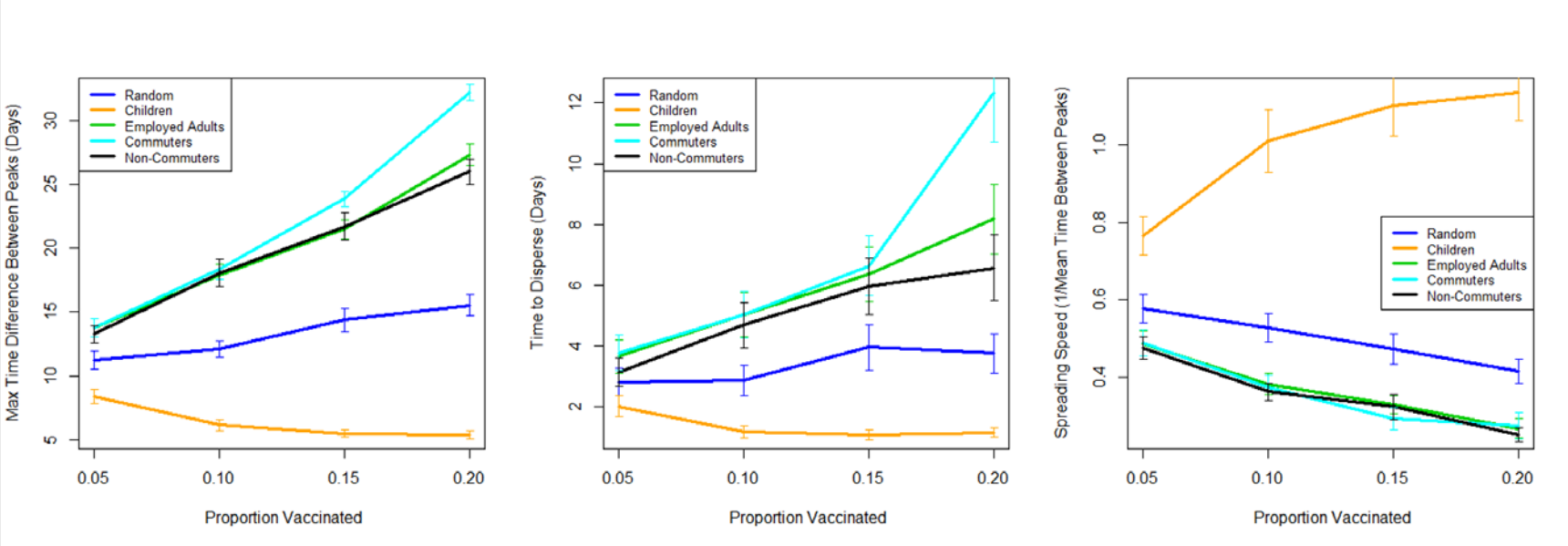

Figure 5.3. Epidemic Timing Under Limited, Targeted Vaccination. Changes in epidemic timing in response to random vaccination and four different targeted strategies when vaccine doses are limited. Plots show total time necessary for the epidemic to spread across the metapopulation (left), time necessary for the epidemic to disperse from the patch of initial introduction (center) and epidemic spreading speed (right).

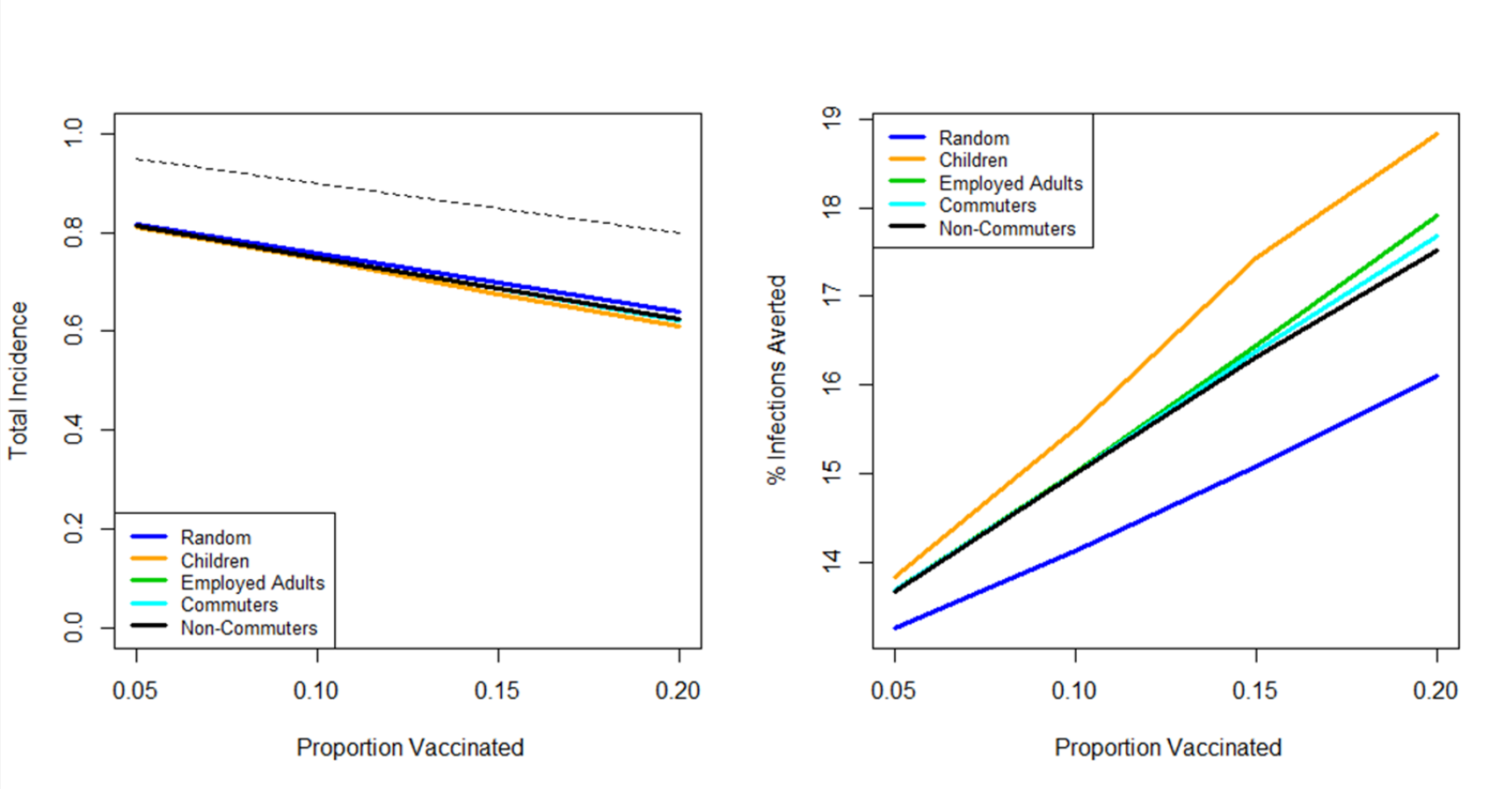

Figure 5.4. Incidence Under Limited, Targeted Vaccination. Reductions in total incidence in response to random vaccination and four different targeted strategies when vaccine doses are limited. Left panel shows overall reduction in incidence across a range of vaccination levels, right panel shows the percent of infections averted. Dashed line in left panel represents the total possible infections if all individuals that had not been vaccinated were to become infected.

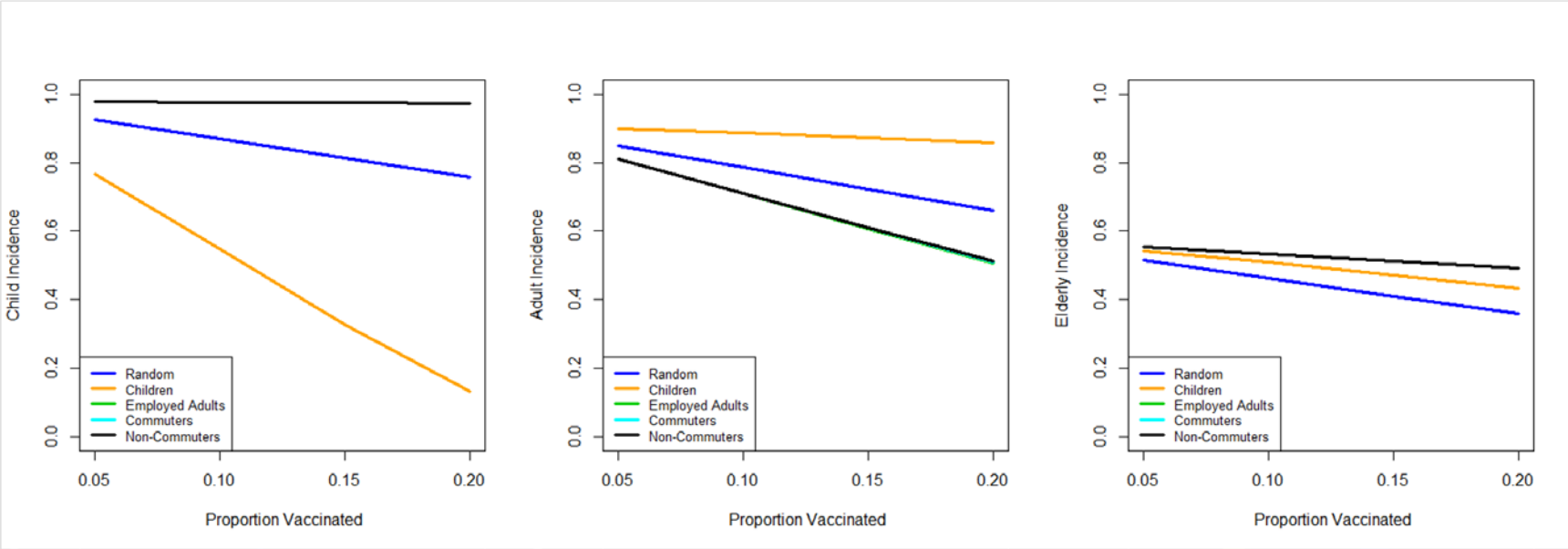

Figure 5.5. Incidence by Age Group Under Limited, Targeted Vaccination. Incidence in children (left), adults (center) and elderly (right) shown.

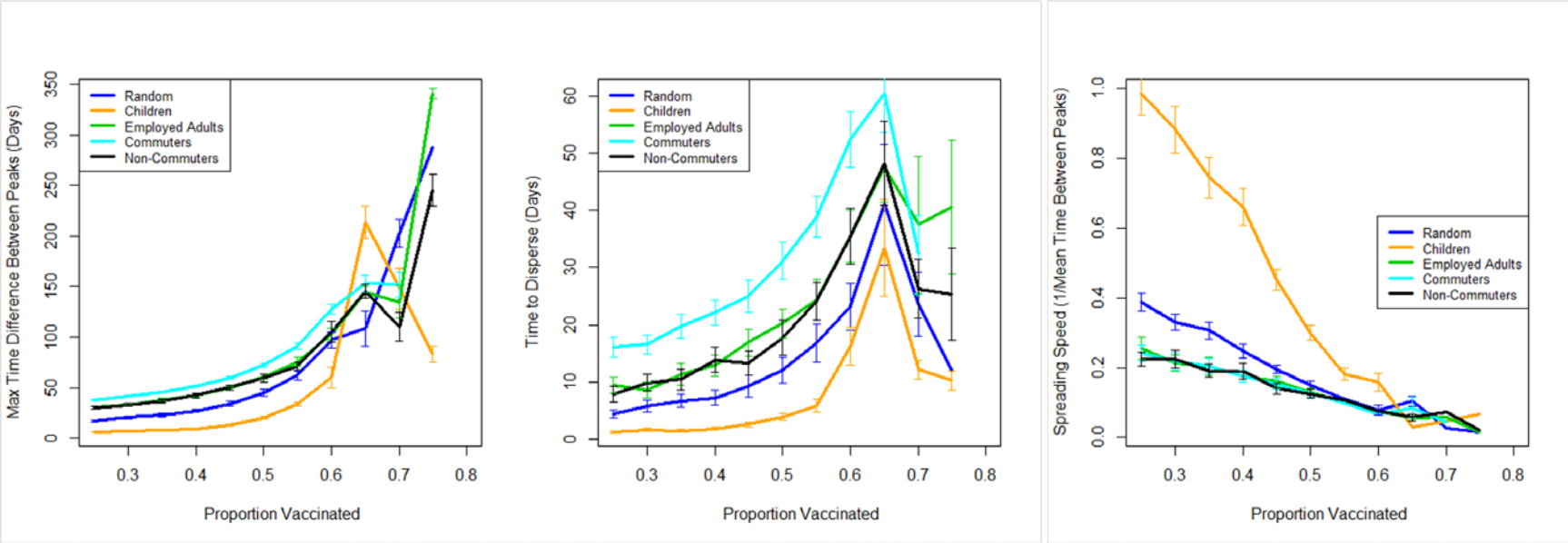

Figure 5.6. Epidemic Timing Under Excess, Targeted Vaccination. Changes in epidemic timing in response to random vaccination and four different targeted strategies when vaccine doses exceed the total number of individuals in the targeted population. Plots show total time necessary for the epidemic to spread across the metapopulation (left), time necessary for the epidemic to disperse from the patch of initial introduction (center) and epidemic spreading speed (right).

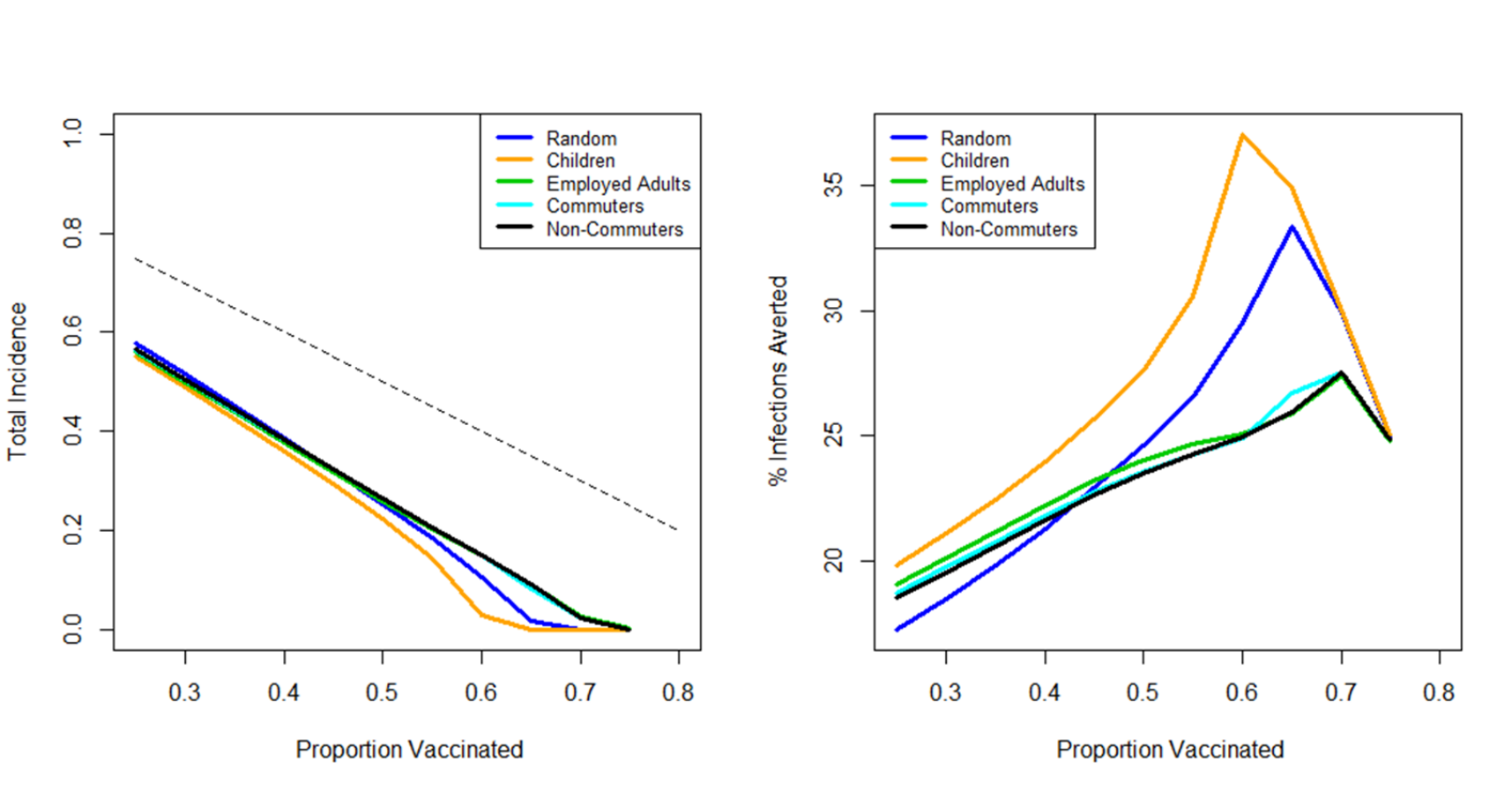

Figure 5.7. Incidence Under Excess, Targeted Vaccination. Reductions in total incidence in response to random vaccination and four different targeted strategies when vaccine doses exceed the total number of individuals in the targeted population. Left panel shows overall reduction in incidence across a range of vaccination levels, right panel shows the percent of infections averted. Dashed line in left panel represents the total possible infections if all individuals that had not been vaccinated were to become infected.

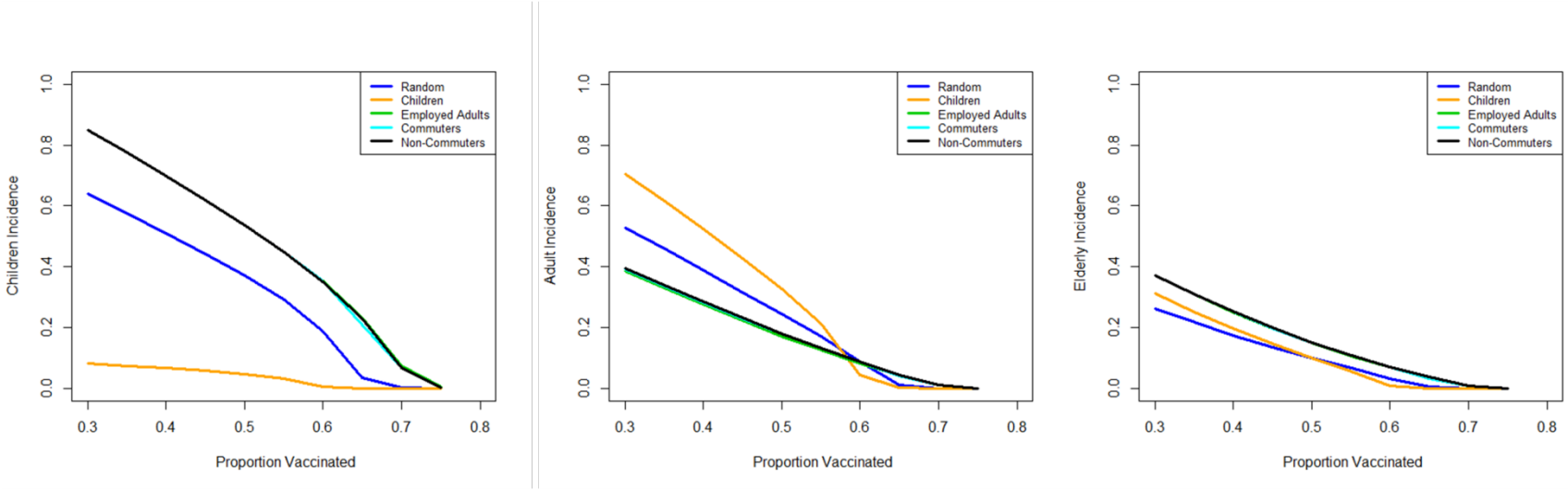

Figure 5.8. Incidence by Age Group Under Excess, Targeted Vaccination. Incidence in children (left), adults (center) and elderly (right) shown.

Chapter 6

Summary and Conclusions

Two of the studies presented in this dissertation utilized estimates of human movement along transportation networks to explore whether underlying patterns in seasonal influenza population structure exist at the regional scale. In addition, the information gleaned from this work was used to design and test a novel control strategy aimed at host groups that are important to transmission. This body of work is one of the first to explore spatial patterns previously suggested through epidemiological data with viral genetic sequence data and enhances our understanding of this ubiquitous human pathogen.

The questions addressed in these studies were informed by a detailed understanding of the nuances of host-parasite dynamics over the geographic range. A review of the literature, presented in **Chapter 2**, demonstrated that pathogens are not evenly distributed within their hosts' ranges and that a variety of factors, both abiotic and biotic, modulate a parasite's ability to evolve in response to changing conditions across the landscape. As a result, parasite genetic variation can be used to gain important insights into host demography, migration and other life-history characteristics, especially in relation to range expansions, contractions and shifts. It is also apparent that there is much more work yet to be done, particularly in relation to ascertaining the relative importance of ecological and evolutionary factors in setting range boundaries, the specific effects of biotic interactions on parasite distributions and the future effects of climate change on host and parasite interactions.

6.1 Effects of human mobility on pathogen evolutionary and ecological dynamics

Epidemics spread along spatial pathways defined, in part, by host mobility networks. While local host movement can spatially structure epidemic dynamics and potentially genetic variation, hosts that move rapidly and far disrupt any underlying spatial patterns that might exist by increasing opportunities for long-distance transmission. Recent work using distance metrics derived from mobility networks rather Euclidean distance measurements previously revealed otherwise undetectable patterns in the spread of disease (Brockmann and Helbing, 2014; Lemey et al., 2014; Viboud et al., 2006b). Building on this work, I explored whether similar patterns in the spread of disease can be detected at the regional scale in **Chapters 3 and 4**, but did not find evidence that influenza epidemics predictably spread between geographic locations based on the volume of passenger travel.

Unlike analyses conducted at the global scale, I found that the regional aviation networks functioned to mix pathogen populations, eroding any structure that may be imposed due to transmission across more local, geographically organized networks. A comparison of the US commuter network and European rail network revealed that the two networks differed in the degree of community partitioning and spatial structure present. The US commuter network was similar to, but not entirely consistent with, geographic distances between states. In comparison, more long-range connections were present in the European rail network; these connections likely allowed for the rapid, long-distance spread of influenza. Furthermore, the high modularity of the US commuting network indicated that semi-insular communities existed at sub-regional scales. Similar partitioning was not observed in the European rail network due to the abundance of long range connections.

Influenza populations within countries were more similar than influenza populations among countries, a finding which suggested that the magnitude of within-country or within-state transmission is much greater than that between locations; epidemic spread beyond country borders is likely enhanced by long-distance travelers, but their effect is marginal once the infection reaches a new country. This finding also brought to light a potential pitfall in the spatial analysis of genetic sequence data based on mobility networks. I found that associations could be driven by high impact points that consisted of pairwise comparisons between sequences that were highly similar and were collected from within the same location. As travel volume over the commuting and rail network was much higher within locations than between locations, including these comparisons in the analysis could cause significant associations to appear when, in fact, genetic distance did not predictably decline in response to increased connectivity through travel. Further studies using high-resolution spatial genetic data and more precise alternative techniques are necessary to clarify the role of human mobility in regional influenza spread.

In **Chapter 5**, I explored the relative effectiveness of vaccination strategies targeted at different host groups. Simulations of epidemic spread through a metapopulation revealed that vaccinating commuters was not as effective as vaccinating children in terms of reducing population-wide incidence, but demonstrated that vaccination strategies targeting employed adults delayed the timing and speed of epidemic spread when epidemics were severe. Delaying epidemic spread could potentially be beneficial when vaccination is limited, as it could provide an opportunity for alternative control strategies, such as the distribution of antivirals or the enforcement of social distancing policies, to be implemented. Nonetheless, the optimal strategy of vaccinating children is based on the fundamental idea of targeting those most

responsible for transmission by identifying the age and/or social group with highest contact rate.

6.2 Conclusions, future directions and a call for data

In conclusion, while the spatial genetic patterns of pathogens can be used to gain insight into the ecology of the host organism as it relates to disease transmission, these patterns are not necessarily straightforward and can be difficult to detect, especially when long-range host movement is common. Furthermore, it is important to note that these patterns can be specific to the particular host, location or spatial scale under investigation. While classic spatial statistics were used in the studies presented here, approaches have recently been developed that apply phylogeographic techniques to these same problems (Bedford et al., 2015; Dellicour et al., 2016; Lemey et al., 2014; Magee et al., 2015; Trovao et al., 2015; Zinder et al., 2014). Utilizing these new approaches will not only prove useful for clarifying the findings presented here, but could also be used to further investigate the regional pathways over which influenza and other similar pathogens are likely to spread during future epidemics.

Identifying pathways of epidemic spread within networks, as well as host groups that are important for transmission can potentially inform the design and implementation of policies aimed at controlling disease outbreaks. Although our targeted vaccination strategy did not outperform the policy of vaccinating children, it did perform better than random vaccination during severe epidemics when vaccine doses were limited and provided the additional benefit of delaying epidemic spread. As this result was obtained in an idealized model population, we do not yet know how it would fare under realistic conditions. Census datasets from various regions exist that would allow for the extension of this model to real-world populations. Recently, detailed human

mobility data obtained through cellular phone records were used to identify regional sources and sinks of malaria transmission (Wesolowski et al., 2012). Information such as this will allow public health officials to pinpoint locations in which surveillance should be increased to best track pathogen spread. Similarly identifying sources and sinks of regional influenza spread could assist in the creation of surveillance and control programs that more effectively contain epidemics from the start.

Finally, this work has highlighted the need for the greater availability of spatial genetic sequence data. The recent explosion of genetic sequencing capability has led to development of novel analysis techniques that integrate knowledge from the previously disparate fields of ecology, evolution, bioinformatics, statistics and public health. Gains from this union will be increasingly realized as datasets become available that are rich in genetic, temporal and spatial information. All of the data used in this work, from genetic sequences to transportation networks to population demographics, were publicly available. Limitations on the extent to which spatial patterns could be recovered stemmed, in part, from our present inability to obtain enough data at the necessary spatial resolution to precisely measure transmission dynamics. As an example, future work in this system should aim to examine the effects of human mobility within and across cities, as this is the spatial scale at which actual influenza transmission occurs. Currently, most publicly available influenza sequence data from the US is recorded only at the state level. Studies conducted at finer spatial resolutions would have a greater ability to illuminate actual pathways over which influenza spreads and additionally could integrate the effects of multiple transportation networks. The greater availability of data will lead to a more detailed understanding of the epidemiological and evolutionary dynamics of pathogens like influenza that have such an important impact on global human health.

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Appendix I

Supplementary Material for Chapter 3

I.1 Supplementary Tables

Table S1. Accession numbers, locations and collection dates of all sequences used.

Subtype	Accession	State	Date	Subtype	Accession	State	Date
H3N2	EU502382	UT	11/13/2003	H3N2	KC892423	AR	12/5/2011
H3N2	EU501336	TX	10/2/2003	H3N2	KC893078	CO	1/11/2012
H3N2	EU502360	TX	10/3/2003	H3N2	CY112122	CO	1/30/2012
H3N2	CY008916	NY	11/12/2003	H3N2	CY112152	CO	2/14/2012
H3N2	CY000065	NY	12/9/2003	H3N2	KC892669	MO	1/17/2012
H3N2	EU502288	NJ	11/20/2003	H3N2	KC893015	MO	1/17/2012
H3N2	CY000889	NY	1/6/2004	H3N2	KC892644	MO	3/6/2012
H3N2	CY000761	NY	1/30/2004	H3N2	CY112181	NE	2/24/2012
H3N2	EU502316	NY	11/19/2003	H3N2	KC892453	MO	2/28/2012
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H3N2	CY001029	NY	1/6/2004	H3N2	KC892250	CO	11/8/2011
H3N2	CY001229	NY	1/6/2004	H3N2	KC892488	VA	1/14/2012
H3N2	CY000917	NY	12/19/2003	H3N2	KC892263	AR	10/7/2011
H3N2	CY000001	NY	12/20/2003	H3N2	KC892818	AR	1/11/2012
H3N2	CY001421	NY	12/1/2003	H3N2	KC892621	KS	12/11/2011
H3N2	CY008868	NY	11/24/2003	H3N2	CY112100	CO	12/14/2011
H3N2	CY009260	NY	1/15/2004	H3N2	KC893022	WY	1/10/2012
H3N2	CY008892	NY	12/15/2003	H3N2	CY112154	CO	2/7/2012
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H3N2	CY009252	NY	1/12/2004	H3N2	KC893134	UT	1/30/2012
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H3N2	EU502423	WV	11/5/2003	H3N2	KC892198	OR	10/3/2011
H3N2	CY091173	CA	12/17/2003	H3N2	KC892618	WA	12/13/2011
H3N2	CY091213	CA	12/19/2003	H3N2	KC892352	WA	1/26/2012
H3N2	CY091221	CA	12/16/2003	H3N2	KC892885	WA	3/8/2012
H3N2	EF473625	NY	4/22/2004	H3N2	KC892444	WA	3/2/2012
H3N2	EU502313	NY	4/22/2004	H3N2	KC892355	WA	2/2/2012
H3N2	CY000025	NY	11/29/2003	H3N2	KC892376	ID	2/2/2012
H3N2	CY001640	NY	11/28/2003	H3N2	KC892379	WA	2/2/2012
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H3N2	CY000957	NY	12/16/2003	H3N2	KC893012	ID	1/16/2012
H3N2	EF473612	NC	12/23/2003	H3N2	KC892815	WA	1/11/2012
H3N2	EU502266	NC	12/23/2003	H3N2	CY112162	WA	2/14/2012
H3N2	EU502293	NM	12/1/2003	H3N2	KC892504	WA	2/25/2012
H3N2	EF473623	NM	12/1/2003	H3N2	CY120898	WA	4/9/2012
H3N2	EU502294	NM	12/1/2003	H3N2	KC893093	SD	1/3/2012
H3N2	EU502436	WY	12/2/2003	H3N2	KC893116	MN	1/30/2012
H3N2	EF473617	OR	12/29/2003	H3N2	KC892517	ND	3/6/2012
H3N2	EU502320	OR	12/29/2003	H3N2	KC892306	MN	2/15/2012
H3N2	CY000377	NY	12/18/2003	H3N2	KC892278	MN	3/8/2012
H3N2	CY000353	NY	11/26/2003	H3N2	KC893126	MN	4/8/2012
H3N2	CY000265	NY	12/11/2003	H3N2	KC893123	WI	4/2/2012
H3N2	CY001221	NY	12/29/2003	H3N2	KC893072	OR	1/4/2012
H3N2	CY000177	NY	12/8/2003	H3N2	CY112120	WA	11/21/2011
H3N2	CY001112	NY	10/28/2003	H3N2	KC892608	NV	11/4/2011
H3N2	CY000909	NY	12/3/2003	H3N2	KC892694	WY	12/30/2011
H3N2	CY000361	NY	12/2/2003	H3N2	KC892871	NV	3/2/2012
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H3N2	CY000769	NY	12/16/2003	H3N2	KC892361	NV	2/7/2012
H3N2	CY000521	NY	12/12/2003	H3N2	CY120908	CA	3/14/2012
H3N2	CY001088	NY	12/1/2003	H3N2	KC892392	NV	4/3/2012
H3N2	CY001096	NY	12/4/2003	H3N2	KC892874	NV	3/4/2012
H3N2	EU502129	AZ	10/23/2003	H3N2	KC892224	NV	4/3/2012
H3N2	CY001512	NY	12/16/2003	H3N2	KC892221	NV	4/6/2012
H3N2	EU502128	AZ	11/10/2003	H3N2	KC892892	PA	3/19/2012
H3N2	CY000129	NY	11/11/2003	H3N2	KC892462	ID	2/13/2012
H3N2	CY091461	CA	12/10/2003	H3N2	KC892879	NV	3/12/2012
H3N2	EU502437	WY	12/9/2003	H3N2	CY120894	CO	4/17/2012
H3N2	EF473609	WY	12/9/2003	H3N2	KC893006	GA	1/15/2012
H3N2	EU502371	TX	11/5/2003	H3N2	KF182366	CA	3/12/2012
H3N2	EU501516	OK	12/8/2003	H3N2	KC892508	NM	2/20/2012
H3N2	CY000073	NY	12/12/2003	H3N2	KC892514	RI	3/7/2012
H3N2	EF473622	AZ	1/28/2004	H3N2	KC892934	FL	3/12/2012
H3N2	CY000777	NY	12/21/2003	H3N2	KC892739	TN	4/10/2012
H3N2	EU502336	SD	1/11/2004	H3N2	KC892921	TN	3/15/2012
H3N2	EU502214	ID	11/6/2003	H3N2	KC892511	TN	3/1/2012
H3N2	CY000785	NY	12/9/2003	H3N2	CY120862	TX	3/15/2012
H3N2	EU501290	TN	12/3/2003	H3N2	KC892974	TN	4/19/2012
H3N2	CY091117	MO	1/9/2004	H3N2	KC892172	IN	2/1/2012
H3N2	EU502127	AZ	1/28/2004	H3N2	KC892732	CT	1/22/2012
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H3N2	EF473626	WI	1/2/2004	H3N2	KC892400	IA	11/17/2011
H3N2	EU502408	WI	1/2/2004	H3N2	KC892257	IA	11/5/2011
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H3N2	EU502398	VT	12/19/2003	H3N2	CY120856	CO	3/9/2012
H3N2	EU501484	NY	1/6/2004	H3N2	KC892909	NE	3/5/2012
H3N2	CY000369	NY	1/5/2004	H3N2	KC892801	NE	1/14/2012
H3N2	CY090981	MO	1/12/2005	H3N2	KC892468	KY	2/15/2012
H3N2	EU502286	NH	10/11/2004	H3N2	CY112183	NE	2/29/2012
H3N2	EU502409	WI	10/8/2004	H3N2	KF182352	TX	3/14/2012
H3N2	EU502345	TN	2/7/2005	H3N2	KF182348	TX	3/20/2012
H3N2	EU502346	TN	2/11/2005	H3N2	KC892428	NE	12/15/2011
H3N2	EU502412	WI	10/18/2004	H3N2	CY112180	NE	3/5/2012
H3N2	EU501578	WA	10/14/2004	H3N2	KC892465	CO	2/5/2012
H3N2	EU502401	WA	10/14/2004	H3N2	KC892159	KY	4/2/2012
H3N2	EU502282	NE	11/9/2004	H3N2	KC892773	IN	5/14/2012
H3N2	CY002024	NY	11/30/2004	H3N2	KC892297	NE	2/6/2012

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H3N2	CY002584	NY	12/1/2004	H3N2	CY112161	NE	2/8/2012
H3N2	CY002464	NY	1/6/2005	H3N2	CY112118	NE	1/9/2012
H3N2	EU502233	MA	1/7/2005	H3N2	CY112182	NE	2/29/2012
H3N2	EU502228	KY	11/27/2004	H3N2	KC892594	WI	5/5/2012
H3N2	EU502230	KY	4/1/2005	H3N2	KC892326	WV	2/5/2012
H3N2	CY006131	NY	1/19/2005	H3N2	KC892975	NE	3/5/2012
H3N2	EU502229	KY	12/3/2004	H3N2	KC892561	CO	3/7/2012
H3N2	EU502136	AZ	1/5/2005	H3N2	KC892710	KY	5/10/2012
H3N2	CY002736	NY	1/4/2005	H3N2	KC892962	MN	11/2/2011
H3N2	EU502290	NJ	2/13/2005	H3N2	KC892998	MN	10/2/2011
H3N2	CY002256	NY	12/29/2004	H3N2	KC892702	VT	12/26/2011
H3N2	EU502248	MO	12/29/2004	H3N2	KC892399	OH	11/5/2011
H3N2	EU502416	WI	1/17/2005	H3N2	KC892416	MN	11/17/2011
H3N2	CY091005	IL	4/6/2005	H3N2	KC892741	NJ	10/6/2011
H3N2	CY090989	SC	2/11/2005	H3N2	KC892521	MS	11/23/2011
H3N2	FJ975056	OK	3/4/2005	H3N2	KC892432	MT	11/30/2011
H3N2	EU502429	WY	1/14/2005	H3N2	KC892696	MD	12/26/2011
H3N2	EU502428	WY	1/14/2005	H3N2	KC893099	AZ	12/9/2011
H3N2	EU502430	WY	1/14/2005	H3N2	KC892266	UT	11/6/2011
H3N2	EU502244	MO	2/11/2005	H3N2	KC892413	UT	11/28/2011
H3N2	EU502247	MO	1/3/2005	H3N2	KC892364	CA	1/18/2012
H3N2	EF462544	OK	2/21/2005	H3N2	CY120884	TX	3/26/2012
H3N2	EU502433	WY	2/2/2005	H3N2	CY112179	WA	2/17/2012
H3N2	EU502432	WY	2/1/2005	H3N2	KC893180	NY	1/16/2012
H3N2	EU502431	WY	2/3/2005	H3N2	KC893183	NY	1/16/2012
H3N2	EU502426	WY	3/10/2005	H3N2	KC892882	WA	3/13/2012
H3N2	EU502256	MT	1/28/2005	H3N2	KC892388	WA	2/29/2012
H3N2	EU502255	MT	1/28/2005	H3N2	CY120896	WA	4/20/2012
H3N2	EU502298	NV	4/22/2005	H3N2	CY112163	WA	2/7/2012
H3N2	EU502392	VA	1/7/2005	H3N2	CY120899	WA	4/14/2012
H3N2	EU502254	MT	10/2/2004	H3N2	CY120861	WA	3/16/2012
H3N2	EF462550	OK	3/4/2005	H3N2	KC892303	DE	2/15/2012
H3N2	EU502373	TX	10/12/2004	H3N2	KC892616	DE	3/12/2012
H3N2	EU502232	LA	1/26/2005	H3N2	KC893081	SC	1/11/2012
H3N2	CY091429	CA	2/7/2005	H3N2	CY112169	NV	2/23/2012
H3N2	EU501469	MS	12/14/2004	H3N2	KC892635	NV	3/1/2012
H3N2	CY092217	NJ	2/10/2005	H3N2	KC892774	SC	1/4/2012
H3N2	CY002408	NY	12/21/2004	H3N2	CY112142	OH	2/2/2012
H3N2	CY006076	NY	2/2/2005	H3N2	CY120892	CA	4/9/2012
H3N2	CY091125	GA	1/25/2005	H3N2	KC893023	OH	3/8/2012
H3N2	EU502274	ND	10/20/2004	H3N2	KC892284	OH	3/8/2012

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H3N2	EU501511	ND	10/20/2004	H3N2	CY120880	OH	3/26/2012
H3N2	EU502169	CO	10/27/2004	H3N2	KC892906	OH	3/12/2012
H3N2	EU502414	WI	11/22/2004	H3N2	KC892988	MI	10/2/2011
H3N2	EU501580	WI	11/6/2004	H3N2	KC892253	CA	10/9/2011
H3N2	CY002600	NY	12/26/2004	H3N2	KC893107	MD	1/18/2012
H3N2	EU502417	WI	1/21/2005	H3N2	KC893166	MD	1/18/2012
H3N2	EU502415	WI	1/17/2005	H3N2	KC892806	VA	1/17/2012
H3N2	EU502413	WI	11/22/2004	H3N2	KC892349	PA	2/9/2012
H3N2	CY003408	NY	12/27/2004	H3N2	CY112106	DC	1/25/2012
H3N2	EU502135	AZ	2/15/2005	H3N2	KC892655	CA	10/26/2011
H3N2	EU502337	SD	12/2/2004	H3N2	KC893090	AL	1/21/2012
H3N2	CY003056	NY	1/24/2005	H3N2	KC892230	DE	4/21/2012
H3N2	EU502210	IA	1/30/2005	H3N2	KC892373	IA	2/16/2012
H3N2	EU502374	TX	12/14/2004	H3N2	KC892474	AL	2/16/2012
H3N2	EU502410	WI	11/29/2004	H3N2	KC893169	VA	2/1/2012
H3N2	EU502283	NE	3/23/2005	H3N2	KC892317	NH	2/20/2012
H3N2	EU502227	KS	1/18/2005	H3N2	KC892573	NY	4/4/2012
H3N2	EF462551	OK	3/2/2005	H3N2	KC892638	CA	11/24/2011
H3N2	EF462549	OK	3/16/2005	H3N2	KC892719	NY	5/14/2012
H3N2	CY002064	NY	12/21/2004	H3N2	CY120890	CO	4/4/2012
H3N2	CY002048	NY	12/27/2004	H3N2	KC892799	IA	1/3/2012
H3N2	CY002032	NY	1/29/2005	H3N2	KC892206	NV	4/2/2012
H3N2	EU502385	UT	1/12/2005	H3N2	KC892838	MI	3/6/2012
H3N2	EU502400	VT	12/13/2004	H3N2	KC892429	IN	11/29/2011
H3N2	EU502418	WI	1/20/2005	H3N2	KC892256	TX	10/16/2011
H3N2	EU502170	CO	1/21/2005	H3N2	KC892268	MT	3/18/2012
H3N2	CY092257	CA	2/8/2005	H3N2	KC892995	UT	1/1/2012
H3N2	CY091549	CA	2/7/2005	H3N2	KC892699	NH	12/28/2011
H3N2	EU502425	WV	1/25/2005	H3N2	CY112099	WA	11/11/2011
H3N2	CY002456	NY	2/22/2005	H3N2	KC892567	SC	2/27/2012
H3N2	CY006147	NY	2/2/2005	H3N2	KC892334	MA	2/21/2012
H3N2	CY002016	NY	1/3/2005	H3N2	KC892809	VT	1/16/2012
H3N2	CY006139	NY	2/1/2005	H3N2	KC892667	RI	4/18/2012
H3N2	EU502278	NE	1/3/2005	H3N2	KC892926	MI	3/5/2012
H3N2	EU502309	NY	1/3/2005	H3N2	CY120883	WA	3/25/2012
H3N2	EU502289	NJ	12/26/2004	H3N2	KC892675	WA	4/15/2012
H3N2	EU502378	TX	2/9/2005	H3N2	KC892192	VA	2/17/2012
H3N2	CY002216	NY	12/9/2004	H3N2	KC892320	VA	2/17/2012
H3N2	CY006371	NY	11/27/2004	H3N2	KC892329	GA	2/6/2012
H3N2	CY003664	NY	11/8/2004	H3N2	KC892323	RI	1/30/2012
H3N2	CY008516	NY	10/19/2004	H3N2	CY112105	CO	1/9/2012
H3N2	EU502394	VA	1/7/2005	H3N2	KC892498	WI	3/3/2012

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H3N2	EU502335	SC	2/4/2005	H3N2	KC892519	WI	5/7/2012
H3N2	CY002472	NY	12/28/2004	H3N2	KC892181	AL	4/4/2012
H3N2	CY002712	NY	11/8/2004	H3N2	KC892367	CA	2/1/2012
H3N2	CY009268	NY	12/10/2004	H3N2	KC893059	AL	3/20/2012
H3N2	CY002504	NY	12/7/2004	H3N2	KC892288	VT	2/2/2012
H3N2	CY006291	NY	2/8/2005	H3N2	KF790169	OK	10/8/2012
H3N2	CY003640	NY	2/9/2005	H3N2	CY141188	FL	12/19/2012
H3N2	CY003648	NY	3/7/2005	H3N2	KF790491	LA	11/6/2012
H3N2	CY002056	NY	1/7/2005	H3N2	CY134692	GA	12/3/2012
H3N2	EU502310	NY	1/5/2005	H3N2	CY134703	SC	10/26/2012
H3N2	EU502330	RI	1/24/2005	H3N2	CY141221	NY	12/24/2012
H3N2	CY002440	NY	12/16/2004	H3N2	CY134649	FL	12/6/2012
H3N2	EU502192	GA	1/6/2005	H3N2	CY134666	MD	11/26/2012
H3N2	EU502184	FL	3/10/2005	H3N2	KF790479	SC	10/29/2012
H3N2	CY002080	NY	12/24/2004	H3N2	CY141255	SC	12/17/2012
H3N2	EU502252	MS	2/27/2005	H3N2	CY183121	TX	1/7/2013
H3N2	CY002288	NY	12/9/2004	H3N2	CY134668	OH	11/28/2012
H3N2	CY002000	NY	1/17/2005	H3N2	KF789707	KY	12/3/2012
H3N2	CY003040	NY	12/28/2004	H3N2	KF789670	VA	12/5/2012
H3N2	EU502375	TX	12/27/2004	H3N2	KF789804	VA	12/5/2012
H3N2	CY006115	NY	11/1/2004	H3N2	KF789782	MI	12/3/2012
H3N2	CY002040	NY	12/22/2004	H3N2	KF789819	VA	12/5/2012
H3N2	CY002720	NY	1/4/2005	H3N2	KF789706	TN	12/7/2012
H3N2	CY002424	NY	11/18/2004	H3N2	KF790495	TN	11/1/2012
H3N2	CY007643	NY	11/18/2004	H3N2	KF790048	SC	10/29/2012
H3N2	CY002768	NY	11/22/2004	H3N2	KF790488	SC	11/2/2012
H3N2	CY003032	NY	11/6/2004	H3N2	KF789899	KY	11/19/2012
H3N2	CY002608	NY	11/11/2004	H3N2	KF789604	KY	11/19/2012
H3N2	CY006435	NY	11/11/2004	H3N2	CY134721	SC	11/14/2012
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H3N2	CY006123	NY	1/7/2005	H3N2	CY171599	IL	1/1/2013
H3N2	CY019811	NY	12/22/2004	H3N2	CY182921	TX	12/23/2012
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H3N2	CY019157	NY	12/22/2004	H3N2	KF886309	SC	2/15/2013
H3N2	CY002264	NY	1/28/2005	H3N2	KF790402	NE	1/11/2013
H3N2	CY002192	NY	12/20/2004	H3N2	KF790093	WI	10/5/2012
H3N2	CY002416	NY	11/5/2004	H3N2	KF790209	MS	10/9/2012
H3N2	CY019165	NY	12/22/2004	H3N2	KM244537	MS	1/4/2013
H3N2	CY002200	NY	1/3/2005	H3N2	KM244534	MS	11/27/2012
H3N2	CY002224	NY	12/22/2004	H3N2	CY134707	GA	11/1/2012
H3N2	CY002760	NY	11/6/2004	H3N2	CY134702	GA	10/31/2012

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H3N2	CY019149	NY	12/22/2004	H3N2	CY168007	MA	12/28/2012
H3N2	CY002240	NY	1/29/2005	H3N2	CY141209	MD	12/18/2012
H3N2	CY002488	NY	3/23/2005	H3N2	CY141197	FL	1/9/2013
H3N2	CY003336	NY	12/28/2004	H3N2	KJ741963	CT	12/31/2012
H3N2	EU501485	NY	11/18/2004	H3N2	KF928626	SC	12/3/2012
H3N2	EU501486	NY	11/18/2004	H3N2	KF199859	SC	12/3/2012
H3N2	EU502306	NY	11/9/2004	H3N2	CY134694	FL	12/6/2012
H3N2	EU502307	NY	11/19/2004	H3N2	CY134670	GA	11/26/2012
H3N2	EU502308	NY	11/19/2004	H3N2	KF789805	GA	12/2/2012
H3N2	EU502191	GA	1/27/2005	H3N2	CY134693	AL	12/3/2012
H3N2	EU502419	WI	1/8/2005	H3N2	CY171447	IL	12/28/2012
H3N2	CY002280	NY	11/4/2004	H3N2	CY134658	AL	12/11/2012
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H3N2	EU502246	MO	10/22/2004	H3N2	CY134719	SC	11/14/2012
H3N2	CY091133	TX	2/16/2005	H3N2	KF789944	FL	1/3/2013
H3N2	CY003048	NY	1/18/2005	H3N2	KF790287	SC	11/7/2012
H3N2	CY002072	NY	3/4/2005	H3N2	KJ741955	CT	12/29/2012
H3N2	EU502427	WY	3/15/2005	H3N2	CY134677	GA	11/29/2012
H3N2	CY019269	NY	1/10/2005	H3N2	KF789596	CO	11/14/2012
H3N2	CY020533	NY	1/10/2005	H3N2	KF790063	DE	12/19/2012
H3N2	CY019277	NY	1/10/2005	H3N2	KF790081	DE	12/19/2012
H3N2	CY019293	NY	1/10/2005	H3N2	KF790242	NV	10/31/2012
H3N2	CY019285	NY	1/10/2005	H3N2	KM244532	MS	11/21/2012
H3N2	EU502424	WV	1/5/2005	H3N2	KM244550	MS	11/28/2012
H3N2	CY002728	NY	12/15/2004	H3N2	KF790265	MS	11/13/2012
H3N2	CY019317	NY	1/10/2005	H3N2	KM244545	MS	11/14/2012
H3N2	CY019301	NY	1/10/2005	H3N2	KM244548	MS	11/21/2012
H3N2	CY002448	NY	2/16/2005	H3N2	KM244547	MS	11/20/2012
H3N2	CY006084	NY	3/8/2005	H3N2	CY134639	OH	12/4/2012
H3N2	CY019309	NY	1/10/2005	H3N2	CY134660	OH	11/15/2012
H3N2	CY002008	NY	2/2/2005	H3N2	CY134687	OH	11/28/2012
H3N2	CY003344	NY	1/4/2005	H3N2	CY134669	OH	11/28/2012
H3N2	CY002432	NY	12/8/2004	H3N2	CY134662	OH	12/4/2012
H3N2	CY003416	NY	12/16/2004	H3N2	CY186155	TX	1/14/2013
H3N2	CY002480	NY	1/5/2005	H3N2	KF789983	FL	10/4/2012
H3N2	CY002592	NY	12/20/2004	H3N2	KF790278	NY	10/16/2012
H3N2	CY019189	NY	1/10/2005	H3N2	CY171735	IL	1/25/2013
H3N2	CY002176	NY	12/1/2004	H3N2	CY171279	IL	12/19/2012
H3N2	CY002784	NY	12/9/2004	H3N2	CY171551	IL	12/31/2012
H3N2	CY002776	NY	2/15/2005	H3N2	CY171519	IL	12/30/2012
H3N2	CY002208	NY	12/20/2004	H3N2	KF789748	LA	12/4/2012

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H3N2	CY003072	NY	12/16/2004	H3N2	CY134690	LA	12/4/2012
H3N2	CY020053	NY	1/10/2005	H3N2	CY171311	IL	12/25/2012
H3N2	CY019253	NY	12/27/2004	H3N2	CY171607	IL	1/1/2013
H3N2	CY019261	NY	12/27/2004	H3N2	KF790178	VT	10/15/2012
H3N2	CY019819	NY	12/27/2004	H3N2	KM244549	MS	11/26/2012
H3N2	CY002248	NY	12/28/2004	H3N2	CY134638	FL	12/2/2012
H3N2	CY019245	NY	12/27/2004	H3N2	KM244533	MS	11/26/2012
H3N2	CY002232	NY	12/27/2004	H3N2	CY134700	FL	10/26/2012
H3N2	CY019181	NY	12/27/2004	H3N2	KM244544	MS	11/9/2012
H3N2	CY021989	NY	12/27/2004	H3N2	CY141185	FL	12/18/2012
H3N2	CY019173	NY	12/27/2004	H3N2	CY134691	AL	12/4/2012
H3N2	CY091525	CA	12/2/2005	H3N2	CY148668	MA	1/20/2013
H3N2	EU502132	AZ	1/11/2006	H3N2	KM244543	MS	1/30/2013
H3N2	EU501835	WI	10/19/2005	H3N2	CY134699	AL	12/5/2012
H3N2	EU502197	GA	1/24/2006	H3N2	CY141192	FL	1/4/2013
H3N2	CY172191	NY	11/10/2005	H3N2	CY141187	FL	12/18/2012
H3N2	CY091501	CA	10/25/2005	H3N2	CY134698	AL	12/5/2012
H3N2	CY172287	NY	2/14/2006	H3N2	KF789680	VA	11/13/2012
H3N2	CY091013	CA	11/30/2005	H3N2	KF789674	MD	11/13/2012
H3N2	EU502249	MO	1/3/2006	H3N2	CY134689	LA	12/4/2012
H3N2	EU502404	WA	11/30/2005	H3N2	CY163422	FL	1/5/2013
H3N2	EU502234	MA	11/30/2005	H3N2	CY141200	FL	12/17/2012
H3N2	CY091509	CA	11/2/2005	H3N2	KF789912	AL	12/18/2012
H3N2	EU502321	OR	11/29/2005	H3N2	KF789606	ND	11/12/2012
H3N2	CY058073	NY	1/1/2006	H3N2	KF789877	AR	12/19/2012
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H3N2	CY091541	CA	12/5/2005	H3N2	KF790425	TX	11/2/2012
H3N2	EU502216	ID	12/21/2005	H3N2	CY134804	TX	11/20/2012
H3N2	CY020077	NY	2/23/2006	H3N2	CY134796	TX	11/20/2012
H3N2	CY020069	NY	2/23/2006	H3N2	CY182897	TX	12/21/2012
H3N2	CY020061	NY	2/23/2006	H3N2	CY183057	TX	1/3/2013
H3N2	CY020357	NY	2/23/2006	H3N2	CY135020	TX	12/1/2012
H3N2	CY019827	NY	2/23/2006	H3N2	CY135164	TX	12/8/2012
H3N2	CY172255	NY	1/24/2006	H3N2	CY141186	FL	12/18/2012
H3N2	CY173599	NY	12/20/2005	H3N2	CY134657	AL	12/11/2012
H3N2	CY172207	NY	1/4/2006	H3N2	CY141179	AL	12/14/2012
H3N2	EU502196	GA	1/23/2006	H3N2	KF790432	OR	10/29/2012
H3N2	CY091045	IL	2/15/2006	H3N2	CY170871	CA	12/24/2012
H3N2	EU516029	OH	3/1/2006	H3N2	KF790229	OK	11/1/2012
H3N2	CY172279	NY	2/7/2006	H3N2	CY183065	TX	1/4/2013

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H3N2	EU516031	OH	4/3/2006	H3N2	CY183025	TX	1/2/2013
H3N2	EU502195	GA	1/18/2006	H3N2	KF790236	NY	10/17/2012
H3N2	CY091141	GA	1/9/2006	H3N2	KF789927	CA	12/18/2012
H3N2	CY172239	NY	1/13/2006	H3N2	KF790502	PA	11/9/2012
H3N2	CY172231	NY	1/12/2006	H3N2	KF790262	NH	11/8/2012
H3N2	CY091517	CA	11/29/2005	H3N2	CY148300	MA	11/12/2012
H3N2	CY091021	TX	12/19/2005	H3N2	KF790461	NM	1/2/2013
H3N2	EU502215	ID	11/27/2005	H3N2	CY148404	MA	12/7/2012
H3N2	EU502273	NC	2/21/2006	H3N2	KF790524	MD	11/11/2012
H3N2	CY172431	NY	3/7/2006	H3N2	CY141253	OK	1/7/2013
H3N2	CY172495	NY	3/14/2006	H3N2	CY170471	CA	1/30/2013
H3N2	CY091029	IL	12/23/2005	H3N2	KF790100	WY	10/5/2012
H3N2	EU502211	IA	12/12/2005	H3N2	KF790138	NC	1/3/2013
H3N2	EU502280	NE	4/1/2006	H3N2	KF789615	OK	2/5/2013
H3N2	CY172271	NY	2/7/2006	H3N2	CY147292	OK	1/28/2013
H3N2	CY172247	NY	1/24/2006	H3N2	KF790019	NM	3/13/2013
H3N2	EU502287	NH	3/6/2006	H3N2	CY171135	IL	12/6/2012
H3N2	CY172399	NY	2/27/2006	H3N2	CY149116	MA	1/15/2013
H3N2	CY091053	CA	2/21/2006	H3N2	KF790398	DC	3/27/2013
H3N2	EU501621	CA	10/11/2005	H3N2	CY141259	SD	1/7/2013
H3N2	EU502323	PA	11/13/2005	H3N2	CY171663	IL	1/7/2013
H3N2	EU502376	TX	11/15/2005	H3N2	CY171127	IL	12/5/2012
H3N2	CY172463	NY	3/12/2006	H3N2	KF886323	IL	1/28/2013
H3N2	CY172471	NY	3/12/2006	H3N2	KF928630	CA	1/8/2013
H3N2	EU502331	RI	3/6/2006	H3N2	KF790325	DE	1/7/2013
H3N2	CY172343	NY	2/16/2006	H3N2	CY171463	IL	12/28/2012
H3N2	EU502314	NY	4/17/2006	H3N2	CY171655	IL	1/7/2013
H3N2	EU502185	FL	12/5/2005	H3N2	KM244546	MS	11/15/2012
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H3N2	EU501905	FL	1/19/2006	H3N2	CY134730	SD	11/20/2012
H3N2	CY058071	FL	1/19/2006	H3N2	KF790323	NM	12/8/2012
H3N2	CY172303	NY	2/15/2006	H3N2	KF789769	OH	11/16/2012
H3N2	CY172455	NY	3/9/2006	H3N2	KF790512	ID	1/4/2013
H3N2	CY172527	NY	3/31/2006	H3N2	CY134648	FL	12/4/2012
H3N2	CY054272	FL	1/19/2006	H3N2	CY141260	SD	12/12/2012
H3N2	CY172383	NY	2/20/2006	H3N2	CY134663	OH	12/4/2012
H3N2	CY091037	TX	2/13/2006	H3N2	KJ741957	CT	12/30/2012
H3N2	CY172503	NY	3/16/2006	H3N2	KF790190	MI	10/2/2012
H3N2	CY172519	NY	3/22/2006	H3N2	KF790051	SD	10/30/2012
H3N2	CY172511	NY	3/20/2006	H3N2	KF789794	SD	10/29/2012
H3N2	CY172215	NY	1/8/2006	H3N2	KF790009	SD	10/29/2012

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H3N2	CY019843	NY	3/1/2006	H3N2	KF790446	WY	11/5/2012
H3N2	CY019333	NY	3/1/2006	H3N2	CY134656	SD	12/13/2012
H3N2	CY019851	NY	3/1/2006	H3N2	KF789775	SD	10/29/2012
H3N2	CY172447	NY	3/8/2006	H3N2	KF789688	SD	10/12/2012
H3N2	CY020109	NY	3/1/2006	H3N2	KF789791	SD	10/29/2012
H3N2	EF462554	OK	1/12/2006	H3N2	KF789826	WA	12/1/2012
H3N2	CY091077	MO	4/5/2006	H3N2	KF928640	IL	12/21/2012
H3N2	EU501986	TN	3/1/2006	H3N2	CY169927	MA	1/24/2013
H3N2	EU502277	NE	1/16/2006	H3N2	CY134673	WA	11/15/2012
H3N2	EU502251	MO	2/3/2006	H3N2	KF789728	NC	3/7/2013
H3N2	EU501966	KY	4/2/2006	H3N2	CY134688	OH	12/4/2012
H3N2	CY091085	IL	4/6/2006	H3N2	KF790213	IA	10/3/2012
H3N2	CY091061	SC	3/28/2006	H3N2	KF789689	NE	11/26/2012
H3N2	EU502292	NJ	1/21/2006	H3N2	CY134667	SD	11/27/2012
H3N2	CY172327	NY	2/15/2006	H3N2	KF790135	NY	1/2/2013
H3N2	CY172295	NY	2/14/2006	H3N2	KF789923	ND	12/6/2012
H3N2	EU502386	UT	12/6/2005	H3N2	KF790452	SD	2/1/2013
H3N2	EF462553	OK	2/25/2006	H3N2	CY170039	MA	2/13/2013
H3N2	EU502421	WI	4/7/2006	H3N2	KF790454	NV	2/1/2013
H3N2	EU199252	WY	2/9/2006	H3N2	KF789646	ID	1/15/2013
H3N2	EU502434	WY	2/9/2006	H3N2	KJ741956	CT	12/30/2012
H3N2	CY091533	CA	11/15/2005	H3N2	CY170639	CA	1/8/2013
H3N2	EU502377	TX	11/28/2005	H3N2	CY169031	MA	12/27/2012
H3N2	CY172199	NY	12/27/2005	H3N2	CY141270	VA	1/3/2013
H3N2	EU502171	CO	12/3/2005	H3N2	CY141195	FL	1/7/2013
H3N2	EU502242	MN	3/13/2006	H3N2	CY170239	MA	1/7/2013
H3N2	EU502090	WY	1/23/2006	H3N2	KF789605	WV	11/20/2012
H3N2	CY054271	NH	1/2/2006	H3N2	CY169767	MA	1/13/2013
H3N2	CY058070	NH	1/2/2006	H3N2	KF789722	OH	12/9/2012
H3N2	EU502391	VA	1/30/2006	H3N2	KF790125	MO	3/15/2013
H3N2	EU502134	AZ	3/2/2006	H3N2	KF789709	MO	3/15/2013
H3N2	EU502133	AZ	2/22/2006	H3N2	CY163424	GA	1/24/2013
H3N2	EU502250	MO	2/24/2006	H3N2	CY134655	SC	12/12/2012
H3N2	CY172311	NY	4/20/2006	H3N2	KF789732	VT	12/10/2012
H3N2	CY020093	NY	2/28/2006	H3N2	CY170399	MA	1/31/2013
H3N2	CY019325	NY	2/28/2006	H3N2	KF886321	AZ	1/6/2013
H3N2	CY172407	NY	2/28/2006	H3N2	KF789953	OH	1/14/2013
H3N2	CY020085	NY	2/28/2006	H3N2	CY141281	WA	1/7/2013
H3N2	CY019939	NY	2/28/2006	H3N2	KF886337	SC	2/6/2013
H3N2	CY019835	NY	2/28/2006	H3N2	KF790333	DC	12/17/2012
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H3N2	EU502271	NC	3/9/2006	H3N2	KF790205	CO	10/13/2012
H3N2	EU502317	OH	1/26/2006	H3N2	KF789582	NC	11/15/2012
H3N2	CY013797	NY	3/22/2006	H3N2	KF790104	CO	10/13/2012
H3N2	CY012792	NY	3/22/2006	H3N2	KF789579	IN	11/14/2012
H3N2	EU502272	NC	2/8/2006	H3N2	KF790244	IN	11/8/2012
H3N2	EU502312	NY	1/26/2006	H3N2	CY141190	FL	1/2/2013
H3N2	EF473473	NY	1/26/2006	H3N2	KJ741959	MO	12/30/2012
H3N2	CY054274	NY	1/26/2006	H3N2	KF789550	NV	2/4/2013
H3N2	CY172263	NY	2/6/2006	H3N2	KF789571	AL	5/22/2013
H3N2	CY091069	TX	4/4/2006	H3N2	CY171367	IL	12/26/2012
H3N2	CY172439	NY	3/7/2006	H3N2	KF790500	KS	11/5/2012
H3N2	CY172359	NY	2/17/2006	H3N2	KM244540	MS	1/14/2013
H3N2	CY172375	NY	2/17/2006	H3N2	KF789787	MI	11/18/2012
H3N2	CY172335	NY	2/16/2006	H3N2	CY134652	NY	12/10/2012
H3N2	CY172367	NY	2/17/2006	H3N2	CY134654	NY	12/13/2012
H3N2	CY172351	NY	2/17/2006	H3N2	CY134644	NY	12/6/2012
H3N2	CY172423	NY	3/7/2006	H3N2	CY134643	NY	12/6/2012
H3N2	CY172319	NY	2/15/2006	H3N2	CY134678	NY	12/6/2012
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H3N2	EU502420	WI	3/29/2006	H3N2	CY168335	MA	1/18/2013
H3N2	CY172391	NY	2/24/2006	H3N2	CY147290	MI	1/16/2013
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H3N2	CY172487	NY	3/13/2006	H3N2	CY141231	NY	1/7/2013
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H3N2	CY020133	NY	3/2/2006	H3N2	KF789885	ME	12/12/2012
H3N2	CY020365	NY	3/2/2006	H3N2	KJ741954	CT	12/30/2012
H3N2	CY019859	NY	3/2/2006	H3N2	CY170831	CA	1/25/2013
H3N2	CY020117	NY	3/2/2006	H3N2	KF790517	CA	1/29/2013
H3N2	CY014159	NY	4/5/2006	H3N2	CY134836	TX	11/24/2012
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H3N2	CY025485	NY	3/5/2007	H3N2	KF789716	CO	12/4/2012
H3N2	EU516019	DE	3/17/2007	H3N2	CY134642	CO	12/4/2012
H3N2	EU100715	WI	12/15/2006	H3N2	KF790439	WI	11/6/2012
H3N2	EU199362	WI	2/14/2007	H3N2	KF789673	MO	11/26/2012
H3N2	CY025843	NY	3/5/2007	H3N2	CY147293	OK	2/1/2013
H3N2	CY026147	CO	1/8/2007	H3N2	CY171383	IL	12/27/2012
H3N2	EU100713	MD	12/17/2006	H3N2	KF790413	WI	1/24/2013
H3N2	CY025739	CA	1/29/2007	H3N2	CY134637	FL	11/26/2012
H3N2	EU199380	MN	3/26/2007	H3N2	KJ741973	CT	12/29/2012
H3N2	CY172895	NY	2/6/2007	H3N2	KJ741974	CT	12/27/2012

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H3N2	CY172751	NY	2/11/2007	H3N2	CY171503	IL	12/29/2012
H3N2	EU100720	FL	1/9/2007	H3N2	KF789759	NV	12/10/2012
H3N2	EU100696	WI	12/27/2006	H3N2	KF790455	CA	1/7/2013
H3N2	EU502586	WI	12/27/2006	H3N2	KJ741972	CT	12/29/2012
H3N2	EU502602	WI	12/27/2006	H3N2	KF789633	LA	2/19/2013
H3N2	EU100697	NY	11/29/2006	H3N2	CY170791	CA	2/2/2013
H3N2	EU502546	NY	11/29/2006	H3N2	KF789740	MN	3/6/2013
H3N2	CY030197	IL	3/14/2007	H3N2	KF790368	OH	11/8/2012
H3N2	CY030205	VA	3/13/2007	H3N2	KF790160	WI	11/1/2012
H3N2	EU199343	CO	2/25/2007	H3N2	CY171103	IL	12/2/2012
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H3N2	EU199276	NJ	1/14/2007	H3N2	CY141214	NE	1/10/2013
H3N2	EU199278	NJ	1/27/2007	H3N2	CY134636	SC	11/26/2012
H3N2	CY026195	CA	3/13/2007	H3N2	CY171247	IL	12/18/2012
H3N2	CY031563	CA	3/12/2007	H3N2	KF790473	NM	1/16/2013
H3N2	CY025835	NY	2/21/2007	H3N2	KF790334	PA	1/10/2013
H3N2	EU199345	WI	3/26/2007	H3N2	CY170895	CA	2/4/2013
H3N2	EU199359	PA	3/9/2007	H3N2	CY169919	MA	1/24/2013
H3N2	CY172767	NY	2/28/2007	H3N2	KF886306	IL	2/13/2013
H3N2	CY025859	AL	3/7/2007	H3N2	KF789640	VT	2/19/2013
H3N2	EU199272	WI	1/15/2007	H3N2	KF789628	KS	2/5/2013
H3N2	CY172831	NY	3/26/2007	H3N2	CY141189	FL	12/27/2012
H3N2	CY172783	NY	3/5/2007	H3N2	KF789619	CT	2/1/2013
H3N2	CY025907	KY	2/21/2007	H3N2	KF886312	IL	1/17/2013
H3N2	CY025747	TX	3/2/2007	H3N2	KF790028	MI	3/28/2013
H3N2	EU199271	NY	2/1/2007	H3N2	CY141219	NJ	1/3/2013
H3N2	EU199279	NJ	2/1/2007	H3N2	KF790066	CO	1/1/2013
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H3N2	EU516100	CA	12/8/2006	H3N2	CY170511	CA	1/23/2013
H3N2	EU100685	CA	12/8/2006	H3N2	CY141251	NC	12/18/2012
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H3N2	EU100716	WI	12/16/2006	H3N2	KM244531	MS	1/22/2013
H3N2	EU100670	WI	12/16/2006	H3N2	KF789906	CA	1/29/2013
H3N2	EU502584	WI	12/16/2006	H3N2	CY141184	DC	1/4/2013
H3N2	EU199255	CO	12/8/2006	H3N2	CY170527	CA	1/8/2013
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H3N2	CY022882	CO	3/12/2007	H3N2	KM244541	MS	1/17/2013
H3N2	EU199280	TN	2/9/2007	H3N2	CY171487	IL	12/28/2012

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H3N2	EU100714	MD	12/12/2006	H3N2	KM244542	MS	1/23/2013
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H3N2	CY026243	CA	3/6/2007	H3N2	CY171263	IL	12/18/2012
H3N2	CY172791	NY	3/7/2007	H3N2	CY171255	IL	12/18/2012
H3N2	CY172903	NY	3/26/2007	H3N2	CY171423	IL	12/27/2012
H3N2	CY172775	NY	3/2/2007	H3N2	KF790478	LA	1/20/2013
H3N2	CY026019	IL	1/15/2007	H3N2	KF790357	MS	1/8/2013
H3N2	CY026027	IL	1/15/2007	H3N2	KM244539	MS	1/9/2013
H3N2	CY026883	KY	2/5/2007	H3N2	KM244535	MS	1/4/2013
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H3N2	CY092249	CA	4/30/2007	H3N2	CY170519	CA	1/13/2013
H3N2	CY022888	CO	4/2/2007	H3N2	CY170455	CA	1/23/2013
H3N2	CY025883	VT	3/1/2007	H3N2	KF790167	WA	10/13/2012
H3N2	CY025541	VT	2/26/2007	H3N2	KF789535	CA	2/2/2013
H3N2	CY172863	NY	4/15/2007	H3N2	KF789725	MT	12/12/2012
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H3N2	EU199365	VT	4/11/2007	H3N2	CY134756	TX	11/12/2012
H3N2	CY172807	NY	3/15/2007	H3N2	KF790448	CA	10/28/2012
H3N2	EU199360	SC	2/28/2007	H3N2	KF789547	PA	2/20/2013
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H3N2	CY025477	IL	2/19/2007	H3N2	CY186139	TX	1/20/2013
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H3N2	EU199259	GA	1/16/2007	H3N2	CY183089	TX	1/5/2013
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H3N2	CY025643	NY	1/17/2007	H3N2	KF790532	MD	4/3/2013
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H3N2	CY022891	CO	4/2/2007	H3N2	CY141213	NE	1/3/2013
H3N2	CY022890	CO	4/2/2007	H3N2	CY170479	CA	1/22/2013
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H3N2	CY027547	CO	1/8/2007	H3N2	KF790429	DE	11/5/2012
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H3N2	EU199257	CO	1/9/2007	H3N2	KF790286	IN	10/22/2012
H3N2	CY026771	WA	2/12/2007	H3N2	KF790275	AZ	10/22/2012
H3N2	EU502580	WA	12/18/2006	H3N2	KF790270	AZ	10/22/2012
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H3N2	CY026843	OR	2/13/2007	H3N2	CY170727	CA	1/31/2013
H3N2	CY027795	OR	2/6/2007	H3N2	KF789613	NC	2/22/2013
H3N2	CY027075	OR	2/13/2007	H3N2	CY141252	OH	1/11/2013
H3N2	EU100698	WA	1/10/2007	H3N2	CY171239	IL	12/18/2012
H3N2	CY026163	CO	3/7/2007	H3N2	CY171119	IL	12/4/2012
H3N2	CY172823	NY	3/23/2007	H3N2	CY147297	OK	3/5/2013
H3N2	CY027107	OR	2/19/2007	H3N2	KF790011	OK	3/13/2013

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H3N2	CY022892	CO	4/2/2007	H3N2	CY170551	CA	1/9/2013
H3N2	CY026827	OR	2/26/2007	H3N2	KF790384	NM	12/10/2012
H3N2	CY028475	TX	3/14/2007	H3N2	KF789842	NC	3/21/2013
H3N2	CY026667	CO	2/14/2007	H3N2	KF790404	IA	5/2/2013
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H3N2	EU199361	ID	1/25/2007	H3N2	CY148500	MA	12/26/2012
H3N2	CY025707	IL	3/1/2007	H3N2	KF789958	WV	1/3/2013
H3N2	CY027123	OR	2/13/2007	H3N2	CY141246	NY	12/14/2012
H3N2	CY028371	OR	2/8/2007	H3N2	CY134726	NY	11/16/2012
H3N2	EU199369	MN	2/4/2007	H3N2	CY169215	MA	12/30/2012
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H3N2	EU199261	NM	1/13/2007	H3N2	CY183169	TX	1/8/2013
H3N2	EU199264	TX	1/23/2007	H3N2	CY141228	NY	1/6/2013
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H3N2	CY028740	VA	3/1/2007	H3N2	CY148492	MA	12/26/2012
H3N2	CY026275	TX	3/9/2007	H3N2	CY134685	NY	12/3/2012
H3N2	EU199375	TX	5/31/2007	H3N2	CY168367	MA	1/21/2013
H3N2	EU199377	SD	1/23/2007	H3N2	CY134696	NY	11/26/2012

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H3N2	CY028299	OH	2/12/2007	H3N2	KF790331	WA	1/19/2013
H3N2	CY026555	TX	2/20/2007	H3N2	CY134676	WA	11/25/2012
H3N2	CY025277	IL	3/9/2007	H3N2	KF789847	WA	1/7/2013
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H3N2	EU516042	PA	3/3/2007	H3N2	CY141254	SC	12/17/2012
H3N2	CY026707	CO	2/26/2007	H3N2	CY148940	MA	1/9/2013
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H3N2	EU516044	NV	10/5/2007	H3N2	CY141256	SC	12/19/2012
H3N2	EU779524	ID	2/1/2008	H3N2	KF790214	ID	10/9/2012
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H3N2	EU516213	TN	12/21/2007	H3N2	CY141205	KY	1/2/2013
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H3N2	EU779510	FL	2/6/2008	H3N2	KM244536	MS	1/4/2013
H3N2	CY032065	SC	2/22/2008	H3N2	KF789600	MT	11/17/2012
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H3N2	EU516208	AZ	12/14/2007	H3N2	CY141282	WA	1/7/2013
H3N2	CY031920	CA	2/4/2008	H3N2	CY141202	GA	1/11/2013
H3N2	CY030030	SC	1/10/2008	H3N2	KF790232	IA	10/18/2012
H3N2	CY032113	TX	1/25/2008	H3N2	KF790248	IA	11/12/2012
H3N2	CY032121	TX	1/28/2008	H3N2	KF790311	NE	12/18/2012

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H3N2	CY032020	NJ	3/6/2008	H3N2	CY141276	WA	12/18/2012
H3N2	CY037863	CA	2/19/2008	H3N2	KJ741970	CT	12/29/2012
H3N2	EU852003	NE	1/24/2008	H3N2	KJ741969	CT	12/29/2012
H3N2	FJ975074	OK	3/1/2008	H3N2	CY141212	NE	12/18/2012
H3N2	CY037567	KY	2/25/2008	H3N2	CY168767	MA	12/24/2012
H3N2	CY038791	CA	2/13/2008	H3N2	CY171687	IL	1/14/2013
H3N2	CY031886	AL	3/14/2008	H3N2	KF790010	WI	4/8/2013
H3N2	CY038815	CA	2/20/2008	H3N2	CY183017	TX	1/2/2013
H3N2	EU516206	NJ	12/19/2007	H3N2	KF790459	ND	1/27/2013
H3N2	EU516062	TX	11/11/2007	H3N2	KF789841	NJ	3/11/2013
H3N2	EU516210	FL	11/14/2007	H3N2	KF790037	ND	3/30/2013
H3N2	EU516077	FL	11/7/2007	H3N2	KJ741953	CT	12/30/2012
H3N2	EU516205	TX	10/13/2007	H3N2	CY141274	VA	1/10/2013
H3N2	CY032029	NC	3/20/2008	H3N2	KF790039	NY	3/27/2013
H3N2	CY030036	LA	1/15/2008	H3N2	KF886335	CA	1/9/2013
H3N2	CY030044	LA	1/22/2008	H3N2	KF790416	IA	1/4/2013
H3N2	CY030012	NV	12/26/2007	H3N2	KF789879	VA	1/4/2013
H3N2	CY173111	NY	1/30/2008	H3N2	KF789630	WY	2/8/2013
H3N2	CY038839	CA	2/21/2008	H3N2	CY141210	MD	1/2/2013
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H3N2	CY032014	NV	1/30/2008	H3N2	KF886341	SC	1/24/2013
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H3N2	CY032200	MD	2/1/2008	H3N2	KF790403	DE	2/1/2013
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H3N2	CY031925	CA	3/4/2008	H3N2	CY130197	OK	10/5/2012
H3N2	FJ532086	IL	2/19/2008	H3N2	KF790514	AZ	12/12/2012
H3N2	CY173183	NY	2/18/2008	H3N2	CY141216	NV	1/11/2013
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H3N2	EU779532	GA	2/26/2008	H3N2	KF789567	ID	2/15/2013
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H3N2	FJ549055	IL	2/19/2008	H3N2	CY148412	MA	12/2/2012
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H3N2	FJ549056	NY	2/13/2008	H3N2	CY148644	MA	12/21/2012
H3N2	CY173175	NY	2/13/2008	H3N2	CY169295	MA	12/31/2012
H3N2	CY034463	WA	2/27/2008	H3N2	CY169599	MA	1/5/2013
H3N2	CY032040	OK	2/19/2008	H3N2	CY168775	MA	12/24/2012
H3N2	CY031884	AL	2/15/2008	H3N2	KJ741961	CT	12/30/2012
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H3N2	CY030017	CO	1/22/2008	H3N2	KF790137	OK	1/4/2013
H3N2	CY031921	CA	2/9/2008	H3N2	CY147304	SC	3/29/2013
H3N2	CY032085	SD	3/28/2008	H3N2	KF886315	SC	1/9/2013
H3N2	CY032627	OK	2/26/2008	H3N2	KF790201	NC	1/3/2013
H3N2	CY044780	MA	3/1/2008	H3N2	CY141268	VA	12/19/2012
H3N2	CY037847	KS	3/5/2008	H3N2	KF790119	LA	4/11/2013
H3N2	EU885532	OR	3/11/2008	H3N2	CY141249	NC	12/27/2012
H3N2	CY032108	TX	1/24/2008	H3N2	KJ741964	CT	12/30/2012
H3N2	CY032032	OK	1/30/2008	H3N2	KF789736	MT	2/21/2013
H3N2	EU716446	MD	1/29/2008	H3N2	CY134713	OK	11/13/2012
H3N2	EU885516	NJ	3/14/2008	H3N2	CY141194	FL	1/4/2013
H3N2	CY031933	CO	2/3/2008	H3N2	KF789560	FL	2/12/2013
H3N2	CY032019	NJ	2/14/2008	H3N2	KJ741962	CT	12/29/2012
H3N2	CY032136	TX	2/5/2008	H3N2	KJ741966	CT	12/30/2012
H3N2	CY032579	OK	2/28/2008	H3N2	KF789840	CA	2/21/2013
H3N2	CY044548	MA	2/7/2008	H3N2	CY147299	CA	3/7/2013
H3N2	CY032189	WA	3/26/2008	H3N2	KF790362	NY	4/10/2013
H3N2	CY032649	TX	2/11/2008	H3N2	KJ741960	CT	12/29/2012
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H3N2	CY034471	CA	3/4/2008	H3N2	KF790389	MN	4/16/2013
H3N2	CY034445	CA	2/20/2008	H3N2	KF789888	NJ	5/15/2013
H3N2	CY032634	AL	2/27/2008	H3N2	KF790032	FL	3/21/2013
H3N2	CY031890	AZ	3/27/2008	H1N1	EU516143	NJ	1/23/2007
H3N2	CY034451	WA	5/7/2008	H1N1	CY026627	NY	2/7/2007
H3N2	EU851993	LA	1/13/2008	H1N1	CY027603	NY	2/16/2007
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H3N2	EU716492	VA	2/5/2008	H1N1	CY026523	CO	1/22/2007
H3N2	CY044540	MA	2/6/2008	H1N1	EU199355	NY	4/2/2007
H3N2	EU851995	LA	1/12/2008	H1N1	CY172631	NY	2/6/2007
H3N2	CY032008	NE	2/6/2008	H1N1	EU716569	CA	12/6/2006
H3N2	CY031938	FL	2/14/2008	H1N1	EU199354	CA	1/29/2007
H3N2	CY034461	WA	3/27/2008	H1N1	EU199348	CA	12/14/2006
H3N2	CY032007	NE	2/6/2008	H1N1	CY026539	CA	2/21/2007
H3N2	CY037799	OH	2/18/2008	H1N1	CY028307	CA	3/1/2007
H3N2	CY030023	OK	1/23/2008	H1N1	CY026587	KY	3/1/2007
H3N2	CY044596	MA	2/15/2008	H1N1	CY026371	MS	2/20/2007
H3N2	CY044429	MA	2/13/2008	H1N1	CY026699	TN	1/18/2007
H3N2	EU885501	FL	2/5/2008	H1N1	EU716572	CA	1/13/2007
H3N2	CY032565	TX	2/12/2008	H1N1	CY028315	TX	2/8/2007
H3N2	CY034443	CA	2/19/2008	H1N1	EU199328	TX	1/31/2007

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H3N2	CY031922	CA	2/9/2008	H1N1	CY026339	TX	3/7/2007
H3N2	CY032167	TX	2/22/2008	H1N1	CY027883	TX	3/5/2007
H3N2	CY044644	MA	2/20/2008	H1N1	CY028323	TX	1/11/2007
H3N2	CY034470	MS	3/3/2008	H1N1	CY025445	TX	3/1/2007
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H3N2	CY031919	CA	2/6/2008	H1N1	CY027043	IL	2/1/2007
H3N2	CY032046	OK	2/13/2008	H1N1	CY028075	TN	1/26/2007
H3N2	CY173159	NY	2/6/2008	H1N1	CY028395	TN	2/14/2007
H3N2	CY032173	TX	3/13/2008	H1N1	CY172711	NY	1/27/2007
H3N2	CY030046	NE	1/24/2008	H1N1	EU199353	SD	1/27/2007
H3N2	CY034469	TX	3/5/2008	H1N1	CY027771	OK	1/22/2007
H3N2	CY044588	MA	2/14/2008	H1N1	EU100704	FL	12/14/2006
H3N2	CY044620	MA	2/19/2008	H1N1	EU100712	WI	12/19/2006
H3N2	CY032043	OK	2/22/2008	H1N1	CY025213	TX	12/20/2006
H3N2	CY044788	MA	3/2/2008	H1N1	CY028339	FL	2/7/2007
H3N2	CY037735	KY	2/27/2008	H1N1	CY026659	FL	3/5/2007
H3N2	CY037687	KY	2/20/2008	H1N1	CY027955	OR	2/5/2007
H3N2	CY031931	CO	1/27/2008	H1N1	CY026899	OR	2/8/2007
H3N2	CY031932	CO	2/4/2008	H1N1	CY027691	OR	2/5/2007
H3N2	CY044708	MA	2/24/2008	H1N1	CY028211	OR	2/7/2007
H3N2	CY030052	SC	1/3/2008	H1N1	CY027083	OR	2/9/2007
H3N2	CY031898	AR	2/8/2008	H1N1	CY027203	MS	1/22/2007
H3N2	CY030051	VA	1/23/2008	H1N1	CY028756	VA	2/6/2007
H3N2	CY032130	TX	2/1/2008	H1N1	CY027747	TN	2/27/2007
H3N2	EU779502	IN	1/22/2008	H1N1	CY037783	TN	1/29/2007
H3N2	CY032101	TX	1/22/2008	H1N1	CY027379	TN	1/29/2007
H3N2	CY032628	OK	2/27/2008	H1N1	CY026891	TN	1/26/2007
H3N2	CY031924	CA	2/12/2008	H1N1	CY027731	TN	3/5/2007
H3N2	CY031895	AR	2/4/2008	H1N1	CY028379	VA	2/19/2007
H3N2	CY031892	AR	1/23/2008	H1N1	CY027835	KS	1/26/2007
H3N2	CY031911	AR	2/13/2008	H1N1	CY028035	KY	1/19/2007
H3N2	EU885507	IN	2/20/2008	H1N1	CY027723	TN	1/29/2007
H3N2	CY032016	NV	2/8/2008	H1N1	CY172695	NY	4/10/2007
H3N2	CY032618	SC	2/29/2008	H1N1	CY025771	FL	2/14/2007
H3N2	CY032022	NM	2/11/2008	H1N1	CY027315	FL	2/7/2007
H3N2	CY173087	NY	1/18/2008	H1N1	CY025659	VT	2/15/2007
H3N2	CY030561	CA	2/2/2008	H1N1	CY025795	VT	1/26/2007
H3N2	CY031923	CA	2/10/2008	H1N1	CY028003	TN	2/15/2007
H3N2	CY037543	CA	2/19/2008	H1N1	CY027131	TN	1/29/2007
H3N2	CY044445	MA	2/24/2008	H1N1	CY172727	NY	2/11/2007

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H3N2	CY032576	AR	2/22/2008	H1N1	CY026963	TX	2/5/2007
H3N2	CY034446	CA	2/20/2008	H1N1	CY037775	TN	2/20/2007
H3N2	CY030037	IL	1/17/2008	H1N1	CY027451	TN	2/26/2007
H3N2	CY031913	AR	2/15/2008	H1N1	CY028083	KY	2/22/2007
H3N2	CY031899	AR	2/11/2008	H1N1	CY028051	KY	2/26/2007
H3N2	CY031906	AR	2/14/2008	H1N1	CY172679	NY	2/28/2007
H3N2	CY031897	AR	2/6/2008	H1N1	EU516296	CA	1/29/2007
H3N2	CY038831	OH	2/21/2008	H1N1	CY027659	TX	1/31/2007
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H3N2	CY031916	CA	2/2/2008	H1N1	CY026211	TX	2/6/2007
H3N2	EU779534	TX	3/12/2008	H1N1	CY026267	TX	2/15/2007
H3N2	CY044628	MA	2/19/2008	H1N1	CY026187	TX	2/15/2007
H3N2	CY044724	MA	2/24/2008	H1N1	CY027323	TX	2/19/2007
H3N2	CY032039	OK	2/14/2008	H1N1	CY026403	TX	2/13/2007
H3N2	CY032118	TX	1/22/2008	H1N1	EU199349	CA	1/23/2007
H3N2	CY032147	TX	2/14/2008	H1N1	CY025389	TX	2/22/2007
H3N2	CY032155	TX	2/19/2008	H1N1	EU199352	CA	1/25/2007
H3N2	CY032002	MS	2/8/2008	H1N1	CY096851	CO	3/1/2007
H3N2	CY031926	CA	3/8/2008	H1N1	CY025357	KY	2/20/2007
H3N2	CY032204	MD	2/5/2008	H1N1	CY025509	KY	1/29/2007
H3N2	CY032024	NM	2/13/2008	H1N1	CY026515	KY	1/23/2007
H3N2	CY031937	CO	2/12/2008	H1N1	CY025261	KY	1/23/2007
H3N2	CY173223	NY	2/27/2008	H1N1	EU100706	IA	12/29/2006
H3N2	CY037671	KY	2/14/2008	H1N1	CY026531	CA	2/14/2007
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H3N2	CY032131	TX	2/5/2008	H1N1	EU199286	NM	2/5/2007
H3N2	CY032063	SC	2/25/2008	H1N1	CY025493	KY	1/18/2007
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H3N2	CY032004	MS	2/5/2008	H1N1	CY027211	CA	3/9/2007
H3N2	EU852009	IA	3/23/2008	H1N1	CY172591	NY	1/29/2007
H3N2	CY032005	MS	2/5/2008	H1N1	CY027227	CO	3/5/2007
H3N2	CY030556	MS	2/7/2008	H1N1	CY027139	OH	2/6/2007
H3N2	CY032001	MS	2/8/2008	H1N1	CY027355	CA	3/7/2007
H3N2	CY037511	MS	2/14/2008	H1N1	CY172703	NY	1/10/2007
H3N2	CY037719	MS	2/25/2008	H1N1	EU199308	IL	12/11/2006
H3N2	CY030552	MS	2/5/2008	H1N1	CY027467	OH	2/23/2007
H3N2	CY030553	MS	2/6/2008	H1N1	CY027763	OH	1/30/2007
H3N2	CY030557	MS	2/6/2008	H1N1	CY172623	NY	2/6/2007
H3N2	CY030555	MS	2/5/2008	H1N1	CY025221	MI	12/28/2006
H3N2	CY032003	MS	2/8/2008	H1N1	CY027243	TN	1/29/2007

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H3N2	CY031935	CO	2/13/2008	H1N1	CY025939	KY	3/7/2007
H3N2	EU716449	TX	1/15/2008	H1N1	CY026227	KY	3/7/2007
H3N2	CY032013	NV	1/17/2008	H1N1	CY027371	KY	2/26/2007
H3N2	CY030038	CO	1/24/2008	H1N1	CY028147	KY	2/6/2007
H3N2	EU716512	WI	1/30/2008	H1N1	CY027675	KY	2/27/2007
H3N2	CY031993	MD	2/5/2008	H1N1	EU199338	TX	2/6/2007
H3N2	CY032010	NE	2/14/2008	H1N1	CY025285	NY	2/22/2007
H3N2	CY173167	NY	2/10/2008	H1N1	CY025373	CA	2/26/2007
H3N2	EU716486	NJ	1/25/2008	H1N1	CY026355	CA	2/9/2007
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H3N2	CY032573	TX	2/13/2008	H1N1	CY027843	CA	1/30/2007
H3N2	CY032629	OK	2/27/2008	H1N1	CY025587	TX	3/6/2007
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H3N2	CY031980	LA	2/1/2008	H1N1	CY041450	CA	2/26/2007
H3N2	CY032622	TX	2/27/2008	H1N1	CY172567	NY	12/27/2006
H3N2	EU779506	MN	1/11/2008	H1N1	CY172559	NY	12/17/2006
H3N2	EU716476	GA	1/22/2008	H1N1	EU199309	WI	12/29/2006
H3N2	FJ975059	OK	1/20/2008	H1N1	EU199350	NE	2/6/2007
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H3N2	CY036999	OH	3/6/2008	H1N1	CY027419	TN	2/13/2007
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H3N2	CY034438	OK	2/21/2008	H1N1	CY027939	VA	2/14/2007
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H3N2	CY032144	TX	2/12/2008	H1N1	CY027483	IL	1/30/2007
H3N2	CY032037	OK	2/12/2008	H1N1	CY027819	IL	1/25/2007
H3N2	CY044580	MA	2/14/2008	H1N1	CY027091	IL	2/1/2007
H3N2	CY032599	TX	2/10/2008	H1N1	CY026971	IL	1/29/2007

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H3N2	CY030043	IL	1/17/2008	H1N1	CY027395	IL	2/1/2007
H3N2	CY032009	NE	2/8/2008	H1N1	CY172607	NY	2/5/2007
H3N2	CY044524	MA	1/31/2008	H1N1	CY027851	KS	1/30/2007
H3N2	CY044676	MA	2/21/2008	H1N1	CY172719	NY	2/9/2007
H3N2	CY044668	MA	2/21/2008	H1N1	CY027595	TX	2/27/2007
H3N2	CY044716	MA	2/24/2008	H1N1	EU199303	PA	11/20/2006
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H3N2	EU885518	TN	3/21/2008	H1N1	CY026619	VT	3/5/2007
H3N2	FJ686925	TN	3/21/2008	H1N1	CY037463	VT	3/2/2007
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H3N2	CY032082	SD	3/6/2008	H1N1	CY026939	VA	2/5/2007
H3N2	FJ975057	OK	1/24/2008	H1N1	CY026731	NY	1/31/2007
H3N2	CY031910	AR	2/13/2008	H1N1	CY026379	NY	1/23/2007
H3N2	CY032177	WA	2/19/2008	H1N1	CY028099	VA	2/22/2007
H3N2	CY034466	WA	2/27/2008	H1N1	CY172671	NY	2/28/2007
H3N2	CY032178	WA	2/18/2008	H1N1	CY028027	OH	3/6/2007
H3N2	CY030027	WA	1/23/2008	H1N1	CY027635	TN	2/22/2007
H3N2	CY032176	WA	2/12/2008	H1N1	CY025995	VA	1/29/2007
H3N2	CY032181	WA	2/22/2008	H1N1	CY027899	CO	3/1/2007
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H3N2	CY037599	KS	2/28/2008	H1N1	CY025563	TX	2/27/2007
H3N2	CY032577	MS	2/26/2008	H1N1	CY027179	TX	2/6/2007
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H3N2	EU885514	WA	3/3/2008	H1N1	CY027755	VA	1/30/2007
H3N2	CY032639	MS	2/29/2008	H1N1	CY027931	OR	2/13/2007
H3N2	CY032188	WA	3/26/2008	H1N1	CY027827	VA	1/25/2007
H3N2	CY034459	WA	3/12/2008	H1N1	CY027491	TN	3/1/2007
H3N2	CY032610	WA	2/27/2008	H1N1	CY025381	AL	2/28/2007
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H3N2	CY032638	MS	2/28/2008	H1N1	CY025365	TX	1/11/2007
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H3N2	EU566967	GA	1/15/2008	H1N1	CY025923	KY	1/16/2007
H3N2	CY044516	MA	1/28/2008	H1N1	CY028195	KY	12/6/2006
H3N2	CY032195	MD	1/17/2008	H1N1	CY027067	OH	2/26/2007
H3N2	CY032575	AZ	3/12/2008	H1N1	CY025915	KY	1/24/2007
H3N2	CY037623	FL	3/10/2008	H1N1	CY027387	OH	2/9/2007
H3N2	CY038871	FL	3/10/2008	H1N1	CY026811	KY	1/24/2007
H3N2	CY173279	NY	3/27/2008	H1N1	CY025229	KY	12/18/2006
H3N2	EU885538	NY	4/21/2008	H1N1	CY025453	KY	1/23/2007

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H3N2	CY031879	AL	2/5/2008	H1N1	CY037655	OH	3/2/2007
H3N2	CY031952	IL	2/4/2008	H1N1	CY026947	OH	3/5/2007
H3N2	CY032033	OK	2/5/2008	H1N1	CY030061	OH	2/12/2007
H3N2	CY032062	SC	2/8/2008	H1N1	CY027171	KY	1/25/2007
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H3N2	EU885522	WA	3/13/2008	H1N1	CY030727	KY	1/24/2007
H3N2	CY037535	KY	2/18/2008	H1N1	CY025635	KY	2/5/2007
H3N2	CY032073	SC	3/20/2008	H1N1	CY027115	TN	2/2/2007
H3N2	EU885536	MN	3/19/2008	H1N1	CY027403	OH	2/5/2007
H3N2	CY037639	KY	3/19/2008	H1N1	CY027259	OH	3/5/2007
H3N2	CY034465	WA	2/27/2008	H1N1	CY027003	OH	2/28/2007
H3N2	CY034449	IL	1/28/2008	H1N1	CY027443	OH	1/30/2007
H3N2	CY030045	MD	1/17/2008	H1N1	CY026011	OH	1/30/2007
H3N2	EU885499	MN	1/6/2008	H1N1	CY025971	OH	2/16/2007
H3N2	CY032203	MD	2/3/2008	H1N1	CY028123	OH	2/19/2007
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H3N2	CY031874	AL	1/31/2008	H1N1	CY026875	KY	1/30/2007
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H3N2	CY034441	AL	2/21/2008	H1N1	CY027051	KY	2/2/2007
H3N2	CY173143	NY	2/5/2008	H1N1	CY028043	KY	2/23/2007
H3N2	CY031959	IL	2/8/2008	H1N1	CY028163	KY	2/13/2007
H3N2	CY032640	AR	2/11/2008	H1N1	CY025245	IL	1/4/2007
H3N2	CY031872	AL	1/23/2008	H1N1	CY025237	IL	1/5/2007
H3N2	CY032036	OK	2/7/2008	H1N1	CY027739	KS	1/24/2007

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H3N2	CY032047	OK	3/4/2008	H1N1	CY027619	TX	2/8/2007
H3N2	CY032048	OK	3/14/2008	H1N1	CY036855	TX	2/5/2007
H3N2	CY036975	OH	2/26/2008	H1N1	CY025683	TX	2/6/2007
H3N2	CY044756	MA	2/26/2008	H1N1	CY031551	KS	1/30/2007
H3N2	CY031967	IL	2/22/2008	H1N1	CY027427	KS	2/12/2007
H3N2	EU852007	IA	3/21/2008	H1N1	CY027347	IL	2/12/2007
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H3N2	CY032567	IL	2/11/2008	H1N1	CY027667	IL	1/26/2007
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H3N2	CY044732	MA	2/25/2008	H1N1	CY025325	IL	2/21/2007
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H3N2	CY032583	SC	2/26/2008	H1N1	CY033465	OR	3/15/2007
H3N2	CY032584	SC	2/25/2008	H1N1	CY028363	KS	2/5/2007
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H3N2	EU516219	VA	12/13/2007	H1N1	CY027035	KS	1/30/2007

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H3N2	FJ686931	MO	2/26/2008	H1N1	CY025963	KS	2/1/2007
H3N2	FJ549038	MO	2/26/2008	H1N1	CY027995	VA	1/29/2007
H3N2	CY031943	IL	1/17/2008	H1N1	CY026931	VA	2/13/2007
H3N2	CY032157	TX	2/11/2008	H1N1	CY031132	VA	2/9/2007
H3N2	EU885503	TN	2/4/2008	H1N1	EU516297	FL	10/31/2006
H3N2	CY032042	OK	2/19/2008	H1N1	EU199333	NY	12/13/2006
H3N2	CY039415	MS	2/14/2008	H1N1	CY172551	NY	12/13/2006
H3N2	CY032651	IL	2/12/2008	H1N1	EU100711	WI	12/9/2006
H3N2	CY031891	AZ	4/9/2008	H1N1	EU100707	MN	12/29/2006
H3N2	CY032076	SC	3/27/2008	H1N1	EU100709	NC	12/28/2006
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H3N2	CY039095	OH	2/18/2008	H1N1	CY028203	TN	1/22/2007
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H3N2	CY034429	AL	2/19/2008	H1N1	CY027859	VA	2/20/2007
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H3N2	CY031907	AR	2/12/2008	H1N1	CY027643	VA	2/14/2007
H3N2	CY044572	MA	2/13/2008	H1N1	CY027971	VA	2/13/2007
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H3N2	CY173199	NY	2/19/2008	H1N1	CY025333	CO	2/12/2007
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H3N2	CY037711	NY	2/25/2008	H1N1	CY025555	MS	1/31/2007
H3N2	CY037823	KY	2/25/2008	H1N1	CY027283	KY	2/21/2007
H3N2	CY030015	AL	1/23/2008	H1N1	CY037447	FL	2/13/2007
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H3N2	CY038855	KY	3/10/2008	H1N1	CY026915	VA	2/21/2007
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H3N2	CY035150	PA	1/22/2008	H1N1	EU516295	OR	12/3/2007
H3N2	CY035182	PA	2/8/2008	H1N1	EU516292	OR	12/6/2007
H3N2	CY035062	PA	1/23/2008	H1N1	EU516247	MA	12/1/2007
H3N2	CY035046	PA	1/17/2008	H1N1	EU516251	NY	12/5/2007
H3N2	CY035166	PA	1/25/2008	H1N1	CY172935	NY	1/21/2008
H3N2	CY031876	AL	2/4/2008	H1N1	FJ532088	TX	1/29/2008
H3N2	CY031962	IL	2/7/2008	H1N1	FJ532071	TX	1/25/2008
H3N2	CY030047	NC	1/17/2008	H1N1	EU516245	TX	12/11/2007
H3N2	EU716482	SD	1/18/2008	H1N1	CY037327	WA	1/10/2008
H3N2	CY031948	IL	1/31/2008	H1N1	EU566989	NM	1/3/2008
H3N2	CY037551	OH	2/19/2008	H1N1	EU516238	WA	12/19/2007
H3N2	CY031882	AL	2/11/2008	H1N1	EU516253	WA	12/14/2007
H3N2	CY030022	OK	1/14/2008	H1N1	FJ532072	ID	2/28/2008
H3N2	CY034437	AZ	2/8/2008	H1N1	EU516303	WA	11/6/2007
H3N2	EU852001	NC	2/11/2008	H1N1	EU516081	WA	11/6/2007
H3N2	EU716437	WI	2/4/2008	H1N1	CY172911	NY	1/14/2008
H3N2	CY031965	IL	2/7/2008	H1N1	CY172927	NY	1/22/2008
H3N2	CY032012	NE	3/20/2008	H1N1	CY172943	NY	1/22/2008
H3N2	CY032079	SD	2/8/2008	H1N1	EU516301	WA	12/27/2007
H3N2	CY032078	SD	2/4/2008	H1N1	EU887027	FL	1/11/2008
H3N2	CY032081	SD	2/25/2008	H1N1	CY173063	NY	2/26/2008
H3N2	CY032084	SD	4/2/2008	H1N1	EU851987	NY	2/5/2008

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H3N2	CY030042	AR	1/16/2008	H1N1	EU566981	IL	12/12/2007
H3N2	CY044492	MA	12/15/2007	H1N1	EU516300	PA	1/2/2008
H3N2	CY031963	IL	2/7/2008	H1N1	CY172967	NY	2/4/2008
H3N2	CY031929	CO	1/22/2008	H1N1	CY172991	NY	2/6/2008
H3N2	CY030020	MD	1/9/2008	H1N1	EU516299	CA	10/24/2007
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H3N2	CY173103	NY	1/24/2008	H1N1	EU516096	CA	10/2/2007
H3N2	CY031992	MD	2/1/2008	H1N1	EU516091	PA	11/13/2007
H3N2	CY037479	OH	2/12/2008	H1N1	EU779630	GA	2/6/2008
H3N2	CY044804	MA	3/12/2008	H1N1	CY044660	MA	2/20/2008
H3N2	CY032049	OK	3/27/2008	H1N1	EU516241	IA	11/28/2007
H3N2	CY032562	FL	1/30/2008	H1N1	EU516092	GA	10/3/2007
H3N2	EU885509	NY	1/24/2008	H1N1	EU516298	FL	12/16/2007
H3N2	CY173135	NY	2/4/2008	H1N1	EU887023	FL	12/16/2007
H3N2	CY031914	AR	2/17/2008	H1N1	CY173031	NY	2/18/2008
H3N2	CY031905	AR	2/14/2008	H1N1	CY173023	NY	2/18/2008
H3N2	CY032201	MD	2/3/2008	H1N1	EU779628	NC	2/14/2008
H3N2	CY032202	MD	2/3/2008	H1N1	CY038762	DC	2/1/2008
H3N2	EU885512	AR	3/2/2008	H1N1	EU887024	PA	12/12/2007
H3N2	CY034462	WA	2/27/2008	H1N1	EU887025	PA	12/12/2007
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H3N2	CY173095	NY	1/24/2008	H1N1	FJ532083	WA	2/18/2008
H3N2	CY031989	MD	1/27/2008	H1N1	EU516259	CO	10/31/2007
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H3N2	EU516217	NC	11/26/2007	H1N1	EU516252	CO	11/12/2007
H3N2	CY032028	NC	2/1/2008	H1N1	EU516240	PA	12/10/2007
H3N2	EU779530	MO	2/20/2008	H1N1	EU851983	MS	1/24/2008
H3N2	CY032067	SC	2/16/2008	H1N1	EU716559	PA	12/20/2007
H3N2	CY037527	KY	2/18/2008	H1N1	EU516302	CO	12/6/2007
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H3N2	CY032027	NC	1/30/2008	H1N1	CY044484	MA	12/4/2007

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H3N2	CY031915	AR	3/14/2008	H1N1	EU779621	MS	1/24/2008
H3N2	CY032642	AR	2/11/2008	H1N1	CY044373	MA	2/3/2008
H3N2	CY037631	NY	3/12/2008	H1N1	EU716563	NY	1/28/2008
H3N2	EU852005	TX	3/19/2008	H1N1	EU779611	LA	1/13/2008
H3N2	CY030040	AL	1/25/2008	H1N1	EU779613	SD	1/9/2008
H3N2	CY031954	IL	2/6/2008	H1N1	EU716619	NJ	1/25/2008
H3N2	CY031958	IL	2/8/2008	H1N1	EU779633	NE	1/21/2008
H3N2	CY032026	NC	1/28/2008	H1N1	CY172983	NY	2/4/2008
H3N2	CY044357	PA	2/6/2008	H1N1	EU887029	ND	12/29/2007
H3N2	CY032186	WA	3/14/2008	H1N1	GQ475830	MT	2/29/2008
H3N2	CY044508	MA	1/28/2008	H1N1	EU779617	TN	1/17/2008
H3N2	CY031964	IL	2/7/2008	H1N1	CY044564	MA	2/12/2008
H3N2	CY037815	KY	2/19/2008	H1N1	CY172975	NY	2/4/2008
H3N2	CY031908	AR	2/12/2008	H1N1	EU516088	TX	12/4/2007
H3N2	CY173255	NY	3/10/2008	H1N1	EU516255	TX	11/26/2007
H3N2	CY037839	KS	3/5/2008	H1N1	EU516089	WA	10/4/2007
H3N2	CY044476	MA	3/3/2008	H1N1	EU779631	CA	1/15/2008
H3N2	CY032626	NJ	2/27/2008	H1N1	EU779614	NY	1/30/2008
H3N2	CY035038	PA	1/23/2008	H1N1	CY173071	NY	3/6/2008
H3N2	CY032059	SC	1/31/2008	H1N1	CY173055	NY	2/26/2008
H3N2	EU716470	WI	2/1/2008	H1N1	CY173047	NY	2/20/2008
H3N2	CY037503	CA	2/13/2008	H1N1	CY173039	NY	2/20/2008
H3N2	CY031999	MS	2/6/2008	H1N1	EU779624	OK	2/20/2008
H3N2	CY031982	LA	2/7/2008	H1N1	EU779625	IN	2/18/2008
H3N2	CY031881	AL	2/11/2008	H1N1	EU516237	IL	12/13/2007
H3N2	CY032183	WA	3/6/2008	H1N1	EU887031	ID	1/22/2008
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H3N2	CY034439	AL	2/20/2008	H1N1	CY044556	MA	2/9/2008
H3N2	CY044700	MA	2/24/2008	H1N1	EU566991	AZ	11/14/2007
H3N2	CY032182	WA	3/6/2008	H1N1	FJ532084	TX	3/6/2008
H3N2	CY034458	WA	3/12/2008	H1N1	EU516246	AZ	12/2/2007
H3N2	CY034460	WA	3/19/2008	H1N1	EU566993	NJ	1/4/2008
H3N2	CY032615	MA	2/26/2008	H1N1	EU567015	NM	12/18/2007
H3N2	CY172175	NY	2/29/2008	H1N1	GQ475792	TN	3/14/2008
H3N2	CY032099	TX	1/20/2008	H1N1	EU887032	NJ	2/18/2008
H3N2	CY034450	WA	3/5/2008	H1N1	EU716571	ID	1/22/2008
H3N2	CY031877	AL	2/5/2008	H1N1	EU566986	NJ	1/11/2008
H3N2	CY031873	AL	1/30/2008	H1N1	EU567007	NJ	1/17/2008
H3N2	CY030039	AR	1/14/2008	H1N1	CY037679	FL	2/14/2008

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H3N2	CY031950	IL	2/4/2008	H1N1	EU516250	FL	12/10/2007
H3N2	CY173191	NY	2/18/2008	H1N1	EU516293	FL	12/4/2007
H3N2	CY031941	FL	3/20/2008	H1N1	CY038807	FL	2/15/2008
H3N2	CY031927	CA	3/18/2008	H1N1	CY173007	NY	2/10/2008
H3N2	CY031961	IL	2/7/2008	H1N1	EU566984	PA	1/7/2008
H3N2	CY032060	SC	2/6/2008	H1N1	EU516086	TX	10/15/2007
H3N2	EU779528	WI	2/4/2008	H1N1	EU716596	MD	1/4/2008
H3N2	CY038863	KY	3/10/2008	H1N1	EU566990	WI	12/5/2007
H3N2	CY032064	SC	2/25/2008	H1N1	CY044341	NJ	2/14/2008
H3N2	CY036991	KS	3/5/2008	H1N1	EU566966	AZ	12/22/2007
H3N2	EU779514	WI	1/23/2008	H1N1	FJ179358	AZ	12/12/2007
H3N2	CY039103	MS	2/18/2008	H1N1	EU516243	AZ	12/6/2007
H3N2	CY031995	MA	2/11/2008	H1N1	FJ179359	AZ	12/12/2007
H3N2	CY031996	MA	2/13/2008	H1N1	EU779622	WY	2/14/2008
H3N2	CY044796	MA	3/11/2008	H1N1	FJ532094	NC	1/9/2008
H3N2	CY031968	IL	3/13/2008	H1N1	FJ532087	NC	1/9/2008
H3N2	CY037831	KY	3/4/2008	H1N1	CY172919	NY	1/17/2008
H3N2	CY037583	KY	2/27/2008	H1N1	FJ179360	PA	12/13/2007
H3N2	CY036951	MS	2/11/2008	H1N1	GQ475714	NJ	2/26/2008
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H3N2	CY030019	LA	1/15/2008	H1N1	GQ466386	GA	1/23/2008
H3N2	CY032117	TX	1/22/2008	H1N1	EU851978	WI	12/30/2007
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H3N2	CY032593	TX	1/28/2008	H1N1	GQ475687	NJ	2/2/2008
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H3N2	CY031878	AL	2/5/2008	H1N1	EU566982	NJ	12/30/2007
H3N2	CY031902	AR	2/14/2008	H1N1	EU516258	NJ	12/16/2007
H3N2	CY032633	IL	2/27/2008	H1N1	EU567013	NJ	1/22/2008
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H3N2	FJ179352	MN	4/7/2008	H1N1	CY044684	MA	2/23/2008
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H3N2	CY032185	WA	3/14/2008	H1N1	EU716598	WA	1/10/2008
H3N2	CY173287	NY	3/28/2008	H1N1	EU887030	WI	1/28/2008
H3N2	EU885530	SC	3/21/2008	H1N1	CY172999	NY	2/9/2008
H3N2	CY031880	AL	2/6/2008	H1N1	EU566970	MD	12/26/2007
H3N2	CY032093	TN	3/19/2008	H1N1	EU566976	PA	1/15/2008
H3N2	CY032095	TN	3/20/2008	H1N1	EU887034	SC	3/28/2008
H3N2	CY032094	TN	3/20/2008	H1N1	CY173079	NY	3/6/2008
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H3N2	EU885534	MN	3/13/2008	H1N1	EU779616	TN	1/15/2008
H3N2	CY032083	SD	3/24/2008	H1N1	JN582063	NY	2/13/2008
H3N2	CY037887	OH	3/4/2008	H1N1	CY089035	MA	2/2/2009
H3N2	CY031893	AR	1/31/2008	H1N1	KC780041	KY	1/26/2009
H3N2	CY032143	TX	2/12/2008	H1N1	CY069413	WA	1/9/2009
H3N2	CY032652	AR	2/12/2008	H1N1	CY100868	NV	2/1/2009
H3N2	CY034434	IL	2/19/2008	H1N1	CY069397	NJ	1/9/2009
H3N2	CY032621	OK	2/22/2008	H1N1	CY080833	MA	2/13/2009
H3N2	CY032086	SD	4/8/2008	H1N1	CY080985	MA	2/19/2009
H3N2	CY044748	MA	2/26/2008	H1N1	CY074331	CA	4/29/2009
H3N2	CY034464	WA	2/27/2008	H1N1	CY089757	MA	2/14/2009
H3N2	GQ895019	GA	5/3/2009	H1N1	CY089083	MA	3/1/2009
H3N2	GQ385820	MD	1/20/2009	H1N1	CY074291	CA	4/29/2009
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H3N2	FJ686935	MA	10/29/2008	H1N1	CY100796	TX	3/1/2009
H3N2	FJ686917	ID	10/7/2008	H1N1	CY100804	NV	1/1/2009
H3N2	FJ686939	ID	10/16/2008	H1N1	KC782273	MI	1/15/2009
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H3N2	GQ385860	OR	2/24/2009	H1N1	CY173503	NY	3/23/2009
H3N2	GQ385822	MN	12/23/2008	H1N1	CY100772	TX	1/1/2009
H3N2	GQ369883	ND	12/15/2008	H1N1	CY074611	CA	4/26/2009
H3N2	CY093287	NJ	1/1/2009	H1N1	CY092337	CA	4/29/2009
H3N2	GQ385902	NE	12/22/2008	H1N1	CY074155	CA	4/29/2009
H3N2	GQ385858	MA	1/9/2009	H1N1	CY064839	CA	4/28/2009
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H3N2	CY050532	NY	4/27/2009	H1N1	CY074259	CA	4/29/2009
H3N2	GQ385932	NM	1/27/2009	H1N1	CY074267	CA	4/29/2009
H3N2	GQ385918	TX	3/18/2009	H1N1	CY074603	CA	4/27/2009
H3N2	CY068593	CA	5/6/2009	H1N1	CY074211	CA	4/29/2009
H3N2	CY068361	CA	4/1/2009	H1N1	CY073845	CA	4/28/2009
H3N2	GQ369814	CO	12/17/2008	H1N1	CY074299	CA	4/29/2009
H3N2	GQ369815	CO	12/24/2008	H1N1	CY064799	CA	4/27/2009
H3N2	FJ686937	CO	10/29/2008	H1N1	CY074627	CA	4/26/2009
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H3N2	CY064815	CA	4/26/2009	H1N1	CY070911	CA	4/28/2009
H3N2	CY067221	CA	4/28/2009	H1N1	CY069365	SC	3/1/2009
H3N2	CY068161	CA	4/28/2009	H1N1	KC780035	TN	3/9/2009
H3N2	GQ369892	PA	12/11/2008	H1N1	KC780089	TX	3/19/2009
H3N2	GQ369926	WI	12/25/2008	H1N1	CY080913	MA	3/10/2009
H3N2	GQ385900	MT	1/26/2009	H1N1	CY080841	MA	2/13/2009
H3N2	FJ686922	MT	12/9/2008	H1N1	CY089059	MA	2/18/2009
H3N2	CY173559	NY	3/16/2009	H1N1	CY074419	CA	4/30/2009
H3N2	GQ385829	WA	1/25/2009	H1N1	CY074451	CA	4/30/2009
H3N2	GQ385935	TX	1/26/2009	H1N1	CY050772	NY	5/9/2009
H3N2	CY173535	NY	2/25/2009	H1N1	CY064871	CA	4/25/2009
H3N2	GQ385923	WA	3/30/2009	H1N1	CY064807	CA	4/27/2009
H3N2	CY072190	CA	5/23/2009	H1N1	CY074547	CA	5/7/2009
H3N2	CY068025	CA	5/23/2009	H1N1	CY074235	CA	4/29/2009

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H3N2	GQ369906	TX	12/26/2008	H1N1	CY074539	CA	5/2/2009
H3N2	GQ895037	NV	12/16/2008	H1N1	CY074107	CA	4/28/2009
H3N2	KC535390	WI	12/23/2008	H1N1	CY074619	CA	4/27/2009
H3N2	GQ369928	WI	12/23/2008	H1N1	CY074371	CA	4/29/2009
H3N2	CY089749	MA	1/16/2009	H1N1	CY074115	CA	4/29/2009
H3N2	GQ385856	MA	1/20/2009	H1N1	CY073813	CA	4/27/2009
H3N2	CY064855	CA	4/27/2009	H1N1	CY074443	CA	5/5/2009
H3N2	CY067229	CA	5/7/2009	H1N1	CY074523	CA	4/30/2009
H3N2	CY068862	CA	4/28/2009	H1N1	CY074507	CA	4/30/2009
H3N2	GQ385920	VT	2/13/2009	H1N1	CY074363	CA	4/29/2009
H3N2	CY093343	TX	2/1/2009	H1N1	CY074139	CA	4/29/2009
H3N2	CY092353	CA	4/29/2009	H1N1	CY074467	CA	5/1/2009
H3N2	GQ385876	WA	3/3/2009	H1N1	CY074203	CA	4/29/2009
H3N2	CY068273	CA	4/29/2009	H1N1	CY074219	CA	4/29/2009
H3N2	CY072206	CA	4/26/2009	H1N1	CY073829	CA	4/27/2009
H3N2	GQ385827	NC	12/29/2008	H1N1	CY074083	CA	4/28/2009
H3N2	GQ385851	WI	2/5/2009	H1N1	CY073805	CA	4/27/2009
H3N2	GQ385835	AZ	2/27/2009	H1N1	CY074347	CA	4/29/2009
H3N2	GQ385906	WY	2/2/2009	H1N1	CY074499	CA	4/30/2009
H3N2	CY050540	NY	4/30/2009	H1N1	CY074555	CA	5/4/2009
H3N2	CY093359	AZ	3/1/2009	H1N1	CY080761	MA	2/24/2009
H3N2	CY064847	CA	4/27/2009	H1N1	CY050476	NY	4/27/2009
H3N2	CY092329	CA	4/28/2009	H1N1	CY074659	CA	4/27/2009
H3N2	CY068345	CA	3/30/2009	H1N1	CY074147	CA	4/28/2009
H3N2	CY093263	AL	2/1/2009	H1N1	CY074323	CA	4/30/2009
H3N2	GQ385926	WA	3/16/2009	H1N1	CY074435	CA	4/30/2009
H3N2	GQ385846	IA	1/2/2009	H1N1	CY092345	CA	4/28/2009
H3N2	CY173575	NY	2/19/2009	H1N1	CY074179	CA	4/29/2009
H3N2	CY093327	NV	2/1/2009	H1N1	CY074123	CA	4/27/2009
H3N2	CY068401	CA	4/30/2009	H1N1	CY080849	MA	2/14/2009
H3N2	CY064823	CA	4/27/2009	H1N1	CY074307	CA	4/29/2009
H3N2	CY068377	CA	4/30/2009	H1N1	CY074283	CA	4/29/2009
H3N2	CY066519	CA	4/28/2009	H1N1	CY069373	SD	3/1/2009
H3N2	CY068417	CA	4/30/2009	H1N1	CY100844	AL	4/1/2009
H3N2	CY068473	CA	5/2/2009	H1N1	CY100836	IL	3/1/2009
H3N2	CY068249	CA	4/28/2009	H1N1	CY074475	CA	4/30/2009
H3N2	CY068726	CA	4/29/2009	H1N1	CY074531	CA	4/30/2009
H3N2	CY064887	CA	4/27/2009	H1N1	CY073821	CA	4/28/2009
H3N2	CY068798	CA	4/28/2009	H1N1	CY080945	MA	1/20/2009
H3N2	GQ385832	WA	4/6/2009	H1N1	KC782260	ND	1/19/2009
H3N2	CY068441	CA	4/30/2009	H1N1	CY089709	MA	2/11/2009
H3N2	CY068425	CA	4/30/2009	H1N1	CY064831	CA	4/27/2009

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H3N2	CY068694	CA	4/27/2009	H1N1	CY074339	CA	4/29/2009
H3N2	CY089741	MA	4/1/2009	H1N1	CY074635	CA	4/27/2009
H3N2	KC535331	WA	5/5/2009	H1N1	CY074643	CA	4/26/2009
H3N2	KC535336	WA	5/1/2009	H1N1	KC782263	MO	5/5/2009
H3N2	KC535337	WA	5/3/2009	H1N1	CY050660	NY	4/27/2009
H3N2	KC535342	WA	5/1/2009	H1N1	CY074483	CA	4/30/2009
H3N2	CY067253	CA	5/4/2009	H1N1	CY073837	CA	4/29/2009
H3N2	CY068545	CA	5/4/2009	H1N1	CY074651	CA	4/27/2009
H3N2	CY068465	CA	4/29/2009	H1N1	CY074171	CA	4/28/2009
H3N2	CY068830	CA	4/26/2009	H1N1	CY074355	CA	4/29/2009
H3N2	CY067985	CA	5/20/2009	H1N1	CY074491	CA	4/30/2009
H3N2	FJ686928	WI	12/3/2008	H1N1	CY070895	CA	4/27/2009
H3N2	CY093295	AR	2/1/2009	H1N1	CY074187	CA	4/29/2009
H3N2	CY068782	CA	4/27/2009	H1N1	CY074379	CA	5/1/2009
H3N2	GQ385825	NH	2/28/2009	H1N1	CY074195	CA	4/29/2009
H3N2	GQ369809	CA	12/20/2008	H1N1	CY089043	MA	2/4/2009
H3N2	CY068193	CA	4/28/2009	H1N1	CY089155	MA	1/30/2009
H3N2	CY068177	CA	4/28/2009	H1N1	CY080753	MA	2/23/2009
H3N2	GQ385849	WI	1/7/2009	H1N1	CY089139	MA	1/22/2009
H3N2	CY089393	MA	1/30/2009	H1N1	CY089147	MA	1/29/2009
H3N2	CY173567	NY	2/9/2009	H1N1	CY080673	MA	2/10/2009
H3N2	CY089773	MA	4/27/2009	H1N1	CY080650	MA	2/10/2009
H3N2	CY068449	CA	4/30/2009	H1N1	CY080785	MA	2/26/2009
H3N2	CY173591	NY	3/2/2009	H1N1	CY089163	MA	2/4/2009
H3N2	CY173583	NY	2/24/2009	H1N1	CY080809	MA	3/1/2009
H3N2	GQ385869	IN	4/15/2009	H1N1	CY080737	MA	2/20/2009
H3N2	CY067929	CA	4/28/2009	H1N1	CY080658	MA	2/11/2009
H3N2	CY050492	NY	4/27/2009	H1N1	CY089067	MA	2/20/2009
H3N2	CY068758	CA	4/28/2009	H1N1	CY080697	MA	2/11/2009
H3N2	CY173543	NY	3/1/2009	H1N1	CY080969	MA	2/12/2009
H3N2	GQ385891	PA	1/22/2009	H1N1	CY089091	MA	2/13/2009
H3N2	KC535318	MD	5/6/2009	H1N1	CY080817	MA	3/3/2009
H3N2	CY050708	NY	5/3/2009	H1N1	CY080594	MA	2/19/2009
H3N2	CY050700	NY	5/3/2009	H1N1	CY080929	MA	3/23/2009
H3N2	CY080475	NY	5/15/2009	H1N1	CY080602	MA	1/30/2009
H3N2	CY050564	NY	4/29/2009	H1N1	CY173479	NY	3/10/2009
H3N2	KC535319	MN	5/4/2009	H1N1	CY080610	MA	4/1/2009
H3N2	GQ895044	KS	5/1/2009	H1N1	CY089075	MA	3/3/2009
H3N2	CY068838	CA	4/25/2009	H1N1	CY080937	MA	3/24/2009
H3N2	CY068625	CA	5/18/2009	H1N1	CY089051	MA	2/19/2009
H3N2	CY081025	MA	2/12/2009	H1N1	CY080721	MA	2/20/2009
H3N2	CY089733	MA	2/27/2009	H1N1	CY080889	MA	3/9/2009

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H3N2	GQ385872	MT	3/3/2009	H1N1	CY080769	MA	2/24/2009
H3N2	CY068289	CA	4/29/2009	H1N1	CY080953	MA	2/9/2009
H3N2	CY068385	CA	4/30/2009	H1N1	CY081001	MA	2/22/2009
H3N2	CY067205	CA	5/1/2009	H1N1	CY080921	MA	3/13/2009
H3N2	CY068878	CA	4/29/2009	H1N1	CY080993	MA	2/23/2009
H3N2	CY064879	CA	4/28/2009	H1N1	CY080626	MA	1/29/2009
H3N2	CY050636	NY	5/1/2009	H1N1	CY088577	MA	1/29/2009
H3N2	CY058764	NY	5/6/2009	H1N1	CY080977	MA	2/13/2009
H3N2	CY068790	CA	4/29/2009	H1N1	CY080729	MA	2/21/2009
H3N2	CY068553	CA	5/3/2009	H1N1	CY080689	MA	2/11/2009
H3N2	CY068257	CA	4/29/2009	H1N1	CY089131	MA	1/14/2009
H3N2	CY068678	CA	4/28/2009	H1N1	CY080705	MA	2/18/2009
H3N2	CY092361	CA	4/29/2009	H1N1	CY080634	MA	1/31/2009
H3N2	CY068633	CA	4/28/2009	H1N1	CY173343	NY	1/28/2009
H3N2	GQ385887	NV	4/8/2009	H1N1	CY089830	MA	1/28/2009
H3N2	CY068233	CA	4/28/2009	H1N1	CY080793	MA	2/27/2009
H3N2	CY068537	CA	5/4/2009	H1N1	CY081009	MA	2/20/2009
H3N2	CY068710	CA	4/29/2009	H1N1	CY080857	MA	2/27/2009
H3N2	CY068481	CA	4/30/2009	H1N1	CY050756	NY	5/13/2009
H3N2	GQ895031	OR	5/25/2009	H1N1	CY074131	CA	4/30/2009
H3N2	CY072198	CA	4/26/2009	H1N1	CY080618	MA	4/27/2009
H3N2	CY068489	CA	5/1/2009	H1N1	CY050748	NY	5/26/2009
H3N2	CY068337	CA	5/2/2009	H1N1	CY073861	CA	4/29/2009
H3N2	CY068225	CA	4/29/2009	H1N1	CY074315	CA	4/29/2009
H3N2	CY068209	CA	4/28/2009	H1N1	CY080825	MA	2/13/2009
H3N2	CY068185	CA	4/29/2009	H1N1	CY080681	MA	2/9/2009
H3N2	CY068305	CA	4/29/2009	H1N1	CY089099	MA	2/22/2009
H3N2	CY068814	CA	4/30/2009	H1N1	CY080745	MA	2/23/2009
H3N2	CY068734	CA	4/28/2009	H1N1	CY089123	MA	3/21/2009
H3N2	CY068774	CA	4/29/2009	H1N1	CY080865	MA	2/28/2009
H3N2	CY093279	CO	5/1/2009	H1N1	CY089115	MA	2/28/2009
H3N2	CY068153	CA	4/28/2009	H1N1	CY089171	MA	3/13/2009
H3N2	CY068750	CA	4/29/2009	H1N1	CY080897	MA	3/9/2009
H3N2	CY068846	CA	4/27/2009	H1N1	CY080905	MA	3/10/2009
H3N2	CY068241	CA	4/29/2009	H1N1	CY080961	MA	2/11/2009
H3N2	CY068313	CA	4/30/2009	H1N1	CY080777	MA	2/25/2009
H3N2	GQ385909	AZ	2/25/2009	H1N1	CY093125	MA	2/12/2009
H3N2	CY068609	CA	5/3/2009	H1N1	CY080642	MA	2/8/2009
H3N2	CY080450	NY	5/17/2009	H1N1	CY089107	MA	2/28/2009
H3N2	CY173519	NY	2/16/2009	H1N1	CY080873	MA	3/1/2009
H3N2	GQ369843	MD	12/5/2008	H1N1	CY089781	MA	2/20/2009
H3N2	CY092369	CA	4/29/2009	H1N1	CY080713	MA	2/20/2009

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H3N2	CY093248	TX	2/1/2009	H1N1	CY092872	IL	1/26/2011
H3N2	GQ895022	TX	2/24/2009	H1N1	KC881748	OR	1/18/2011
H3N2	KF765565	TX	4/1/2009	H1N1	KC882173	CA	12/8/2010
H3N2	CY068321	CA	4/29/2009	H1N1	KC882160	NY	12/7/2010
H3N2	CY050580	NY	5/2/2009	H1N1	KC881582	IL	12/29/2010
H3N2	CY068585	CA	5/11/2009	H1N1	KC882150	ID	2/7/2011
H3N2	CY068129	CA	4/28/2009	H1N1	CY097797	DC	12/26/2010
H3N2	CY068009	CA	5/26/2009	H1N1	CY097821	DC	12/24/2010
H3N2	CY068017	CA	5/26/2009	H1N1	CY097868	DC	1/1/2011
H3N2	CY068121	CA	4/27/2009	H1N1	CY090027	DC	1/28/2011
H3N2	CY067953	CA	4/30/2009	H1N1	CY097860	DC	1/1/2011
H3N2	KC535458	GA	5/1/2009	H1N1	KC882015	AZ	3/8/2011
H3N2	CY055083	NY	5/24/2009	H1N1	KC881922	UT	2/18/2011
H3N2	GQ895050	SC	3/9/2009	H1N1	KC882147	TX	2/16/2011
H3N2	CY093255	FL	5/1/2009	H1N1	KC881988	PA	2/22/2011
H3N2	CY068433	CA	4/30/2009	H1N1	KC882217	TX	3/6/2011
H3N2	KC535324	KS	5/9/2009	H1N1	KC881754	OR	1/28/2011
H3N2	CY068033	CA	5/11/2009	H1N1	KC882208	PA	3/13/2011
H3N2	CY068049	CA	5/11/2009	H1N1	KC882043	PA	2/23/2011
H3N2	CY173551	NY	3/16/2009	H1N1	KC882018	MD	2/2/2011
H3N2	CY068617	CA	5/5/2009	H1N1	KC882339	MD	2/2/2011
H3N2	CY089765	MA	5/11/2009	H1N1	KC881697	NJ	3/3/2011
H3N2	CY068041	CA	5/26/2009	H1N1	KC881789	NC	1/18/2011
H3N2	CY067921	CA	4/27/2009	H1N1	CY134473	MA	1/27/2011
H3N2	CY068822	CA	4/27/2009	H1N1	KC881783	VT	1/14/2011
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H3N2	CY067237	CA	5/2/2009	H1N1	KC881756	NJ	1/13/2011
H3N2	CY068686	CA	4/28/2009	H1N1	KC881576	WI	1/6/2011
H3N2	CY068137	CA	4/28/2009	H1N1	KC881920	MA	2/3/2011
H3N2	CY067245	CA	5/1/2009	H1N1	KC882087	NY	1/29/2011
H3N2	CY068457	CA	5/1/2009	H1N1	KC881916	ME	3/11/2011
H3N2	CY068854	CA	4/26/2009	H1N1	CY134465	MA	1/13/2011
H3N2	CY068353	CA	4/30/2009	H1N1	KC882012	MA	3/7/2011
H3N2	CY068577	CA	5/11/2009	H1N1	CY129862	MA	2/16/2011
H3N2	CY067969	CA	5/4/2009	H1N1	KC881931	NY	2/21/2011
H3N2	CY068217	CA	4/28/2009	H1N1	CY134569	MA	2/17/2011
H3N2	CY068806	CA	4/29/2009	H1N1	KC882257	CA	2/15/2011
H3N2	CY067213	CA	4/30/2009	H1N1	KC881648	WI	3/17/2011
H3N2	CY068702	CA	4/28/2009	H1N1	KC881758	IA	1/5/2011
H3N2	CY068393	CA	4/30/2009	H1N1	KC881676	GA	3/5/2011
H3N2	CY067977	CA	5/4/2009	H1N1	KC882125	FL	2/3/2011
H3N2	CY068569	CA	5/9/2009	H1N1	CY092888	SC	1/25/2011

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H3N2	CY068105	CA	4/27/2009	H1N1	KC882102	PA	11/16/2010
H3N2	CY068529	CA	5/6/2009	H1N1	KC881857	PA	11/17/2010
H3N2	CY068513	CA	5/6/2009	H1N1	KC881791	NY	1/4/2011
H3N2	CY064863	CA	4/27/2009	H1N1	KC881679	MS	2/23/2011
H3N2	CY068497	CA	5/1/2009	H1N1	KC881877	MS	2/23/2011
H3N2	CY068297	CA	4/27/2009	H1N1	KC882188	CA	2/9/2011
H3N2	CY068742	CA	4/28/2009	H1N1	KC881735	PA	1/22/2011
H3N2	CY068329	CA	5/1/2009	H1N1	KC882322	NE	2/25/2011
H3N2	CY068169	CA	4/29/2009	H1N1	KC881851	NH	10/4/2010
H3N2	CY068505	CA	5/1/2009	H1N1	KC881632	CT	1/12/2011
H3N2	CY068870	CA	4/28/2009	H1N1	CY129654	NY	3/24/2011
H3N2	CY069349	WA	2/9/2009	H1N1	KC882220	WA	3/8/2011
H3N2	CY068766	CA	4/28/2009	H1N1	KC882259	WY	1/3/2011
H3N2	CY092377	CA	5/1/2009	H1N1	CY111206	MA	1/19/2011
H3N2	CY067197	CA	4/29/2009	H1N1	CY134497	MA	2/7/2011
H3N2	CY050820	NY	5/20/2009	H1N1	KC881937	NM	2/21/2011
H3N2	CY050804	NY	5/17/2009	H1N1	KC881912	NM	2/7/2011
H3N2	CY068001	CA	5/19/2009	H1N1	KC881943	NM	2/9/2011
H3N2	CY068409	CA	4/30/2009	H1N1	KC882138	NM	3/7/2011
H3N2	CY050732	NY	5/5/2009	H1N1	KC882111	CA	10/29/2010
H3N2	CY050684	NY	4/29/2009	H1N1	KC882168	IA	11/29/2010
H3N2	CY068089	CA	4/25/2009	H1N1	KC882099	MT	11/22/2010
H3N2	CY068113	CA	4/25/2009	H1N1	KC882290	CA	2/21/2011
H3N2	CY068521	CA	5/6/2009	H1N1	CY092880	CA	1/28/2011
H3N2	CY067961	CA	5/9/2009	H1N1	CY176562	MA	2/4/2011
H3N2	CY070919	CA	5/9/2009	H1N1	KC881725	WI	2/14/2011
H3N2	CY050812	NY	5/15/2009	H1N1	KC882187	NY	3/14/2011
H3N2	CY050692	NY	4/27/2009	H1N1	KC881596	FL	5/24/2011
H3N2	CY068718	CA	4/28/2009	H1N1	CY134585	MA	2/21/2011
H3N2	CY050620	NY	5/2/2009	H1N1	KC882090	KS	2/8/2011
H3N2	KC535453	NY	5/23/2009	H1N1	KC881653	TX	3/1/2011
H3N2	CY050724	NY	4/30/2009	H1N1	CY111538	MA	2/3/2011
H3N2	CY068281	CA	4/29/2009	H1N1	CY134553	MA	2/16/2011
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H3N2	CY058796	NY	5/19/2009	H1N1	KC881634	NC	12/23/2010
H3N2	CY067993	CA	5/11/2009	H1N1	KC881719	NC	3/1/2011
H3N2	CY068265	CA	4/30/2009	H1N1	KC882151	GA	11/15/2010
H3N2	CY067945	CA	5/4/2009	H1N1	KC882293	CA	3/13/2011
H3N2	CY050468	NY	4/26/2009	H1N1	KC881722	WI	2/6/2011
H3N2	CY050508	NY	4/28/2009	H1N1	KC881854	NV	2/13/2011
H3N2	CY050596	NY	4/27/2009	H1N1	KC881714	IL	3/9/2011

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H3N2	CY050556	NY	4/28/2009	H1N1	KC881876	AZ	2/1/2011
H3N2	CY058780	NY	5/18/2009	H1N1	KC881814	TN	3/8/2011
H3N2	CY080459	NY	5/4/2009	H1N1	KC881573	NV	1/20/2011
H3N2	CY080483	NY	5/23/2009	H1N1	KC882114	TX	11/30/2010
H3N2	CY058756	NY	5/1/2009	H1N1	KC882071	MA	1/8/2011
H3N2	CY084393	NY	5/6/2009	H1N1	KC882331	VA	1/6/2011
H3N2	CY050484	NY	4/28/2009	H1N1	CY129870	DC	1/10/2011
H3N2	CY050836	NY	5/11/2009	H1N1	CY129878	DC	1/13/2011
H3N2	CY050668	NY	5/1/2009	H1N1	KC881898	MD	1/10/2011
H3N2	CY050452	NY	4/27/2009	H1N1	KC881728	DC	2/12/2011
H3N2	CY050460	NY	4/27/2009	H1N1	CY097837	DC	12/30/2010
H3N2	CY050604	NY	4/27/2009	H1N1	KC882078	GA	12/31/2010
H3N2	CY050588	NY	4/28/2009	H1N1	CY097813	DC	12/28/2010
H3N2	CY050516	NY	4/28/2009	H1N1	KC882349	MD	1/24/2011
H3N2	CY058772	NY	5/13/2009	H1N1	KC881787	ME	2/1/2011
H3N2	CY050796	NY	5/13/2009	H1N1	KC881701	MD	1/14/2011
H3N2	CY050572	NY	4/28/2009	H1N1	KC882366	CO	12/29/2010
H3N2	CY058804	NY	5/24/2009	H1N1	KC882117	CA	10/19/2010
H3N2	CY080467	NY	5/16/2009	H1N1	KC881705	NC	1/20/2011
H3N2	CY050780	NY	5/18/2009	H1N1	KC881716	NC	1/20/2011
H3N2	CY055099	NY	5/20/2009	H1N1	CY111262	MA	2/1/2011
H3N2	CY050716	NY	4/27/2009	H1N1	CY134521	MA	2/12/2011
H3N2	CY050500	NY	4/28/2009	H1N1	CY167468	TN	12/10/2010
H3N2	CY050740	NY	4/28/2009	H1N1	CY167660	TN	3/3/2011
H3N2	CY050676	NY	4/29/2009	H1N1	KC882073	MO	11/30/2010
H3N2	CY089629	NY	5/21/2009	H1N1	KC882081	CT	2/13/2011
H3N2	CY084385	NY	4/28/2009	H1N1	KC881643	WI	1/15/2011
H3N2	KC535452	MD	5/11/2009	H1N1	KC882176	AR	11/30/2010
H3N2	CY050524	NY	4/28/2009	H1N1	KC881850	MS	1/13/2011
H3N2	CY058748	NY	4/28/2009	H1N1	CY111286	MA	2/11/2011
H3N2	CY050628	NY	4/29/2009	H1N1	KC881744	WA	1/11/2011
H3N2	KC882784	CA	12/8/2010	H1N1	KC881609	WA	1/5/2011
H3N2	KC882775	WA	12/2/2010	H1N1	KC882314	WI	2/25/2011
H3N2	CY084298	NV	12/6/2010	H1N1	KC881760	KS	1/19/2011
H3N2	KC882702	SC	12/2/2010	H1N1	KC881949	KS	1/19/2011
H3N2	CY111382	MA	3/5/2011	H1N1	KC881785	TX	1/23/2011
H3N2	KC882820	IL	1/4/2011	H1N1	KC881997	NH	2/11/2011
H3N2	KC882781	AZ	11/9/2010	H1N1	KC881598	NE	1/20/2011
H3N2	KC883278	SC	10/3/2010	H1N1	CY134489	MA	1/27/2011
H3N2	KC882974	KS	2/14/2011	H1N1	CY092896	SC	1/29/2011
H3N2	KC883070	IL	1/22/2011	H1N1	KC882398	DE	2/12/2011
H3N2	KC882992	IL	1/22/2011	H1N1	KC882336	MD	2/22/2011

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H3N2	KC883261	MD	12/22/2010	H1N1	KC882346	ME	2/17/2011
H3N2	CY093232	DC	11/23/2010	H1N1	CY111398	MA	3/8/2011
H3N2	KC883264	CO	2/6/2011	H1N1	KC881909	NY	12/9/2010
H3N2	KC883000	FL	2/3/2011	H1N1	KC882032	UT	10/12/2010
H3N2	KC883342	NH	1/17/2011	H1N1	KC882418	NC	1/31/2011
H3N2	KC882589	AR	1/6/2011	H1N1	KC882037	KS	3/1/2011
H3N2	KC882979	IN	1/15/2011	H1N1	KC882214	OR	2/7/2011
H3N2	KC882950	VA	1/11/2011	H1N1	KC882165	MN	12/5/2010
H3N2	KC883039	AL	4/4/2011	H1N1	KC882154	IA	12/23/2010
H3N2	CY167732	TN	3/16/2011	H1N1	KC882170	DE	12/7/2010
H3N2	KC882834	NH	11/23/2010	H1N1	KC882054	WI	10/2/2010
H3N2	KC882577	NC	12/9/2010	H1N1	KC881764	DC	1/18/2011
H3N2	KC883364	IN	2/17/2011	H1N1	KC881884	MT	2/2/2011
H3N2	KC883320	DC	1/2/2011	H1N1	KC881636	FL	1/4/2011
H3N2	KC882551	WV	1/8/2011	H1N1	KC881848	IN	1/16/2011
H3N2	KC882709	IN	12/13/2010	H1N1	KC881628	NC	1/15/2011
H3N2	KC882548	WV	1/2/2011	H1N1	KC882184	MN	4/19/2011
H3N2	KC883362	FL	2/12/2011	H1N1	KC881585	NM	3/29/2011
H3N2	KC883147	MO	3/2/2011	H1N1	KC881924	NC	2/16/2011
H3N2	KC882772	OR	11/23/2010	H1N1	KC881772	NC	1/27/2011
H3N2	CY111318	MA	2/18/2011	H1N1	CY111278	MA	2/7/2011
H3N2	CY084311	TX	12/29/2010	H1N1	KC881579	UT	1/18/2011
H3N2	KC882908	CA	1/16/2011	H1N1	KC881766	RI	1/7/2011
H3N2	KC882883	NJ	11/28/2010	H1N1	CY097829	DC	12/29/2010
H3N2	CY093224	DC	11/17/2010	H1N1	KC882411	DE	2/4/2011
H3N2	KC882867	DC	12/29/2010	H1N1	KC882419	DE	2/4/2011
H3N2	KC883137	NY	3/1/2011	H1N1	KC881864	IL	1/12/2011
H3N2	CY116699	MA	1/19/2011	H1N1	KC882084	IA	2/13/2011
H3N2	KC883198	RI	3/7/2011	H1N1	CY111294	MA	2/15/2011
H3N2	KC882698	MT	10/24/2010	H1N1	KC881873	VA	2/15/2011
H3N2	KC882681	GA	10/22/2010	H1N1	CY134537	MA	2/14/2011
H3N2	KC883323	VT	1/10/2011	H1N1	KC882075	VA	2/15/2011
H3N2	KC882855	MN	12/19/2010	H1N1	KC882285	NJ	2/22/2011
H3N2	KC883120	MN	1/4/2011	H1N1	KC881827	KY	11/1/2010
H3N2	KC882843	MN	12/7/2010	H1N1	KC881830	KY	11/1/2010
H3N2	KC882845	MN	11/25/2010	H1N1	KC881802	TX	1/5/2011
H3N2	KC882870	MN	11/23/2010	H1N1	KC882052	TX	1/5/2011
H3N2	KC882851	MN	12/6/2010	H1N1	KC881630	WV	1/1/2011
H3N2	KC882609	NV	2/8/2011	H1N1	KC882231	KY	12/8/2010
H3N2	KC882541	ME	12/28/2010	H1N1	KC881866	OH	1/11/2011
H3N2	KC882873	MN	12/28/2010	H1N1	CY092417	MO	1/25/2011
H3N2	KC882455	WY	12/21/2010	H1N1	CY167476	TN	12/16/2010

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H3N2	KC883223	NE	3/10/2011	H1N1	CY167492	TN	1/14/2011
H3N2	KC882488	NE	1/20/2011	H1N1	CY167548	TN	2/2/2011
H3N2	CY116707	MA	2/1/2011	H1N1	CY167716	TN	3/25/2011
H3N2	KC882896	KS	12/26/2010	H1N1	CY167556	TN	2/4/2011
H3N2	CY167620	TN	2/25/2011	H1N1	KC882211	WA	2/10/2011
H3N2	CY167628	TN	3/7/2011	H1N1	KC882196	IN	2/20/2011
H3N2	CY111238	MA	1/15/2011	H1N1	KC882235	OH	2/1/2011
H3N2	CY111174	MA	1/13/2011	H1N1	KC882334	MD	2/25/2011
H3N2	CY111358	MA	2/28/2011	H1N1	KC882096	NC	11/22/2010
H3N2	CY111302	MA	2/16/2011	H1N1	KC882232	AL	1/4/2011
H3N2	CY134609	MA	2/25/2011	H1N1	KC881910	MI	2/23/2011
H3N2	KC883233	MA	12/31/2010	H1N1	KC882278	MI	3/30/2011
H3N2	CY134529	MA	2/13/2011	H1N1	KC882205	UT	3/10/2011
H3N2	CY111342	MA	2/24/2011	H1N1	CY111254	MA	1/27/2011
H3N2	CY111142	MA	1/3/2011	H1N1	KC881960	RI	2/2/2011
H3N2	KC882621	MA	1/9/2011	H1N1	KC882029	KY	10/11/2010
H3N2	KC882536	ME	1/3/2011	H1N1	KC881822	PA	2/28/2011
H3N2	KC882563	NJ	1/11/2011	H1N1	KC881658	CO	3/23/2011
H3N2	KC882557	NJ	1/11/2011	H1N1	KC882039	NY	3/20/2011
H3N2	KC883165	VT	4/12/2011	H1N1	KC882301	MO	1/10/2011
H3N2	CY111446	MA	3/17/2011	H1N1	KC881868	AZ	12/25/2010
H3N2	KC882813	ND	1/14/2011	H1N1	KC882013	KS	12/1/2010
H3N2	CY111390	MA	2/26/2011	H1N1	KC881569	NE	1/8/2011
H3N2	KC882849	VT	12/21/2010	H1N1	KC881835	NE	2/12/2011
H3N2	KC882806	WI	12/28/2010	H1N1	KC881862	SC	1/5/2011
H3N2	KC882856	VT	12/22/2010	H1N1	KC882123	CO	3/8/2011
H3N2	KC882521	NJ	2/3/2011	H1N1	KC881892	WI	1/20/2011
H3N2	KC882595	NC	2/1/2011	H1N1	KC881833	KY	11/10/2010
H3N2	KC882499	MA	3/4/2011	H1N1	CY176442	OH	1/21/2011
H3N2	KC882862	DE	12/20/2010	H1N1	KC882362	IN	2/7/2011
H3N2	KC882879	VT	1/5/2011	H1N1	KC882343	IN	1/19/2011
H3N2	KC883156	NY	4/13/2011	H1N1	KC882263	KY	12/6/2010
H3N2	KC882941	NH	1/31/2011	H1N1	KC881750	AR	1/13/2011
H3N2	CY134545	MA	2/15/2011	H1N1	KC881952	SD	1/12/2011
H3N2	KC882739	LA	12/7/2010	H1N1	KC881639	SD	1/12/2011
H3N2	CY111246	MA	1/28/2011	H1N1	KC882120	DE	11/10/2010
H3N2	KC882764	NV	11/5/2010	H1N1	KC882261	IN	12/13/2010
H3N2	KC883207	KY	10/18/2010	H1N1	KC882395	MD	3/2/2011
H3N2	KC882882	VT	1/10/2011	H1N1	KC881972	MN	2/18/2011
H3N2	KC882497	MA	12/15/2010	H1N1	KC881905	MN	2/18/2011
H3N2	CY111134	MA	1/4/2011	H1N1	KC882223	CA	3/2/2011
H3N2	KC882888	NJ	12/7/2010	H1N1	KC881592	NC	2/25/2011

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H3N2	KC883302	GA	12/31/2010	H1N1	KC881612	CA	1/17/2011
H3N2	CY139586	MA	1/25/2011	H1N1	KC882202	WI	2/25/2011
H3N2	CY111214	MA	1/19/2011	H1N1	CY111374	MA	3/3/2011
H3N2	KC883104	DE	3/6/2011	H1N1	KC881682	TN	2/23/2011
H3N2	CY111182	MA	1/13/2011	H1N1	KC881624	MN	1/6/2011
H3N2	KC882512	PA	12/12/2010	H1N1	KC881606	OK	1/4/2011
H3N2	CY111454	MA	3/23/2011	H1N1	CY167724	TN	4/13/2011
H3N2	KC882822	SD	1/6/2011	H1N1	KC882255	MO	12/21/2010
H3N2	KC883110	VT	3/6/2011	H1N1	KC882253	ME	12/28/2010
H3N2	CY091565	SC	1/28/2011	H1N1	KC882288	AR	4/14/2011
H3N2	KC882662	SC	11/12/2010	H1N1	KC882251	CT	12/14/2010
H3N2	KC883356	SC	2/14/2011	H1N1	KC881741	CA	1/7/2011
H3N2	CY111350	MA	2/26/2011	H1N1	CY167748	TN	3/31/2011
H3N2	KC882917	WA	1/22/2011	H1N1	CY167756	TN	4/4/2011
H3N2	CY111326	MA	2/21/2011	H1N1	CY167309	TN	3/17/2011
H3N2	CY111310	MA	2/18/2011	H1N1	CY167580	TN	2/11/2011
H3N2	CY084327	NC	1/4/2011	H1N1	CY167588	TN	2/14/2011
H3N2	KC882946	VT	2/7/2011	H1N1	KC882157	RI	11/18/2010
H3N2	KC882553	NJ	12/28/2010	H1N1	KC881637	AL	12/28/2010
H3N2	KC883129	NY	1/31/2011	H1N1	KC881615	CA	1/27/2011
H3N2	CY111422	MA	3/12/2011	H1N1	KC881729	OR	12/21/2010
H3N2	KC882953	MN	1/19/2011	H1N1	KC881805	TN	2/23/2011
H3N2	KC882591	RI	1/25/2011	H1N1	KC882199	MT	3/3/2011
H3N2	KC882944	VT	2/7/2011	H1N1	KC882295	MO	3/9/2011
H3N2	CY117581	MA	2/14/2011	H1N1	KC881663	FL	3/15/2011
H3N2	CY134601	MA	2/24/2011	H1N1	KC881810	LA	3/22/2011
H3N2	KC883142	DE	4/11/2011	H1N1	KC882403	LA	3/24/2011
H3N2	CY134505	MA	2/10/2011	H1N1	KC881882	NC	1/14/2011
H3N2	KC883114	VA	2/2/2011	H1N1	KC881856	WA	2/17/2011
H3N2	CY134593	MA	2/22/2011	H1N1	KC882192	CT	4/2/2011
H3N2	KC883306	TN	12/27/2010	H1N1	KC882127	WY	1/28/2011
H3N2	KC882893	VT	1/18/2011	H1N1	CY092904	GA	1/27/2011
H3N2	KC882523	MD	2/7/2011	H1N1	KC882136	NM	4/19/2011
H3N2	KC882502	RI	3/3/2011	H1N1	KC881890	CO	1/24/2011
H3N2	KC883427	MD	3/27/2011	H1N1	KC882226	NE	3/3/2011
H3N2	KC883209	PA	10/28/2010	H1N1	KC881706	NY	4/13/2011
H3N2	KC882721	ND	12/13/2010	H1N1	KC881707	NY	4/13/2011
H3N2	KC883297	LA	10/7/2010	H1N1	KC891090	RI	2/29/2012
H3N2	KC882509	WY	12/16/2010	H1N1	KC891378	OR	12/16/2011
H3N2	KC882729	WI	11/12/2010	H1N1	KC891263	FL	12/20/2011
H3N2	KC882618	RI	3/7/2011	H1N1	KC891219	MD	4/1/2012
H3N2	KC882462	FL	12/10/2010	H1N1	KC891078	WA	2/13/2012

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H3N2	CY084303	FL	12/10/2010	H1N1	CY148003	GA	2/1/2012
H3N2	KC882935	NH	1/13/2011	H1N1	KC891059	SC	11/29/2011
H3N2	KC883292	CA	10/5/2010	H1N1	KC891355	NY	12/14/2011
H3N2	KC882777	CA	11/13/2010	H1N1	KC891483	NJ	1/17/2012
H3N2	KC882752	MA	1/9/2011	H1N1	CY148251	GA	2/1/2012
H3N2	CY134481	MA	1/27/2011	H1N1	KC891289	GA	3/5/2012
H3N2	CY111190	MA	1/21/2011	H1N1	KC891503	DE	2/12/2012
H3N2	CY111166	MA	1/12/2011	H1N1	KC891573	DE	2/12/2012
H3N2	CY134513	MA	2/12/2011	H1N1	KC891210	CA	11/16/2011
H3N2	CY111270	MA	2/7/2011	H1N1	KC891250	FL	12/7/2011
H3N2	KC882491	OK	12/7/2010	H1N1	KC891202	FL	12/7/2011
H3N2	KC883307	MI	1/4/2011	H1N1	KC891023	FL	10/30/2011
H3N2	KC882624	NE	1/27/2011	H1N1	KC891201	FL	10/30/2011
H3N2	CY111230	MA	1/13/2011	H1N1	KC891317	VT	12/22/2011
H3N2	KC883017	UT	3/10/2011	H1N1	KC891468	NH	1/30/2012
H3N2	KC883374	MT	4/5/2011	H1N1	KC891341	MN	3/20/2012
H3N2	KC883240	NC	1/27/2011	H1N1	CY176706	MN	2/27/2012
H3N2	CY084300	NV	11/4/2010	H1N1	KC891015	CA	1/18/2012
H3N2	KC882604	WY	11/28/2010	H1N1	KC891364	FL	1/3/2012
H3N2	KC882836	NY	12/1/2010	H1N1	KC891106	NY	3/22/2012
H3N2	CY117589	MA	3/9/2011	H1N1	KC891264	PA	3/17/2012
H3N2	KC882891	DC	12/31/2010	H1N1	KC891556	IL	4/16/2012
H3N2	KC882801	AL	11/3/2010	H1N1	KC891193	IL	4/16/2012
H3N2	KC882665	SC	11/28/2010	H1N1	KC891026	WI	10/16/2011
H3N2	KC882811	WI	1/6/2011	H1N1	KC891320	IN	3/2/2012
H3N2	CY111222	MA	1/13/2011	H1N1	KC891010	VT	2/6/2012
H3N2	KC882968	IA	2/19/2011	H1N1	KC891382	VT	2/1/2012
H3N2	CY084299	AL	12/16/2010	H1N1	KC891385	UT	1/17/2012
H3N2	KC882465	AL	12/16/2010	H1N1	KC891372	UT	1/17/2012
H3N2	KC882999	MT	2/9/2011	H1N1	KC891205	CO	11/26/2011
H3N2	KC883353	MT	1/10/2011	H1N1	KC891149	KY	3/29/2012
H3N2	KC883424	KS	3/29/2011	H1N1	KC891246	NM	3/6/2012
H3N2	KC883102	NH	3/1/2011	H1N1	KC891032	WV	1/31/2012
H3N2	KC883258	ID	1/5/2011	H1N1	KC891035	OR	1/24/2012
H3N2	KC882526	ME	2/3/2011	H1N1	KC891063	MD	2/14/2012
H3N2	CY111334	MA	2/23/2011	H1N1	KC508625	AZ	2/29/2012
H3N2	CY084330	SC	1/3/2011	H1N1	KC891260	PA	12/19/2011
H3N2	KC882584	ID	1/2/2011	H1N1	KC891461	ID	1/27/2012
H3N2	KC882479	TX	12/31/2010	H1N1	KC891143	CO	3/28/2012
H3N2	CY084328	OK	1/5/2011	H1N1	KC891306	CO	3/28/2012
H3N2	CY084324	MA	1/10/2011	H1N1	KC891096	ND	2/26/2012
H3N2	KC883350	FL	1/17/2011	H1N1	KC891099	ND	2/26/2012

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H3N2	KC883407	WA	3/8/2011	H1N1	KC891471	NM	1/26/2012
H3N2	KC883008	MT	3/2/2011	H1N1	KC891177	LA	4/3/2012
H3N2	CY084302	CO	12/17/2010	H1N1	KJ411983	AZ	4/13/2012
H3N2	KC882674	UT	10/14/2010	H1N1	KC891043	TN	2/2/2012
H3N2	CY084326	NV	1/18/2011	H1N1	KC891424	MA	3/12/2012
H3N2	KC883086	NV	4/4/2011	H1N1	KC891522	TX	3/19/2012
H3N2	KC882902	CA	1/15/2011	H1N1	KC891395	FL	5/1/2012
H3N2	KC883038	WY	3/23/2011	H1N1	KC891057	TX	3/14/2012
H3N2	KC883435	MN	4/18/2011	H1N1	KC891115	NY	3/5/2012
H3N2	KC883084	OR	3/28/2011	H1N1	KC891417	NY	3/5/2012
H3N2	KC882685	UT	11/3/2010	H1N1	JX905426	FL	2/27/2012
H3N2	CY084306	OK	10/18/2010	H1N1	KC891020	TX	3/14/2012
H3N2	CY125717	MA	2/21/2011	H1N1	KC891276	TX	3/2/2012
H3N2	KC882876	VT	1/2/2011	H1N1	KC891228	IA	4/12/2012
H3N2	KC883327	VA	12/27/2010	H1N1	CY176698	NY	3/21/2012
H3N2	CY111430	MA	3/16/2011	H1N1	CY147995	GA	2/1/2012
H3N2	KC882719	MT	12/26/2010	H1N1	CY148211	GA	2/1/2012
H3N2	CY111546	MA	2/8/2011	H1N1	CY148099	GA	2/1/2012
H3N2	CY111414	MA	3/14/2011	H1N1	CY148091	GA	2/1/2012
H3N2	KC883131	IA	4/1/2011	H1N1	CY148083	GA	2/1/2012
H3N2	CY084316	CO	1/18/2011	H1N1	CY148203	GA	2/1/2012
H3N2	CY116715	MA	3/1/2011	H1N1	CY148075	GA	2/1/2012
H3N2	CY134561	MA	2/14/2011	H1N1	CY147979	GA	2/1/2012
H3N2	KC882530	CO	3/25/2011	H1N1	CY148163	GA	2/1/2012
H3N2	KC883135	WV	3/29/2011	H1N1	CY147987	GA	2/1/2012
H3N2	KC883281	UT	12/4/2010	H1N1	KC891452	UT	2/2/2012
H3N2	KC883012	OH	3/1/2011	H1N1	KC891394	WI	5/24/2012
H3N2	CY111158	MA	1/11/2011	H1N1	KC891489	NV	1/23/2012
H3N2	KC883288	WI	11/2/2010	H1N1	KC891084	CA	2/14/2012
H3N2	KC882574	AL	11/7/2010	H1N1	KC891069	NY	2/12/2012
H3N2	CY084317	DE	1/4/2011	H1N1	KC891121	WI	4/1/2012
H3N2	KC883106	VT	3/4/2011	H1N1	KC891049	WI	4/1/2012
H3N2	CY111126	MA	1/3/2011	H1N1	KC891419	OR	3/27/2012
H3N2	KC883348	DE	2/8/2011	H1N1	KC891390	MD	5/15/2012
H3N2	KC882924	DE	1/25/2011	H1N1	KC891392	ID	4/18/2012
H3N2	KC882804	IL	12/21/2010	H1N1	KC891393	ID	4/18/2012
H3N2	KC883291	WI	12/1/2010	H1N1	CY148067	GA	2/1/2012
H3N2	KC882682	UT	11/15/2010	H1N1	CY148059	GA	2/1/2012
H3N2	KC882707	MT	12/9/2010	H1N1	KC891455	DE	1/22/2012
H3N2	KC882744	UT	1/18/2011	H1N1	CY148267	GA	2/1/2012
H3N2	KC883044	GA	4/12/2011	H1N1	KC508624	AZ	2/23/2012

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H3N2	KC883034	MI	3/18/2011	H1N1	KC513476	AZ	4/4/2012
H3N2	KC883121	CT	3/3/2011	H1N1	KC513478	AZ	4/4/2012
H3N2	KC883420	VA	3/2/2011	H1N1	CY148155	GA	2/1/2012
H3N2	KC883338	CA	2/1/2011	H1N1	CY147971	GA	2/1/2012
H3N2	KC882938	NH	2/1/2011	H1N1	CY147963	GA	2/1/2012
H3N2	KC883429	VT	5/3/2011	H1N1	CY148171	GA	2/1/2012
H3N2	KC883003	WI	2/25/2011	H1N1	KC891231	OR	4/11/2012
H3N2	CY111438	MA	3/17/2011	H1N1	KC891391	ID	5/1/2012
H3N2	KC883152	CT	4/2/2011	H1N1	KC891474	NE	2/9/2012
H3N2	CY111470	MA	4/25/2011	H1N1	KC891239	ME	3/6/2012
H3N2	CY111366	MA	3/2/2011	H1N1	KC891267	RI	3/21/2012
H3N2	KC883158	MN	3/18/2011	H1N1	KC891437	CA	3/30/2012
H3N2	KC883018	WI	3/6/2011	H1N1	KC891055	UT	5/8/2012
H3N2	CY134577	MA	2/18/2011	H1N1	KC891181	NM	4/30/2012
H3N2	KC883160	MN	5/8/2011	H1N1	CY148259	GA	2/1/2012
H3N2	KC882538	PA	3/15/2011	H1N1	KC891129	IL	2/13/2012
H3N2	KC883387	WI	5/3/2011	H1N1	KC891179	IL	2/29/2012
H3N2	KC883315	CT	11/24/2010	H1N1	KC891280	TN	3/5/2012
H3N2	KC883246	ID	3/15/2011	H1N1	KC891102	MI	3/4/2012
H3N2	CY117597	MA	3/21/2011	H1N1	KC891234	AZ	1/24/2012
H3N2	CY167564	TN	2/7/2011	H1N1	KC891087	KY	2/10/2012
H3N2	KC882758	TX	10/14/2010	H1N1	KC891158	KY	2/19/2012
H3N2	KC883150	NH	4/11/2011	H1N1	KC891350	UT	3/15/2012
H3N2	KC882695	KY	11/9/2010	H1N1	KC891184	ID	4/8/2012
H3N2	KC882518	MA	2/7/2011	H1N1	KC891037	NC	2/7/2012
H3N2	KC882506	KY	12/15/2010	H1N1	KC891313	CA	5/1/2012
H3N2	CY167572	TN	2/7/2011	H1N1	KC891480	MD	1/28/2012
H3N2	KC883345	KS	1/21/2011	H1N1	KC891029	MO	2/6/2012
H3N2	KC883022	IN	3/12/2011	H1N1	KC891464	TX	2/1/2012
H3N2	CY167612	TN	2/22/2011	H1N1	KC891054	TX	1/7/2012
H3N2	CY084314	CA	1/11/2011	H1N1	KC891222	FL	4/3/2012
H3N2	KC883139	NE	4/4/2011	H1N1	KC891427	GA	2/24/2012
H3N2	CY111150	MA	1/5/2011	H1N1	KC891251	GA	2/24/2012
H3N2	KC883057	MA	1/5/2011	H1N1	KC891135	IL	3/8/2012
H3N2	CY091557	TX	1/25/2011	H1N1	KC891358	TX	1/9/2012
H3N2	KC883390	TX	1/12/2011	H1N1	KC891248	ID	2/18/2012
H3N2	KC882459	TX	12/7/2010	H1N1	KC891161	NV	4/4/2012
H3N2	CY084309	TX	12/21/2010	H1N1	KC891492	GA	1/29/2012
H3N2	CY084310	TX	12/29/2010	H1N1	KC891325	CA	12/28/2011
H3N2	KC883234	IN	12/19/2010	H1N1	KC891007	UT	2/1/2012
H3N2	KC882630	KY	1/18/2011	H1N1	KC891093	TX	2/26/2012
H3N2	KC882742	TX	12/28/2010	H1N1	KC513480	AZ	4/3/2012

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H3N2	CY084312	AZ	1/7/2011	H1N1	KC891132	IL	3/12/2012
H3N2	KC882482	CA	12/14/2010	H1N1	KC891050	IL	3/12/2012
H3N2	CY084297	AZ	12/6/2010	H1N1	KC891051	IL	3/8/2012
H3N2	KC882493	AZ	12/6/2010	H1N1	KC891118	NH	4/11/2012
H3N2	KC883359	ND	2/8/2011	H1N1	KC891415	PA	4/16/2012
H3N2	KC883049	WI	4/15/2011	H1N1	KC891273	WY	3/10/2012
H3N2	KC883030	MS	4/12/2011	H1N1	KC891196	VA	4/25/2012
H3N2	KC882615	MS	3/15/2011	H1N1	KC891339	LA	3/15/2012
H3N2	KC883413	AZ	2/17/2011	H1N1	KC891548	CA	1/19/2012
H3N2	CY111406	MA	3/13/2011	H1N1	KC891446	CA	1/19/2012
H3N2	KC883054	FL	5/1/2011	H1N1	KC891126	SC	4/8/2012
H3N2	KC882982	AL	1/5/2011	H1N1	KC891534	TX	2/23/2012
H3N2	KC893175	MS	2/8/2011	H1N1	KC891425	AL	3/19/2012
H3N2	KC882929	DE	1/25/2011	H1N1	KC891170	WA	3/20/2012
H3N2	KC883415	NM	4/7/2011	H1N1	KC891582	MD	3/8/2012
H3N2	KC882724	FL	12/29/2010	H1N1	KC891109	NY	3/19/2012
H3N2	KC882736	WA	12/10/2010	H1N1	KC891283	WA	2/24/2012
H3N2	CY167644	TN	3/2/2011	H1N1	KC891152	NC	3/28/2012
H3N2	CY167652	TN	3/7/2011	H1N1	KC891406	NM	5/3/2012
H3N2	CY167317	TN	3/31/2011	H1N1	KC891190	NJ	5/2/2012
H3N2	CY084313	AZ	1/10/2011	H1N1	KC891164	NM	3/29/2012
H3N2	KC883380	MI	4/5/2011	H1N1	KC891388	NM	3/29/2012
H3N2	KC882830	DE	11/30/2010	H1N1	KC891066	KS	2/13/2012
H3N2	KC882533	NE	2/25/2011	H1N1	KC891047	IL	3/2/2012
H3N2	KC882860	IA	12/30/2010	H1N1	KC891138	IL	3/2/2012
H3N2	CY167516	TN	1/21/2011	H1N1	KC891389	NH	3/10/2012
H3N2	CY084315	CO	1/3/2011	H1N1	KC891528	TX	3/2/2012
H3N2	CY111198	MA	1/18/2011	H1N1	KC891477	WI	2/3/2012
H3N2	CY084333	TX	1/11/2011	H1N1	KC891187	IA	4/14/2012
H3N2	KC882601	CO	11/23/2010	H1N1	KC513475	AZ	3/14/2012
H3N2	KC882692	FL	10/30/2010	H1N1	KC891343	VA	3/9/2012
H3N2	KC882734	TX	12/6/2010	H1N1	KC891574	NY	4/17/2012
H3N2	KC882598	MS	2/8/2011	H1N1	KC891314	NM	4/9/2012
H3N2	KC882994	WI	2/8/2011	H1N1	KC891225	MT	3/26/2012
H3N2	KC882918	VT	1/27/2011	H1N1	KC891559	TX	3/16/2012
H3N2	KC882568	GA	2/10/2011	H1N1	KC891323	AL	1/6/2012
H3N2	KC883377	WI	4/12/2011	H1N1	KC891588	TX	1/10/2012
H3N2	CY167540	TN	2/4/2011	H1N1	KC891449	NC	1/23/2012
H3N2	CY167692	TN	3/18/2011	H1N1	KC891360	ME	1/11/2012
H3N2	CY167700	TN	3/22/2011	H1N1	KC891363	TX	1/15/2012
H3N2	CY167676	TN	3/18/2011	H1N1	CY125783	MA	3/26/2012
H3N2	CY167764	TN	4/7/2011	H1N1	KC891040	UT	2/9/2012

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H3N2	CY167604	TN	2/18/2011	H1N1	KC891072	OK	2/21/2012
H3N2	CY167532	TN	1/28/2011	H1N1	KC891307	TX	4/1/2012
H3N2	CY167684	TN	3/15/2011	H1N1	KC891167	TX	4/1/2012
H3N2	CY167708	TN	3/15/2011	H1N1	KC891384	CO	1/4/2012
H3N2	CY167668	TN	3/15/2011	H1N1	KC891408	NC	3/1/2012
H3N2	CY167596	TN	2/16/2011	H1N1	KC891513	TX	3/8/2012
H3N2	CY167740	TN	3/23/2011	H1N1	KC891516	CA	2/20/2012
H3N2	KC883419	MO	1/5/2011	H1N1	KC891216	NC	4/26/2012
H3N2	KC882606	NY	11/14/2010	H1N1	KC891458	MO	1/18/2012
H3N2	CY084331	SC	1/18/2011	H1N1	KC891075	ID	1/31/2012
H3N2	KC883029	WI	3/30/2011	H1N1	CY176714	OH	3/12/2012
H3N2	KC882690	FL	11/1/2010	H1N1	KC891123	ME	4/4/2012
H3N2	CY084325	NV	1/18/2011	H1N1	KC891495	WI	1/10/2012
H3N2	KC883285	SD	12/15/2010	H1N1	KC891509	TX	1/26/2012
H3N2	KC882716	SD	12/15/2010	H1N1	KC891500	TX	2/24/2012
H3N2	CY084332	TX	1/7/2011	H1N1	KC891569	TX	2/25/2012
H3N2	KC882799	WI	10/23/2010	H1N1	KC891506	TX	1/26/2012
H3N2	KC882570	CO	12/8/2010	H1N1	KC891540	TX	1/26/2012
H3N2	CY084301	AZ	12/20/2010	H1N1	KC891541	TX	2/21/2012
H3N2	KC883203	MD	1/7/2011	H1N1	KC891543	TX	2/25/2012
H3N2	KC883183	CA	1/3/2011	H1N1	KC891367	CO	1/4/2012
H3N2	KC883311	SC	1/19/2011	H1N1	CY125775	MA	2/21/2012
H3N2	KC883333	LA	1/12/2011	H1N1	KC891270	NV	3/3/2012
H3N2	CY084318	FL	1/17/2011	H1N1	KC513481	AZ	3/10/2012
H3N2	KC883075	OK	2/8/2011	H1N1	KC891242	KS	3/13/2012
H3N2	KC883249	OK	11/3/2010	H1N1	KC891519	TX	3/12/2012
H3N2	KC882712	GA	11/24/2010	H1N1	CY176530	NC	3/8/2012
H3N2	KC883252	AR	11/22/2010	H1N1	KC891176	IA	3/17/2012
H3N2	CY167524	TN	1/24/2011	H1N1	KC891346	CO	3/21/2012
H3N2	KC883451	MS	2/8/2011	H1N1	KC891443	NH	3/10/2012
H3N2	KC883077	LA	2/17/2011	H1N1	KC891562	TX	3/27/2012
H3N2	KC882955	MN	1/21/2011	H1N1	KC891146	WY	4/5/2012
H3N2	CY092281	CA	1/16/2011	H1N1	KC891282	SC	2/27/2012
H3N2	CY091573	IL	1/19/2011	H1N1	KC891291	GA	3/7/2012
H3N2	KC882514	PA	1/4/2011	H1N1	KC891112	NY	3/7/2012
H3N2	KC883024	GA	3/15/2011	H1N1	KC891173	OK	3/5/2012
H3N2	CY111478	MA	3/11/2011	H1N1	KC891563	IL	1/25/2012
H3N2	CY111462	MA	3/29/2011	H1N1	KC891566	IL	1/25/2012
H3N2	KC882900	NM	11/30/2010	H1N1	KC891060	TX	2/12/2012
H3N2	KC883116	MN	2/19/2011	H1N1	CY176690	NY	3/6/2012
H3N2	KC883221	ID	3/6/2011	H1N1	KC891081	WA	2/13/2012
H3N2	KC883336	NV	1/27/2011	H1N1	KC891019	TX	3/7/2012

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H3N2	CY080268	OK	11/20/2010	H1N1	KC891305	TX	3/7/2012
H3N2	CY080269	OK	11/22/2010	H1N1	KF647920	MN	10/29/2012
H3N2	KC882545	MD	11/16/2010	H1N1	KF648213	WI	10/15/2012
H3N2	KC883059	TX	2/8/2011	H1N1	KF647925	WY	12/4/2012
H3N2	KC883394	WA	2/2/2011	H1N1	KF648122	WY	12/26/2012
H3N2	KC882483	CA	1/3/2011	H1N1	KF648274	SC	11/13/2012
H3N2	KC883126	MO	2/11/2011	H1N1	KF648244	SC	10/22/2012
H3N2	KC883095	NM	3/8/2011	H1N1	KF199855	SC	10/10/2012
H3N2	KC882977	DC	2/15/2011	H1N1	CY130173	SC	10/3/2012
H3N2	KC882962	VT	2/12/2011	H1N1	KF928610	SC	10/2/2012
H3N2	KC882793	OR	12/20/2010	H1N1	CY130176	SC	10/4/2012
H3N2	KC883299	LA	12/29/2010	H1N1	CY171159	IL	12/7/2012
H3N2	KC882639	TX	2/5/2011	H1N1	KF648273	IN	1/14/2013
H3N2	KC882633	WY	2/17/2011	H1N1	KF648023	NY	12/2/2012
H3N2	KC883443	NM	1/24/2011	H1N1	KF648106	MA	1/2/2013
H3N2	KC882840	IA	12/13/2010	H1N1	KF648105	MA	1/2/2013
H3N2	KC882817	OH	1/17/2011	H1N1	KF648206	NY	10/2/2012
H3N2	KC883433	MN	3/18/2011	H1N1	KF648261	NY	10/2/2012
H3N2	CY084305	OH	12/30/2010	H1N1	KF648005	IN	11/25/2012
H3N2	KC882923	DE	1/23/2011	H1N1	CY168807	MA	12/25/2012
H3N2	CY167500	TN	1/21/2011	H1N1	CY168879	MA	12/26/2012
H3N2	KC883371	TN	3/16/2011	H1N1	KF648276	RI	12/5/2012
H3N2	KC883093	CA	3/25/2011	H1N1	CY168423	MA	1/30/2013
H3N2	KC882439	IA	12/30/2010	H1N1	CY148316	MA	12/23/2012
H3N2	KC883099	WA	4/6/2011	H1N1	CY169975	MA	2/3/2013
H3N2	KC883219	WY	1/12/2011	H1N1	KF648250	KY	2/8/2013
H3N2	KC882958	CT	2/6/2011	H1N1	CY183217	TX	1/9/2013
H3N2	KC882790	TX	12/20/2010	H1N1	CY170695	CA	1/15/2013
H3N2	CY167508	TN	1/24/2011	H1N1	KF886313	CA	1/23/2013
H3N2	KC883216	MS	1/3/2011	H1N1	KF648104	OH	1/8/2013
H3N2	CY091581	CA	1/14/2011	H1N1	KF648220	OK	2/12/2013
H3N2	CY167484	TN	1/7/2011	H1N1	KF648124	FL	3/11/2013
H3N2	KC893178	MS	2/8/2011	H1N1	KF648201	GA	4/8/2013
H3N2	KC882965	IA	2/18/2011	H1N1	CY186067	TX	1/21/2013
H3N2	KC882914	NM	1/18/2011	H1N1	KF648100	TX	12/15/2012
H3N2	KC882628	RI	1/31/2011	H1N1	KF647924	WI	11/14/2012
H3N2	KC882644	ID	2/8/2011	H1N1	KF886333	CA	1/30/2013
H3N2	KC882579	ID	11/23/2010	H1N1	CY170839	CA	1/19/2013
H3N2	KC882829	KS	10/21/2010	H1N1	CY141258	SD	1/4/2013
H3N2	CY167282	TN	12/8/2010	H1N1	CY169863	MA	1/21/2013
H3N2	KC882678	AL	10/28/2010	H1N1	CY183145	TX	1/8/2013
H3N2	KC883212	CO	1/2/2011	H1N1	CY186043	TX	2/5/2013

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H3N2	KC882727	IL	12/24/2010	H1N1	KF648256	CA	1/22/2013
H3N2	KC883062	WI	2/23/2011	H1N1	KF648136	CA	1/22/2013
H3N2	KC882705	OH	11/16/2010	H1N1	KF647968	ID	2/8/2013
H3N2	CY084329	OK	1/7/2011	H1N1	CY170927	CA	1/26/2013
H3N2	CY084308	TX	12/21/2010	H1N1	KF647974	IL	3/11/2013
H3N2	KC883201	NE	1/7/2011	H1N1	KF648045	NM	3/14/2013
H3N2	KC883317	IA	12/19/2010	H1N1	CY147208	IL	4/9/2013
H3N2	CY092273	CA	1/28/2011	H1N1	KF647933	TX	10/18/2012
H3N2	CY092265	CA	1/28/2011	H1N1	KF648153	FL	3/13/2013
H3N2	KC882471	OK	12/23/2010	H1N1	CY147203	CA	1/29/2013
H3N2	CY084307	OK	12/23/2010	H1N1	CY147209	AL	4/19/2013
H3N2	KC883329	CT	1/7/2011	H1N1	CY163419	NY	3/26/2013
H3N2	KC882612	PA	2/17/2011	H1N1	KF648036	NJ	3/19/2013
H3N2	KC883080	LA	3/15/2011	H1N1	KF648221	WI	5/24/2013
H3N2	CY167636	TN	2/24/2011	H1N1	KF648196	NC	4/9/2013
H3N2	KC883367	FL	3/17/2011	H1N1	KF648164	LA	4/11/2013
H3N2	KC883408	NV	3/7/2011	H1N1	KF648063	NJ	12/8/2012
H3N2	KC882930	KS	1/7/2011	H1N1	CY170079	MA	3/17/2013
H3N2	KC882984	UT	2/12/2011	H1N1	CY170087	MA	3/18/2013
H3N2	KC882971	KS	2/1/2011	H1N1	KF648073	PA	12/19/2012
H3N2	KC883383	KY	3/9/2011	H1N1	KF647915	IN	2/2/2013
H3N2	JQ290164	WV	11/21/2011	H1N1	KF648152	VT	4/8/2013
H3N2	JN866186	ME	10/10/2011	H1N1	KF648094	PA	12/19/2012
H3N2	JX905419	UT	3/29/2012	H1N1	KF648091	TX	12/17/2012
H3N2	JX905414	UT	3/29/2012	H1N1	KF648075	PA	12/18/2012
H3N2	JQ070792	IN	10/22/2011	H1N1	KF648095	PA	12/18/2012
H3N2	JN992750	IN	10/22/2011	H1N1	KF647987	PA	1/18/2013
H3N2	JQ070784	IN	10/22/2011	H1N1	KF648183	TN	1/9/2013
H3N2	JQ290172	IA	11/14/2011	H1N1	KF647917	NE	2/6/2013
H3N2	JQ290180	IA	11/14/2011	H1N1	KF648041	KS	3/21/2013
H3N2	JQ070760	IA	11/14/2011	H1N1	KF647938	PA	11/23/2012
H3N2	JQ070776	IA	11/14/2011	H1N1	CY141237	NY	1/20/2013
H3N2	JQ290188	IA	11/14/2011	H1N1	CY141236	NY	1/18/2013
H3N2	JQ070768	IA	11/14/2011	H1N1	CY141238	NY	1/20/2013
H3N2	KC892260	FL	10/20/2011	H1N1	CY147202	NY	1/22/2013
H3N2	KC892312	MT	4/4/2012	H1N1	KF648255	NY	1/22/2013
H3N2	KC893075	CA	1/10/2012	H1N1	CY141233	NY	1/7/2013
H3N2	KC892829	CA	2/20/2012	H1N1	KF648147	GA	1/2/2013
H3N2	KC892796	CA	1/4/2012	H1N1	CY141272	VA	1/10/2013
H3N2	KC893047	OR	10/4/2011	H1N1	CY163412	GA	2/21/2013
H3N2	KC892706	MS	5/14/2012	H1N1	CY163416	KY	3/12/2013
H3N2	KC892274	MA	4/20/2012	H1N1	KF648093	NC	2/13/2013

Subtype	Accession	State	Date	Subtype	Accession	State	Date
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H3N2	CY120913	OH	2/14/2012	H1N1	KF647914	PA	2/14/2013
H3N2	KC893171	TX	2/6/2012	H1N1	CY147201	CA	1/17/2013
H3N2	KC892294	ME	2/3/2012	H1N1	KF648039	KY	3/30/2013
H3N2	KC892776	DE	12/28/2011	H1N1	KF648162	PA	4/9/2013
H3N2	KC892477	MI	2/2/2012	H1N1	CY163414	NY	2/25/2013
H3N2	KC892965	MI	12/25/2011	H1N1	KF648219	CA	1/12/2013
H3N2	KC892626	NH	3/4/2012	H1N1	KF648163	UT	4/14/2013
H3N2	KC893054	RI	4/17/2012	H1N1	KF648252	WA	1/18/2013
H3N2	KC893132	RI	4/17/2012	H1N1	CY168535	MA	12/19/2012
H3N2	KF182358	IL	2/29/2012	H1N1	CY182929	TX	12/28/2012
H3N2	KC892405	MA	11/23/2011	H1N1	CY170255	MA	1/7/2013
H3N2	KC892953	FL	11/29/2011	H1N1	CY147205	MS	1/31/2013
H3N2	KC893002	TX	12/16/2011	H1N1	CY163417	CO	3/22/2013
H3N2	KC892758	NY	12/23/2011	H1N1	KF647966	TX	3/3/2013
H3N2	KC892485	VT	3/16/2012	H1N1	KF886308	GA	3/14/2013
H3N2	KC892576	MD	4/24/2012	H1N1	KF647964	MN	3/1/2013
H3N2	KC892564	GA	3/4/2012	H1N1	CY141273	VA	1/11/2013
H3N2	KC892896	NY	5/10/2012	H1N1	CY183329	TX	1/15/2013
H3N2	KC893122	NJ	2/3/2012	H1N1	KF886304	IL	2/4/2013
H3N2	KC892168	SC	4/9/2012	H1N1	CY141275	VA	1/15/2013
H3N2	KC892724	FL	5/3/2012	H1N1	KF886298	CA	2/8/2013
H3N2	KC892793	TX	1/5/2012	H1N1	CY141217	NV	1/15/2013
H3N2	KC892850	CA	3/21/2012	H1N1	KF886299	SC	2/6/2013
H3N2	CY120885	CA	3/29/2012	H1N1	CY170671	CA	1/8/2013
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H3N2	CY120895	CO	3/20/2012	H1N1	CY171543	IL	12/30/2012
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H3N2	KC892790	FL	1/9/2012	H1N1	KF648198	CA	3/9/2013
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H3N2	KC893057	VA	4/4/2012	H1N1	CY163408	NV	2/14/2013
H3N2	KC892552	NM	3/1/2012	H1N1	KF648027	NM	4/10/2013
H3N2	CY130180	WA	5/13/2012	H1N1	KF648114	WI	1/2/2013
H3N2	CY120893	WA	4/8/2012	H1N1	KF886307	CA	1/7/2013
H3N2	CY120882	WA	3/24/2012	H1N1	KF648265	NM	1/4/2013
H3N2	CY120887	NV	4/3/2012	H1N1	CY163418	NY	3/27/2013
H3N2	KF182353	CA	5/22/2012	H1N1	KF648138	FL	1/23/2013
H3N2	CY130178	NJ	5/3/2012	H1N1	KF648253	MO	2/5/2013
H3N2	KC892549	OR	3/8/2012	H1N1	CY163411	OH	2/21/2013
H3N2	CY112168	NV	3/5/2012	H1N1	KF648193	TN	3/26/2013
H3N2	KC892876	NV	3/13/2012	H1N1	CY186099	TX	2/8/2013

Subtype	Accession	State	Date	Subtype	Accession	State	Date
H3N2	KC513479	AZ	3/31/2012	H1N1	CY163413	TX	2/14/2013
H3N2	CY120881	CA	3/26/2012	H1N1	KF648235	MS	5/20/2013
H3N2	KC892677	CA	5/4/2012	H1N1	KF886345	SC	1/15/2013
H3N2	KC892632	TX	3/2/2012	H1N1	CY134632	FL	12/7/2012
H3N2	CY120891	CA	4/9/2012	H1N1	CY141198	FL	1/16/2013
H3N2	CY120905	NV	4/16/2012	H1N1	CY134634	FL	12/12/2012
H3N2	KC892863	AZ	4/5/2012	H1N1	CY134633	FL	12/13/2012
H3N2	KC892937	WI	11/5/2011	H1N1	KF647994	FL	12/12/2012
H3N2	KC892978	NY	10/2/2011	H1N1	KF648240	TN	10/31/2012
H3N2	KC892165	OH	4/3/2012	H1N1	KF647927	CA	10/19/2012
H3N2	KC892186	IN	3/26/2012	H1N1	KF648189	CA	3/8/2013
H3N2	KC892269	KY	11/4/2011	H1N1	KF647963	LA	2/19/2013
H3N2	KC893060	OH	2/19/2012	H1N1	KF648180	KY	12/25/2012
H3N2	CY120875	OH	3/26/2012	H1N1	KF648110	NY	1/7/2013
H3N2	KC892339	KY	2/3/2012	H1N1	KF886319	SC	2/1/2013
H3N2	CY120868	OH	3/26/2012	H1N1	KF647941	MD	11/8/2012
H3N2	CY120879	OH	3/26/2012	H1N1	KF648092	PA	12/4/2012
H3N2	KC892992	IN	10/3/2011	H1N1	CY182713	TX	12/12/2012
H3N2	KC892751	NM	12/29/2011	H1N1	KF648178	TX	1/5/2013
H3N2	KC892190	CO	10/23/2011	H1N1	CY135116	TX	12/6/2012
H3N2	KC893019	SC	12/19/2011	H1N1	CY135108	TX	12/6/2012
H3N2	KC892358	OR	2/2/2012	H1N1	KF886326	OK	1/28/2013
H3N2	KC892394	WY	2/6/2012	H1N1	CY186187	TX	1/27/2013
H3N2	KC893009	MT	1/17/2012	H1N1	CY186131	TX	1/30/2013
H3N2	KF182350	CA	1/18/2012	H1N1	KF648010	NH	11/24/2012
H3N2	KC892766	IN	12/8/2011	H1N1	KF647967	FL	2/26/2013
H3N2	KC892761	WI	1/2/2012	H1N1	KF648149	UT	1/20/2013
H3N2	KF182344	CA	1/24/2012	H1N1	KF648115	NJ	11/20/2012
H3N2	KC892300	KS	2/1/2012	H1N1	KF647953	FL	5/7/2013
H3N2	KC892482	FL	2/24/2012	H1N1	CY170095	MA	4/26/2013
H3N2	KC892489	WI	12/18/2011	H1N1	KF648230	UT	5/12/2013
H3N2	KC892822	NM	2/16/2012	H1N1	KF648182	MN	12/20/2012
H3N2	CY120909	CO	2/23/2012	H1N1	KF647996	MN	12/13/2012
H3N2	KC892153	MS	2/18/2012	H1N1	KF648067	NM	1/6/2013
H3N2	CY112187	CO	2/23/2012	H1N1	KF648272	NM	1/6/2013
H3N2	CY120865	FL	3/19/2012	H1N1	KF648246	UT	2/3/2013
H3N2	CY112170	OK	3/1/2012	H1N1	KF648049	AZ	1/14/2013
H3N2	KC892591	VA	5/15/2012	H1N1	KF648001	CO	3/23/2013
H3N2	KC892716	UT	5/16/2012	H1N1	KF647905	NY	5/8/2013
H3N2	KC892410	CO	11/22/2011	H1N1	CY163410	OH	2/21/2013
H3N2	KC893084	MS	1/12/2012	H1N1	KF886342	IL	1/28/2013
H3N2	KC892931	OR	3/29/2012	H1N1	CY147206	MS	3/4/2013

Subtype	Accession	State	Date	Subtype	Accession	State	Date
H3N2	KC892769	CO	12/25/2011	H1N1	KF648229	CA	5/3/2013
H3N2	CY120863	TX	3/15/2012	H1N1	KF647918	AL	2/25/2013
H3N2	CY120864	TX	3/16/2012	H1N1	CY163421	FL	5/2/2013
H3N2	CY120867	TX	3/22/2012	H1N1	KF648087	FL	5/2/2013

Season	H3N2		H1N1	
	Sequences (Full)	Locations	Sequences (Full)	Locations
2003-2004	191	29	-	-
2004-2005	189	34	-	-
2005-2006	147	30	-	-
2006-2007	211	34	371	28
2007-2008	662 (760)	38	165	34
2008-2009	302	32	196	16
2010-2011	410	49	247	48
2011-2012	400	49	216	44
2012-2013	564 (1276)	49	171	39

Table S2. Number of sequences per season and number of locations (US states) represented for influenza A/H3N2 and A/H1N1. Numbers in parentheses indicate the total number of publicly available sequences for those seasons; because of the extremely large sample size as compared to other seasons, subsamples were taken from states in these seasons that contributed an excessive number of sequences.

Season	Root Height	Growth Rate	Clock Rate	Clade	Clade Divergence Date	Sequences	Locations
2003-2004	1.424 (1.02-1.909)	3.669 (1.87-5.555)	0.005572 (0.003461-0.007759)	1	2003.598 (2003.424 - 2003.738)	30	12
				2	2003.282 (2002.925 - 2003.581)	59	17
2004-2005	1.656 (1.087-2.278)	3.764 (2.005-5.592)	0.004694 (0.003013-0.006469)	NA	NA	NA	NA
2005-2006	1.35 (0.951-1.816)	2.636 (1.243-4.181)	0.009151 (0.006521-0.02082)	1	2005.337 (2005.066 - 2005.572)	49	17
				2	2005.784 (2005.662 - 2005.886)	29	10
2006-2007	1.647 (1.137-2.251)	2.713 (1.306-4.2)	0.007733 (0.005568-0.009923)	1	2006.684 (2006.533 - 2006.819)	50	15
				2	2006.684 (2006.533 - 2006.819)	112	29
2007-2008	1.528 (1.165-1.962)	3.391 (2.142-4.782)	0.006833 (0.005487-0.008296)	1	2007.344 (2007.223 - 2007.578)	78	29
				2	2007.752 (2007.613 - 2007.876)	28	16
				3	2007.752 (2007.613 - 2007.876)	159	32
				4	2007.679 (2007.536 - 2007.811)	107	25
				5	2007.679 (2007.536 - 2007.811)	277	32
2008-2009	1.532 (1.007-2.073)	2.084 (1.163-2.964)	0.006681 (0.005259-0.008227)	NA	NA	NA	NA
2010-2011	1.947 (1.488-2.42)	3.486 (2.362-4.683)	0.005383 (0.004137-0.006641)	1	2010.523 (2010.320 - 2010.709)	23	16
				2	2010.566 (2010.401 - 2010.731)	62	23

2011-2012	2.205 (1.723-2.741)	2.697 (1.906-3.531)	0.00577 (0.0041006-0.0062034)	1	2011.397 (2011.773-2011.365)	41	21
				2	2011.191 (2011.577-2011.14)	67	23
				3	2011.301 (2011.69-2011.263)	49	26
				4	2011.805 (2011.897-2011.65)	23	9
2012-2013	2.841 (2.178-3.603)	2.088 (1.347-2.864)	0.004942 (0.003892-0.006008)	1	2012.591 (2012.418 - 2012.746)	21	11
				2	2012.621 (2012.445 - 2012.774)	20	9
				3	2012.450 (2012.263 - 2012.618)	33	22
				4	2012.354 (2012.137 - 2012.561)	35	15
				5	2012.354 (2012.137 - 2012.561)	37	19
				6	2012.616 (2012.466 - 2012.750)	46	23

Table S3. Summary of epidemiological and evolutionary dynamics of H3N2 epidemics based on phylogenetic analyses of each influenza season. 'Root Height' is measured in years before present, with the present time equal to the latest sampling date. 'Clock rate' is measured in substitutions/site/year. 'Sequences' represents the number of sequences analyzed per clade and 'Locations' represents the number of states these sequences were collected from.

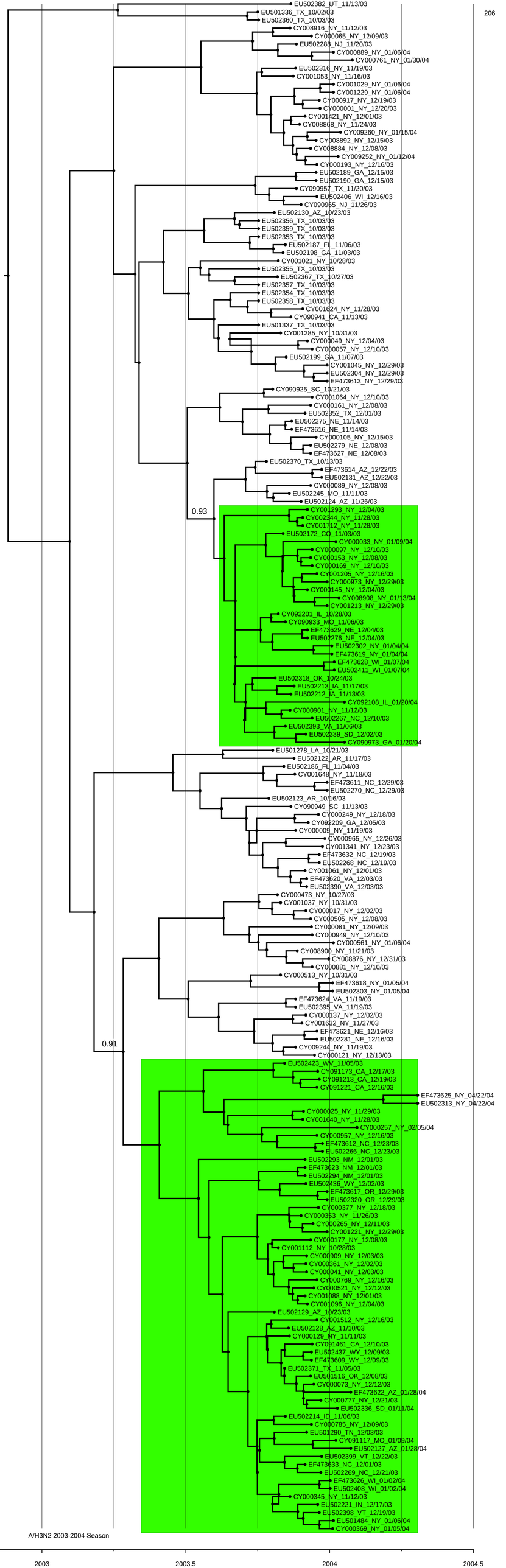
Season	Root Height	Growth Rate	Clock Rate	Clade	Clade Divergence Date	Sequences	Locations
2006-2007	4.102 (2.868-5.429)	1.031 (0.567-1.51)	0.004611 (0.003438-0.005903)	1	2006.686 (2006.51 - 2006.831)	35	10
				2	2006.467 (2006.176 - 2006.732)	38	11
				3	2006.780 (2006.621 - 2006.917)	28	9
2007-2008	4.237 (2.288-6.999)	1.541 (0.648-2.473)	0.002746 (0.00122-0.004286)	1	2006.960 (2006.143 - 2007.573)	23	13
2008-2009	1.363 (0.944-1.874)	1.645 (0.59-2.679)	0.006018 (0.003936-0.008157)	NA	NA	NA	NA
2010-2011	2.26 (1.705-2.901)	2.083 (1.329-2.909)	0.004176 (0.003123-0.005239)	1	2010.549 (2010.443 - 2010.803)	23	14
				2	2010.364 (2010.22 - 2010.667)	25	17
				3	2010.374 (2010.253 - 2010.627)	86	38
2011-2012	1.913 (1.459-2.418)	1.8 (0.946-2.701)	0.005543 (0.004205-0.006926)	1	2011.870 (2011.763 - 2011.964)	33	15
				2	2011.615 (2011.424 - 2011.790)	113	35
2012-2013	3.028 (2.188-3.941)	0.933 (0.388-1.524)	0.005109 (0.003875-0.006435)	1	2012.708 (2012.623 - 2012.846)	29	14

Table S4. Summary of epidemiological and evolutionary dynamics of H1N1 epidemics based on phylogenetic analyses of each influenza season. 'Root Height' is measured in years before present, with the present time equal to the latest sampling date. 'Clock rate' is measured in substitutions/site/year. 'Sequences' represents the number of sequences analyzed per clade and 'Locations' represents the number of states these sequences were collected from.

I.2 Supplementary Figures and Captions

Figures S1-S9. Phylogenetic trees estimated using influenza A/H3N2 HA sequences sampled from a single subtype within a single influenza season (labeled at bottom left) in the US using a Bayesian method. Clades used for association tests are highlighted in green. Posterior probability values (>0.9) are labeled for nodes leading to clades used in the correlation analysis. Horizontal axis is measured in years.

Figures S10-S15. Phylogenetic trees estimated using influenza A/H1N1 HA sequences sampled from a single subtype within a single influenza season (labeled at bottom left) in the US using a Bayesian method. Clades used for association tests are highlighted in green. Posterior probability values (>0.9) are labeled for nodes leading to clades used in the correlation analysis. Horizontal axis is measured in years.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CY000105_NY_12/15/03
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EF473627_NE_12/08/03
EU502370_TX_10/13/03
EF473614_AZ_12/22/03
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CY000097_NY_12/10/03
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CY000169_NY_12/10/03
CY001205_NY_12/16/03
CY000973_NY_12/29/03
CY000145_NY_12/04/03
CY008908_NY_01/13/04
CY001213_NY_12/29/03
CY092201_IL_10/28/03
CY090933_MO_11/06/03
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EU502276_NE_12/04/03
EU502302_NY_01/04/04
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EF473628_WI_01/07/04
EU502411_WI_01/07/04
EU502318_OK_10/24/03
EU502213_IA_11/17/03
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EF473611_NC_12/29/03
EU502270_NC_12/29/03
EU502123_AR_10/16/03
CY090949_SC_11/13/03
CY000249_NY_12/18/03
CY092209_GA_12/05/03
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A/H3N2 2004-2005 Season

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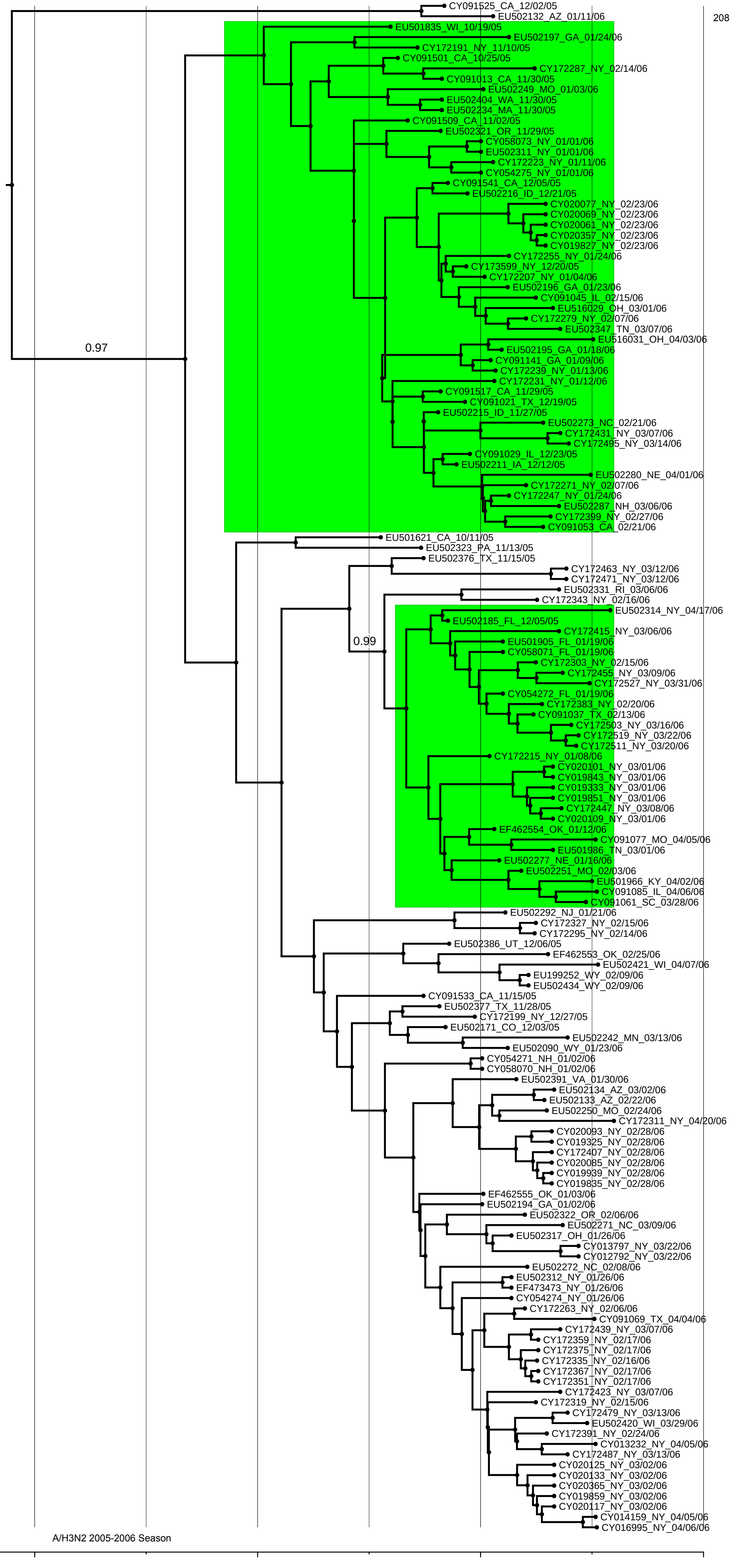
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A/H3N2 2005-2006 Season
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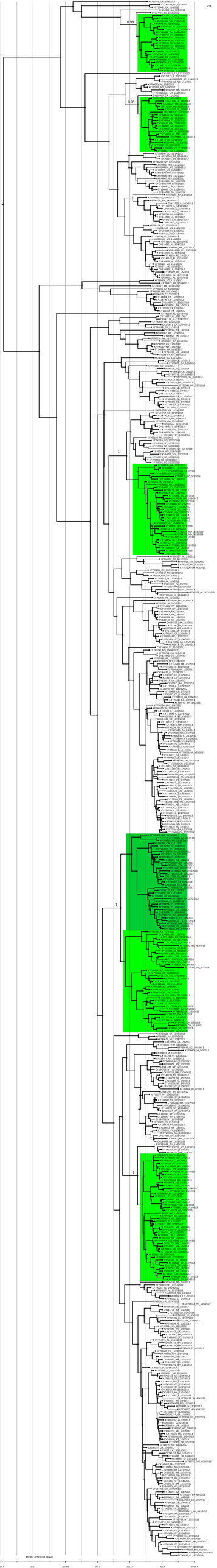
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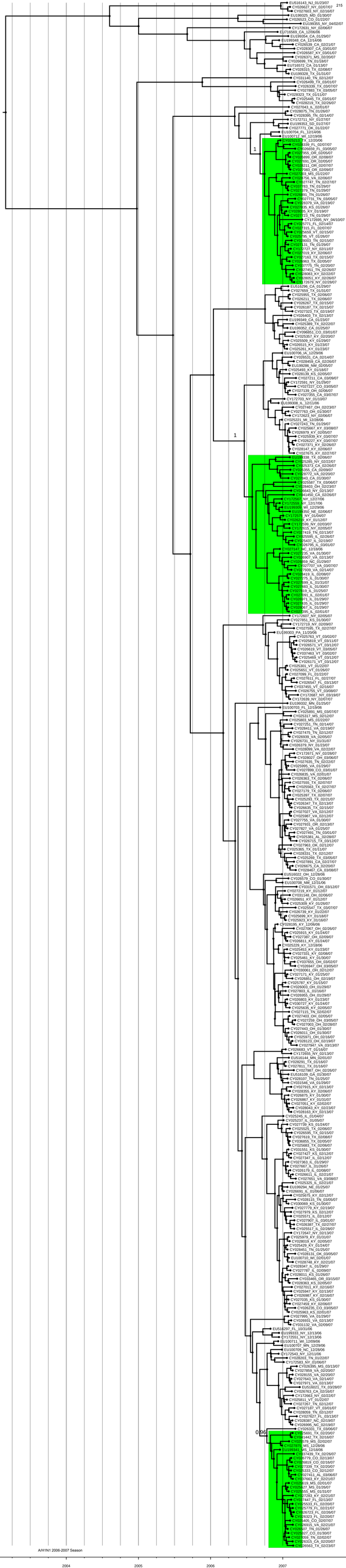
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A/H1N1 2007-2008 Season

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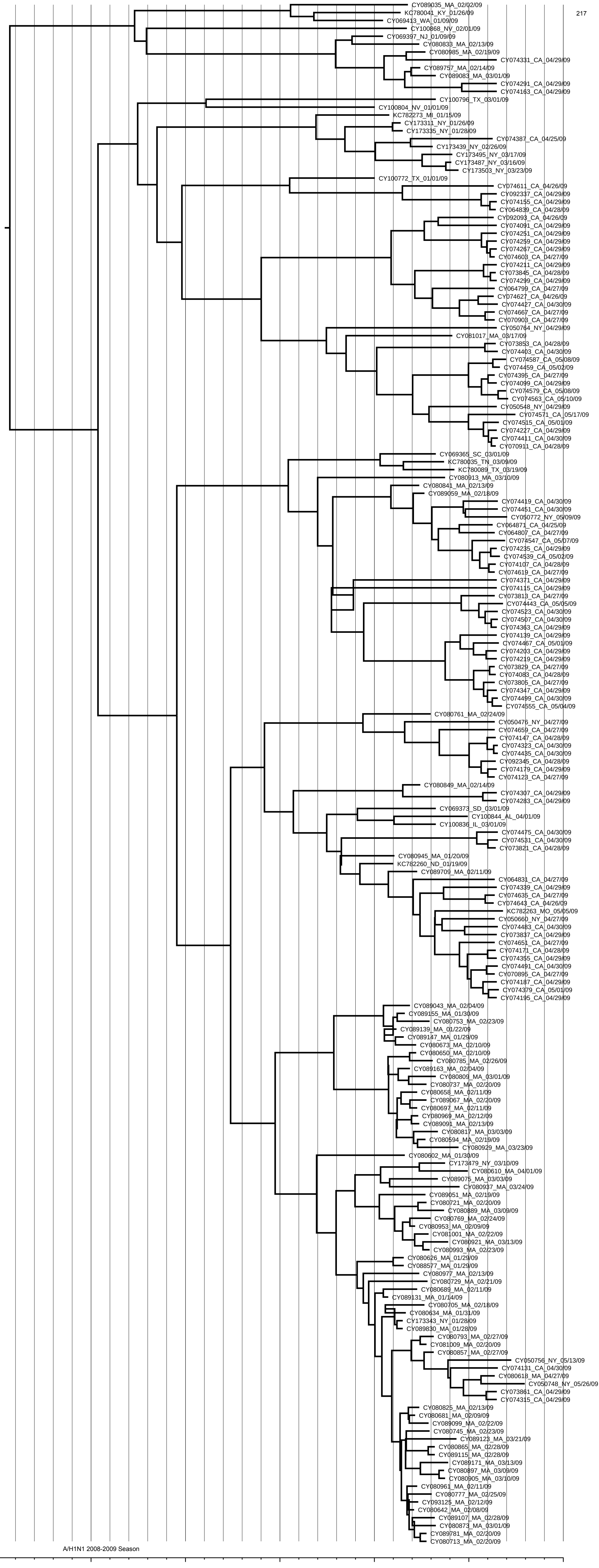
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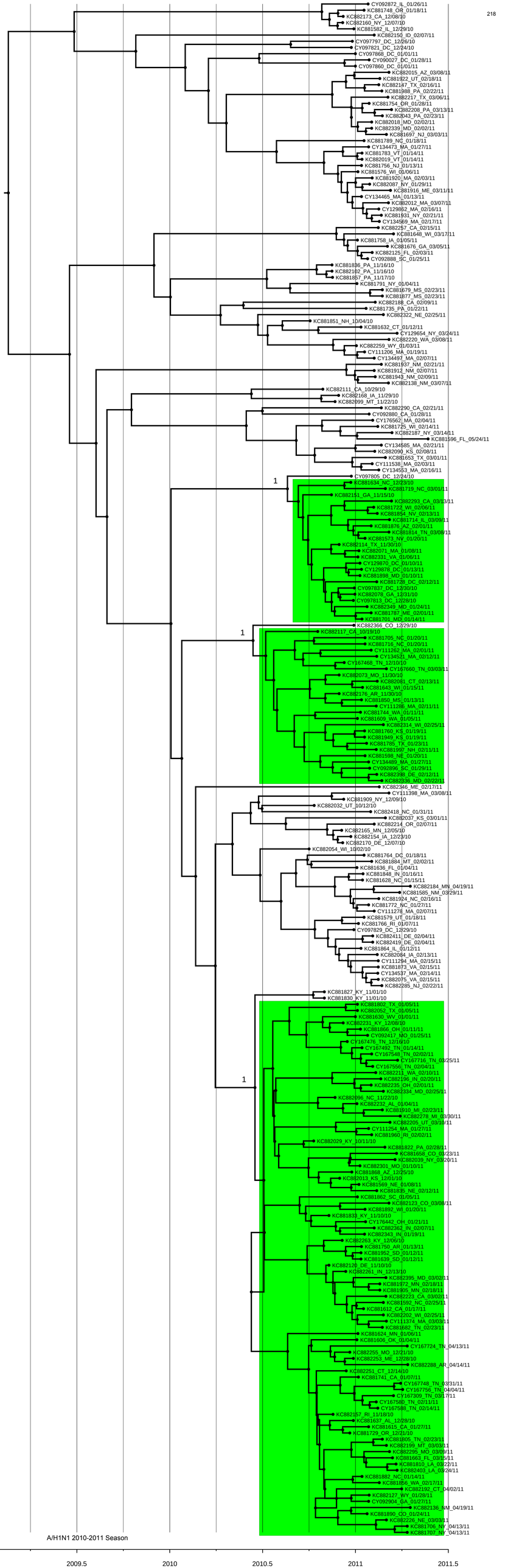
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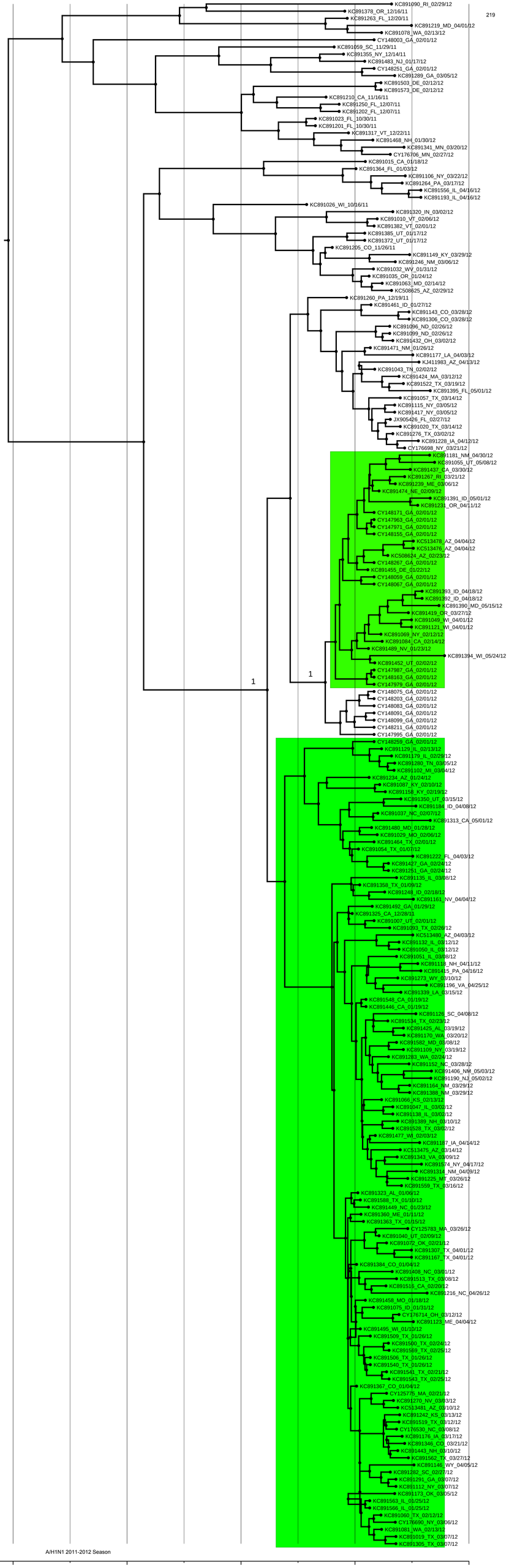
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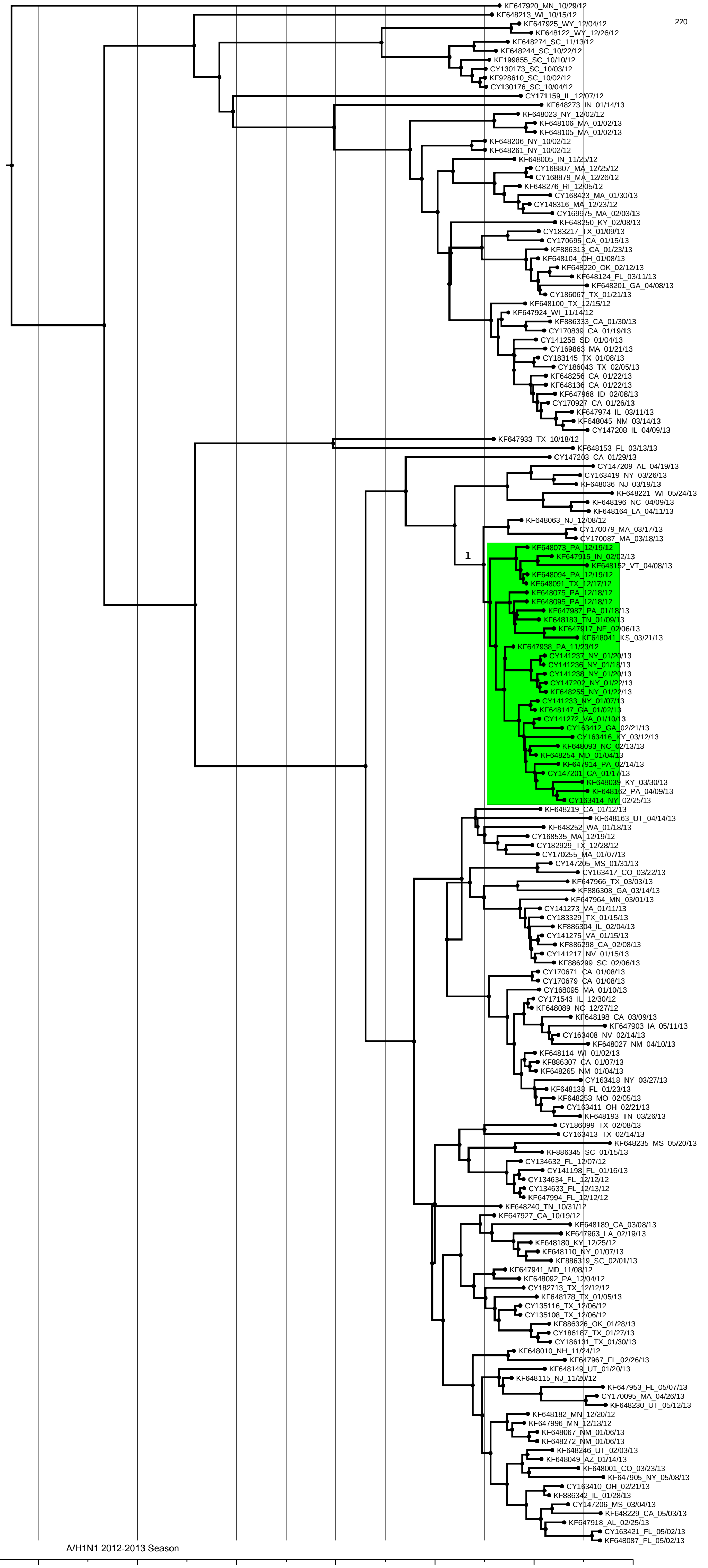
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KF648001_CO_03/23/13
KF647905_NY_05/08/13
CY163410_OH_02/21/13
KF886342_IL_01/28/13
CY147206_MS_03/04/13
KF648229_CA_05/03/13
KF647918_AL_02/25/13
CY163421_FL_05/02/13
KF648087_FL_05/02/13
A/H1N1 2012-2013 Season
2010.5
2011
2011.5
2012
2012.5
2013
2013.5

Appendix II

Supplementary Material for Chapter 4

II.1 Supplementary Tables

Table S1. List of Accession Numbers, Dates and Countries. "Used" column indicates whether or not a sequence was part of a clade used in the spatial analysis

ACCESSION	DATE	Used	Country	ACCESSION	DATE	Used	Country
AB477004	1/29/2008	y	NL	FJ654307	1/8/2008	y	GR
AB477005	2/11/2008	y	NL	FJ654308	12/11/2007	y	SE
AB477007	2/15/2008	y	NL	FJ654309	1/22/2008	y	IT
AB477008	12/21/2007	y	NL	FJ654310	1/2/2008	y	PT
CY034598	2/27/2008	y	DE	FJ654311	1/10/2008	y	DE
CY034599	2/27/2008	y	DE	FJ654312	1/3/2008	y	ES
CY034600	2/27/2008	y	DE	FJ654313	1/21/2008	y	BG
CY034601	2/27/2008	y	DE	FJ654314	1/14/2008	y	CZ
CY034602	2/27/2008	y	DE	FJ654315	2/12/2008	-	UA
CY034605	2/27/2008	y	DE	FJ654316	1/14/2008	y	RO
CY034607	2/27/2008	y	DE	FJ654318	1/31/2008	y	PT
CY034608	2/27/2008	y	DE	FJ654319	12/21/2007	y	ES
CY034610	2/27/2008	y	DE	FJ654320	1/25/2008	-	HU
CY034611	2/27/2008	y	DE	FJ654321	1/10/2008	y	SI
CY034615	2/27/2008	y	DE	FJ654322	1/10/2008	y	SI
CY034616	2/27/2008	y	DE	FJ654323	1/21/2008	y	RO
CY034617	2/27/2008	y	DE	FJ654324	2/13/2008	y	IT
CY034618	2/27/2008	y	DE	FJ654325	1/31/2008	-	HR
CY036666	11/21/2007	y	NO	FJ654329	1/23/2008	-	LV
CY036667	11/27/2007	y	NO	FJ654330	2/6/2008	-	UA
CY036668	1/14/2008	y	NO	FJ654334	1/17/2008	y	AT
CY036677	12/2/2007	y	NO	FJ654339	12/24/2007	y	SE
CY036682	1/23/2008	y	NO	FN423713	6/1/2009	y	LU
CY036683	1/28/2008	y	NO	GQ183633	5/10/2009	y	FI
CY039527	4/29/2009	y	NL	GQ184630	5/21/2009	-	RU
CY043334	6/4/2009	y	DK	GQ214138	4/30/2009	-	FR
CY043342	6/4/2009	y	DK	GQ214144	4/30/2009	y	FR
CY043350	6/9/2009	y	DK	GQ214151	4/29/2009	-	FR
CY045482	5/4/2009	y	DE	GQ214156	5/1/2009	y	FR
CY045490	5/6/2009	y	DE	GQ219586	5/21/2009	-	RU
CY045495	6/3/2009	y	DE	GQ227545	5/8/2009	y	SE
CY046061	6/20/2009	y	IT	GQ232099	5/21/2009	y	IT
CY046062	6/16/2009	y	IT	GQ247726	5/26/2009	-	RU
CY046063	6/10/2009	y	IT	GQ249333	5/1/2009	y	FR

ACCESSION	DATE	Used	Country	ACCESSION	DATE	Used	Country
CY046064	7/17/2009	y	IT	GQ249337	5/11/2009	y	FR
CY046065	7/17/2009	y	IT	GQ251035	5/3/2009	y	IT
CY046066	7/21/2009	y	IT	GQ255897	5/22/2009	-	RU
CY046946	5/29/2009	y	NO	GQ255900	5/26/2009	-	RU
CY046952	6/28/2009	y	NO	GQ283484	5/27/2009	y	IT
CY051984	5/16/2009	y	NO	GQ283488	5/26/2009	y	FI
CY051985	5/27/2009	y	NO	GQ283493	5/28/2009	y	FI
CY051986	7/27/2009	y	NO	GQ329066	5/23/2009	y	FR
CY051987	7/29/2009	y	NO	GQ329070	6/2/2009	y	FR
CY051988	8/11/2009	y	NO	GQ329076	6/2/2009	y	FR
CY051989	8/10/2009	y	NO	GQ329082	5/22/2009	y	FR
CY051990	8/19/2009	y	NO	GQ329088	5/6/2009	y	FR
CY051991	8/11/2009	y	NO	GQ329093	6/2/2009	y	FR
CY051992	8/28/2009	y	NO	GQ329100	5/17/2009	y	FR
CY051993	8/27/2009	y	NO	GQ329106	5/6/2009	y	FR
CY051994	8/31/2009	y	NO	GQ330645	6/3/2009	-	RU
CY051998	9/8/2009	y	NO	GQ351290	6/14/2009	y	IT
CY052003	9/1/2009	-	NO	GQ351319	6/6/2009	y	IT
CY052004	8/27/2009	y	NO	GQ359765	5/29/2009	y	SE
CY052005	9/9/2009	-	NO	GQ360060	5/30/2009	y	SE
CY052006	9/9/2009	y	NO	GQ365368	6/1/2009	y	SE
CY052008	9/20/2009	-	NO	GQ365658	4/29/2009	y	DE
CY052009	10/2/2009	-	NO	GQ365666	5/2/2009	y	DE
CY052010	10/14/2009	-	NO	GQ365674	5/4/2009	y	DE
CY052011	10/12/2009	-	NO	GQ375284	5/26/2009	-	RU
CY052012	10/19/2009	-	NO	GQ392022	7/9/2009	-	RU
CY052013	10/24/2009	-	NO	GQ392029	6/17/2009	y	IT
CY052014	10/23/2009	y	NO	GQ421199	6/8/2009	y	IT
CY053416	11/1/2009	-	RU	GQ421200	6/11/2009	y	IT
CY053627	11/10/2009	-	RU	GQ421201	7/1/2009	y	IT
CY053681	11/1/2009	-	RU	GQ421203	7/12/2009	y	IT
CY053689	11/1/2009	-	RU	GQ464408	4/28/2009	y	ES
CY053728	11/1/2009	-	RU	GQ494354	6/20/2009	-	RU
CY053736	11/1/2009	-	RU	GQ496142	7/22/2009	-	RU
CY053744	11/1/2009	-	RU	GQ496149	7/24/2009	-	RU
CY053752	11/1/2009	-	RU	GQ527167	8/12/2009	-	RU
CY054630	11/1/2009	-	RU	GU211227	9/22/2009	-	RU
CY054638	11/1/2009	-	RU	GU220604	8/4/2009	-	RS
CY054646	11/1/2009	-	RU	GU290047	6/27/2009	y	CZ
CY054654	11/1/2009	-	RU	GU290055	7/15/2009	y	CZ
CY054662	11/1/2009	-	RU	GU292341	7/24/2009	y	FI
CY054670	11/12/2009	-	RU	GU371256	11/16/2009	-	RU

ACCESSION	DATE	Used	Country	ACCESSION	DATE	Used	Country
CY054678	11/5/2009	-	RU	GU371263	11/11/2009	-	RU
CY056939	10/30/2009	-	BE	GU433025	7/19/2009	-	RU
CY056947	11/20/2009	y	DK	GU433033	7/21/2009	-	RU
CY056955	12/13/2009	-	GR	GU451254	11/14/2009	-	RU
CY056963	12/7/2009	-	DK	GU480943	8/10/2009	-	RU
CY056971	12/10/2009	-	DK	GU560008	11/18/2009	-	RU
CY056979	12/2/2009	-	DK	GU560016	11/22/2009	-	RU
CY056987	12/7/2009	-	PO	GU562450	11/25/2009	-	RU
CY057045	10/26/2009	-	GB	GU562458	1/4/2010	-	RU
CY057049	11/5/2009	-	GB	GU576500	7/15/2009	y	IT
CY057050	10/29/2009	-	GB	GU576501	7/16/2009	y	IT
CY057059	10/17/2009	-	GB	GU576502	7/17/2009	y	IT
CY057062	11/18/2009	-	GB	GU576504	7/17/2009	y	IT
CY057069	11/19/2009	-	GB	GU576506	7/17/2009	y	IT
CY057350	12/4/2009	-	DE	GU576508	8/3/2009	y	IT
CY061267	10/29/2009	y	BE	GU576510	8/5/2009	y	IT
CY062675	11/13/2009	y	ES	GU576512	8/6/2009	y	IT
CY062691	11/24/2009	-	DK	GU576514	8/16/2009	y	IT
CY062699	11/27/2009	y	DK	GU576515	8/19/2009	y	IT
CY062707	12/13/2009	-	GR	GU576517	8/19/2009	y	IT
CY062715	12/13/2009	-	GR	GU576519	8/21/2009	y	IT
CY062723	12/13/2009	-	GR	GU576521	8/21/2009	y	IT
CY062731	12/15/2009	-	GR	GU576522	8/31/2009	y	IT
CY062739	11/19/2009	-	DE	GU576540	12/31/2009	y	IT
CY062755	11/26/2009	-	ES	GU576542	1/9/2010	-	IT
CY062763	12/2/2009	-	ES	GU592889	12/18/2009	-	RU
CY062771	12/4/2009	-	ES	GU592905	12/14/2009	-	RU
CY062779	12/10/2009	-	BE	GU727825	12/4/2009	-	RU
CY062787	11/10/2009	y	DK	HM101145	11/25/2009	-	RU
CY062795	11/20/2009	-	DK	HM104477	12/5/2009	-	RU
CY062803	11/26/2009	-	AT	HM124383	3/2/2010	-	RU
CY062811	11/11/2009	-	DK	HM157254	12/4/2009	-	RU
CY062819	12/7/2009	-	DK	HM173599	11/12/2009	-	RU
CY062827	12/3/2009	-	PO	HM189312	11/2/2009	-	RU
CY062835	12/30/2009	-	GR	HM189320	11/25/2009	-	RU
CY062843	12/30/2009	-	GR	HM189352	11/10/2009	-	RU
CY062851	12/17/2009	-	GR	HM189357	11/5/2009	-	RU
CY062859	12/18/2009	-	GR	HM189358	11/18/2009	-	RU
CY062867	12/18/2009	-	GR	HM189359	8/25/2009	-	RU
CY062875	12/19/2009	-	GR	HM189360	11/10/2009	-	RU
CY062899	12/20/2009	y	GR	HM189361	11/26/2009	-	RU
CY062907	12/21/2009	-	GR	HM189362	9/25/2009	-	RU

ACCESSION	DATE	Used	Country	ACCESSION	DATE	Used	Country
CY062915	12/26/2009	-	GR	HM189363	9/25/2009	-	RU
CY062923	12/26/2009	y	GR	HM189364	9/25/2009	-	RU
CY062931	12/18/2009	-	DE	HM189365	9/25/2009	-	RU
CY062947	12/17/2009	-	ES	HM189366	9/26/2009	-	RU
CY062955	12/24/2009	-	ES	HM189367	7/16/2009	-	RU
CY062963	12/23/2009	-	ES	HM189368	11/26/2009	-	RU
CY062971	12/28/2009	-	DK	HM189369	7/15/2009	-	RU
CY062979	1/5/2010	y	DE	HM189370	8/16/2009	-	RU
CY062987	1/5/2010	y	AT	HM189371	12/1/2009	-	RU
CY062995	12/21/2009	-	EE	HM189372	10/1/2009	-	RU
CY063003	1/4/2010	-	EE	HM189373	10/24/2009	-	RU
CY063011	1/7/2010	-	EE	HM189374	11/24/2009	-	RU
CY063019	12/15/2009	-	ES	HM189375	11/24/2009	-	RU
CY063027	12/30/2009	-	ES	HM189376	11/24/2009	-	RU
CY063035	12/30/2009	-	ES	HM189377	7/25/2009	-	RU
CY063043	12/10/2009	-	DE	HM189378	11/19/2009	-	RU
CY063051	12/15/2009	y	BE	HM189379	12/9/2009	-	RU
CY063059	12/30/2009	-	BE	HM189380	7/30/2009	-	RU
CY063582	11/10/2009	y	NO	HM189381	8/25/2009	-	RU
CY063590	12/9/2009	-	GR	HM189382	8/13/2009	-	RU
CY063598	11/20/2009	-	DE	HM189383	11/24/2009	-	RU
CY063606	12/2/2009	-	DK	HM189384	8/4/2009	-	RU
CY063638	12/29/2009	-	GR	HM189385	7/28/2009	-	RU
CY063646	12/29/2009	-	GR	HM189386	11/9/2009	-	RU
CY063654	12/18/2009	-	GR	HM189387	11/21/2009	-	RU
CY064772	12/11/2009	-	DE	HM189388	8/5/2009	-	RU
CY065115	11/15/2009	-	NL	HM189389	9/10/2009	-	RU
CY065131	11/16/2009	-	NL	HM189390	11/30/2009	-	RU
CY065158	6/23/2009	y	GB	HM189391	11/23/2009	-	RU
CY065206	4/28/2009	y	GB	HM189392	9/21/2009	-	RU
CY065350	5/3/2009	y	GB	HM189393	9/17/2009	-	RU
CY065446	5/11/2009	y	GB	HM189394	9/21/2009	-	RU
CY065598	6/3/2009	y	GB	HM189395	9/21/2009	-	RU
CY065776	11/30/2009	-	NL	HM189396	11/23/2009	-	RU
CY065784	12/4/2009	-	NL	HM189397	11/21/2009	-	RU
CY065792	8/25/2009	y	NL	HM189398	11/23/2009	-	RU
CY065808	10/31/2009	-	NL	HM189399	8/17/2009	-	RU
CY065816	11/5/2009	-	NL	HM189400	7/13/2009	-	RU
CY065824	11/17/2009	-	NL	HM189401	8/10/2009	-	RU
CY065832	11/7/2009	-	NL	HM189402	8/12/2009	-	RU
CY065840	12/1/2009	-	NL	HM189403	11/18/2009	-	RU
CY065856	11/19/2009	-	NL	HM189404	11/25/2009	-	RU

ACCESSION	DATE	Used	Country	ACCESSION	DATE	Used	Country
CY065864	10/23/2009	-	NL	HM189405	11/23/2009	-	RU
CY065872	1/4/2010	-	NL	HM189406	11/20/2009	-	RU
CY065880	9/4/2009	-	NL	HM189407	8/12/2009	-	RU
CY065888	12/7/2009	y	NL	HM189408	11/23/2009	-	RU
CY065896	12/2/2009	-	NL	HM189409	11/30/2009	-	RU
CY065904	9/10/2009	-	NL	HM189410	11/2/2009	-	RU
CY065912	9/10/2009	-	NL	HM189413	11/4/2009	-	RU
CY065920	9/30/2009	-	NL	HM189414	10/31/2009	-	RU
CY066599	12/15/2009	-	GR	HM189415	7/15/2009	-	RU
CY066607	12/15/2009	-	GR	HM189416	7/15/2009	-	RU
CY066615	12/15/2009	y	GR	HM189417	11/18/2009	-	RU
CY066623	12/15/2009	-	GR	HM189418	11/18/2009	-	RU
CY066631	11/19/2009	-	DE	HM189420	7/18/2009	-	RU
CY066647	11/20/2009	-	DE	HM189421	11/13/2009	-	RU
CY066663	11/30/2009	-	DE	HM189423	11/12/2009	-	RU
CY066671	12/10/2009	-	BE	HM189424	8/14/2009	-	RU
CY066679	11/20/2009	-	DK	HM189425	8/13/2009	-	RU
CY066687	11/25/2009	-	DK	HM189426	7/16/2009	-	RU
CY066695	11/27/2009	-	DK	HM189427	7/17/2009	-	RU
CY066703	11/19/2009	-	AT	HM189428	8/5/2009	-	RU
CY066711	11/24/2009	-	AT	HM189429	7/18/2009	-	RU
CY066719	11/17/2009	-	ES	HM567592	5/24/2009	y	IE
CY066727	10/30/2009	-	BE	HM567736	5/31/2009	y	GB
CY066735	11/3/2009	-	BE	HM567808	5/26/2009	y	IE
CY066743	11/4/2009	-	BE	HM567816	6/1/2009	y	IE
CY066823	10/28/2009	-	BE	HM567824	6/5/2009	y	IE
CY066831	11/3/2009	-	ES	HM567832	5/26/2009	y	IE
CY066839	11/11/2009	-	ES	HM567840	5/29/2009	y	IE
CY066847	11/13/2009	-	ES	HM567848	5/31/2009	y	IE
CY066935	11/19/2009	-	DK	HM567896	6/5/2009	y	GB
CY066943	11/23/2009	-	DK	HM567928	6/9/2009	y	GB
CY066951	11/24/2009	-	DK	HM567936	6/7/2009	y	GB
CY066959	11/26/2009	-	DK	HM567944	6/7/2009	y	GB
CY066967	11/26/2009	y	DK	HM567968	11/20/2009	-	GB
CY066975	11/24/2009	y	DK	HM567984	11/18/2009	-	GB
CY066983	11/9/2009	-	BE	HM568008	11/23/2009	-	GB
CY066991	11/18/2009	-	BE	HM568024	11/23/2009	-	GB
CY066999	11/16/2009	-	DE	HM568040	11/25/2009	-	GB
CY067007	11/25/2009	-	DE	HM568048	10/20/2009	-	GB
CY067015	11/13/2009	-	DE	HM568144	9/10/2009	-	GB
CY067023	11/13/2009	-	DE	HM569740	3/2/2010	-	RU
CY067031	11/21/2009	y	DK	HQ228025	6/12/2009	y	FI

ACCESSION	DATE	Used	Country	ACCESSION	DATE	Used	Country
CY067039	11/21/2009	-	DK	HQ228026	6/12/2009	y	FI
CY067047	11/22/2009	y	DK	HQ228028	6/11/2009	y	FI
CY067055	11/28/2009	-	DK	HQ228029	6/13/2009	y	FI
CY067063	12/13/2009	-	GR	HQ228030	6/15/2009	y	FI
CY067071	12/13/2009	y	GR	HQ228031	6/20/2009	y	FI
CY067079	12/13/2009	-	GR	HQ228032	6/18/2009	y	FI
CY067087	12/13/2009	-	GR	HQ228033	6/19/2009	y	FI
CY067103	12/13/2009	-	GR	HQ228034	6/18/2009	y	FI
CY067111	12/13/2009	-	GR	HQ228035	6/19/2009	y	FI
CY067119	12/13/2009	-	GR	HQ228036	6/19/2009	y	FI
CY067127	12/16/2009	-	GR	HQ228037	6/19/2009	y	FI
CY067135	12/15/2009	-	GR	HQ228038	6/18/2009	y	FI
CY067151	12/15/2009	-	GR	HQ228039	6/18/2009	y	FI
CY067159	12/17/2009	-	GR	HQ228040	6/18/2009	y	FI
CY067167	12/8/2009	-	DE	HQ228041	6/18/2009	y	FI
CY067175	12/9/2009	-	DE	HQ228042	6/23/2009	y	FI
CY067635	10/27/2009	-	NO	HQ228043	6/28/2009	y	FI
CY067651	11/18/2009	y	BE	HQ228044	7/3/2009	y	FI
CY069114	11/17/2009	-	ES	HQ228045	7/4/2009	y	FI
CY069122	11/24/2009	y	ES	HQ228046	7/4/2009	y	FI
CY069130	11/26/2009	-	ES	HQ228047	7/3/2009	y	FI
CY069138	11/30/2009	-	ES	HQ228048	7/7/2009	y	FI
CY069146	11/23/2009	-	DE	HQ228049	7/9/2009	y	FI
CY069162	12/21/2009	-	GR	HQ228050	7/9/2009	y	FI
CY069170	12/21/2009	-	GR	HQ228051	7/12/2009	y	FI
CY069186	12/26/2009	y	GR	HQ228052	7/13/2009	y	FI
CY069194	12/26/2009	-	GR	HQ228053	7/14/2009	y	FI
CY069218	11/30/2009	y	DE	HQ228054	7/14/2009	y	FI
CY069226	12/4/2009	y	DE	HQ228055	7/15/2009	y	FI
CY069234	12/9/2009	-	DE	HQ228056	7/15/2009	y	FI
CY069757	6/30/2009	y	GB	HQ228057	8/31/2009	y	FI
CY069781	5/2/2009	y	GB	HQ228059	9/8/2009	y	FI
CY069821	5/4/2009	y	GB	HQ228061	7/9/2009	y	FI
CY069853	5/11/2009	y	GB	HQ228062	7/21/2009	y	FI
CY069893	6/2/2009	y	GB	HQ228063	7/22/2009	y	FI
CY070158	6/10/2009	y	GB	HQ228064	7/27/2009	y	FI
CY070170	6/29/2009	y	GB	HQ228065	7/27/2009	y	FI
CY070171	6/23/2009	y	GB	HQ228067	9/9/2009	-	FI
CY070178	6/29/2009	y	GB	HQ228070	9/18/2009	-	FI
CY070201	7/1/2009	y	GB	HQ228071	9/18/2009	-	FI
CY070204	7/2/2009	y	GB	HQ228072	9/23/2009	-	FI
CY070220	7/7/2009	y	GB	HQ228073	10/16/2009	-	FI

ACCESSION	DATE	Used	Country	ACCESSION	DATE	Used	Country
CY070225	6/22/2009	y	GB	HQ228074	7/20/2009	y	FI
CY070226	6/21/2009	y	GB	HQ228075	7/17/2009	y	FI
CY070227	7/7/2009	y	GB	HQ228076	7/16/2009	y	FI
CY070238	6/30/2009	y	GB	HQ228079	7/20/2009	y	FI
CY070239	6/30/2009	y	GB	HQ228084	10/5/2009	-	FI
CY070243	7/12/2009	y	GB	HQ228085	9/30/2009	-	FI
CY070245	7/8/2009	y	GB	HQ228088	11/12/2009	y	FI
CY070265	7/14/2009	y	GB	HQ228089	11/24/2009	-	FI
CY070281	7/17/2009	y	GB	HQ228090	11/21/2009	y	FI
CY070286	5/17/2009	y	GB	HQ228091	11/20/2009	-	FI
CY070320	7/23/2009	y	GB	HQ228092	11/16/2009	-	FI
CY070329	7/25/2009	y	GB	HQ228093	11/19/2009	y	FI
CY070332	7/29/2009	y	GB	HQ228094	11/28/2009	y	FI
CY070335	7/30/2009	y	GB	HQ228095	10/12/2009	-	FI
CY070338	7/13/2009	y	GB	HQ228096	10/13/2009	-	FI
CY070363	9/2/2009	-	GB	HQ228097	10/9/2009	y	FI
CY070364	9/2/2009	-	GB	HQ228098	10/20/2009	-	FI
CY070369	9/9/2009	-	GB	HQ228099	10/20/2009	-	FI
CY070379	9/7/2009	-	GB	HQ228100	10/21/2009	-	FI
CY070383	9/14/2009	-	GB	HQ228101	10/20/2009	-	FI
CY070385	9/15/2009	-	GB	HQ228102	10/14/2009	y	FI
CY070395	9/21/2009	-	GB	HQ228103	10/21/2009	y	FI
CY070408	9/27/2009	-	GB	HQ228104	10/26/2009	-	FI
CY070426	10/1/2009	-	GB	HQ228105	10/26/2009	-	FI
CY070434	9/28/2009	y	GB	HQ228106	10/26/2009	-	FI
CY070435	9/27/2009	-	GB	HQ228107	10/27/2009	y	FI
CY070446	10/4/2009	-	GB	HQ228108	10/27/2009	-	FI
CY070451	10/5/2009	-	GB	HQ228109	10/27/2009	-	FI
CY070467	10/12/2009	-	GB	HQ228110	10/26/2009	y	FI
CY070470	10/11/2009	-	GB	HQ228111	11/11/2009	y	FI
CY070482	10/14/2009	-	GB	HQ228112	11/14/2009	y	FI
CY070485	10/14/2009	-	GB	HQ228113	11/18/2009	-	FI
CY070504	10/16/2009	-	GB	HQ228114	11/14/2009	-	FI
CY070516	10/16/2009	y	GB	HQ228115	11/6/2009	y	FI
CY070523	10/20/2009	-	GB	HQ228116	10/12/2009	-	FI
CY070528	10/21/2009	-	GB	HQ228117	11/15/2009	-	FI
CY070535	11/1/2009	y	GB	HQ228118	11/19/2009	-	FI
CY070549	11/3/2009	-	GB	HQ228119	11/10/2009	-	FI
CY070556	11/2/2009	y	GB	HQ228121	11/12/2009	-	FI
CY070563	11/4/2009	-	GB	HQ228123	11/17/2009	-	FI
CY070564	10/26/2009	-	GB	HQ228124	10/22/2009	-	FI
CY070566	11/6/2009	-	GB	HQ228125	11/13/2009	-	FI

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CY070572	11/9/2009	-	GB	HQ228126	11/19/2009	-	FI
CY070587	11/17/2009	y	GB	HQ228127	12/16/2009	y	FI
CY070591	11/17/2009	-	GB	HQ228128	11/20/2009	y	FI
CY070596	11/20/2009	y	GB	HQ228129	11/20/2009	-	FI
CY070601	11/18/2009	-	GB	HQ228130	11/24/2009	-	FI
CY070604	11/17/2009	y	GB	HQ228131	11/24/2009	y	FI
CY070605	11/11/2009	-	GB	HQ228132	11/25/2009	-	FI
CY070608	11/14/2009	-	GB	HQ228133	12/9/2009	-	FI
CY070609	11/13/2009	y	GB	HQ228134	11/8/2009	y	FI
CY070614	11/23/2009	-	GB	HQ228135	11/9/2009	-	FI
CY070618	11/24/2009	-	GB	HQ228136	11/6/2009	y	FI
CY070619	11/24/2009	-	GB	HQ228137	11/5/2009	-	FI
CY070620	11/23/2009	-	GB	HQ228138	11/5/2009	-	FI
CY070629	11/25/2009	-	GB	HQ228139	11/2/2009	-	FI
CY070630	11/23/2009	-	GB	HQ228140	12/24/2009	-	FI
CY070633	11/24/2009	-	GB	HQ228141	12/1/2009	-	FI
CY070634	11/20/2009	-	GB	HQ228142	12/6/2009	-	FI
CY070635	11/22/2009	-	GB	HQ228143	10/27/2009	-	FI
CY070642	11/25/2009	-	GB	HQ228144	1/12/2010	y	FI
CY070647	12/8/2009	-	GB	HQ228145	1/13/2010	-	FI
CY070650	12/11/2009	-	GB	HQ228146	2/2/2010	-	FI
CY070652	12/9/2009	-	GB	HQ228147	1/26/2010	-	FI
CY070653	12/11/2009	-	GB	HQ420235	11/20/2009	-	PO
CY070662	12/15/2009	-	GB	HQ834746	10/13/2010	-	RU
CY070679	5/21/2009	y	GB	HQ891281	12/3/2010	-	RU
CY070689	5/24/2009	y	GB	JF340083	1/25/2010	-	RU
CY070690	5/24/2009	y	GB	JF429392	11/21/2009	-	FR
CY070709	5/29/2009	y	GB	JF429393	11/25/2009	-	FR
CY070711	5/24/2009	y	GB	JF429394	11/17/2009	-	FR
CY070717	6/1/2009	y	GB	JF429395	11/23/2009	-	FR
CY070724	6/3/2009	y	GB	JF429396	9/14/2009	-	FR
CY070733	12/29/2009	-	GB	JF682629	1/25/2011	y	CZ
CY070738	11/25/2009	-	GB	JF701798	1/30/2008	y	FR
CY071055	1/5/2010	-	AT	JF701802	1/30/2008	y	FR
CY071063	12/23/2009	-	EE	JF701804	2/4/2008	y	FR
CY071071	1/7/2010	-	EE	JF701806	2/6/2008	y	FR
CY071079	12/2/2009	y	DE	JF701808	2/1/2008	y	FR
CY071087	12/2/2009	y	DE	JF701812	2/12/2008	y	FR
CY071095	12/11/2009	-	ES	JF701813	2/18/2008	y	FR
CY071103	12/16/2009	-	BE	JF701818	2/25/2008	y	FR
CY071111	12/22/2009	-	DE	JF701821	2/24/2008	y	FR
CY071127	12/31/2009	-	GR	JF701824	2/19/2008	y	FR

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CY071135	1/13/2010	-	GR	JF701826	2/16/2008	y	FR
CY071143	1/14/2010	-	GR	JF701827	2/13/2008	y	FR
CY071151	1/19/2010	-	GR	JF906183	2/12/2010	-	NL
CY071159	1/11/2010	-	GR	JN185093	1/25/2011	-	RU
CY071167	1/21/2010	y	GR	JN185098	1/24/2011	-	RU
CY071175	1/24/2010	-	GR	JN185100	2/9/2011	-	RU
CY071191	12/2/2009	-	DE	JN185102	2/2/2011	-	RU
CY071199	12/23/2009	-	DE	JN185103	2/7/2011	-	RU
CY071207	1/8/2010	-	DE	JN185106	2/8/2011	-	RU
CY071215	1/11/2010	-	DE	JN185107	1/23/2011	-	RU
CY071223	11/19/2009	y	NO	JN185108	1/23/2011	-	RU
CY071231	12/29/2009	-	PO	JN185110	1/24/2011	-	RU
CY071239	12/29/2009	-	PO	JN185111	2/3/2011	-	RU
CY071247	11/24/2009	y	ES	JN185113	1/24/2011	-	RU
CY071255	12/16/2009	-	ES	JN185114	2/7/2011	-	RU
CY071263	1/30/2010	-	GR	JN185115	1/26/2011	-	RU
CY071271	2/2/2010	-	GR	JN185116	1/26/2011	-	RU
CY071279	2/5/2010	-	GR	JN185117	2/10/2011	-	RU
CY071287	2/5/2010	-	GR	JN596858	8/6/2009	-	RU
CY071295	1/18/2010	-	GR	JN601076	11/23/2010	-	FI
CY071303	1/25/2010	-	GR	JN601077	11/29/2010	-	FI
CY071311	1/27/2010	-	GR	JN601078	12/3/2010	-	FI
CY071319	2/3/2010	-	GR	JN601079	12/3/2010	-	FI
CY071375	2/5/2010	-	DE	JN601080	12/3/2010	-	FI
CY072222	11/25/2009	y	DE	JN601081	12/3/2010	-	FI
CY072230	11/26/2009	-	DE	JN601082	12/8/2010	-	FI
CY072238	11/30/2009	-	DE	JN601083	12/7/2010	-	FI
CY072246	11/23/2009	y	DK	JN601084	12/3/2010	-	FI
CY072254	11/24/2009	y	DK	JN601085	12/7/2010	-	FI
CY072262	12/2/2009	-	PO	JN601086	12/9/2010	y	FI
CY072270	12/2/2009	-	PO	JN601087	12/9/2010	-	FI
CY072278	12/3/2009	y	PO	JN601088	12/9/2010	-	FI
CY072286	12/3/2009	-	PO	JN601089	12/9/2010	y	FI
CY072294	12/7/2009	-	PO	JN601090	12/9/2010	-	FI
CY072302	12/7/2009	-	PO	JN601091	12/9/2010	-	FI
CY072310	12/8/2009	-	PO	JN601092	12/13/2010	-	FI
CY072342	12/13/2009	-	GR	JN601093	12/13/2010	-	FI
CY072350	12/13/2009	-	GR	JN601094	12/14/2010	-	FI
CY072358	12/20/2009	-	GR	JN601095	12/9/2010	-	FI
CY072366	12/20/2009	-	GR	JN601096	12/9/2010	-	FI
CY072374	12/25/2009	y	GR	JN601097	12/9/2010	-	FI
CY072382	12/26/2009	-	GR	JN601098	12/13/2010	y	FI

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CY072390	12/26/2009	-	GR	JN601099	12/13/2010	-	FI
CY072398	12/28/2009	-	GR	JN601100	12/14/2010	-	FI
CY072406	12/29/2009	-	GR	JN601101	12/13/2010	y	FI
CY072414	12/30/2009	-	GR	JN601102	12/14/2010	-	FI
CY072422	12/30/2009	-	GR	JN601103	12/14/2010	-	FI
CY072430	12/30/2009	-	GR	JN601104	12/14/2010	-	FI
CY072438	12/30/2009	-	GR	JN601105	12/13/2010	-	FI
CY072446	12/30/2009	-	GR	JN601106	12/13/2010	y	FI
CY072454	12/17/2009	-	GR	JN601107	12/14/2010	-	FI
CY072462	12/17/2009	-	GR	JN601108	12/14/2010	-	FI
CY072470	12/17/2009	-	GR	JN601109	1/12/2011	-	FI
CY072478	12/18/2009	-	GR	JN601110	1/14/2011	-	FI
CY072486	12/18/2009	-	GR	JN704791	2/22/2011	-	RU
CY072494	12/20/2009	-	GR	JN714484	12/31/2010	-	RU
CY072518	12/20/2009	-	GR	JN714492	1/26/2011	-	RU
CY072526	1/7/2010	-	EE	JN714500	2/22/2011	-	RU
CY072542	12/9/2009	-	PO	JN714508	2/5/2011	-	RU
CY072550	12/9/2009	-	PO	JN714513	2/4/2011	-	RU
CY073006	12/26/2009	-	GR	JN714514	2/8/2011	-	RU
CY073118	10/31/2009	-	RU	JN714517	3/14/2011	-	RU
CY073182	12/15/2009	-	RS	JN714518	2/11/2011	-	RU
CY073190	11/18/2009	-	RS	JN714520	1/2/2011	-	RU
CY073198	11/18/2009	-	RS	JN714522	1/27/2011	-	RU
CY073206	12/14/2009	-	RS	JN714524	1/25/2011	-	RU
CY073214	12/14/2009	-	RS	JN714525	1/25/2011	-	RU
CY073222	12/10/2009	-	RS	JN714526	1/28/2011	-	RU
CY073230	12/10/2009	-	RS	JN714527	1/28/2011	-	RU
CY073238	11/29/2009	-	RS	JN714528	1/25/2011	-	RU
CY073246	11/29/2009	-	RS	JN714529	1/28/2011	-	RU
CY073254	12/23/2009	-	GR	JQ041354	2/3/2011	-	RU
CY073481	11/13/2009	-	DE	JQ173148	7/27/2009	y	FI
CY073489	12/15/2009	-	GR	JQ173156	5/10/2009	y	FI
CY073497	12/1/2009	y	DE	JQ173164	11/25/2009	y	FI
CY073505	12/20/2009	-	GR	JQ409126	5/25/2009	y	FI
CY073725	12/7/2009	-	DK	JQ409134	6/13/2009	y	FI
CY073733	2/5/2010	-	EE	JQ409142	6/13/2009	y	FI
CY073741	11/18/2009	-	DK	JQ431196	8/21/2009	y	FR
CY073749	11/26/2009	-	DK	JQ431197	8/11/2009	y	FR
CY073765	12/3/2009	-	ES	JQ431205	8/17/2009	y	FR
CY073773	1/5/2010	-	AT	JQ431206	8/13/2009	y	FR
CY073877	12/15/2009	-	GR	JQ431207	8/13/2009	y	FR
CY075059	1/6/2010	-	GR	JQ431208	8/24/2009	y	FR

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CY075067	1/6/2010	y	GR	JQ431209	8/24/2009	y	FR
CY075075	2/17/2010	-	GR	JQ431210	8/19/2009	y	FR
CY075475	11/2/2009	-	RU	JQ431211	8/26/2009	y	FR
CY075477	11/3/2009	-	RU	JQ431212	8/14/2009	y	FR
CY075479	11/10/2009	-	RU	JQ431213	8/20/2009	y	FR
CY075480	8/13/2009	-	RU	JQ431215	8/19/2009	y	FR
CY075482	11/13/2009	-	RU	JQ431216	8/21/2009	y	FR
CY075483	11/14/2009	-	RU	JQ431217	8/18/2009	y	FR
CY075485	10/26/2009	-	RU	JQ431218	8/22/2009	y	FR
CY075487	10/28/2009	-	RU	JQ431219	8/26/2009	y	FR
CY075488	10/29/2009	-	RU	JQ431221	8/24/2009	y	FR
CY083248	11/3/2009	-	RU	JQ612499	10/26/2009	-	HU
CY083543	11/10/2009	-	HU	JQ612507	1/12/2010	-	HU
CY083551	11/10/2009	-	HU	JX625395	6/30/2009	y	GB
CY083559	12/4/2009	y	HU	JX625459	7/13/2009	y	GB
CY083690	11/30/2009	-	ES	JX625467	7/17/2009	y	GB
CY083729	11/26/2009	y	DE	JX625513	10/9/2009	-	GB
CY083745	12/11/2009	-	ES	JX625702	11/28/2010	-	GB
CY083761	11/25/2009	-	DK	JX625710	11/29/2010	y	GB
CY083768	12/10/2009	-	GR	JX625742	11/30/2010	-	GB
CY083776	11/25/2009	y	DK	JX625782	12/6/2010	-	GB
CY083787	11/30/2009	y	DK	JX625798	12/10/2010	-	GB
CY083805	12/17/2009	-	ES	JX625806	12/9/2010	-	GB
CY083825	12/3/2009	-	PO	JX625862	12/13/2010	y	GB
CY083902	12/13/2009	-	GR	JX625870	12/14/2010	y	GB
CY083910	11/23/2009	y	DK	JX625886	12/16/2010	-	GB
CY083918	12/3/2009	-	PO	JX625894	12/14/2010	y	GB
CY083926	12/11/2009	-	PO	JX625910	12/16/2010	-	GB
CY083934	12/11/2009	-	PO	JX625934	12/20/2010	y	GB
CY088613	11/26/2009	-	DE	JX625950	12/16/2010	y	GB
CY088621	12/21/2009	-	DK	KC222636	7/22/2009	y	DE
CY088729	11/18/2009	-	NL	KC620386	7/21/2009	y	DE
CY090861	2/9/2010	-	NL	KF560302	4/15/2011	y	FI
CY091601	2/7/2011	-	RU	KF860844	9/1/2009	-	ES
CY091609	2/14/2011	-	RU	KF860845	11/14/2009	y	ES
CY091613	2/21/2011	-	RU	KF860846	1/29/2010	y	ES
CY091616	1/26/2011	-	RU	KF897777	9/14/2010	-	FR
CY091620	1/27/2011	-	RU	KF897785	12/26/2010	-	FR
CY097892	1/14/2011	-	RU	KF897793	12/20/2010	-	FR
CY097900	1/21/2011	-	RU	KF897801	12/22/2010	-	FR
CY097932	2/3/2011	-	RU	KF897809	1/1/2011	y	FR
CY097980	1/18/2011	y	HU	KJ549778	7/22/2009	y	DE

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CY097988	1/27/2011	y	HU	KP456197	3/13/2008	-	UA
CY097996	1/27/2011	y	HU	KP456205	1/14/2008	y	RO
CY098004	1/18/2011	-	CZ	KP456268	1/2/2008	y	PT
CY098028	1/31/2011	-	RU	KP456364	1/9/2008	y	GB
CY098036	2/2/2011	-	RU	KP456386	3/3/2008	-	UA
CY098060	1/31/2011	-	RU	KP456439	1/21/2008	y	RO
CY103841	3/11/2011	-	RU	KP456446	1/10/2008	y	DE
CY103843	3/11/2011	-	RU	KP456509	1/10/2008	y	RO
CY103845	1/31/2011	-	RU	KP456565	1/10/2008	y	SI
CY103847	2/2/2011	-	RU	KP456666	12/14/2007	y	FR
CY103851	2/4/2011	-	RU	KP456714	1/22/2008	y	IT
CY103853	2/20/2011	-	RU	KP456896	10/12/2007	y	NL
CY103855	2/20/2011	-	RU	KP456929	12/11/2007	y	SE
CY107260	11/12/2009	-	GB	KP457217	1/3/2008	y	ES
CY107340	10/15/2009	-	GB	KP457268	1/25/2008	-	HU
CY107403	11/5/2009	-	GB	KP457295	12/11/2007	y	NO
CY107418	12/14/2009	-	GB	KP457321	11/26/2007	y	NO
CY107453	2/4/2010	y	GB	KP457328	1/21/2008	y	BG
CY107472	6/10/2009	y	GB	KP457365	2/6/2008	-	UA
CY107585	6/3/2009	y	GB	KP457403	12/31/2007	y	GB
CY107693	6/24/2009	y	GB	KP457648	2/19/2008	-	UA
CY115862	8/11/2009	y	NL	KP457914	12/24/2007	y	SE
CY129435	1/19/2011	y	GB	KP458144	1/15/2008	y	RO
CY129451	1/28/2011	y	GR	KP458150	3/27/2008	-	UA
CY129459	2/12/2011	y	GR	KP458193	12/10/2007	y	NO
CY129467	2/12/2011	y	GR	KP458208	1/8/2008	y	GR
CY129475	2/25/2011	-	GR	KP458248	2/13/2008	y	IT
CY129485	2/27/2011	y	GR	KP458257	12/17/2007	-	FR
CY129499	1/18/2010	y	DE	KP458277	1/23/2008	-	LV
CY129546	1/13/2011	y	DK	KP458391	11/15/2007	y	GB
CY129550	1/26/2011	-	EE	KP458403	1/29/2008	y	NO
CY129558	2/14/2011	y	PO	KP458424	12/8/2007	y	NO
CY129590	2/8/2011	y	DE	KP458513	3/3/2008	-	UA
CY129598	1/13/2011	y	DE	KP458638	1/10/2008	y	SI
CY129606	2/18/2011	y	DE	KP458677	1/2/2008	y	NO
CY129614	2/23/2011	-	DE	KP458745	2/12/2008	-	UA
CY129622	2/1/2011	-	DE	KP458776	12/7/2007	y	NO
CY129630	2/10/2011	y	DE	KP458980	1/14/2008	y	RO
CY129638	2/18/2011	y	DE	KP459033	3/6/2008	-	UA
CY129662	1/19/2011	-	GR	KP459059	12/21/2007	y	NL
CY129670	1/27/2011	-	GR	KP459061	1/6/2008	y	BE
CY129678	2/1/2011	y	GR	KP459165	12/19/2007	-	LV

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CY129686	2/18/2011	-	GR	KP459215	1/15/2008	y	RO
CY129694	2/24/2010	y	GR	LN845774	3/18/2010	-	GB
CY129702	2/4/2011	y	GR	LN846336	12/16/2010	-	GB
CY129710	2/11/2011	y	GR	LN846344	12/16/2010	y	GB
CY129718	2/25/2011	y	GR	LN846470	12/22/2010	y	GB
CY129726	2/27/2011	-	GR	LN846494	2/4/2010	-	GB
CY129734	2/21/2011	-	ES	LN846518	12/20/2010	y	GB
CY129830	1/5/2011	y	GB	LN846550	12/8/2009	y	GB
CY129886	2/21/2011	y	BE	LN846558	1/4/2011	-	GB
CY129894	2/11/2011	y	DE	LN846566	12/21/2010	y	GB
CY129902	2/15/2011	-	DE	LN846631	1/12/2011	y	GB
CY129910	1/25/2011	-	DK	LN846639	1/9/2011	-	GB
CY129918	1/21/2011	y	DK	LN846655	12/2/2010	-	GB
CY129926	1/19/2011	y	DK	LN846795	12/30/2010	y	GB
CY129934	1/20/2011	y	DK	LN849998	12/18/2010	y	GB
CY129942	2/4/2011	y	DK	LN850014	1/12/2011	y	GB
CY129950	1/27/2011	-	EE	LN850054	12/15/2010	y	GB
CY129958	2/1/2011	-	EE	LN850133	12/15/2010	y	GB
CY129966	2/2/2011	-	EE	LN850284	12/18/2010	y	GB
CY129974	1/31/2011	-	PO	LN850308	12/14/2010	y	GB
CY129982	2/4/2011	-	PO	LN850364	12/2/2010	y	GB
CY176397	2/23/2011	y	PO	LN850719	11/30/2010	y	GB
CY176474	1/27/2011	-	GR	LN866284	12/23/2010	y	GB
CY176482	2/12/2011	y	GR	LN866301	12/22/2010	y	GB
CY176546	1/5/2011	-	GB	LN866317	11/25/2010	-	GB
CY176570	1/25/2011	y	DK	LN867325	12/9/2010	y	GB
CY176578	1/14/2011	y	DK	LN867357	12/12/2010	-	GB
CY176586	2/7/2011	y	DK	LN867365	12/21/2010	y	GB
CY176594	2/8/2011	y	PO	LN867431	1/1/2011	-	GB
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CY176802	1/19/2011	y	GR	LN867470	1/8/2011	-	GB
CY176810	1/28/2011	y	GR	LN867494	12/23/2010	y	GB
EU685785	1/10/2008	y	FR	LN867502	11/30/2010	y	GB
EU685786	1/13/2008	y	FR	LN867518	12/17/2010	-	GB
FJ264950	2/13/2008	y	DK	LN867660	12/23/2010	y	GB
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FJ654305	12/12/2007	y	NO	LN867852	12/17/2010	y	GB
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Table S2. European Country Codes

Country	Code
Albania	AL
Austria	AT
Belgium	BE
Bulgaria	BG
Croatia	HR
Cyprus	CY
CzechRepublic	CZ
Denmark	DK
Estonia	EE
Finland	FI
France	FR
Germany	DE
Greece	GR
Hungary	HU
Iceland	IS
Ireland	IE
Italy	IT
Latvia	LV
Liechtenstein	LI
Lithuania	LT
Luxembourg	LU
Malta	MT
Moldova	MD
Netherlands	NL
Norway	NO
Poland	PO
Portugal	PT
Romania	RO
Russia	RU
Slovakia	SK
Slovenia	SI
Spain	ES
Sweden	SE
Switzerland	CH
Yugoslavia	MK
Turkey	TR
Ukraine	UA
UnitedKingdom	GB

Table S3. Summary of Available Sequences. Number of sequences available on Genbank per season and per European country.

Country	2007-2008	2008-2009	2009-2010	2010-2011	Total
AT	1	0	6	0	7
BE	2	0	14	1	17
BG	2	0	0	0	2
CZ	1	2	0	2	5
DE	16	9	36	10	71
DK	1	3	35	9	48
EE	0	0	7	4	11
ES	3	1	28	1	33
FI	0	50	67	36	153
FR	16	31	5	5	57
GB	6	50	76	53	185
GR	2	0	85	17	104
HR	1	0	0	0	1
HU	2	0	5	3	10
IE	0	7	0	0	7
IT	4	30	2	0	36
LU	0	1	0	0	1
LV	3	0	0	0	3
NL	6	3	21	0	30
NO	16	15	14	0	45
PO	0	0	18	5	23
PT	3	0	0	0	3
RO	8	0	0	0	8
RS	0	1	9	0	10
RU	0	43	90	53	186
SE	4	4	0	0	8
SI	4	0	0	0	4
UA	10	0	0	0	10
Total	**111**	**250**	**518**	**199**	**1078**

Table S4. Summary of Sequences Used. Number of sequences used per season and per European country. Asterisk indicates countries for which no rail passenger volume data was available.

Country	2007-2008	2008-2009	2009-2010	2010-2011	Total
AT	1	0	1	0	2
BE	2	0	3	1	6
BG	2	0	0	0	2
CZ	1	2		1	4
DE	16	9	9	6	40
DK	1	3	12	8	24
EE	0	0	0	0	0
ES	3	1	5	0	9
FI	0	50	20	6	76
FR	15	29	0	1	45
GB	6	50	10	33	99
GR	2	0	9	11	22
HR	0	0	0	0	0
HU	0	0	1	3	4
IE	0	7	0	0	7
IT	4	30	1	0	35
LU	0	1	0	0	1
LV	0	0	0	0	0
NL	6	3	1	0	10
NO	16	15	5	0	36
PO	0	0	1	3	4
PT	3	0	0	0	3
RO	8	0	0	0	8
RS*	0	0	0	0	0
RU*	0	0	0	0	0
SE	4	4	0	0	8
SI	4	0	0	0	4
UA*	0	0	0	0	0
Total	**94**	**204**	**78**	**73**	**449**

Season	Root Height	Growth Rate	Clock Rate	Clade	Clade Divergence Date	Sequences	Locations
2007-2008	2.634 (1.324-4.180)	0.688 (0-1.719)	0.00692 (0.0034451-0.010297)	1	2007.485 (2007.055 - 2007.835)	32	7
				2	2007.115 (2006.515 - 2007.605)	62	15
2008-2009 (Pandemic)	0.581 (0.466-0.714)	7.027 (4.433-9.665)	0.0086752 (0.0068082-0.010757)	1	2009.084 (2008.954 - 2009.194)	204	13
2009-2010	1.211 (1.022-1.398)	6.513 (5.166-7.798)	0.0057427 (0.0048251-0.0067179)	2	2009.535 (2009.405 - 2009.645)	44	11
				3	2009.575 (2009.495 - 2009.635)	15	4
				4	2009.675 (2009.595 - 2009.745)	19	5
2010-2011	1.18 (0.884-1.535)	3.8 (2.215-5.542)	0.007906 (0.0060384-030097321)	1	2010.715 (2010.625 - 2010.785)	14	5
				2	2010.725 (2010.635 - 2010.815)	22	8
				3	2010.755 (2010.665 - 2010.835)	37	5

Table S5. Summary of epidemiological and evolutionary dynamics of European H1N1 epidemics based on phylogenetic analyses of each influenza season. 'Root Height' is measured in years before present, with the present time equal to the latest sampling date. 'Clock rate' is measured in substitutions/site/year. 'Sequences' represents the number of sequences analyzed per clade and 'Locations' represents the number of states these sequences were collected from.

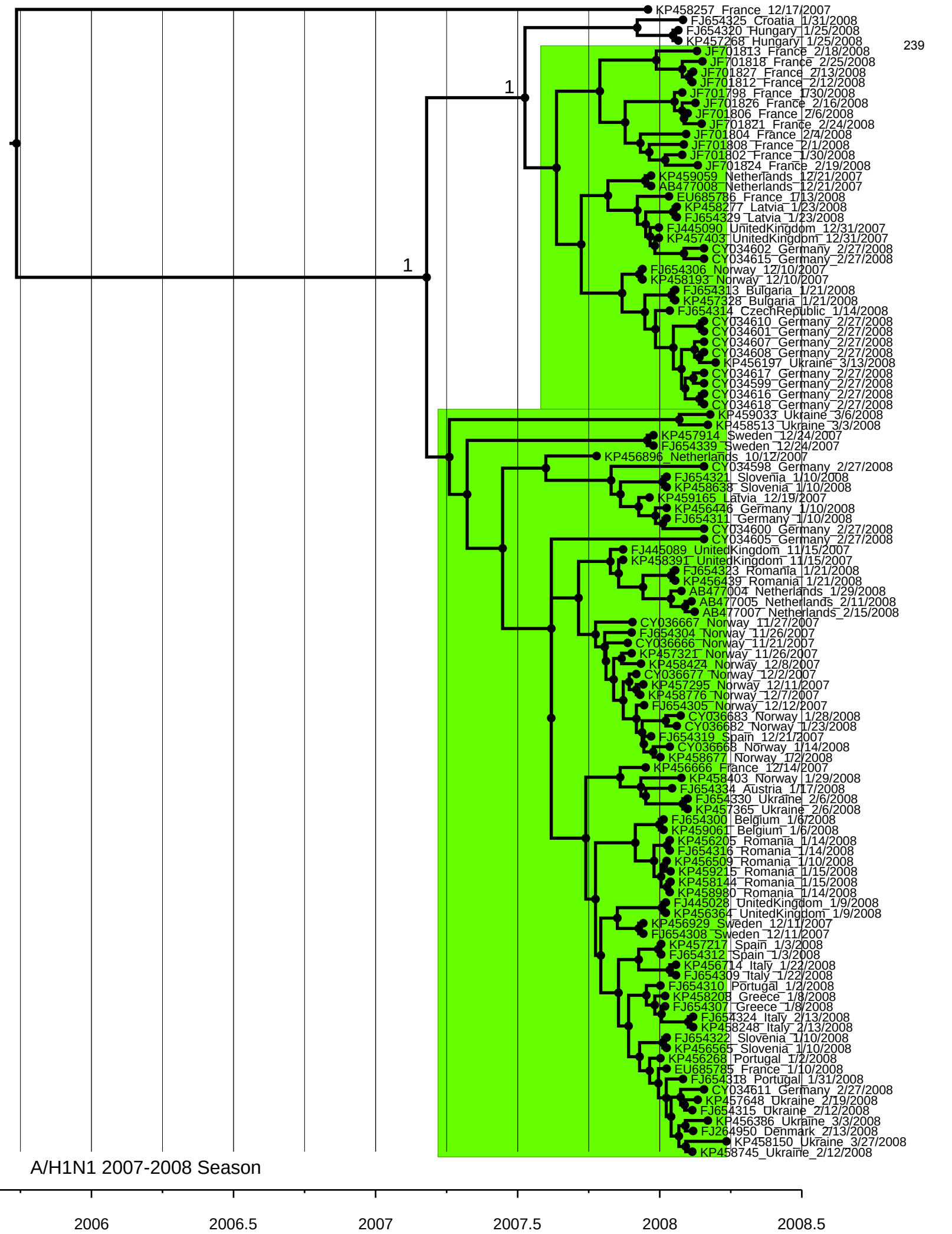
II.2 Supplementary Figures and Captions

Figure S1. Phylogenetic tree estimated using influenza A/H1N1 HA sequences sampled from a single subtype within the 2007-2008 influenza season using a Bayesian method. Clades used for association tests are highlighted in green and have a posterior probability values >0.9. Horizontal axis is measured in years.

Figure S2. Phylogenetic tree estimated using influenza A/H1N1 HA sequences sampled from a single subtype within the 2008-2009 influenza season using a Bayesian method. Clades used for association tests are highlighted in green and have a posterior probability values >0.9. Horizontal axis is measured in years.

Figure S3. Phylogenetic tree estimated using influenza A/H1N1 HA sequences sampled from a single subtype within the 2009-2010 influenza season using a Bayesian method. Clades used for association tests are highlighted in green and have a posterior probability values >0.9. Horizontal axis is measured in years.

Figure S4. Phylogenetic tree estimated using influenza A/H1N1 HA sequences sampled from a single subtype within the 2010-2011 influenza season using a Bayesian method. Clades used for association tests are highlighted in green and have a posterior probability values >0.9. Horizontal axis is measured in years.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A/H1N1 2007-2008 Season
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240
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2009.3
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2009.6
2009.7

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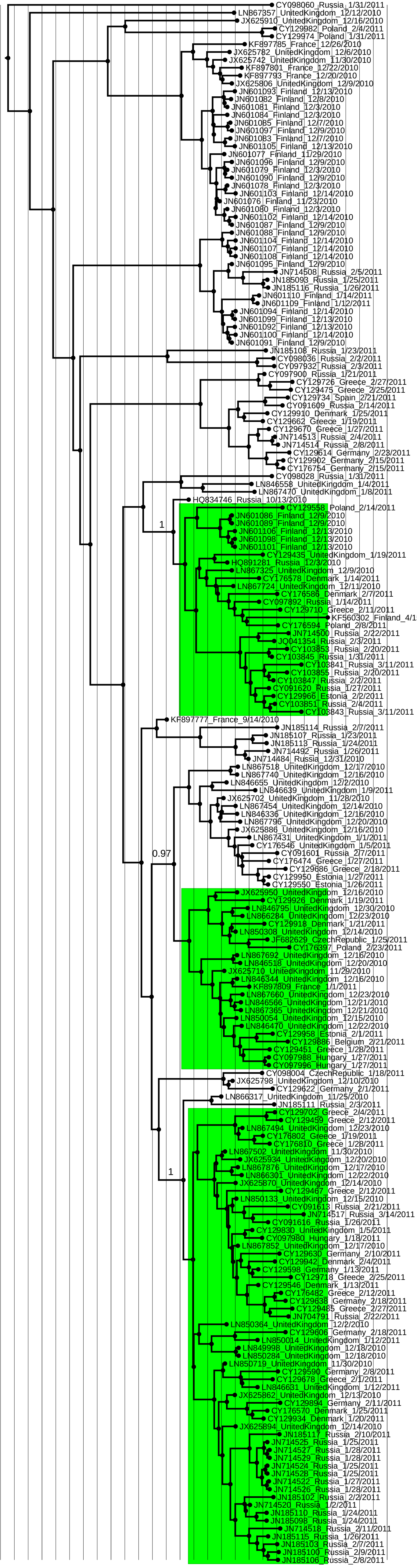
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A/H1N1 2010-2011 Season
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2011.5