

Landscape Epidemiology of Vector-Borne Diseases

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Key Words

vector, host, pathogen, climate, spatial dynamics, nidus, refugia

Abstract

Landscape epidemiology describes how the temporal dynamics of host, vector, and pathogen populations interact spatially within a permissive environment to enable transmission. The spatially defined focus, or nidus, of transmission may be characterized by vegetation as well as by climate, latitude, elevation, and geology. The ecological complexity, dimensions, and temporal stability of the nidus are determined largely by pathogen natural history and vector bionomics. Host populations, transmission efficiency, and therefore pathogen amplification vary spatially, thereby creating a heterogeneous surface that may be defined by remote sensing and statistical tools. The current review describes the evolution of landscape epidemiology as a science and exemplifies selected aspects by contrasting the ecology of two different recent disease outbreaks in North America caused by West Nile virus, an explosive, highly virulent mosquito-borne virus producing ephemeral nidi, and *Borrelia burgdorferi*, a slowly amplifying chronic pathogen producing semipermanent nidi.

Vector: competent arthropod that carries a pathogen to and infects a vertebrate host

WNV: West Nile virus

Amplification: increase of a pathogen and therefore the number of infections within the environment

Nidus: place where pathogen transmission occurs (from Latin meaning “nest,” synonym of focus)

Reservoir host: arthropod or vertebrate host that provides a long-term source of infection

Anthroponoses: diseases in which humans function as the primary vertebrate host

INTRODUCTION

Geographical information systems, remote sensing, and modern computing have provided new tools to re-examine old, and perhaps synthesize contemporary, concepts concerning the landscape epidemiology of vector-borne diseases. The current review extends previous summaries focused on methods of study (3, 7, 52, 56), defines the components of vector-borne disease foci, examines factors driving their dynamics in time and space, and describes how expanding human populations have altered their ecology, thereby enhancing the risk of transmission. The emergence and ongoing epidemics of Lyme borreliosis (*Spirochaetales*, *Spirochaetaceae*, *Borrelia burgdorferi*) and West Nile virus (*Flaviviridae*, *Flavivirus*, WNV) in North America provide excellent comparative examples of how different vector biology and landscape dynamics determine foci composition, enable enzootic amplification, and determine human infection (51, 59, 61, 77). Although most examples in the current review relate to these two pathogens, the overarching concepts should be extrapolative to other arthropod-borne pathogens.

Landscape epidemiology is linked closely to its ecological parallel, landscape ecology, a science with beginnings in the early 1930s to study interactions between the environment and vegetation (122). Geomorphology and climate combine to delineate plant communities and therefore ecosystem structure. These biomes were first classified at a global scale in the early 1900s by Köppen, who proposed that climatic zones could be effectively defined by their resulting plant communities. This classification system was updated recently for the 1951–2000 period (88) and broadly delineates ecosystems with varying capacity to support different vectors, hosts, and pathogens. Some pathogens such as WNV have invaded almost all but the most extreme climates, whereas others, such as Barmah Forest virus, seem more restrictive in their distribution. However, landscapes are spatially and temporally dynamic. The increasing size and expanding distribution of the global human population

have destabilized climax communities that have been intruded upon by agriculture and human habitation and must respond to anthropogenic-driven climate and ecosystem change (31). The resulting heterogeneous matrix ([http://www.eoearth.org/article/Anthropogenic.biomes](http://www.eoearth.org/article/Anthropogenic_biomes)) consists of habitat patches that change in dimension owing to human and other activities and are linked by a series of transitional boundaries (or ecotones) characterized by their distinct and diverse vegetative types, enhanced primary productivity, species diversity, and complex interactions (also referred to as the edge effect).

Concurrent with the emergence of landscape ecology as a science, Pavloskiy proposed the concept of nidality (or focality) of disease (86, 87), where pathogens are associated with specific landscapes. The nidus of infection contains three critical elements: (a) competent and infectious vectors, (b) competent vertebrate reservoirs, and (c) susceptible recipient (tangential) hosts such as humans or domestic animals. In his original concept based on tick-borne pathogens in Russia, humans became infected when they traveled into the nidus and contacted the infectious vector or perhaps the reservoir host. The disjunct distribution of infection and residence complicated the initial understanding of the epidemiology of transmission, especially for highly clustered tick-borne pathogens such as tick-borne encephalitis virus (83). This nidality concept blended with landscape ecology has led to the emergence of the contemporary science of landscape epidemiology (37), in which diseases may be associated with distinct landscape features or ecological settings where vector, host, and pathogen intersect within a permissive climate (**Figure 1**). When placed into the recent context of anthropogenically altered biomes or anthromes (31), the nidus now ranges from remote, sparsely inhabited landscapes to residential settings and may be delineated by various mapping and statistical tools (56). For many vector-borne anthroponoses, the nidus may be the human residence where commensal vectors reside and blood feed.

COMPONENTS OF THE NIDUS

Climate

Although delineated spatially by landscape features, disease foci invariably arise within a permissive climate where competent host and vector populations intersect (**Figure 1**). Within these environments, moisture governs vegetative structure and the extent of suitable habitat, whereas temperature governs the rates at which processes occur. Climate varies spatially and temporally at different scales, which may be divided into seasonal (intraannual), annual (interannual), and long-term (decadal or longer) change. For transmission to occur, climate must attain seasonal ranges within the tolerances of host and vector species and be suitable for pathogen replication within the poikilothermic arthropod vector. Most pathogens have a minimal thermal developmental threshold below which replication, and therefore transmission, will not occur. This is especially pertinent for arboviruses within diapausing insects, where termination, temperature increases, and even reproductive activity may be necessary for pathogen replication and detection (5). Seasonal changes in day length, temperature, and precipitation also delineate ecosystem primary productivity, food availability, and therefore host and vector reproductive periods. During unfavorable weather periods, nidus dimensions often contract to spatially delimited refugia that enable host and/or vector and pathogen persistence. Under permissive temperatures, moisture-related focus contraction actually may enhance host-vector contact and therefore transmission. In central Florida, for example, droughts limit favorable habitat and concentrate the mosquito vector *Culex nigripalpus* and its avian hosts at densely vegetated palm hammocks, where the transmission of St. Louis encephalitis virus (SLEV) is enhanced (25) and synchronized by episodic rainfall events that raise humidity and stimulate vector dispersal for oviposition and then blood feeding (26). During unfavorable periods, vertebrate reservoir host populations may survive by remaining metabolically active,

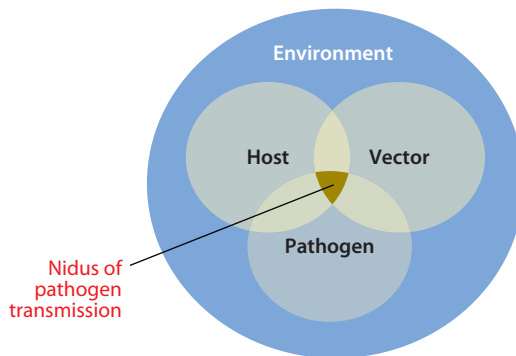


Figure 1

Conceptual nidus showing how vector, host, and pathogen populations intersect within a permissive environment to enable pathogen transmission.

entering hibernation, or migrating, whereas vector populations may remain active at permissive refugia, enter aestivation (summer), quiescence or diapause (winter), or become regionally extinct and require annual reintroduction. Despite the negative effect of elevated temperatures on vector survival (94, 96), most amplification transmission occurs during the warmest periods of the year, because the rate of pathogen replication in the vector typically increases and therefore the duration of extrinsic incubation decreases as a curvilinear function of ambient temperature (104).

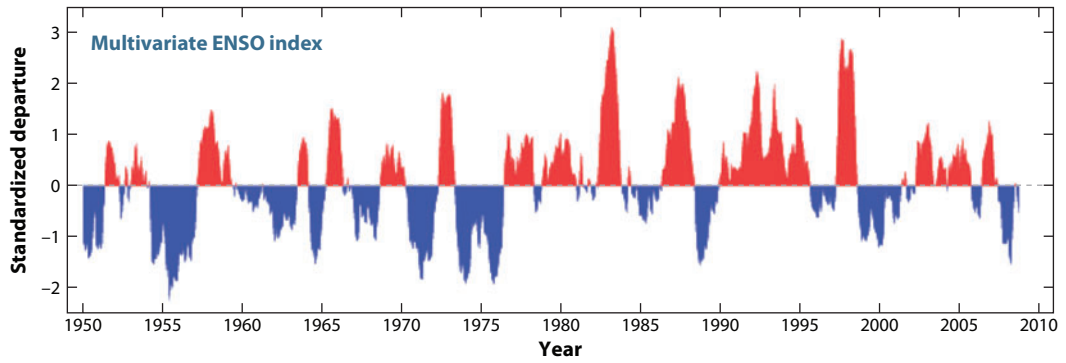
The duration and intensity of favorable periods often fluctuate due to climate cycles or show long-term patterns related to change. Intermediate duration changes in ocean temperatures create interannual variation in climate over broad areas often affecting pathogen dynamics. The El Niño phase of the El Niño–Southern Oscillation (ENSO) allows cloud formation to move from the western Pacific to the Hawaiian Islands, thereby increasing the frequency and intensity of rainfall events in parts of the New World, including the United States (**Figure 2**), while leading to droughts in the Western Pacific, including Australia. Warming of the Indian Ocean occurs concurrently with the ENSO shift, resulting in increased rainfall, the accumulation of surface water, and greening of the vegetation in east Africa, a precursor to outbreaks of Rift Valley Fever virus (68).

Refugia: place where pathogens or hosts persist during unfavorable periods

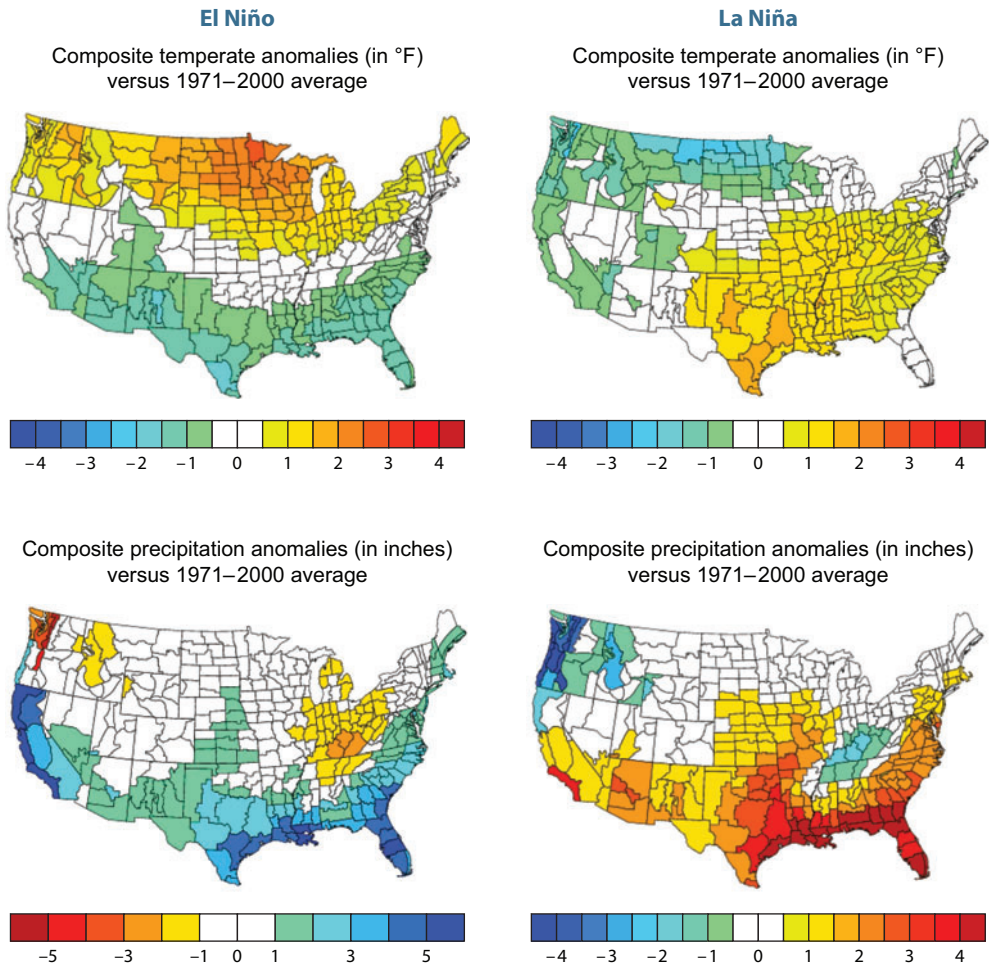
SLEV: St. Louis encephalitis virus

El Niño–Southern Oscillation (ENSO): temporal and spatial changes in the temperature of the Pacific Ocean

a



b



The three- to eight-year ENSO cycle may be altered by the Pacific Decadal Oscillation (PDO), which has been linked to rainfall, vegetation, rodent populations, and plague epizootic dynamics in the southwestern United States (12). In contrast, hot and dry La Niña conditions (**Figure 2**) between ENSO episodes have been associated historically with outbreaks of SLEV in North America, such as those in the Ohio River drainage in the 1970s (79).

Warm temperature anomalies have their greatest impact on nidus dynamics near the distributional limits of pathogens. WNV, for example, has caused recurring outbreaks in the upper midwestern United States and Canadian prairies during anomalously warm summers but has had reduced activity during cool summers (104). Collectively, climate variation at intermediate scales may be used to forecast habitat change, host and vector dynamics, and the risk of pathogen transmission, especially in Mediterranean-type climates such as California, where the extent of immature vector habitat during the spring-summer period is dictated by the quantity of winter precipitation (97).

Climate has been altered by overriding global trends that have warmed the earth by 0.75°C over the past 100 years, caused sea levels to rise, and led to increased annual variation in temperature and precipitation (116). Global warming has been disproportionately greatest at northern latitudes, leading to expansions in vector distributions, increases in the length of transmission seasons, and the introduction of pathogens such as several Blue-tongue virus serotypes into northern Europe (90) and WNV into central Canada. Pathogen transmission seems to progress most effectively

under warm temperatures, because vector populations increase rapidly in abundance and generation times are shortened; blood feeding and oviposition occur more frequently, increasing the frequency of host-vector contact; and rapid pathogen development within the vector shortens the duration of the extrinsic incubation period, thereby increasing the efficiency of transmission. Collectively, changes in these temperature-sensitive variables increase vectorial capacity (95) or the force of transmission that, in part, determines the shape of amplification and epidemic curves and establishes the receptivity of new areas for pathogen invasion. The response of the pathogen to temperature usually is species or even genotype specific and often defines the distributional limits of outbreaks. Historically, for example, outbreaks of western equine encephalitis virus (WEEV) were confined to areas north and SLEV to areas south of the 21°C June isotherm (49), most likely due to differences in the thermodynamics of viral replication in the mosquito host (104).

Urbanization alters climate within cities and surrounding landscapes by forming heat islands. Atmospheric pollutants in combination with extensive concrete and asphalt substrates absorb heat during the day and then radiate this heat back into the atmosphere at night, resulting in average temperatures that may be 2 to 5°C warmer than outlying vegetated areas (64). **Figure 3a** shows the impact of vegetation on the summer heat profile in New York City, whereas **Figure 3b** shows diagrammatically a temperature profile through an urban heat island. As urbanization intensifies, cities become progressively warmer. **Figure 3c**, for example, shows an increase in mean annual temperature in Los Angeles during a 50-year period of

Figure 2

Climate cycles. (a) Annual changes in the El Niño–Southern Oscillation (ENSO) index (<http://www.cdc.noaa.gov/people/klaus.wolter/MEI/>) and (b) anomaly of composite spatial temperature and precipitation in the United States during El Niño (November–March 1982–1983, 1972–1973, 1957–1958, 1965–1966, 1986–1987, 1991–1992, 1968–1969, 1997–1998, and 2002–2003) and La Niña (November–March 1954–1955, 1955–1956, 1970–1971, 1973–1974, 1975–1976, 1988–1989, and 1999–2000) periods (<http://www.cdc.noaa.gov/enso/enso.comp.html>).

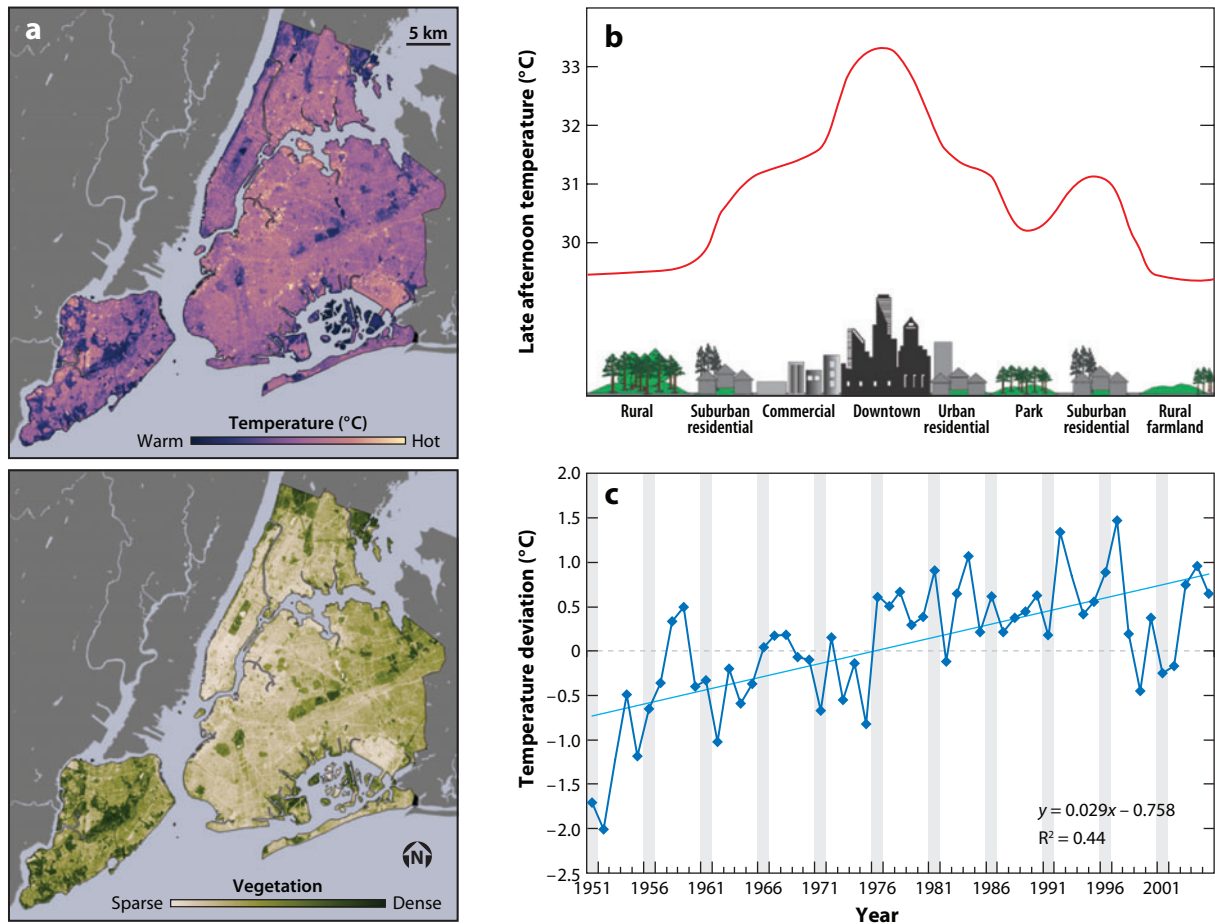


Figure 3

Urban heat islands. (a) Infrared satellite data (*top*) measured by NASA's Landsat Enhanced Thematic Mapper Plus on August 14, 2002, one of the hottest days in New York City's summer. Landsat also collected vegetation data (*bottom*). Images from NASA Earth Observatory Web page (<http://earthobservatory.nasa.gov/IOTD/view.php?id=6800>). (b) Afternoon temperatures in Atlanta, Georgia, showing the urban heat island effect (http://adaptation.rncan.gc.ca/perspective/health_3_e.php). (c) Yearly changes in the mean annual temperature measured at Santa Ana, Los Angeles, California.

continuous population growth. In addition to temperature, urbanization alters winds due to temperature differentials, creates urban canyons that tend to stagnate air movement, and increases precipitation runoff due to the high percentage of impervious surfaces that preclude percolation. In dry areas such as southern California, runoff from domestic landscaping creates curb drizzle that recharges underground drainage systems and produces large numbers of *Culex* vectors of WNV (118).

Vegetation

Ecosystem structure and productivity are determined by plant communities, which can be mapped remotely using aerial photography and satellite imagery. Plants provide cover for host and vector populations as well as food for vertebrates in the form of the plants themselves and the animals that feed on them. Vectors such as mosquitoes have evolved specific questing behaviors to locate plant sugar for flight energy (133) and blood meals for egg

production (13). Plant communities can be characterized at varying spatial scales. The NASA Terrestrial Observation and Prediction System (<http://ecocast.arc.nasa.gov/>), for example, utilizes eight-day MODIS imagery to derive soil moisture, leaf area, and gross primary productivity measures at a resolution of 1 km (78). Areas with high soil wetness and primary productivity during summer delineate areas suitable for mosquito production and for plants and insects, potential food items for bird populations. Areas with increased vector mosquito and avian abundance potentially have increased transmission of arboviruses such as WNV. On a fine scale, ecotones frequently are utilized by upland bird species such as mourning doves and house finches for roosting and nesting and by mosquitoes for flight paths and host seeking. **Figure 4** shows the abundance of adult female *Culex tarsalis* collected by unbaited suction traps operated along transects intersecting desert scrub vegetation and citrus orchard habitat moving upland from larval habitat (72). Note the repeated significant increase of mosquito abundance along the scrub–orchard ecotone. Vegetative associations also have been linked to the different life stages of *Ixodes scapularis* (the tick vector of Lyme borreliosis) at the interface of forests and residential properties in New York and Connecticut (19, 35, 77). In both instances, ecotones seem to define areas of high risk for human infection.

Hosts

Vertebrates function as intermediate or definitive hosts as well as reservoir, maintenance, or amplifying hosts for vector-borne pathogens. The response of vertebrates to infection depends upon the species of host and pathogen. Depending on this combination, the vertebrate host may be (a) refractory to infection (105), (b) susceptible to rapidly developing acute infections that may cause mortality or resolve, imparting permanent immunity [e.g., many avian hosts of WNV (103)], or (c) susceptible to developing chronic long-lasting infections that are a continual source of pathogens for vector

infection [e.g., mice infected with Lyme spirochetes (65)]. Typically, humans are the amplifying hosts for anthroponoses, but are dead-end hosts for most zoonoses, even though they may develop serious disease (e.g., WNV neuroinvasive or Lyme arthritis diseases). Because most hosts develop permanent protective immunity following infection, amplification transmission frequently depends on “herd immunity,” that is contingent upon host longevity and the rate of recruitment of young (such as hatching year birds) into the host population (44). Therefore, it is the location of these immunologically naive young of the year in time and space that may delineate the nidus. Nestling house finches and mourning doves, for example, are highly competent experimental hosts for SLEV (74), whereas adult birds produce a comparatively lower viremia that is less able to infect mosquitoes (101). Because these avian species frequently nest along vegetative ecotones, SLEV amplification may occur most efficiently when vectors are abundant during the vernal nesting season and quest at ecotonal vegetation (**Figure 4**). Aggregations of highly susceptible hosts at nesting colonies or communal roosts also may delineate areas of increased transmission and therefore the risk of human infection. During the 2004 Los Angeles WNV epidemic, for example, *Culex* mosquito and human infection incidence were aggregated spatially during late summer within foraging distance of American crow roosts delineated by the clustering pattern of birds testing positive at necropsy (98). In this example, landscape features such as a remnant stand of mature cottonwoods created conditions attractive to huge numbers of communally roosting American crows that formed the centroid of a nidus of intense WNV transmission in east Los Angeles.

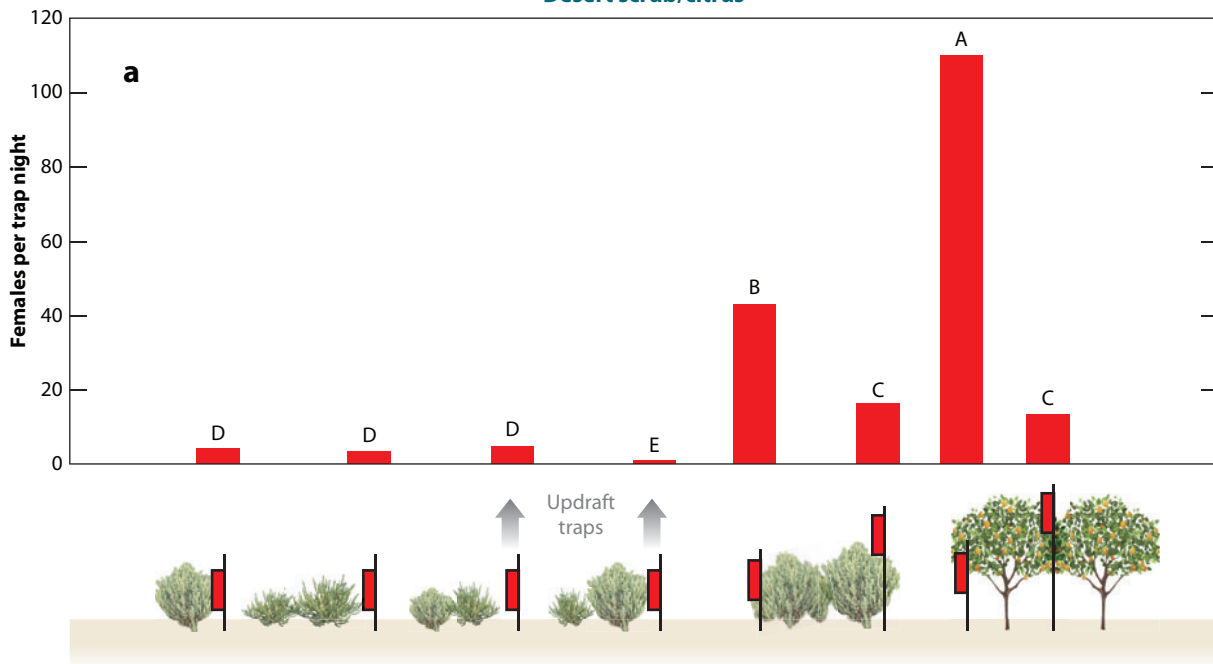
Vectors

Arthropods may function as intermediate or definitive hosts as well as reservoir, maintenance, and/or amplifying hosts for vector-borne pathogens. Like vertebrates, they may be refractory to infection but, if competent,

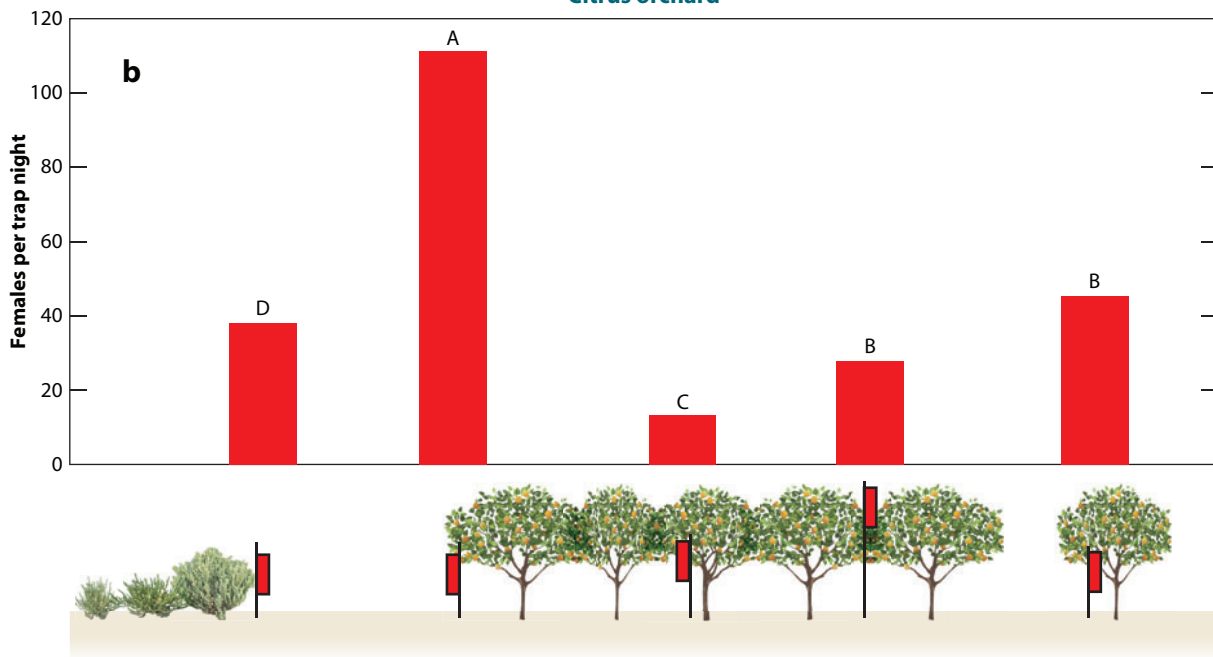
Vertebrate host: competent animal that provides a pathogen source for vector infection

Zoonoses: diseases in which nonhuman animals function as the primary vertebrate host(s)

Desert scrub/citrus



Citrus orchard



typically remain infected and then infectious throughout life after pathogen dissemination. Questing behavior and resulting host selection, in combination with abundance, survival, and vector infection competence, markedly affect transmission dynamics over varying temporal and spatial scales. Coalescing these factors into the vectorial capacity equation (39) provides a method of comparing epidemiological efficiency among vector species (110) and within species over different landscapes and seasons.

Vector biology dictates the dynamics of pathogen transmission and nidus persistence. Vectors such as mosquitoes typically have short life cycles, rapid gonotrophic cycles, multiple blood meals during adult life, and therefore frequent, but intermittent, host contact. Outbreaks of WNV, for example, typically go through rapid phases of silent introduction, explosive epidemic transmission, and then rapid subsidence during successive seasons (47), due in part to the rapid immunization and/or depopulation of avian host populations (129). In WNV epidemics, pathogen persistence becomes a paramount obstacle to long-term nidus maintenance, but vector and host vagility ensures rapid dispersal to alternative receptive areas, resulting in expanding waves of infection (92). In marked contrast, ticks blood feed only once during each life stage and have life cycles that last multiple years, typically producing slowly developing but persistent outbreaks (33). For Lyme spirochetes, both vector and host may serve as effective long-term pathogen reservoirs (121), but the effective dispersal of the pathogen may be limited to the dimensions of rodent and deer home ranges (73). Attachment of *Ixodes* ticks to song birds enables rapid and long-range transport (22), but conditions must be receptive for both tick and spirochete

upon detachment for the establishment of a new nidus.

Pathogens

Nidus complexity depends on the transmission requirements of the pathogen. For arthropods such as malaria or dengue virus that utilize humans as the amplifying host, human dwellings are the primary nidus of infection (48), and vector abundance and transmission intensity frequently vary with socioeconomic risk factors, including housing quality and municipal infrastructure (42). Urbanization has simplified the diversity of the peridomestic fauna to commensal species such as *Aedes aegypti* and the *Culex pipiens* complex that breed, rest and blood feed in or near the home. Transmission typically clusters within portions of cities that have deteriorating or little infrastructure and other enabling landscape features. Zoonotic transmission cycles are more complex, because pathogens are maintained and then amplified within a nonhuman host–vector cycle, before tangential transmission to domestic animals or humans. Often, additional bridge vector species with catholic blood-feeding habitats are necessary to transmit pathogens acquired from enzootic hosts to humans, possibly when humans and domestic animals enter rural or sylvan nidi or when bridge vectors disperse into residential areas. Enzootic transmission may be less efficient in sylvan than in urban environments because vectors are exposed to a diverse array of blood meal hosts that express differing pathogen competence, whereas in suburban/urban settings there may be a greater concentration of competent hosts (55, 119). Successful transmission of tick-borne pathogens is affected by host size in addition to species diversity, so that an effective nidus

Figure 4

Ecotones. Number of *Culex tarsalis* female mosquitoes collected per trap-night in replicate down- or updraft suction traps along a transect intersecting (a) desert scrub and (b) citrus orchard habitat. Geometric means shown by bars with the same letter were not statistically different (72).

Niche: function or position of an organism within the ecosystem

for Lyme spirochetes must contain small bird and rodent hosts for the immature tick stages and large hosts such as deer for the adult stage (35, 69).

NIDUS DYNAMICS IN TIME AND SPACE

Time and space cannot be separated in nidus or patch dynamics, especially in rural environments. Without catastrophic or anthropogenic intervention, seasonal changes expand the dimensions of permissive habitats, thereby enlarging existing foci and creating new intermittent foci across heterogeneous landscapes (32, 43). Seasonal and associated spatial changes allow increases in vector and host populations, thereby facilitating contact and pathogen amplification. In the Coachella Valley of California, for example, mosquito-borne viruses annually amplify and then disperse from overwintering refugia at the Salton Sea into upland agricultural and residential habitats (106). Dispersal seems facilitated by the dispersive behavior of the mosquito vector, *Cx. tarsalis* (107). Adult mosquito control may limit vernal pathogen dispersal when bird movements are limited during nesting (71). In contrast, unfavorable conditions such as drought can cause a reduction in patch size, concentrating vector and host populations at refugia and thereby enhancing transmission (115). Similar patch dynamics and host exploitation may have led to the gradual dispersal of ticks and Lyme spirochetes throughout the northeastern United States (45).

Anthropogenic influences such as expanding agriculture or urbanization can markedly change historic nidus dynamics by altering patch size and expanding ecotonal areas, thereby juxtaposing reservoir hosts, domestic animals, and human hosts to vector populations and enhancing tangential transmission. Both WNV and Lyme spirochetes seem to exploit these fragmented landscapes (15, 18). In vast monocultural agricultural settings, farmsteads effectively function as epidemiological islands, bringing nesting/roosting avian hosts

and nocturnally questing mosquitoes together in time and space, facilitating the transmission of WNV and other arboviruses (**Figure 5a**). This concept also applies to small communities within agroecosystems or to parkland or wetlands within or adjacent to urban continuums (**Figure 5b**). The scenario seems similar for tick-borne pathogens such as Lyme spirochetes, where in the northeastern United States agriculture has subsided, allowing reforestation and the expansion of deer populations (9). When residences were inserted within these subclimax landscapes, domestic landscaping engulfed by secondary forest created ecotonal transitions, suitable rodent habitat, and ample browse for deer. Engorged ticks shed from deer browsing on residential landscaping and rodents feeding near homes provide the principal sources of immature ticks and Lyme spirochete infection of humans, respectively (34).

PATHOGEN DISPERSAL

Regardless of scale and nidus composition, landscapes consist of a heterogeneous patchwork of variably permissive habitats which must be negotiated by dispersive hosts or vectors for pathogens to persist and amplify. Vector and vertebrate host species as well as pathogens exhibit contagious distributions as they discover and exploit optimal microhabitats that fulfill niche and nidus requirements. At the pathogen nidus, persistence of transmission and the requirement for dispersal depends in part on the response of the primary hosts to infection. Highly virulent pathogens such as WNV rapidly sweep through naïve avian populations, resulting either in depopulation among highly susceptible species such as American crows (20) or in high seroprevalence among surviving species (100). Introductions of pathogens into naïve host populations therefore may be critical for WNV maintenance, because rates of host depopulation and/or immunization seem to exceed replacement with naïve juveniles, leading to focal subsidence (129). In contrast, less virulent pathogens such as Lyme spirochetes produce long-term infections in both vector ticks



Figure 5

Epidemiological islands. (a) Farmland in rural California showing how farmsteads function as a nidus for mosquito-borne virus transmission by bringing mosquitoes and birds together for nocturnal roosting and host seeking. (b) Remotely viewed parkland within the urban continuum of Los Angeles showing how a nidus may be created by residual vegetation.

and rodent hosts (65, 121) that overlap seasonal reproductive or recruitment periods, thereby limiting the necessity for dispersal to new areas. Once a Lyme nidus is created, it typically persists over time and infections can be detected indefinitely within tick, rodent, and adjacent human populations (33).

Refugia

Refugia are favorable areas where hosts and/or pathogens may survive adverse conditions in a temporally inhospitable landscape, such as winter hibernacula at northern latitudes, permanent springs or riparian corridors in arid landscapes, or peridomestic environments within agroecosystems. The importance and size of refugia depend on the severity of unfavorable conditions that delimit their suitability. Extremely harsh conditions or anthropogenic effects can eliminate refugia and therefore that portion of the population that depends upon

them. Harsh winters or long dry seasons reduce host and vector population size and spatial distribution, reduce the probability of pathogen persistence, create a genetic bottleneck that reduces diversity of the founding pathogen population, and may delay or limit amplification during succeeding permissive periods. In contrast, mild winters or short dry periods may enable early and rapid amplification, leading to outbreaks during the subsequent transmission season. The nidus must encompass or be within the dispersal ranges of host and vector refugia for persistence and early-season amplification.

Determining the mechanism(s) of pathogen persistence at temperate latitudes has been difficult, especially for mosquito-borne arboviruses such as WNV (102). Current evidence indicates that continued bird-bird transmission may occur at temperate American crow roosts (24), perhaps leading to infections in predators or scavengers (38). In addition, several competent passeriform bird host species develop chronic

infections lasting several months (102), but proof that these infections ever relapse is lacking. Some female *Culex* destined for diapause are infected vertically, survive winter, and then transmit this infection in spring at diapause termination (1, 82). In contrast, both long-lived tick vectors and hosts with persistent infections can provide effective overwintering mechanisms for pathogens such as Lyme spirochetes (121).

Dispersion and Dispersal

Dispersion is a statistical term describing the distribution of organisms over a landscape, whereas dispersal describes their movement or spread. Most landscapes are heterogeneous in structure, resulting in a contagious or clumped dispersion pattern of both hosts and pathogens. During winter and early spring at temperate latitudes, host and pathogen distributions typically are confined to refugia or points of introduction and are therefore highly clumped. Following the amelioration of conditions enabling transmission, amplification typically begins at or near refugia. As favorable conditions persist seasonally, the size and number of foci increase as more microhabitats become permissive for vector, host, and pathogen and therefore the intensity of clustering decreases. Dispersal to create new foci may employ a variety of mechanisms depending upon their spatial scale. Invasive species typically exploit disjunct habitats over large spatial scales. These species usually are generalists and highly adaptive, have a high reproductive rate, and often are human commensals such as *Ae. aegypti* (124). For pathogens, the invasion process may involve long-distance importation [such as the introduction of WNV into New York City (61)] or gradual dispersal [such as the expansion of the range of Lyme spirochetes in the northeastern United States (73) or dengue viruses in North and South America (42)] and may be associated with or follow the invasion of host or vector species. The invasion of *Aedes albopictus* into Italy, for example, enabled a subsequent outbreak of chikungunya virus

(CHIKV) (89). Italy would not have been permissive for the introduction of CHIKV had not *Ae. albopictus* become established previously. Mosquitoes frequently are transported by humans through travel or commerce, and faunal changes may occur in locations along air or water shipping routes. The mosquito fauna of Guam, for example, changed markedly due to the movement of cargo from Southeast Asia first during WWII (126) and then the Vietnam Conflict (99). Invading zoonotic pathogens must be able to exploit new hosts and vectors after introduction or environments that have undergone modification, permitting the invasion of commensals. WNV, for example, successfully infects a wide variety of avian and mosquito hosts (59), facilitating its rapid and widespread dispersal into temperate and subtropical latitudes (61). The house sparrow is a European commensal that was introduced into North America during the 1850s and now is distributed widely in peridomestic habitats, serving as a competent host for the invasive WNV (67). The negative impact of WNV and concurrent decrease in the abundance of competitors such as house finches and predators such as western scrub-jays have coincided with a marked increase in house sparrow abundance in the Central Valley of California (127).

Pathogen dispersal is facilitated by both host and vector movements. Birds are especially important dispersal hosts for both WNV and Lyme spirochetes because of their long-range migrations (93) and wide-ranging foraging flights, especially by hatching year birds after fledging (73, 80). Although the role of birds in arbovirus dispersal has been extensively investigated, there have been few definitive results. Autumnal southbound migrants presumably infected at northern latitudes have been recovered more frequently (70, 75) than viremic northbound migrants. Genetic differences between SLEV and other arboviruses isolated in North and South America indicate infrequent genetic exchange between the continents (60). The failure to detect outbreaks of the temperate encephalitis including WNV in the Neotropics also

indicates minimal amplification, perhaps due to extensive avian diversity, cross-protective immunity from local viruses, or the moderate competence of a different guild of mosquitoes.

Postfledging movements by passeriform birds seem critical in encephalitis dispersal over moderate distances. These foraging flights during mid- to late summer may have been sufficient to account for the rapid east-to-west movement of WNV in North America (92) and the northward dispersal of WNV >1,000 km within California during the summer of 2004. On a smaller scale, moribund and highly viremic American crows previously infected at their nightly roost seem important in seeding WNV into new peridomestic habitats (85). Similarly, ground-foraging passeriform birds may be important dispersal agents of immature *Ixodes* infected with spirochetes (11, 132), whereas the large home range of deer, the primary host of adult *Ix. scapularis*, is important in tick dispersal even though deer are not a competent reservoir for *B. burgdorferi* (35).

Mosquitoes are important in dispersing viruses such as WNV, although vagility varies among species and environments. Long-distance movements of mosquitoes and arboviruses have been associated with storm fronts (114) and prevailing wind patterns (54), resulting in the intercontinental dispersal of both vectors and pathogens (113). On a local scale in the arid western United States, rural species such as *Cx. tarsalis* are extremely vagile, and marked-and-released females have been recaptured as far as 35 km downwind in a single night (6).

Barriers

Nidus dimensions may be defined by abrupt transitions in landscape such as mountain ranges, rivers and oceans or by more gradual transitions in vegetation that delimit both host and pathogen. Even minor and often inapparent differences in landscape composition can alter host and/or vector microhabitats and therefore conditions permissive for pathogen amplification. In addition to the changes in pathogen

genetics mentioned above, barriers such as mountain ranges can lead to important changes in vector genetics. The Tehachapi Mountains at the end of the Central Valley of California and perhaps temperature gradients limit gene flow among *Cx. pipiens* complex (120) and *Cx. tarsalis* (123) populations.

Rivers apparently slowed the western expansion of *Ix. scapularis* in Connecticut (125) and New York (128). The breadth and velocity of the Connecticut and Hudson Rivers near the Northeast coast were temporary barriers for deer and mice dispersal (but not birds), which led to higher rates of Lyme disease on their eastern shores than on their western shores during the 1970s and 1980s. In contrast, rivers and associated riparian forests served as corridors for Lyme spirochete expansion in the Midwest in primarily agricultural landscapes (57).

ANTHROPOGENIC FACTORS

The expanding human population has markedly affected the epidemiology of vector-borne diseases by creating vast urban continuums, altering landscape structure, providing rapid mechanisms for host and pathogen dispersal, and altering climate on several scales, from the local creation of heat islands to the global production of greenhouse gases (50). The most marked anthropogenic impact has been the creation of varying forms of the home microhabitat or nidus, enabling the transmission of anthroponoses by endophagic commensals. The extent of these habitats has dramatically expanded with extensive urbanization in tropical areas (41). For dengue viruses, data on human demography and infection, housing construction and municipal structure, and one or two vector mosquito species may be sufficient to define and model spatial patterns of transmission over urban landscapes (14, 76). For zoonoses, the increase in ecotonal areas has been associated with residences and associated landscaping becoming interspersed among climax and subclimax vegetation or within agroecosystems, especially monocultures such as rice. As indicated above, these fragmented

Global positioning system (GPS): using multiple earth-orbiting satellites to establish location

Geographical information system (GIS): software to store, analyze and visualize GPS related data

landscapes bring reservoir hosts, vectors, and humans together, enhancing amplification and the risk for tangential transmission. This has been an especially critical aspect of Lyme spirochete epidemiology in eastern North America (19, 27, 77). Forest patch size and dynamics due to anthropogenic change and other disturbance markedly alters biodiversity (36) and therefore the efficiency of amplification transmission (69). The above factors may define human risk at or near residences, but for some zoonoses, pathogen persistence and amplification depend entirely upon enzootic amplification in host and vector populations, with distributions that may not include residential settings. Human risk for these pathogens depends either on humans visiting these foci or hosts or on vectors carrying the pathogen into residential settings. Human behaviors relating to occupation or recreation are critical in determining the location and extent of exposure. In contrast to the northeastern United States, where Lyme spirochete risk is greatest around the home, risk in the Midwest and California has been associated with recreation or other activities that bring humans into rural nidi (30, 66). For WNV, risk is related not only to spatial factors, but also to photoperiod and diel activity behaviors, because the primary *Culex* vectors blood feed nocturnally (2, 109). Human behaviors, such as smoking and dog walking, that bring humans outside the protection of screened or air-conditioned homes at night elevate the risk of infection. Such behaviors are less important in the tropics, where homes are of open construction and indoor resting and endophagic vectors transmit pathogens inside the home.

METHODS OF STUDY

The ability to quantitatively describe epidemiological patterns over diverse landscapes is dependent upon spatially linking sampling data with landscape, environmental, and socioeconomic factors. Extensive reviews have focused on specific aspects of these geographical, statistical, and epidemiological problems (3, 7, 37, 52, 53, 56, 58).

Sampling

Carefully designed sampling protocols are the foundation of landscape epidemiology. No amount of statistical manipulation or landscape descriptors can overcome sampling biases or inadequate scale created by poor data collection. Sampling design depends entirely on nidus structure and transmission complexity and the distribution of hosts and vectors. For anthroponoses transmitted within the home, ground or remote surveys can delineate the spatial extent and heterogeneity of the area at risk, allowing carefully devised sampling schemes (76). In contrast, zoonoses require a complex paradigm that must account for landscape composition and enzootic transmission among animal hosts and vectors and then vectors to humans (84). Sampling protocols often are complicated by access, and frequently the habitat has to be modified, for example by cutting trails or natural corridors exploited to enable access, realizing that the data gathered may not be representative spatially. Delineating pathogen distributions must account for biases related to the host population, which has its own heterogeneous or clumped distribution. The effect of prior knowledge and access on developing mosquito sampling strategies was evaluated previously in rural southern California (108).

Global Positioning and Geographic Information Systems

Knowing the exact location of each sampling point has been greatly enhanced by accurate, portable, and relatively inexpensive global positioning tools. Use of global positioning system (GPS) data has been facilitated by geographic information systems (GIS) and relational databases that capture, store, analyze, and present data linked spatially to specific GPS locations. These computational tools allow users to query and analyze spatial information, create maps, and view results in various formats. In combination, GPS and GIS tools allow the precise tracking of pathogens in relation to landscape and other environmental

features. Most software used in GIS allows the creation of data surfaces through interpolation of point data using statistical methods such as kriging (63). Spatially linked data surfaces then can be analyzed using approaches, such as multiple regression, that account for spatial dependency and autocorrelation (40). GPS and GIS have been used to develop risk maps for Lyme disease at several spatial scales, including regional (57), state-wide (84), and local community (27), and to depict the distribution of WNV cases in Chicago and Detroit in relation to neighborhood classification, vegetation, and population density (112).


Spatial Statistics

At least three types of spatial data are important in the study of vector-borne diseases: (a) point data observed for the entire population or in proportion to their actual occurrence (e.g., public-reported dead birds within a city), (b) lattice data aggregated for areas within a contiguous sampling grid (e.g., human cases of a notifiable disease by county for a state), and (c) geostatistical data observed at selected sampling locations within a continuous spatial domain (e.g., mosquito counts at a set of trap locations) that often are limited by practical considerations (23).

Analysis of spatial point patterns has been facilitated by free software products (see **Supplemental Appendix**, follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). The degree of clustering may be described simply by the coefficient of variation, but tests based on a comparison of observed point patterns and those expected from a random or other distribution are more informative. Examples include the Knox test, which compares observed and expected counts of pairs that are close in space and time (8), and the Kolmogorov-Smirnov test (117), which assesses clustering about a point or goodness of fit for a known distribution. The geographic size and location of clusters can be delineated using the spatial scan statistics implemented in SaTScanTM software (62).

For example, clusters of dead American crows reported by the public were delimited by this statistic and then used to forecast the location of WNV human cases (81). These clustering techniques also may assist in understanding the ecology of transmission. The distribution of WNV-infected dead birds reported by the public, the infection incidence within *Culex quinquefasciatus* populations, and the degree of human case clustering in southern California during the outbreak of 2004 were consistent with the distribution, abundance, and behaviors of the predominant corvid species (98). Few human cases were detected where there were few corvids and therefore relatively few dead birds. By comparison, in Kern County, California, 43 human cases were reported, but these cases did not show significant spatial clustering because the most important bird species, the western scrub-jay, is highly territorial, resulting in an even distribution of dead birds. In contrast, American crows were the dominant corvid in Los Angeles, and dead birds of this species were highly clustered about communal roosts during late summer. Grouping of the data for SaTScan in time and space requires a priori knowledge of distributional patterns within the data and perhaps forces the resolved patterns based on these assumptions (129). New statistical methods are needed to resolve irregularly shaped clusters and the temporal dynamics of cluster formation and persistence with minimal a priori constraints.

For lattice and geostatistical data, exploratory analyses test whether global clustering exists (e.g., Moran's I) and, if so, where the clustering is located (e.g., local Moran's I or G_i^*) (3). Such analyses have been used to detect areas with elevated WNV prevalence in humans (111) and to determine the spatial dimensions of clustering in *Ix. scapularis* in the eastern United States (28). Variography is used to estimate the range of spatial autocorrelation, and kriging to create a continuous surface by interpolating among sampling sites. Spatially varying explanatory variables have been used in regression models to describe variation in vector abundance (28, 29) or disease risk to humans

 **Supplemental Material**

(16, 131), with spatial structure only incorporated through spatial variation in the explanatory variable(s). If spatial autocorrelation in an outcome variable remains after inclusion of all relevant predictor variables, additional spatial error terms may be estimated to account for unobserved factors or biological processes, such as vector or host dispersal. Models of this type are becoming more common in vector-borne disease research (10, 130).

Remote Sensing

Remotely sensed variables usually describe the environment of the hosts or vectors, thereby providing a surrogate for distribution and perhaps abundance. Remote sensing in its simplest and finest granularity may employ aerial photography or more distant and coarse measurement using sensors onboard Earth-orbiting satellites. These sensors measure the intensity of radiation within one or more spectral bands, typically within the visible-infrared portion of the spectrum, from which data products can be derived such as land cover classes, surface temperatures, or vegetation indices. The selection of an appropriate sensor involves a trade-off between spatial resolution (<1 m to several kilometers), temporal resolution (daily to near-monthly), and spectral resolution (monochrome-hyperspectral). Selection of an appropriate sensor depends on the objectives of the study, the ecology of the vectors, hosts, and pathogens, and the scale at which transmission takes place (46, 52).

Forecasting

The goal of forecasting is to translate linkages among environmental variables and vectors, hosts or pathogens, into predictions of outcome measures such as vector abundance or human infection. These predictive outcomes can be evaluated in real time by surveillance. Although models have been developed to explain some component(s) of the epidemiology of many vector-borne diseases, prediction is challenging and skillful forecasts are rare. A major limitation in the translation of results

of scientific research and model-building into forms that can be automated and updated in real time with new surveillance information is the requirement of considerable expertise in computing and data management. Also, most modeling studies have been retrospective and resulting models evaluated based on skill in predicting past epidemiologic outcomes. Perhaps the best example of a successful prospective forecast of vector-borne disease risk has been the prediction of the Rift Valley Fever virus outbreaks in the Horn of Africa based on ENSO and remote sensing (4).

A challenge to applying climate forecasts or other model output operationally is that public health and vector control agencies are reluctant to respond proactively until evidence from surveillance indicates that a threat to human health is imminent or ongoing. The cost of delays and, conversely, the value of forecasting, depend on the balance between the costs of early prevention versus a reactive response to an ongoing epidemic. For vector-borne diseases at temperate latitudes, this balance typically favors early preventive measures to arrest amplification prior to reaching epidemic levels and is linked strongly to seasonal climate variation during late winter-early summer (97). Because the cost of even a single human case of many vector-borne diseases is often high (134), prevention through vector control may be cost effective. The temporal scale of forecasts is important, and an ideal system would integrate short-range forecasts based on weather, seasonal forecasts prior to vernal virus amplification, and long-range forecasts under various scenarios for climate change (17).

Predictions can be presented in several forms, including predicted values, intervals to indicate the range within which values are likely to fall, or probabilities of each set of epidemiologically relevant outcomes. A variety of new quantitative methods and advances in computing, including the rise of open-source software, has enhanced the utility of forecasting. Simulation modeling and hierarchical Bayesian methods (21) provide ways to account for the many sources of variation inherent in vector-borne

disease epidemiology, including variation in the predictors themselves [e.g., ensembles of long-range climate scenarios (91), unobserved processes, and spatial and temporal autocorrelation (10)]. These models have the advantage of incorporating prior information into parameter estimates that can be iteratively updated as new information is acquired.

SUMMARY

The advent of modern observational equipment such as GPS and remote sensing combined with high-speed computing and GIS software has transitioned the science of landscape

epidemiology from observational investigation to a quantitative science that now is based on statistical inference. Modeling change in time and space to define temporal patterns and spatial distributions remains a challenge for epidemiologists to fully understand conditions of nidus formation, expansion, and subsidence. Translating forecasted risk and observed patterns from surveillance programs into effective response plans has been hampered technically by modeling limitations and skill, rapid processing of surveillance information, and the collective will of public health programs to proactively respond in an escalating fashion prior to human illness and outbreak conditions.

SUMMARY POINTS

1. Landscapes are defined by vegetative patterns and formed by the interactions of geology and climate.
2. Landscapes that allow vertebrate host, vector, and pathogen populations to interact within a permissive environment delineate the nidus, or focus, of transmission.
3. Nidus complexity depends upon pathogen natural history and vector bionomics.
4. Nidus stability varies with vector-host contact rates, pathogen virulence, and host replacement patterns.
5. Anthropogenic factors related to agriculture or urbanization simplify ecosystem complexity and may facilitate pathogen transmission.
6. New remote-sensing, statistical, and computing tools have enabled landscape epidemiology to transition from a descriptive to a quantitative science.

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31. Reconstructed the climate-vegetation system of Köppen-Geiger to visualize human impacts.

37. Coined the term landscape epidemiology.

49. Recognized the spatial separation of encephalitis outbreaks caused by two North American viruses based on temperature requirements for replication.

56. Reviewed statistical tools to investigate landscape epidemiology of vector-borne diseases.

62. Introduced SatSCAN, an important tool for statistical cluster analysis.

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