

Review

Impacts of Climate, Land Use, and Biological Invasion on the Ecology of Immature *Aedes* Mosquitoes: Implications for La Crosse Emergence

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Abstract: Arthropod-borne viruses (arboviruses) cause many diseases worldwide and their transmission is likely to change with land use and climate changes. La Crosse virus (LACV) is historically transmitted by the native mosquito *Aedes triseriatus* (Say) in the upper Midwestern US, but the invasive congeners *Aedes albopictus* (Skuse) and *A. japonicus* (Theobald), which co-occur with *A. triseriatus* in water-holding containers, may be important accessory vectors in the Appalachian region where La Crosse encephalitis is an emerging disease. This review focuses on evidence for how climate, land use, and biological invasions may have direct abiotic and indirect community-level impacts on immature developmental stages (eggs and larvae) of *Aedes* mosquitoes. Because vector-borne diseases usually vary in space and time and are related to the ecology of the vector species, we propose that the ecology of its mosquito vectors, particularly at their immature stages, has played an important role in the emergence of La Crosse encephalitis in the Appalachian region and represents a model for investigating the effects of environmental changes on other vector-borne diseases. We summarize the health effects of LACV and associated socioeconomic costs that make it the most important native mosquito-borne disease in the US. We review of the transmission of LACV, and present evidence for the impacts of climate, land use, and biological invasions on *Aedes* mosquito communities. Finally, we discuss important questions about the ecology of LACV mosquito vectors that may improve our understanding of the impacts of environmental changes on LACV and other arboviruses.

Keywords: *Aedes albopictus*, *Aedes triseriatus*, Culicidae, disease ecology, disease vectors, interspecific competition, predation, invasion, La Crosse encephalitis, global change biology

INTRODUCTION

In the past 60 years, many infectious diseases have emerged so that their epidemiology or symptoms are distinct from any disease seen previously (e.g., Ebola virus, severe acute

respiratory syndrome, and Nipah virus) (Daszak et al. 2000). Many other infectious diseases were thought to be under control but are now re-emerging and causing morbidity or mortality at greater rates or in areas or populations not previously affected (Barrett et al. 1998; Weiss and McMichael 2004; Wilcox and Colwell 2005). Vector-borne diseases are a significant proportion of emerging and re-emerging infectious diseases (Jones et al. 2008). The

most medically important vectors of disease are mosquitoes and among the most important pathogens they transmit are arboviruses (Weaver and Reisen 2010).

An important and emerging mosquito-borne disease is La Crosse virus (LACV) encephalitis. LACV encephalitis is the most common mosquito-borne disease native to North America (Calisher 1994) and second most reported mosquito-borne disease behind introduced WNV encephalitis. LACV encephalitis is caused by LACV, which is a bunyavirus belonging to the Californian (CAL) serogroup of viruses (Family: *Bunyaviridae*, genus: *Orthobunyavirus*) (Tsai 1991), and is historically transmitted by the native North American treehole mosquito *Aedes triseriatus* (Say). LACV encephalitis has experienced a dramatic geographic shift in the last 20 years (Fig. 1). It was formerly almost entirely confined to sparsely populated areas in the upper Midwest with few cases in the Appalachian region (Kappus et al. 1982) but has emerged in the Appalachian region (Jones et al. 1999), which now yields the highest incidence risk in the nation among children 15 years and younger (Haddow and Odai 2009). The emergence of LACV encephalitis in the Appalachian region has broadly coincided with the invasion and spread of the Asian Tiger mosquito, *Aedes albopictus* (Skuse), and the Asian bush mosquito, *Aedes japonicus* (Theobald) (= *Ochlerotatus japonicus*; Reinert 2000), which co-occur with *A. triseriatus* as larvae in water-holding containers (e.g., Livdahl and Willey 1991; Swanson et al. 2000; Szumlas et al. 1996; Barker et al. 2003a, b; Joy and Sullivan 2005; Bevins 2007a). *Aedes albopictus* and *A. japonicus* invaded the US via used tires in the mid-1980s and mid-1990s, respectively. Both species have since spread throughout the Appalachian

region, and *A. japonicus* is also present in the upper Midwest in apparently lower numbers (Darsie and Ward 2005; Morris et al. 2007; Hughes et al. 2008). *A. albopictus* and *A. japonicus* are competent laboratory vectors of LACV (Grimstad et al. 1989; Cully et al. 1992; Sardelis et al. 2002). LACV has been isolated from field populations of both *A. albopictus* (Gerhardt et al. 2001; Haddow et al. 2009; Lambert et al. 2010; Westby et al. 2011) and *A. japonicus* (Westby et al. 2011). Thus, both invaders may affect the incidence of LACV in the Appalachian region by acting as important accessory vectors and by affecting the distribution and abundance of *A. triseriatus* by competing with the native species for resources in water-holding containers.

Despite this dramatic emergence in the Appalachian region and the invasions of *A. albopictus* and *A. japonicus*, LACV has received relatively little attention, even in reviews of emerging arboviruses (Jones et al. 2008; Weaver and Reisen 2010). LACV cases are typically under-diagnosed (Calisher 1994; Utz et al. 2003), which may contribute to the limited attention to this disease. However, we propose that the dramatic geographic shift of LACV toward the Appalachian region is unlikely to be due to differential rates of diagnosis between the Appalachian region and the upper Midwest and is more likely dependent on the environment. *Aedes albopictus* is the best-studied invasive mosquito (Juliano and Lounibos 2005; Juliano 2009). Despite this background, relatively little is known about how invasion of *A. albopictus* affects *A. triseriatus*, and how interactions among these species may alter LACV encephalitis risk. Even less is known about the recent invasion of *A. japonicus* and its interactions with *A. triseriatus* or *A. albopictus* (Juliano and Lounibos 2005). We propose that management of

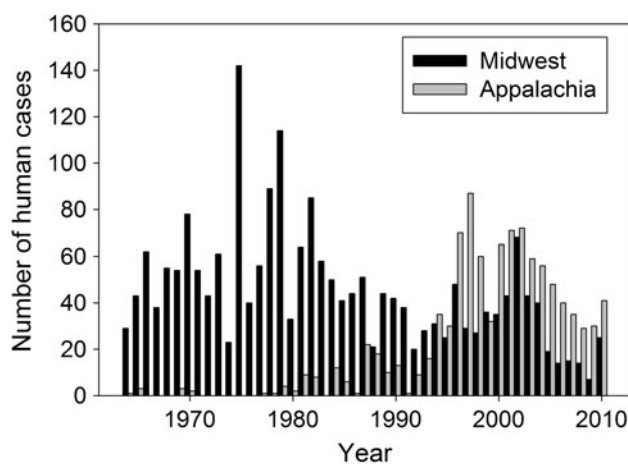


Figure 1. Number of cases with CAL serogroup viral disease in Midwestern (Ohio, Wisconsin, Minnesota, Illinois) and Appalachian (West Virginia, North Carolina, Tennessee) states of the United States (CDC 2011).

LACV encephalitis requires an understanding of how climate change, land use change, and biotic invasions, affect the ecologies of *A. triseriatus*, *A. albopictus*, and *A. japonicus*. In this review, we define land use change as conversion of forest to peridomestic habitats including single rural homes, small towns, or larger suburbs, all of which increase numbers of artificial water-holding containers.

Incidence of arboviral diseases varies in space and time within a region (Reisen 2010). For arboviral pathogens to persist and to spread, mosquito vectors must encounter vertebrate hosts and favorable environments so that spatiotemporal disease risk is directly related to the ecology of the vector (Andreadis et al. 2004; Yasuoka and Levins 2007; Reisen 2010). Thus, the ecologies of LACV vectors, particularly eggs and larvae, and their responses to environmental changes, may be the key processes driving the regional emergence of LACV encephalitis. In this review, we postulate that human settlement facilitates invasions by *A. albopictus* and *A. japonicus*, increasing the risk of transmission of LACV encephalitis in the Appalachian region. Further, such land use changes combined with impending climate change will affect future transmission in the Appalachian region and other parts in the US. We also suggest that climate and land use changes may be altering ecological interactions among *A. triseriatus*, *A. albopictus*, and *A. japonicus* at the finer scale of individual water-holding containers that are development sites for larvae of these mosquitoes. Because of their tendency to bite humans, increased production of adult *A. albopictus* and *A. japonicus* with human settlement and climate change are likely to increase LACV risk. Regional coexistence of *A. triseriatus*, *A. albopictus*, and *A. japonicus* in a fragmented forest–peridomestic landscape and diverse local climates is especially likely to increase LACV transmission if they each contribute to simultaneous zoonotic and bridge transmission, or maintain LACV in a location throughout multiple seasons (Juliano and Lounibos 2005; Juliano 2009).

We begin with a review of the transmission cycle of LACV and describe recent changes in its geographic distribution. We summarize the health and socioeconomic effects of LACV encephalitis that make it an important mosquito-borne disease in the US. We then focus on the ecologies of *A. triseriatus*, *A. albopictus*, and *A. japonicus*, and how environmental changes may increase risk of LACV encephalitis by influencing the distributions and abundances of the egg and larval stages of these *Aedes*. Terrestrial adult mosquitoes are the direct cause of disease in humans, and ecological factors acting on adults (e.g., seasonal cold

stress, desiccation, availability of hosts) have been an important traditional focus of investigations of ecology of mosquito-borne disease (e.g., Reisen 2010). However, the ecology of mosquito host–vector interactions is only one component of mosquito population dynamics. Ecology of eggs and larvae is also critical for understanding and managing mosquito-borne disease and arguably may have a greater role than adult ecology in affecting the diseases transmitted by mosquitoes that develop in water-holding containers. Physical factors act directly on eggs and larvae to affect the production, distribution, and coexistence of adults (e.g., Hanson and Craig 1995; Teng and Apperson 2000), and we review evidence for differential responses of immature *A. triseriatus*, *A. albopictus*, and *A. japonicus* to these factors. Container-dwelling mosquito larvae are strongly affected by interspecific competition, predation, and parasitism, and by density-dependent effects, which are largely absent at the adult stage. Such community-level effects can regulate the production and fitness of adults (Livdahl and Willey 1991; Lounibos et al. 2003b). Thus, we focus also on how these biotic interactions regulate populations and coexistence of *A. triseriatus*, *A. albopictus*, and *A. japonicus*, and how climate and land use may modify these processes. We postulate that climate and land use play significant roles in LACV encephalitis risk by affecting the ecology of immature *Aedes* mosquitoes. Our goal is to outline a paradigm for investigating the ecology of these *Aedes* that will contribute to better management of LACV over different land uses and climates. Because all arthropod vectors are sensitive to environmental changes, we hope that ideas and approaches in our review will be relevant beyond understanding LACV, and will guide future efforts to understand how climate and land use changes affect mosquito ecology and public health.

Health Impacts of LACV

LACV is an important cause of pediatric encephalitis in endemic regions of the US. LACV encephalitis is the second most common mosquito-borne encephalitis behind WNV encephalitis, with a total of 3,590 cases of confirmed and probable CAL serogroup viral illnesses from 1964 to 2009 (29–167 cases per year; CDC 2011). Almost all of these CAL illnesses were LACV (Calisher 1994; CDC 2011). LACV cases usually exhibit symptoms of fever, headache, myalgia, malaise, and occasionally prostration (Calisher 1994). It is likely that LACV infection is under-reported because LACV is often not specifically identified (Calisher 1994). Mild

LACV infections are often misdiagnosed as “flu” or “summer cold” (Utz et al. 2003) and severe LACV infections as herpes simplex encephalitis (Sokol et al. 2001). Cryptic infections may be as high as 300,000 per year in the US (Rust et al. 1999).

Severe LACV cases can lead to encephalitis, with permanent neurologic sequelae or death in approximately 0.5% of cases (Rust et al. 1999). Although mortality is low compared to other arboviral diseases (Utz et al. 2003), a substantial socioeconomic burden is associated with LACV. For example, in North Carolina, direct and indirect costs of 25 cases totaled nearly \$800,000 (mean \pm SD: \$32,974 \pm \$34,793 per case) over nearly 90 accumulated life years. Projected costs of lifelong neurologic sequelae are as high as \$3,090,798 per patient. Lost workdays due to a LACV case are estimated to be an order of magnitude greater than those from dengue epidemics in Puerto Rico (Von Allmen et al. 1977; Torres 1997).

Biology of LACV Vectors

Aedes triseriatus is the natural vector and overwintering host of LACV. The virus has been repeatedly isolated from *A. triseriatus* in the field (e.g., Sudia et al. 1971; Watts et al. 1974; Szumlas et al. 1996; Nasci et al. 2000). Laboratory transmission experiments (Watts et al. 1972, 1973; Woodring et al. 1998), and the spatial and temporal association of *A. triseriatus* with zoonotic and human hosts with antibodies to LACV (e.g., Thompson and Evans 1965; Wright and DeFoliart 1970), all implicate *A. triseriatus* as the main vector. *Aedes triseriatus* circulates LACV naturally among eastern chipmunks (*Tamias striatus*), gray squirrels (*Sciurus carolinensis*), red foxes (*Vulpes fulva*), and possibly other small mammals (Calisher 1994; Grimstad 1988) in hardwood forests containing habitat—such as water-holding treeholes—for vector immature-stage (eggs and larvae). *Aedes triseriatus* transovarially transmits LACV and the virus overwinters in diapausing *A. triseriatus* eggs (Watts et al. 1974).

Historically, most cases of LACV encephalitis have been reported from Wisconsin, Minnesota, Illinois, and Ohio (Fig. 1). However, in the past 20 years, LACV has emerged in West Virginia, Tennessee, and North Carolina (Fig. 1). Encroachment of human dwellings into hardwood forests may have facilitated the emergence of LACV in the Appalachian region since *A. triseriatus* can also colonize artificial and natural containers in shaded peridomestic environments (Szumlas et al. 1996; Debboun et al. 2005;

Kling et al. 2007; Yee 2008). Complicating the epidemiology of LACV is the spread of the invasive congeners *A. albopictus* and *A. japonicus* into the Appalachian region. *A. albopictus* is a particularly aggressive day-time biter of small mammals and humans, making it an effective bridge vector of LACV (Estrada-Franco and Craig Jr. 1995). *Aedes japonicus* is also a day-time biter of a variety of hosts including humans (Andreadis et al. 2001). LACV has been isolated from *A. albopictus* eggs and adults (Gerhardt et al. 2001; Haddow et al. 2009; Lambert et al. 2010; Westby et al. 2011) and *A. japonicus* adults (Westby et al. 2011) in the field. For both species, LACV positive adults have been found at case sites of LACV encephalitis in eastern Tennessee (Haddow et al. 2009; Westby et al. 2011), implicating these species as vectors of human cases in the Appalachian region. Laboratory infection and oral transmission rates for *A. albopictus* may be equal to or greater than those for *A. triseriatus* (Grimstad et al. 1989; Cully et al. 1992), although disseminated infection (Hughes et al. 2006) and transoviral transmission (Tesh and Gubler 1975) rates are lower.

Environmental Effects on La Crosse Vectors

Direct Effects on Immature Stages

Aedes albopictus appears to require higher temperatures than *A. triseriatus* to complete larval development (Teng and Apperson 2000). We may expect strong selection on adult *A. albopictus* to oviposit in areas that receive more radiant energy and thus be more likely to utilize containers in sunlit peridomestic areas warmed by built structures (McIntyre 2000). *A. albopictus* and *A. japonicus* show a greater oviposition preference for sunlit peridomestic areas compared to *A. triseriatus*, which prefer to oviposit in forested areas (Barker et al. 2003a, b; Joy and Sullivan 2005). The role of microclimate in female oviposition choice and immature survival of these *Aedes* mosquitoes is still poorly understood.

Aedes triseriatus is widely regarded as extremely tolerant of a range of temperatures and is distributed from Florida to eastern Canada (Darsie and Ward 2005). Since its arrival, *A. japonicus* has spread as far south as Georgia (Gray et al. 2005) and north into eastern Canada (Thielman and Hunter 2006). *Aedes albopictus* has spread south into Florida and as far north as the latitude at which daily mean January temperatures reach -5°C in the eastern US, which was predicted by its northern distribution in its native

range (Nawrocki and Hawley 1987). The more limited distribution of *A. albopictus* to regions of warmer temperatures and higher humidity appears to be due to lower overwintering egg survivorship (Andreadis 2009). Climate change is expected to increase mean temperatures and milder winters across much of North America (IPCC 2007) and thus may both favor the northward spread of all *Aedes* mosquitoes and—more importantly—the movement of *A. albopictus* into areas already occupied by *A. triseriatus* and *A. japonicus*. Overwintering survival of *Aedes* eggs depends on temperature minimum and duration of exposure (Hawley et al. 1989; Hanson and Craig 1994, 1995). In laboratory experiments, the absolute minimum temperature that cold-acclimatized diapausing *A. albopictus* eggs can withstand can be as low as -12°C (Hanson and Craig 1994), but there has been survivorship of *A. albopictus* eggs in the field when briefly exposed to these temperatures (Hanson and Craig 1995). It is likely that northern *A. albopictus* populations overwinter in areas where mean temperatures reach -5°C only if females oviposit in containers that are not subjected to prolonged extreme cold. Artificial containers in peridomestic areas (e.g., disused tires, trash receptacles) may be particularly well buffered against cold temperatures and increase overwintering success of *A. albopictus*. Thus, increasing conversion of forest into peridomestic areas may combine with climate change to promote the northward expansion of *A. albopictus*. Arboviral infections commonly affect overwintering *Aedes* mortality and the fitness of infected larvae. Mortality of overwintering LACV infected *A. triseriatus* eggs is greater than for uninfected eggs (McGaw et al. 1998). Species-specific overwintering mortality effects of LACV infection would affect LACV vectors but effects of LACV on overwintering *A. albopictus* or *A. japonicus*, vertical transmission of LACV in *A. japonicus*, and fitness of larvae infected with LACV have not been tested.

Aedes japonicus may be excluded from warm rock pool habitats, suggesting that a temperature barrier may inhibit *A. japonicus* populations from occupying southern areas of the US with relatively high summer temperatures (Andreadis and Wolfe 2010). Thus, climate change may also limit the spread southward of *A. japonicus* or even favor a retraction of this species' southern range. However, as with *A. albopictus*, any regional climate changes are likely to interact strongly with climate variation among individual containers. Topographical diversity is also likely to contribute to local climate variability and affect both northern and southern distributions of *Aedes* mosquitoes in complex

ways. Such regional and local scale variation in climate may be especially prominent in the Appalachian region, with its mountainous landscapes (Joy and Sullivan 2005).

Community-Level Effects on Immature Stages

Water-holding containers have low primary productivity (Fish and Carpenter 1982; Carpenter 1983). Almost all food resources are derived from allochthonous inputs of organic detritus and associated microorganisms (Carpenter 1983; Merritt et al. 1992; Kitching 2000; Kaufman et al. 2001). Thus, populations of *Aedes* in containers are often resource limited (Kitching 2000, 2001) and competition for microbial food is likely the strongest ecological process structuring communities (Kitching 2001; Juliano and Lounibos 2005). Some container habitats harbor predators and parasites that can regulate populations of *Aedes* mosquitoes. Prominent predators include the mosquito *Toxorhynchites rutilus* (Coquillett) and the midge *Corethrella appendiculata* (Graham) (Lounibos et al. 2001). Common parasites include the gregarine gut parasites *Ascogregarina barretti* (Vavra) and *Ascogregarina taiwanensis* (Lien and Levine) (Tseng 2007), and obligate intracellular microsporidia (Andreadis 2007). Pathogenic viruses have been isolated from *A. triseriatus* and *A. albopictus* (Becnel and White 2007), but little is known about how they affect the ecology of either species.

Competition, predation, and parasitism can impact roles of *A. albopictus* and *A. japonicus* in disease transmission. When an invasive mosquito replaces a resident mosquito via competition, disease transmission changes if the invader is a more or less efficient vector (Juliano and Lounibos 2005). Intensity of competition and resultant changes in adult body size or condition can affect the transmission of LACV (Grimstad and Haramis 1984; Grimstad et al. 1989; Grimstad and Walker 1991). When an invasive vector escapes enemies from its native range, distribution and abundance of that species may be enhanced. Likewise, native enemies may limit spread and impact of invasive mosquitoes (Juliano et al. 2010). These biotic interactions among larvae are well documented for *A. triseriatus* and *A. albopictus*, but not for *A. japonicus*. Further, these effects likely will change with climate and land use.

Competition

Laboratory and field experiments consistently show *A. albopictus* to be superior in competition for food resources to

A. triseriatus (Livdahl and Willey 1991; Novak et al. 1993; Teng and Apperson 2000; Aliabadi and Juliano 2002; Yee et al. 2007; Juliano 2009). Despite the competitive superiority of *A. albopictus*, there is little evidence for competitive exclusion of *A. triseriatus* (Juliano and Lounibos 2005). Experiments on competition between *A. albopictus* and *A. japonicus* show clear competitive superiority for *A. albopictus* (Armistead et al. 2008). No studies have tested competition between *A. japonicus* and *A. triseriatus* but the spread of *A. japonicus* is associated with a decline of *A. triseriatus* and other native species in waste tire sites in Connecticut (allopatric to *A. albopictus*) suggesting competitive displacement (Andreadis and Wolfe 2010). In the Appalachian region, *A. japonicus* are becoming the most abundant mosquito species in artificial containers where all three *Aedes* species coexist (Joy and Sullivan 2005; Bevins 2007a; Grim et al. 2007).

Superior overwintering survival and earlier hatching may enable *A. triseriatus* and *A. japonicus* to exploit vacant habitats early in the spring and to persist throughout the summer despite being competitively inferior to *A. albopictus* (Barker et al. 2003a, b; Swanson et al. 2000). The requirement for higher temperatures by *A. albopictus* to attain the same development rate as *A. triseriatus*, may also contribute to the dominance of *A. triseriatus* in northern, cooler regions of North America (Juliano and Lounibos 2005). Alternative hypotheses for the regional persistence of *A. triseriatus* after the invasion of *A. albopictus* involve varying outcomes to interspecific competition across habitat gradients (Juliano 2009). One form of competition among these *Aedes*, interference competition via direct physical or chemical negative effects, may relax the impacts of resource competition on *A. triseriatus* and promote its persistence. *A. triseriatus* and *A. albopictus* hatch when eggs are flooded and delay hatching, to varying degrees, in response to older larvae feeding in the water (Edgerly et al. 1993). Later stage *Aedes* larvae are likely to be superior resource competitors and less susceptible to toxic effects of excretory products (e.g., ammonium) than younger *Aedes* larvae (Walker et al. 1991; Sunahara and Mogi 2002). *A. albopictus* is both least sensitive to delayed-hatching effects and more likely as a fourth-instar larva to produce this inhibitory effect than *A. triseriatus* (Edgerly et al. 1993). Delayed hatching of *A. triseriatus* may result in avoiding later stage *A. albopictus* and limited delayed-hatching response of *A. albopictus* may decrease *A. triseriatus* vulnerability to competition. However, as yet, no studies have considered how land use or climate changes may modify

this asymmetrical interaction or interference competition involving *A. japonicus*.

Advantage in resource competition between *A. triseriatus* and *A. albopictus* appears to change with the nature of the container and resource, with *A. albopictus* having a strong advantage in discarded tires but coexistence expected in treeholes (Livdahl and Willey 1991). Because the frequency of natural versus artificial containers and the type and amount of detritus inputs likely change from forested to peridomestic areas, it is probable that land use change alters the competitive outcomes among *A. triseriatus*, *A. albopictus*, and perhaps *A. japonicus*, yielding another hypothesis for regional coexistence of these competitors. In the laboratory, the outcome of competition between *A. triseriatus* and *A. albopictus* appears to vary with the amount of total detritus and the ratio of leaf detritus to drowned insect detritus (Yee et al. 2007). The competitive advantage of *A. albopictus* is reduced with greater total detritus and greater proportions of insect detritus (Yee et al. 2007), suggesting that coexistence is more likely in habitats with greater total or animal detritus inputs. Different temporal patterns of detritus input also alter competitive interactions between *A. triseriatus* and *A. albopictus*, with multiple small, evenly spaced inputs reducing competitive asymmetry compared to single large pulses (Bevins 2007b). This result suggests that patterns of detritus input may also contribute to coexistence between competing *Aedes* species.

Forested areas are also less likely to be dominated by non-native vegetation than are urban areas (Thuiller et al. 2008). Different leaf species support different quantities (and possibly different species) of microorganisms (Walker et al. 1991; Yee and Juliano 2006), which in turn affects the quantity or quality of food for *Aedes* mosquitoes (Murrell and Juliano 2008; Reiskind et al. 2009). Differential feeding of mosquito species on microorganism species or an overabundance of microorganisms available to both species alter or even reverse interspecific competitive advantage between *A. triseriatus* and *A. albopictus*, allowing their regional coexistence (Yee et al. 2007). To date no experiments have directly tested competitive outcomes among *A. triseriatus*, *A. albopictus*, and *A. japonicus* with detritus types chosen to represent different land use patterns. The nutritional quality of leaf detritus is highly dependent on the concentrations of nitrogen and carbon-based secondary compounds of the detritus (e.g., phenolics, tannins, and lignin) (Strand et al. 1999; Tuchman et al. 2003). Leaf species decomposition rate increases with nitrogen:carbon

(N:C) ratio (Peterson and Cummins 1974). High concentrations of carbon-based secondary metabolites are also likely to affect *Aedes* communities by being toxic to larvae, altering microbial food communities, and influencing the impacts of parasites (Sota 1993; Mercer and Anderson 1994).

Predation

Intraguild predation also may limit invasion of *A. albopictus* into containers with *A. triseriatus*. Fourth-instar larvae of *A. triseriatus* are more likely to prey upon newly hatched conspecifics and *A. albopictus*, and newly hatched *A. triseriatus* are less vulnerable to such intraguild predation (Edgerly et al. 1999). Intraguild predation early in the season may be especially important for the persistence of *A. triseriatus* throughout the summer. However, no studies have considered how land use or climate change may modify intraguild predation or tested for intraguild predation involving *A. japonicus*. Top-down predation also may structure *A. triseriatus* and *A. albopictus* communities, and that predators are likely affected by land use and climate. *Toxorhynchites rutilus* and *Corethrella appendiculata* produce strong top-down effects in treeholes and other containers in forests, which are dominated by *A. triseriatus* and where *A. albopictus* is less common (Bradshaw and Holzapfel 1983, 1985; Kesavaraju et al. 2008). Laboratory and field tests show that *A. albopictus* is more vulnerable to these predators (Kesavaraju and Juliano 2004; Griswold and Lounibos 2005; Juliano et al. 2010), in part because *A. triseriatus* shows reduced movement and foraging, which reduces predation risk, in response to water-borne cues from either *T. rutilus* or *C. appendiculata* predation, whereas *A. albopictus* show much more limited behavioral changes (Kesavaraju and Juliano 2004, Kesavaraju et al. 2007). Few studies have examined the role of top-down predation in *A. japonicus* invasion, but as with *A. triseriatus*, *A. japonicus* shows greater reduction of movement and foraging in response to water-borne cues from *T. rutilus* than does *A. albopictus* (Kesavaraju et al. 2011). These predators are less common in open peridomestic areas and thus wooded areas appear to act as barriers to *A. albopictus* spread (Kesavaraju et al. 2008; Juliano et al. 2010). Thus, reduction in forested areas with increased urbanization would likely reduce predation and facilitate the spread of *A. albopictus*, while intact forest may act as a barrier to invasion of *A. albopictus*.

Parasitism

Parasitism by gregarines has been shown to affect the interaction of *A. triseriatus* and *A. albopictus*, and these parasites themselves are likely affected by climate. The gregarine parasites of *A. triseriatus* and *A. albopictus* (*A. barretti* and *A. taiwanensis*, respectively) cannot infect each other's hosts, so species-specific effects of climate on the development and spread of each parasite would likely have an impact on mosquito assemblage composition. When *A. albopictus* invades a new area, gregarine parasitism is reduced for several years (Munstermann and Wesson 1990; Blackmore et al. 1995; Aliabadi and Juliano 2002). *Aedes triseriatus* in such newly invaded areas are typically more heavily parasitized than *A. albopictus*, and this asymmetry in parasite load accentuates competitive advantage of *A. albopictus* (Aliabadi and Juliano 2002). It is unclear how climate or land use change may impinge on gregarine parasites, but Van Rhein et al. (2000) showed that the drying of treeholes greatly reduced intensity and frequency of parasitism by *A. barretti*, suggesting that climate shifts toward aridity may reduce parasitism and increase *Aedes* populations. To our knowledge, no research has investigated community effects of parasites of *A. japonicus*.

Geographic Variation

Predicting the impacts of climate and land use on LACV vectors may be complicated by geographic variation in ecological processes, which can result from varying abiotic or biotic environments favoring one species over the other, or from inherent geographic differentiation of local populations. Differences among populations of *A. albopictus* and *A. triseriatus* have been documented for numerous life-history traits. However, except for differences in diapause incidence (Shroyer and Craig 1983; Lounibos et al. 2003a) and susceptibility to and transmission of LACV (Grimstad et al. 1977), no interregional differences can be attributed to differences in latitudinal climate, LACV distribution, predator abundances, or competitor abundances (Juliano 1996; Frankino and Juliano 1999; Armbruster and Conn 2006; Leisnham et al. 2009). These findings suggest that highly local factors may select for life-history differentiation, or that local variation results from strong founder effects, genetic drift, or other non-selective processes. Geographic variation in susceptibility to and transmission of LACV presents an interesting pattern of lower susceptibility and transmission among *A. triseriatus* from LACV-

endemic areas of the upper Midwest (Grimstad et al. 1977), suggesting that LACV selects for resistance among its vectors (Grimstad et al. 1977). This study included only one *A. triseriatus* population from the Appalachian region (Cashiers, NC), which showed high susceptibility and transmission, as was typical of populations from non-endemic regions (Grimstad et al. 1977). This result suggests that: first, LACV was in fact rare or absent in the Appalachian region at the time of Grimstad et al.'s study, and that subsequent emergence of LACV in this region represents a real change in LACV distribution and abundance; second, susceptibility and transmission by newly invasive vectors *A. albopictus* and *A. japonicus* in a LACV-endemic region may be similarly high, making new invaders particularly important as LACV vectors.

Future Research and Conclusions

For a better understanding of LACV encephalitis, we require investigations of the (i) impacts of biotic interactions (competition, predation, parasitism, vector–host interactions) involving *A. triseriatus*, *A. albopictus*, and *A. japonicus* in the field in both the Midwestern and Appalachian regions; (ii) potential effects of climate change, land use change, and their interaction, on those biotic interactions; and (iii) means to predict the temporal and spatial consequences of these biotic interactions on the distributions, abundances, animal and human host contacts of these vectors, and their vector competence. Knowing the composition of *Aedes* communities, including species co-occurrence patterns and abundances, across different land uses will be valuable. Such surveys must determine if containers along forest-to-peridomestic gradients have different leaf litter inputs, hydroperiods, and temperatures that may modify the impacts of climate change on mosquito communities. Experiments under controlled laboratory conditions can be useful for testing potential effects of particular factors (e.g., leaf detritus, hydroperiod, and temperature) on interspecific competition, predation, and parasitism. Other experiments may test the effects of desiccation and temperature on survival of *Aedes* eggs and their effects on population growth rates. Field manipulations of climate or land use variables across latitude will be necessary to determine the actual importance of these factors. Models of the effects of microclimate on the population parameters of *Aedes* under different climate scenarios will be necessary to integrate interactive effects of climate and land use on mosquito performance across the

dynamic landscapes in both the Midwestern and Appalachian regions. Re-examination of susceptibility to and transmission of LACV by *A. triseriatus* populations from the Midwestern and Appalachian regions, and currently non-endemic areas (e.g., Florida), would be extremely interesting as a way of testing predictions of the hypothesis that LACV selects for resistance among *A. triseriatus*. Similar comparative studies of susceptibility to and transmission of LACV by invasive vectors *A. albopictus* and *A. japonicus* from these regions would also be informative for understanding the consequences of invasions of novel vectors into LACV-endemic areas.

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