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Dendrochronological reconstruction of the epicentre and early spread of emerald ash borer in North America

Nathan W. Siegert[1*,†], Deborah G. McCullough[1], Andrew M. Liebhold[2] and Frank W. Telewski[3]

[1]*Departments of Entomology and Forestry, Michigan State University, East Lansing, MI 48824-1115, USA,* [2]*US Forest Service, Northern Research Station, Morgantown, WV 26505, USA,* [3]*Department of Plant Biology, Michigan State University, East Lansing, MI 48824-1312, USA*

*Correspondence: N. W. Siegert, Departments of Entomology and Forestry, 243 Natural Sciences Bldg., Michigan State University, East Lansing, MI 48824-1115, USA.
E-mail: nwsiegert@fs.fed.us

†Present Address: US Forest Service, Northeastern Area State and Private Forestry, Forest Health Protection, Durham, NH 03824, USA

ABSTRACT

Aim Emerald ash borer *Agrilus planipennis* was identified in 2002 as the cause of extensive ash (*Fraxinus* spp.) decline and mortality in Detroit, Michigan, and has since killed millions of ash trees in the US and Canada. When discovered, it was not clear how long it had been present or at what location the invading colony started. We used dendrochronological methods to document the onset and progression of ash mortality and the spatio-temporal dynamics of the invasion. Reconstructing the progression of ash mortality serves as a proxy to draw inferences about the colonization and spread of emerald ash borer in North America.

Location Southeastern Michigan, USA.

Methods We collected increment cores from dead, declining or non-symptomatic ash trees on a systematic 4.8 × 4.8 or 2.4 × 2.4 km grid in 2004–2006. Geo-referenced samples were cross-dated to determine the earliest date emerald ash borer-killed trees in each location. Interpolated dates of ash mortality were analysed to determine rates and patterns of emerald ash borer spread across the 1.5 million ha study area.

Results We identified a location in southeastern Michigan where ash trees were killed by emerald ash borer as early as 1997. Rates of ash mortality subsequently progressed at 3.84 km year^{-1} from 1998 to 2001 and then increased to 12.97 km year^{-1} from 2001 to 2003 as satellite colonies coalesced with the primary infestation. From 1998 to 2003, new satellites formed at a rate of 7.4 per year, with average jump distances of 24.5 km.

Main conclusions Emerald ash borer was likely established in southeastern Michigan by at least the early to mid-1990s. Anthropogenic-aided stratified dispersal and the coalescence of satellite colonies with the primary population resulted in biphasic range expansion, rapidly expanding the footprint of the invasion. Our reconstruction of the emerald ash borer invasion demonstrates this invaders' remarkable capacity for population growth and spread.

Keywords

***Agrilus planipennis*, biological invasions, dendroentomology, epicentre, invasive forest pest, stratified dispersal.**

INTRODUCTION

Invasive forest pests affect a range of ecosystem processes and alter community dynamics (Asner & Beatty, 1996; Mack *et al.*, 2000; Hale *et al.*, 2008; Krushelnycky & Gillespie, 2008) and cost regulatory agencies, plant-based industries and property owners billions of dollars annually (Aukema *et al.*, 2011). Biological invasions of non-indigenous species can be characterized by three distinct phases: arrival, establishment and spread (Mack *et al.*, 2002; Lockwood *et al.*, 2007; Liebhold &

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Tobin, 2008). International trade regulations and inspections have undoubtedly reduced the arrival of non-indigenous species, but these efforts have largely been offset by increases in global commerce and travel, resulting in a steady accumulation of non-native plant pests (Niemelä & Mattson, 1996; Work *et al.*, 2005; Liebhold *et al.*, 2006; McCullough *et al.*, 2006; Tatem & Hay, 2007; Aukema *et al.*, 2010).

Once a non-indigenous species becomes established, its spread is strongly influenced by the organism's capacity for dispersal. Species solely capable of short-distance dispersal, typically characterized by diffusive movement, tend to expand their range continuously along the periphery of the primary population (Shigesada & Kawasaki, 1997). Other organisms are capable of both short- and long-distance dispersal and spread via the formation of satellite colonies well beyond the main invasion front. These satellite colonies typically continue to grow in size through diffusion and, over time, coalesce with the expanding primary population. This process, termed 'stratified diffusion', may greatly increase the rate of radial expansion and has been documented in many species (Moody & Mack, 1988; Shigesada & Kawasaki, 1997).

Emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), a phloem-feeding insect native to parts of Asia, was identified in 2002 as the cause of ash (*Fraxinus* spp.) decline and mortality in the greater metropolitan area of Detroit, Michigan, USA, and shortly thereafter, in Windsor, Ontario, Canada (Cappaert *et al.*, 2005; Poland & McCullough, 2006). Since then, emerald ash borer has killed tens of millions of ash trees in forest, riparian and urban areas, becoming the most destructive and costly forest insect to invade North America (Aukema *et al.*, 2011). As of February 2014, emerald ash borer populations had been identified in at least 21 additional states and the province of Quebec (Emerald Ash Borer Information, 2014). Emerald ash borer has also invaded the Moscow region of Russia and now threatens ash in Europe (Baranchikov *et al.*, 2008; Kenis & Branco, 2010; Eyre *et al.*, 2013; Orlova-Bienkowskaja, 2013).

In its native habitat, emerald ash borer functions as a secondary pest, colonizing and killing severely stressed or declining ash trees (Liu *et al.*, 2003). North American ash species, however, have no evolutionary history with emerald ash borer or with native congeners. While stressed trees are preferentially colonized (McCullough *et al.*, 2009a,b; Siegert *et al.*, 2010), emerald ash borer also attacks and kills healthy trees, and native ash species could eventually be functionally extirpated from North American forest systems (Poland & McCullough, 2006; Klooster *et al.*, 2014; Herms & McCullough, 2014). Cultivars of green ash (*Fraxinus pennsylvanica* Marsh.) and white ash (*Fraxinus americana* L.) have been popular landscape trees for decades and comprise more than 20% of the urban forest canopy in some areas (MacFarland & Meyer, 2005; Poland & McCullough, 2006). Projected costs of treating or replacing even 45% of the landscape ash trees in urban areas with emerald ash borer infestations were estimated at \$10.7 billion USD from 2009 to 2019 (Kovacs *et al.*, 2010). Aukema *et al.* (2011) further estimated costs of emerald ash borer to municipalities and private property owners exceed \$1 billion USD annually.

While nearly all native ash species are threatened, there are consistent interspecific differences in emerald ash borer host preference or host resistance (Anulewicz *et al.*, 2008; Rebek *et al.*, 2008; Tanis & McCullough, 2012). Adult beetles select hosts for leaf-feeding, which occurs throughout their 3–6 week life span, and mature females lay eggs in bark cracks or crevices between bouts of feeding and resting (Cappaert *et al.*, 2005; Mercader *et al.*, 2012). Larvae feed on cambium and phloem in galleries that typically score the outer sapwood, thus disrupting nutrient and water transport. While some native wood-boring insects will colonize severely stressed, newly dead or recently cut ash trees (Drooz, 1985; Johnson & Lyon, 1994; Solomon, 1995), the s-shaped, serpentine galleries of emerald ash borer larvae are readily distinguishable. In newly infested, healthy trees, emerald ash borer often requires 2 years for development, but as densities build and trees become stressed, development is usually completed in 1 year (Cappaert *et al.*, 2005; Siegert *et al.*, 2010; Tluczek *et al.*, 2011). Intensive stem analyses of infested trees at localized outlier sites in Michigan and several other states have shown ash trees are typically infested for at least 3–5 years before tree mortality occurs (Siegert *et al.*, 2007; McCullough & Mercader, 2012; N.W.Siegert & D.G. McCullough, unpublished data). Green ash, which is widely distributed in forests and commonly used in landscapes, and black ash (*Fraxinus nigra* Marsh.), which typically grows in northern swamps or bogs, are highly preferred hosts of emerald ash borer and are particularly vulnerable (Anulewicz *et al.*, 2007, 2008; Rebek *et al.*, 2008).

Following the initial detection of emerald ash borer in 2002, regulatory officials began efforts to delimit the extent of the infestation. Detecting low-density populations of emerald ash borer, however, was and remains challenging (Cappaert *et al.*, 2005; Herms & McCullough, 2014). Newly infested trees typically exhibit none of the external symptoms that characterize heavily infested trees, such as holes left by woodpeckers preying on late instar larvae, epicormic sprouts, or progressive canopy thinning and dieback (Cappaert *et al.*, 2005; McCullough *et al.*, 2009b; Poland *et al.*, 2011). The small adult beetles (7.0–13 mm long) spend most of their life span in the canopy and are seldom observed, even in high-density populations. Moreover, emerald ash borer adults do not produce long-distance pheromones (Rodriguez-Saona *et al.*, 2006; Crook & Mastro, 2010), and artificial traps baited with host volatiles are not highly effective, particularly when emerald ash borer populations are at very low densities (McCullough *et al.*, 2011; Mercader *et al.*, 2012, 2013). By autumn 2003, regulatory agencies in the US had quarantined six counties in southeastern Michigan (Federal Register, 2003). The quarantine, which regulated transport of ash trees, logs, firewood and related material, was established well beyond the suspected primary infestation, based on visual surveys of dead, declining and symptomatic trees (Rauscher & Mastro, 2004). The number of dead and declining trees in the greater Detroit area suggested that emerald ash borer had been present for some time, but the location of the epicentre of the infestation was unknown.

The distinct larval galleries, lack of host resistance and relatively rapid host mortality caused by emerald ash borer provided a unique opportunity to use dendrochronology to reconstruct the historical spatio-temporal dynamics of this biological invasion across the area in southeastern Michigan that encompassed the primary emerald ash borer population. We reconstructed establishment and spread of the founding population across this diverse, heterogeneous environment using cross-dating to identify the year of mortality of trees killed by emerald ash borer. Our data represent a robust, high-resolution record of the progression of emerald ash borer during the period when it was unknown and unmanaged. Our goals were to document: (1) the colonization and spread of the primary population; (2) the formation of satellite colonies beyond the main invasion front of the primary population; and (3) the coalescence of satellite colonies with the expanding primary population over time. Results provide a historical perspective of the invasion of this notable pest and document the importance of isolated satellite colonies forming ahead of the primary population front in the spread of this species.

METHODS

Study area

To reconstruct the origin and progression of emerald ash borer-induced ash mortality, we sampled ash trees across a geographical area, roughly 1.5 million ha in size (> 15,000 km^2) that encompassed the original six Michigan counties quarantined for emerald ash borer by regulatory officials in 2002–2003 (Fig. 1a). Our study area extended beyond the original quarantine (Fig. 1a), extending from 41.73° to 42.96° N and from 82.44° to 84.29° W, and ash trees at the periphery of our study area generally appeared to be healthy and exhibited no signs or symptoms of emerald ash borer infestation. The study area included urban and residential areas, forested parks, small woodlots and agricultural fields.

We systematically sampled green ash trees at least every 4.8 × 4.8 km throughout the study area (n = 1085 trees sampled) (Fig. 1b). Green ash was selected for sampling because of its nearly ubiquitous distribution in this region and because it is highly preferred and vulnerable to emerald ash borer (Anulewicz *et al.*, 2007, 2008). We delineated an area, *c.* 900 km^2 in size, in the centre of the sampling grid where a relatively high proportion of ash trees were dead. We suspected this area encompassed the core infestation of the primary emerald ash borer population and therefore intensified our sampling by selecting trees on at least a 2.4 × 2.4 km grid.

Sample collection and measurement

Extensive visual surveys were conducted with vehicles and on foot in natural and urban settings within each cell of our systematic sampling grid to identify green ash trees that appeared to have the most advanced emerald ash borer infestation. Traits of such trees included extensive emerald ash borer larval galleries, few remaining fine branches or twigs and bark that was sloughing and separating from the sapwood. Our next priority were trees that had been killed more recently by emerald ash borer; these trees also had extensive larval galleries but typically retained most or all fine branches and twigs, and there was little, if any, bark separation from wood. If we did not find ash killed by emerald ash borer, we then prioritized declining trees with obvious signs of emerald ash borer infestation including bark cracks over the distinctive larval galleries and exit holes of emerged adult beetles (Cappaert *et al.*, 2005; McCullough *et al.*, 2008). When we could find no dead or declining ash within a grid cell, we sampled non-symptomatic ash trees (Fig. 1b). Additional trees were occasionally sampled within a cell to aid in ageing and cross-dating at a given location. GPS coordinates (ETrex Legend, Garmin International, Olathe, KS, USA) were recorded for each sample tree.

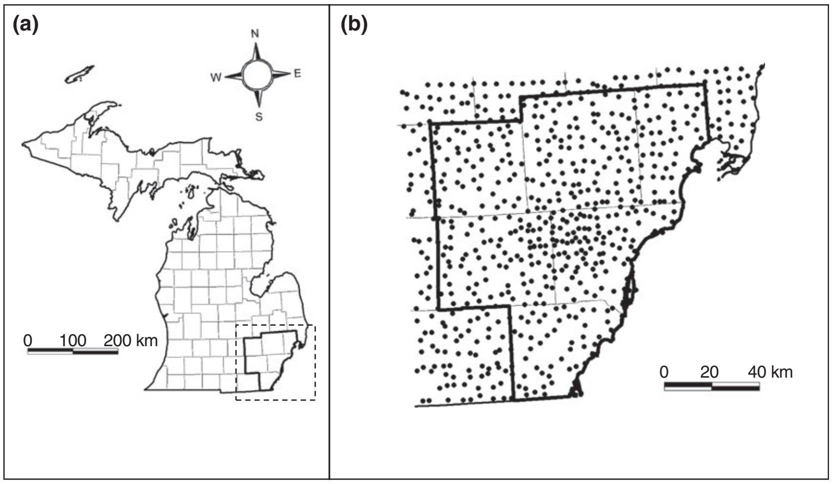

Figure 1 Extent of study area (outlined with dashed line) in southeastern Michigan (a) and locations of sample trees (solid black circles) used in reconstructing the temporal and spatial dynamics of emerald ash borer (*Agrilus planipennis*) (b). Initial 2002–2003 quarantine area is denoted by the bold outline.

Sampling consisted of collecting two increment cores from each of the selected tree(s) in each cell using 5.15-mm (core diameter) increment borers (Suunto, Helsinki, Finland) (n = 1976 increment cores collected). Generally, increment cores were collected at breast height (1.5 m) from two different aspects of each sample tree, avoiding areas where ring patterns were likely to be distorted (e.g. areas with decay, near branches or comprised of tension wood). In a few cases, cross sections of the main stem rather than increment cores were collected at breast height from felled or downed trees.

Samples (cores and cross sections) were dried, and cores were glued onto wooden mounts. Samples were surfaced with successively finer grit sandpaper ranging from ANSI 80 grit (177–210 μm) to ANSI 220 grit (53–74 μm) (Orvis & Grissino-Mayer, 2002) to expose the annual growth rings. Additional polishing of increment core surfaces with ANSI 320 grit (32.5–36.0 μm) to ANSI 400 grit (20.6–23.6 μm) sandpaper was conducted as needed to clearly distinguish growth rings. Ring widths from each increment core were then measured to the nearest 0.01 mm under 10× magnification using a Velmex measuring system (Velmex, Inc., Bloomfield, NY, USA) coupled with a linear encoder (Metronics, Inc., Bedford, NH, USA) and Measure J2X software (VoorTech Consulting, Holderness, NH, USA). Rings widths from each cross section were similarly measured along two radii and cross-dated. In cases where an increment core spanned the diameter of the tree and included two complete ring series (i.e. one ring series extending from the outer bark to the pith and another complete ring series extending from the pith to the outer bark on the opposite side of the tree), both ring series were measured and individually cross-dated (n = 2421 complete ring series).

Cross-dating samples

Skeleton plots, which graphically represent the width of each annual growth ring relative to the average width of the three tree rings on either side, were generated from ring width measurements for each increment core. Ring porous trees, such as ash, have annual growth rings with a characteristic band of large water-conducting pores produced at the beginning of the growing season (i.e. earlywood/springwood) followed by a band of much smaller pores produced later in the growing season (i.e. latewood/summerwood) and rarely have false or missing rings (Phipps, 1985; Fritts, 2001). Increment cores were first cross-dated to other cores collected from the same tree and then to increment cores collected from other nearby sample trees within a grid cell or adjacent cells. Increment cores and skeleton plots from live, non-symptomatic ash trees were inspected first and dates assigned to each growth ring. Skeleton plots were used to visually cross-date the remaining increment cores, matching marker years (i.e. narrow rings caused by adverse growing conditions and wide rings produced during years with more favourable growing conditions) to determine the precise year of formation of each growth ring (Stokes & Smiley, 1968). Notable marker years that were especially persistent throughout the large study area included narrow rings produced in 1895, 1918, 1925, 1934, 1965, 1988 and 1996, and wide rings produced in 1902, 1937, 1975 and 1980 (Fig. 2).

Visual cross-dating results were verified using COFECHA software, a quality control program used to assess cross-dating and ring measurement accuracy (Holmes, 1983; Grissino-Mayer, 2001). COFECHA was used iteratively as needed at local scales (e.g. county-level or smaller) and then for the entire study area to verify cross-dating results overall. If COFECHA flagged increment cores that could potentially cross-date to a different year, indicating a possible error in the visual cross-dating or ring series measurement, increment cores and skeleton plots were re-examined for measurement errors and visually cross-dated again within individual trees and to other nearby sample trees to ensure the maximum degree of confidence in cross-dating accuracy. In cases where cross-dating results were more ambiguous, such as with

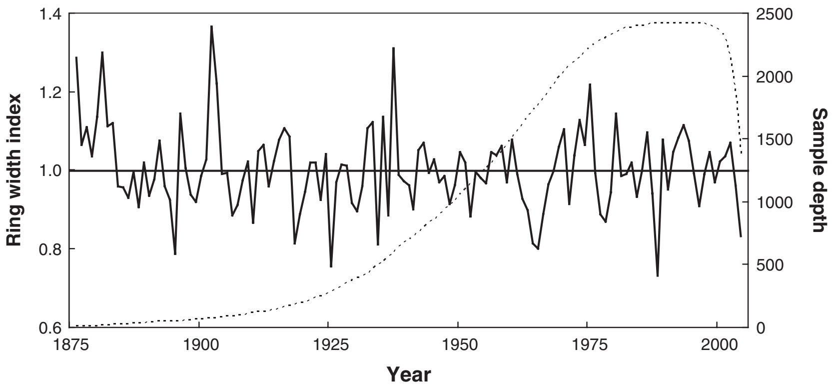

Figure 2 The standard chronology (solid line) and sample depth (dotted line) of *Fraxinus pennsylvanica* increment cores (n = 2421 total cores) sampled for the reconstruction of emerald ash borer (*Agrilus planipennis*) establishment and spread in southeastern Michigan, USA. Tree ring series used to develop the standard chronology averaged 53.6 year in length and cross-dated relatively well throughout the heterogeneous environment of the greater Detroit metropolitan area (series intercorrelation = 0.366; average mean sensitivity = 0.236).

complacent ring series where ring widths were not as variable year to year, field notes taken at the time of sample collection (i.e. qualitative measures of tree decline and emerald ash borer infestation such as percentage leaf cover, missing outer bark and presence of fine branches and twigs, bark splits, emerald ash borer exit holes or exposed larval galleries) were used to aid in determination of the year of mortality. For instance, if COFECHA software indicated that a given core may have cross-dated 4 years earlier than visual cross-dating indicated (e.g. 2001 as opposed to 2005), field notes such as '70% leaf cover in 2005' enabled us to confirm the terminal year of growth.

ARSTAN software (Cook & Holmes, 1999) was applied to individual cores to remove growth trends and standardize cross-dated tree ring series before generating a standard chronology of green ash radial growth for the study area (Fig. 2). To remove low frequency variability due to biological or stand-level effects, tree ring series were detrended using a cubic smoothing spline of 50% frequency response of 67% of the length of each series.

Spatial interpolation and reconstructed population dynamics

Spatial interpolation of the earliest date that emerald ash borer was responsible for tree mortality from 645 geographically referenced sample trees was used to reconstruct the origin and progression of emerald ash borer-induced ash mortality in southeastern Michigan. Sample trees used for the spatial interpolation represent a subset of the 1085 total trees sampled and were selected based on the earliest date that emerald ash borer tree mortality occurred within each cell. The remaining 440 trees represent additional samples that were occasionally collected from other trees within a cell to aid in ageing and cross-dating at a given location. Points were imported to the ARCVIEW 3.2 geographical information system (Environmental Systems Research Institute, Redlands, CA, USA) and interpolated with the Spatial Analyst extension using inverse distance weighting of the 12 nearest neighbours to each sample point. An inverse distance exponent value of 2 was used in the interpolation procedure. Inverse distance-based weighted interpolation was used to estimate interpolated values on at least a 4.8 × 4.8 km grid (Watson & Philip, 1985).

Based on the reconstructed spatial and temporal dynamics of emerald ash borer-caused ash mortality, the number of satellite colonies established each year was determined. Distance from the midpoint of each satellite colony to the nearest edge of the primary, continuously infested population was measured to the nearest 0.01 km using the Measure tool in ARCVIEW 3.2. Satellite colonies were defined as any emerald ash borer-induced tree mortality among our sample points that was disjunct from the primary population in a given year, as determined by the inverse distance-based weighted interpolation procedure described above. To characterize the radial expansion of the primary population each year, distances to the edge of the primary population were also measured along 32 transects extending every 11.25° (i.e. 11.25, 22.5, 33.75, 45…360°) from the reconstructed epicentre of the emerald ash borer infestation. Linear regression was used to evaluate the rate of formation of satellite colonies and radial expansion of the primary population over time using SYSTAT version 10 (Systat Software, Inc., Chicago, IL, USA).

RESULTS

Tree ring series, which averaged 53.6 year in length, were used to develop a standard chronology of ash growth from 1876 to 2004 (n = 2421 total cores) (Fig. 2) across the study area of southeastern Michigan (Fig. 1a,b). More than 75% of the chronology's ring widths (i.e. 1907–2004) had sample depths of ≥ 100 cores, while the remainder ranged from 8 to 94 cores (Fig. 2). Sampled trees cross-dated relatively well throughout the widely diverse, heterogeneous environment of the greater Detroit metropolitan area. Series intercorrelation, which is the average correlation of each tree ring series with a chronology derived from all other tree ring series and measures the strength of the signal common to all sampled trees at a site, was 0.366 across the mosaic of urban and residential areas, forested parks, small woodlots and agricultural fields included in our study area. Mean sensitivity, which is the relative change in ring width from 1 year to the next and provides a measure of the relative ease of cross-dating, averaged 0.236 for all samples collected across the entire study area. Chronologies of ash growth developed from nearby trees generally had slightly improved statistics, as would be expected. County-level tree ring chronologies, for example, had series intercorrelations that averaged (± SE) 0.394 ± 0.012 (range: 0.285–0.457) and average mean sensitivities of 0.239 ± 0.003 (range: 0.222–0.259).

Reconstruction of the epicentre and progression of ash mortality caused by emerald ash borer across the study area was achieved after cross-dating each sample tree to determine its terminal year of growth. The earliest year that emerald ash borer was found to be responsible for killing ash trees in southeastern Michigan was 1997 in the suburban community of Canton in Canton Township in northwestern Wayne County (Fig. 3). Tree mortality progressively radiated from the epicentre of the emerald ash borer invasion in subsequent years with isolated pockets of tree mortality occurring beyond the apparent epicentre of the infestation (Fig. 3). From 1998 to 2003, isolated groups of emerald ash borer-killed trees formed at a rate of 7.4 per year ($r^2 = 0.956$; $P = 0.004$) (Fig. 4a) with average jump distances of 24.5 km (lower 95% CI = 20.3 km; upper 95% CI = 28.8 km) (Fig. 4b). In 1998, new isolated groups of emerald ash borer-killed trees became established at an average distance of 8.2 km (Fig. 5a), with a maximum distance of 12.9 km (Fig. 5b), from the edge of the reconstructed epicentre of the infestation. In contrast, from 1999 to 2002, distances of isolated groups of emerald ash borer-killed trees

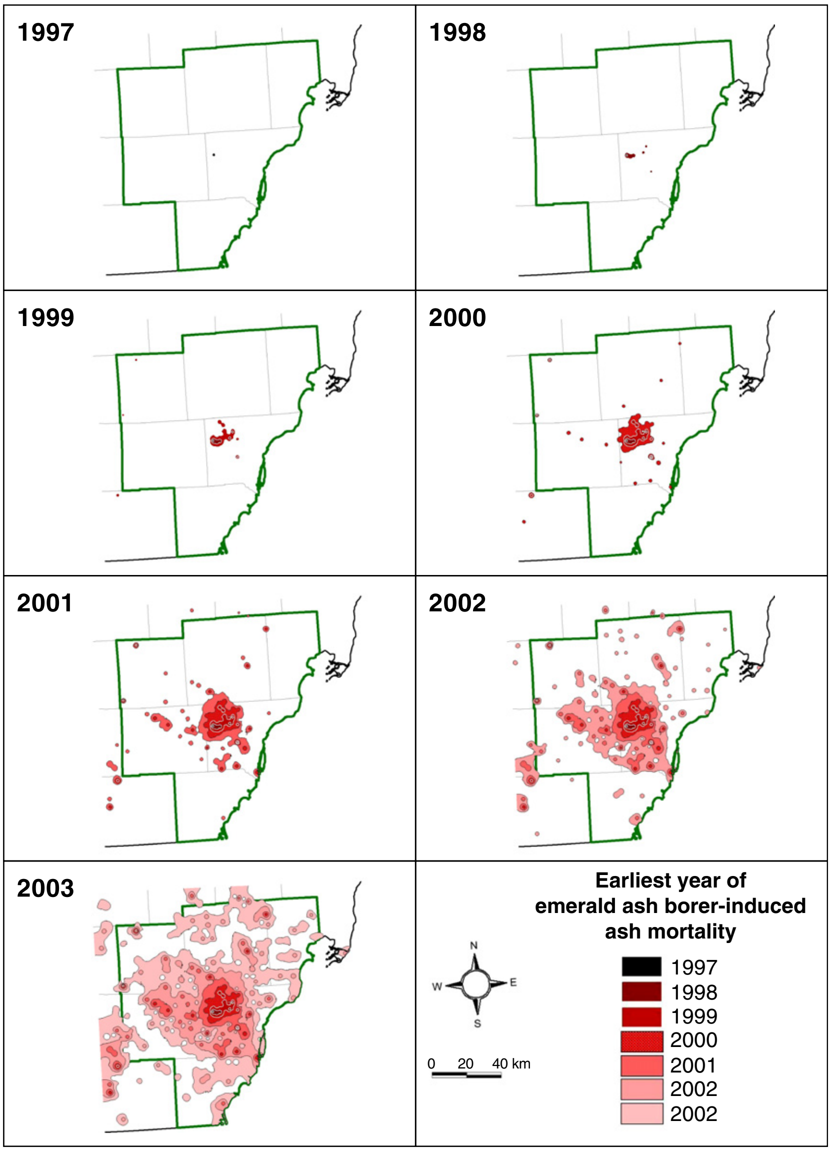

Figure 3 Interpolated reconstruction of the earliest emerald ash borer (*Agrilus planipennis*)-induced ash mortality across study area, 1997–2003. Initial 2002–2003 quarantine area is denoted by the green outline.

averaged (± SE) 27.4 ± 3.2 km from the edge of the reconstructed epicentre of emerald ash borer infestation (Fig. 5a), with maximum distances of 64.7 ± 1.9 km (Fig. 5b). Range expansion of the continuously infested emerald ash borer region initially occurred at 3.84 km year^{-1} from 1998 to 2001 (Fig. 6: dashed trend line; $r^2 = 0.980$; $P = 0.01$), then increased to 12.97 km year^{-1} from 2001 to 2003 (Fig. 6: solid trend line; $r^2 = 0.999$; $P = 0.025$) as an increasing number of formerly isolated groups of emerald ash borer-killed trees coalesced with the expanding primary emerald ash borer infestation (Fig. 3).

DISCUSSION

The initial colonization arrival phase of a typical biological invasion is rarely observed, largely because relatively few individual organisms are involved, and it is thus not easily detectable. For this same reason, establishment and early spread is also typically not observed. Invasion of North America by emerald ash borer, however, provided a unique opportunity to use dendrochronology to accurately reconstruct the historical establishment and spread dynamics of this destructive pest. Our approach was facilitated by specific features of this invasion, including the readily distinguishable galleries of emerald ash borer larvae, and the relatively rapid rates of emerald ash borer population growth and ash mortality following establishment (Mercader *et al.*, 2011a,b). Whole-tree dissections of emerald ash borer-killed trees and dendrochronological dating of the establishment of isolated satellite colonies in Michigan and several other states have consistently indicated that the earliest tree mortality at newly infested sites lags arrival of emerald ash borer by 3–5 years (Siegert *et al.*, 2007; McCullough & Mercader, 2012; N.W.Siegert & D.G. McCullough, unpublished data). The onset of ash mortality varies, depending on the size of the founding emerald ash borer population and the species, density and health of the hosts. Expansion at the periphery of the primary population and formation of satellite colonies

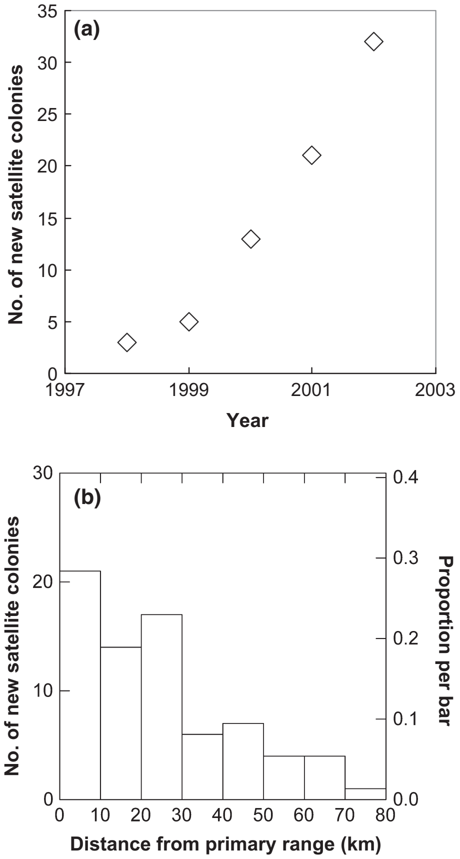

Figure 4 Number of new satellite colonies by year (a) and jump distances from the primary emerald ash borer (*Agrilus planipennis*) population (b). From 1998 to 2002, new emerald ash borer satellite colonies formed at a rate of 7.4 per year ($r^2 = 0.956$; $P = 0.004$) with average jump distances of 24.5 km (lower 95% CI = 20.3 km; upper 95% CI = 28.8 km).

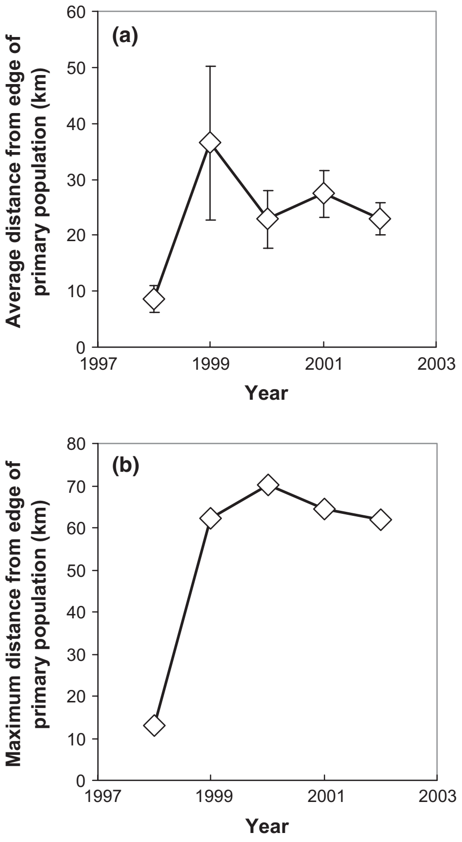

Figure 5 Average (± SE) (a) and maximum distance (km) (b) of new satellite colonies from the nearest edge of the primary emerald ash borer (*Agrilus planipennis*) population each year. In 1998, new satellite colonies became established an average distance of 8.2 km, with a maximum distance of 12.9 km, from the edge of the primary population. In contrast, from 1999 to 2002, distances of new satellite colonies averaged (± SE) 27.4 ± 3.2 km from the edge of the primary emerald ash borer population, with maximum distances of 64.7 ± 1.9 km.

would typically occur at low densities, similar to emerald ash borer densities we have observed at outlier sites. Thus, the progression of ash mortality serves as a suitable surrogate for the spread of emerald ash borer, albeit lagged by a few years.

Our results showed that ash trees were killed by emerald ash borer in 1997 (5 years prior to its detection in 2002) in the suburban community of Canton in Wayne County in southeastern Michigan, *c.* 40 km west of Detroit. This highly urbanized area is adjacent to major highways, includes a sizeable industrial area with large warehouses and is located 25–60 km from international air and marine ports. Although we do not know exactly how emerald ash borer arrived in southeastern Michigan, solid wood packing material associated with containerized shipping is known to be a high-risk pathway for introductions of non-native subcortical insects (United States Department of Agriculture Animal & Plant Health Inspection Service (USDA APHIS), 2003; Work *et al.*, 2005; Haack, 2006). Intensive examination and whole-tree dissections of multiple ash trees at the reconstructed epicentre of the invasion in southeastern Michigan were not feasible given our resources and time constraints. While the early progression of ash mortality generally radiated out from the Canton area in subsequent years forming the core of the reconstructed primary population, it is likely that our sampling did not detect the original tree colonized and killed by emerald ash borer. Moreover, given the 2-year life cycle that predominates in low-density populations and the temporal lag between emerald ash borer arrival and the onset of ash mortality, emerald ash borer was undoubtedly established well before 1997. We conclude, therefore, that emerald ash borer was introduced and became established in Canton, Michigan, no later than the early to mid-1990s, and possibly as early as the late 1980s.

A temporal lag between the establishment of a non-indigenous species and its detection is a common feature of biotic invasions (Crooks & Soule, 1999; Sakai *et al.*, 2001; Mack *et al.*, 2002; Memmott *et al.*, 2005; Liebhold & Tobin, 2006) and, in some cases, simply reflects exponential increases in population density over time (Skellam, 1951). In other situations, population growth rates may increase as an invader

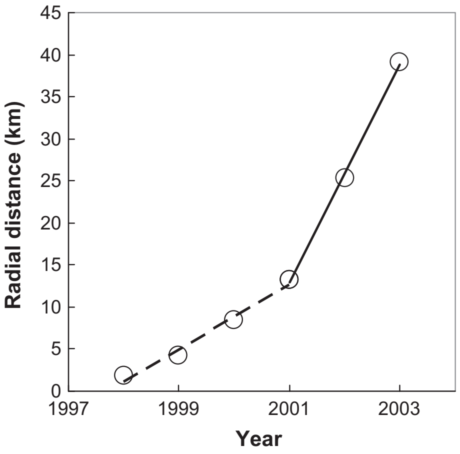

Figure 6 Biphasic range expansion of the primary population of emerald ash borer (*Agrilus planipennis*) as determined by the reconstructed establishment and spread in southeastern Michigan. Following establishment, range expansion initially occurred at 3.84 km year^{-1} from 1998 to 2001 (dashed trend line; $r^2 = 0.980$; $P = 0.01$) and then increased to 12.97 km year^{-1} from 2001 to 2003 (solid trend line; $r^2 = 0.999$; $P = 0.025$) as an increasing number of satellite colonies coalesced with the primary population.

overcomes Allee effects (Lewis & Kareiva, 1993; Taylor & Hastings, 2005) or result from changes in host or habitat quality (Griffen & Drake, 2008). In this specific case, detection was also delayed by the paucity of information on emerald ash borer, which was not recognized as a potentially serious pest prior to its detection in North America (Jendek, 1994; Cappaert *et al.*, 2005; Poland & McCullough, 2006).

The biphasic range expansion of emerald ash borer and the progression of ash mortality across southeastern Michigan are typical of biological invasions in which new satellite colonies are generated close enough to the primary population that coalescence occurs relatively quickly (Shigesada & Kawasaki, 1997). Tree mortality progressively radiated from the epicentre of the primary population at 3.84 km year^{-1} from 1998 to 2001, but from 2001 to 2003, this rate increased dramatically to 12.97 km year^{-1}. The accelerated spread rate in 2001–2003 reflects satellite colonies that became established well beyond the primary population and then coalesced with each other and the primary population during that timeframe.

The expansion of ash mortality likely resulted from a combination of natural emerald ash borer dispersal and inadvertent human-assisted transport of infested ash material across southeastern Michigan. Large-scale dispersal studies conducted in emerald ash borer infestations with a known origin have shown a high proportion (> 80%) of eggs are laid on trees within 100 m of the point where the parent beetles emerged (Mercader *et al.*, 2009, 2012; Siegert *et al.*, 2010). Adult emerald ash borer beetles, particularly mature females, are relatively strong fliers (Taylor *et al.*, 2010), however, and even in newly established infestations, a small proportion of female beetles bypass apparently suitable hosts to oviposit on trees ≥ 750 m from their emergence point (Siegert *et al.*, 2010; McCullough *et al.*, 2011; Mercader *et al.*, 2012).

Anthropogenic transport of infested ash nursery trees, logs and firewood played a key role in both the growth of the primary population of emerald ash borer and the establishment of satellite colonies across southeastern Michigan and beyond. Trace-back and trace-forward investigations launched by regulatory officials soon after the discovery of emerald ash borer identified numerous infestations directly attributable to infested but non-symptomatic ash nursery trees planted in commercial, residential or right-of-way settings (Rauscher, 2005; McCullough & Siegert, 2007). Other infestations were associated with infested firewood transported to campgrounds and sawmills where ash logs were processed (McCullough & Siegert, 2007; Storer *et al.*, 2007; United States Department of Agriculture Animal & Plant Health Inspection Service (USDA APHIS), 2010; Haack *et al.*, 2010). Previous efforts to estimate or model emerald ash borer spread similarly noted the important contribution of human-assisted transport of infested ash material underlying stratified diffusion (BenDor *et al.*, 2006; Muirhead *et al.*, 2006; Prasad *et al.*, 2010).

It is important to note that spread of emerald ash borer and the expansion of ash mortality documented by our study occurred well before emerald ash borer was detected and identified in North America. Since late 2002, state and federal quarantines have regulated transport of ash trees, logs, firewood and related material from areas known to be infested. These efforts, coupled with a growing public awareness of emerald ash borer and ongoing outreach activities to convey the risk of moving infested material, should presumably diminish the likelihood of new satellite colonies becoming established. Nevertheless, previously unknown emerald ash borer infestations continue to be detected every year (Emerald Ash Borer Information, 2014).

Dendrochronology has long been used to track the temporal occurrence and impacts of fire, drought, insect outbreaks and other forest disturbances (e.g. Swetnam & Lynch, 1993; Swetnam *et al.*, 1999; Ryerson *et al.*, 2003; Rentch *et al.*, 2009), but has rarely been applied to evaluate spread of an invasive organism and certainly not on the spatial scale of our study. In two previous studies, dendrochronology was used to assess the establishment and spread of non-native woody plants, Norway maple (*Acer platanoides*) across a 7.3 km^2 area on Mackinac Island, Michigan (Wangen & Webster, 2006), and hawthorn (*Crataegus monogyna*) into a 5 km^2 grassland in New Zealand (Williams *et al.*, 2010). In another instance, spread of a root rot pathogen affecting Port Orford cedar (*Chamaecyparis lawsoniana*) across a 37 km^2 area in Oregon and northern California was examined using dendrochronology (Jules *et al.*, 2002).

To maximize our chances of identifying the origin of the emerald ash borer infestation in southeastern Michigan, we preferentially sampled dead and declining trees, rather than prioritizing sites where trees would be relatively sensitive to climatic fluctuations (e.g. xeric sites). Many trees we sampled, therefore, would inevitably have annual growth rings that were more similar in width (i.e. complacent) than if trees had been selected from sites where yearly fluctuations in limiting factors such as water availability would have produced larger or smaller rings (i.e. sensitive). This would contribute to lowering the series intercorrelation and average mean sensitivity of the chronology. Additionally, this chronology was developed for the entire 1.5 million ha (15,000 km^2) study area which would presumably incorporate more variability into the chronology statistics. In general, mean sensitivity values in the 0.20–0.29 range are considered intermediate, and series intercorrelation values > 0.5 are desirable (Grissino-Mayer, 2001). These descriptive statistics, however, vary by species, regional climate, and, as in this case, the geographical extent of the study area (Fritts, 2001; Grissino-Mayer, 2001). Despite our sampling criteria and the broad expanse of the area encompassed by our sampling, the increment cores and cross sections cross-dated relatively well (series intercorrelation = 0.366; average mean sensitivity = 0.236) throughout the diverse, heterogeneous environment of southeastern Michigan.

Our results have important implications for managing emerald ash borer specifically, but more generally demonstrate the importance of early detection, and the role satellite colonies can play in accelerating the spread of invasive pests. Kovacs *et al.* (2011) showed that if the localized satellite colonies of emerald ash borer detected in 2005–2010 could have been prevented or contained, it would have saved or delayed economic costs associated with treating or replacing landscape ash trees by more than $7 billion USD over the next decade.

Detectability was shown to be a critical factor influencing the success of arthropod eradication programmes around the globe (Tobin *et al.*, 2014), and Mehta *et al.* (2007) demonstrated the economic benefits associated with allocation of resources towards early detection versus costs of control or management of an invasive pest. Early detection, however, is particularly challenging for non-native cryptic or subcortical insects that do not produce long-range pheromones. While emerald ash borer has rapidly become the most economically damaging forest pest in North America (Aukema *et al.*, 2011; Kovacs *et al.*, 2011), the increasing rate of new detections of non-native phloem- and wood-boring species in the USA (Aukema *et al.*, 2010), many of which have no known pheromones, suggest similar patterns of biological invasion may occur in the future.

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BIOSKETCH

Nathan W. Siegert is a forest entomologist, whose work focuses on the behaviour and ecology of native and non-native forest insects to help maintain healthy productive forests and better manage forest ecosystems. He is broadly interested in the ecological and evolutionary aspects of plant–insect interactions, population dynamics of forest insects and invasive species biology.

Author contributions: The initial concept for this work was developed by D.G.M. and N.W.S. N.W.S. oversaw data collection and analyses; N.W.S., D.G.M. and A.M.L. contributed expertise on emerald ash borer and invasion ecology; F.W.T. and N.W.S. contributed dendrochronology expertise. All authors contributed to the writing, which was led by N.W.S. and D.G.M.

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