RESEARCH ARTICLE

Temporal dynamics and drivers of landscape-level spread by emerald ash borer

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Abstract

1. Non-native insects pose threats to forest health and often spread via stratified dispersal in which long-distance jumps cause elevated rates of range expansion. Quantifying patterns and developing models of spread are central to understanding drivers of invasion and forecasting future invasions.

2. We investigated the utility of models for characterizing and predicting spread of emerald ash borer (EAB), quantified temporal dynamics of spread and identified correlates of county-level invasion risk.

3. We estimated rates and frequency of EAB spread and length of long-distance jumps throughout the contiguous USA from 1997 to 2018 and compared observed patterns with model predictions. A time-to-event model was then developed at the county level to assess the influence of habitat characteristics and propagule pressure on invasion risk. The final model was used to forecast invasion risk across the contiguous USA.

4. Range expansion by EAB accorded well with model predictions. Following the initial establishment phase, range expansion rates were biphasic, shifting to a faster, linear pattern around 2002 and then declining from 2015 onwards. From 2003 onwards, EAB invaded 6–134 new counties per year, including a mean of 14 discrete jumps per year averaging 93 ± 7 *SE* km.

5. Risk of spread was positively associated with proximity to previously invaded areas, human population density and densities of ash and non-ash trees in rural forests but negatively associated with temperature.

6. *Synthesis and applications*. At the regional level, the invasion by emerald ash borer appears to be entering the saturation phase, indicating that most high-risk counties in the eastern USA have been invaded. Even though spread has recently slowed, counties in close proximity to invaded areas and that have high densities of humans and trees are at the greatest risk of becoming invaded. Taken together, our findings provide insight into historical and future dynamics of range expansion by emerald ash borer, which can be used to guide risk assessments for potential invaders capable of frequent long-distance dispersal.

KEYWORDS
Agrilus planipennis, Cox proportional hazards, emerald ash borer, *Fraxinus*, invasion, landscape, spatiotemporal, stratified dispersal

1 | INTRODUCTION

Spread of non-native insects results from population growth coupled with dispersal, which can be categorized into two types, short- and long-distance (Kot, Lewis, & van den Driessche, 1996; Liebhold & Tobin, 2008). Short-distance dispersal is typically achieved by active movement by insects, such as flight, whereas long-distance dispersal is frequently attributed to human activities (Gilbert, Grégoire, Freise, & Heitland, 2004; Koch, Yemshanov, Magarey, & Smith, 2012; Liebhold & Tobin, 2008). These two types of movement often occur in tandem to manifest as stratified dispersal (Hengeveld, 1989; Liebhold & Tobin, 2008).

Theoretical models of spread developed by Shigesada, Kawasaki, and Takeda (1995) posit that range expansion undergoes three phases. The first is establishment, a lag phase during which spread is minimal while populations build in the novel habitat. Next is expansion, during which spread occurs, followed by saturation, characterized by deaccelerating rates of spread as suitable habitat is exhausted. Under this framework, spread rates during expansion can be linear and monophasic, linear and biphasic, or constantly increasing, referred to as type 1, 2 or 3 radial range expansion, respectively (Shigesada et al., 1995). Type 1 range expansion is typical of invaders that settle in close proximity to natal patches whereas types 2 and 3 range expansions are typical of invaders with stratified dispersal (Shigesada et al., 1995).

Quantifying patterns and drivers of invader spread can provide natural resource managers with critical information for designing and implementing management programs (Liebhold & Kean, 2019; Sadof, Hughes, Witte, Peterson, & Ginzel, 2017). Predictive models of range expansion can improve the efficacy of detection, delimitation, eradication and barrier-zone management (Liebhold et al., 2016; Sharov, Leonard, Liebhold, Roberts, & Dickerson, 2002) while providing insight into underlying drivers of invasion. Limited ecological information may be available for new invaders (Herms & McCullough, 2014) and thus initial management guidelines may have to rely on models developed for or patterns displayed by invaders with similar ecology.

Invasions by bark- and wood-boring insect species have increased with use of solid-wood packaging materials and international trade (Aukema et al., 2010; Brockerhoff & Liebhold, 2017; Meurisse, Rassati, Hurley, Brockerhoff, & Haack, 2019), intensifying the need to identify potentially common drivers of post-establishment spread by borers. Spread of bark and wood-borers is often characterized by long-distance jumps and can be challenging to predict because it often occurs cryptically via human-aided movement of infested material such as firewood (Jacobi, Goodrich, & Cleaver, 2011; Jacobi, Hardin, Goodrich, & Cleaver, 2012; Koch et al., 2012) and/ or there may exist significant lags between invasion and detection. Habitat characteristics such as the diversity and abundance of host trees (Guo, Fei, Potter, Liebhold, & Wen, 2019; Hudgins, Liebhold, & Leung, 2017; Liebhold et al., 2013), human population density in source and destination locations (Gilbert et al., 2004), and climate can affect spread. Evaluating the relative influence of these factors for individual species is necessary for forecasting invasion risk and, potentially, guiding risk assessments for spread of future invaders.

Emerald ash borer *Agrilus planipennis* Fairmaire (EAB) is a phloem and wood boring beetle native to eastern Asia that was initially discovered in North America near Detroit, MI, USA in 2002 (Poland & McCullough, 2006), and apparently invaded Europe around that same time (Baranchikov, Mozolevskaya, Yurchenko, & Kenis, 2008; Valenta, Moser, Kapeller, & Essl, 2017). The insect likely became established in North America in the early 1990s, began killing trees by 1997 (Siegert, McCullough, Liebhold, & Telewski, 2014), and has since killed millions of *Fraxinus* spp. in the eastern USA (Herms & McCullough, 2014; Morin, Liebhold, Pugh, & Crocker, 2017), resulting in significant biomass losses (Fei, Morin, Oswalt, & Liebhold, 2019). Initial radial range expansion by EAB at the sub-county level occurred at ~4 km/year between 1998 and 2001, and ~13 km/year between 2001 and 2003 (Siegert et al., 2014).

Spread of EAB is facilitated by human activity, particularly movement of infested firewood (BenDor, Metcalf, Fontenot, Sangunett, & Hannon, 2006; Muirhead et al., 2006; Prasad et al., 2010; Yemshanov et al., 2015). Sub-county level analyses in the USA have highlighted the role of human activity and spatially proximate invasions (BenDor et al., 2006; Muirhead et al., 2006; Prasad et al., 2010; Yemshanov et al., 2015) as well as ash phloem resources in aiding the spread of EAB (Mercader et al., 2016; Mercader, Siegert, Liebhold, & McCullough, 2009, 2011). Spread at the county level—the spatial unit at which quarantines on ash materials are imposed—such as radial spread rates and changes therein, frequency or length of long-distance jumps, and the effects of propagule pressure and habitat characteristics on invasion risk have not been quantified; however, such knowledge of spread dynamics is critical for developing successful management and quarantine programs.

We investigated patterns of spread across the United States from 1997 to 2018 and examined the utility of theoretical models for characterizing range expansion by EAB, an invader with highly stratified dispersal. Study aims were to (a) quantify rates of radial range expansion and assess if the range has expanded in a manner consistent with invasion theory, (b) characterize patterns of short- versus long-distance dispersal through time and (c) quantify drivers of invasion risk at the county level across the contiguous USA and forecast invasion risk. We intend that our research findings will provide insight into the past and future invasion dynamics of EAB in North America while elucidating patterns that might help guide future risk assessments for invasions by other wood borers.

2 | MATERIALS AND METHODS

New records of established EAB populations in the USA are reported by state and federal forest health agencies along with discoveries made by citizens. The United States Department of Agriculture, Animal and Plant Health Inspection Service (USDA APHIS) has annually compiled these records into county-level data detailing the distribution of EAB since 2002 (Figure 1). We defined 'adjoining' versus
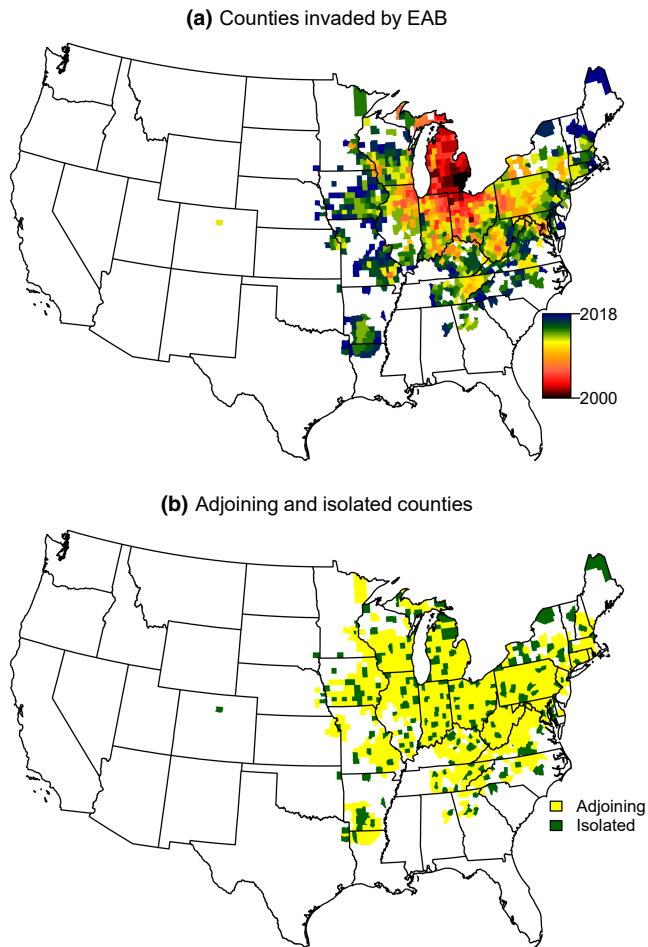
(a) Counties invaded by EAB

(b) Adjoining and isolated counties

FIGURE 1 (a) Progression of emerald ash borer invasion in the USA at the county level as of 31 December 2018 according to data from United States Department of Agriculture, Animal and Plant Health Inspection Service. (b) Same as in panel (a), except counties with invaded neighbouring counties prior to the year they became invaded are depicted in yellow (i.e. adjoining counties) and counties without invaded neighbours prior to their invasion are depicted in green (i.e. isolated counties)

'isolated' counties as those that became invaded in year t and were or were not, respectively, neighbouring at least one county invaded as of year $t - 1$ (Figure 1b). For most counties, there likely exists a lag of random length between establishment and detection that introduces random variation for which we are not able to account. Nonetheless, we use the terms 'invaded' and 'detected' interchangeably. Analyses throughout were conducted using R version 3.5.0 (R Core Team, 2018).

2.1 | Radial range expansion

We assessed if radial range expansion at the county level followed a type 1, 2 or 3 range expansion as defined by Shigesada et al. (1995). The effective range radius (ERR, km) of the invaded area per annum was calculated using county areas ($ERR_t = \sqrt{\frac{\sum_i^n Area_i}{\pi}}$, where i is a unique county identifier for each county invaded by year t). Maps

by Siegert et al. (2014) detailing historical EAB invasion at a sub-county level in southeastern Michigan indicated that 13 counties were invaded between 1997 and 2003. We combined these data with USDA APHIS data, in which six counties were known invaded as of 2002, by recording the earliest year of invasion reported between the two data sources for each county (i.e. some counties invaded in 2002–2004 according to the USDA APHIS data were re-assigned to earlier invasion years). A comparison of range expansion rates using county level versus sub-county level data from Siegert et al. (2014) is provided in Figure S1.

Range expansion can be categorized as a type 1, 2 or 3 expansion depending on changes in spread rates between the end of the establishment phase and the onset of the saturation phase (Shigesada et al., 1995). The end of the EAB establishment phase likely occurred in ~1997, the first year in which trees were known to have been killed by EAB and landscape-level spread commenced (Siegert et al., 2014). To identify changes in spread rates, piecewise regressions were fit using the SEGMENTED package in R (Muggeo, 2008), which can be used to objectively identify breakpoints in bivariate relationships. The segmented() function was parameterized to search for three breakpoints in the relationship between ERR and year (1997–2018), but the approximate years of breakpoints were not specified. Potential breakpoints could include (a) a single increase in spread rates, indicative of type 2 expansion (b) several increases in spread, potentially indicative of type 3 expansion (i.e. nonlinear increases in spread) and (c) deaccelerating spread indicative of the saturation phase. For example, only one breakpoint located at the onset of the saturation phase would indicate type 1 expansion. Three breakpoints—2002, 2012 and 2015—were identified (see Section 3), however, potentially indicating type 3 expansion. To further disentangle a type 2 versus 3 range expansion, we quantified ln(ERR) as a function of time across 1997–2014. For this analysis, which was conducted to determine if spread increased nonlinearly, data from 2015 onwards were considered part of the saturation phase and not included.

Rates of increase in the ERR with time (years; 1997–2018) were then characterized using a generalized additive model (GAM) in which time was fit as a smoothing function. For this analysis, increases in ERR, for example, from 2002 to 2003 and 2003 to 2004 were paired with time values of '2003' and '2004', respectively. GAMs were fit using the MGCV package (Wood, 2011). We caution that county shape and size could influence modelled results; however, no temporal trends in the size of invaded counties were detected (Figure S2) and finer resolution data documenting the invasion are not available. Moreover, Siegert et al. (2014) estimated radial spread from a network of trees for which year of death was reconstructed using dendrochronology, likely a much more sensitive and accurate sampling approach than those used to detect county level invasions comprising the USDA APHIS data. Thus, data from Siegert et al. (2014) were not included in any ensuing analyses, which focused solely on county level USDA APHIS data (2002–2018).

2.2 | Invasion of adjoining and isolated counties

We quantified patterns in the number of counties invaded per year. Three separate GAMs were used to estimate the number of newly invaded counties per year as a function of a smoothing term for time (2003–2018), with one model fit using all counties, another model fit to adjoining counties and a third fit to isolated counties. Spread distances between counties were estimated by assigning randomly spaced points across each county and calculating the minimum distance between points located in each newly invaded county and points located across all previously invaded counties. The number of points placed in each county was set to the highest value of either one point per 100 km^2 or a minimum of 15 total points. The randomly spaced points were generated using the spsample() function in the SP package (Bivand, Pebesma, & Gómez-Rubio, 2013; Pebesma & Bivand, 2005) and distances were calculated using the pointDistance() function from the RASTER package in R (Hijmans, 2017). This approach precluded spread distances of zero km into adjacent counties and was analogous to methods used by Kovacs et al. (2010) in developing the dispersal kernel we used to forecast spread (see below).

Effective management immediately following discovery of a newly invading species hinges on reliable forecasts for lengths of long-distance jumps. For isolated counties, we estimated the $M \pm 95\%$ confidence limits for jump distances. Moreover, theoretical models from Shigesada et al. (1995) provide a useful framework for estimating potential jump distances for invaders with type 2 range expansion based on the rate of range expansion during the first phase of biphasic expansion. Given that spread by EAB closely resembled type 2 biphasic expansion (see Section 3), we compared expected jump distances, L, with observed mean (±95 CI) jump distances using:

$$L = 2ct_s,\qquad(1)$$

where L is the expected length (km) of long-distance jumps, c is the rate (km/year) of expansion during the first phase of biphasic range expansion and t_s is the time in years from establishment until range expansion switches to a faster, constant rate (Shigesada et al., 1995). The parameter c was estimated using two different approaches: (a) as the slope coefficient for a segment spanning 1997–2002 estimated from our piecewise regression analysis of county-level data (see Section 3) and (b) as the slope coefficient from a regression of radial spread distances on year (1997–2002) using sub-county level data from Siegert et al. (2014). In both instances, slopes and 95% confidence intervals were estimated and input into Equation 1. This approach enabled us to compare sensitivity of predicted jump distances when using data collected at different scales. The parameter t_s was assigned a value of 5 (=2002 − 1997), given that spread accelerated to an approximately constant rate following 2002 (see Section 3).

2.3 | Risk of invasion at the county level

We used a Cox proportional hazards model, which enabled the inclusion of time-dependent and time-independent predictors (Therneau, Crowson, & Atkinson, 2019; Thomas & Reyes, 2014), to estimate time-to-invasion as a function of propagule pressure and habitat invasibility. Similar survival analyses have been used to quantify invasion risk as a hazard function (Hastings et al., 2005; Jules, Kauffman, Ritts, & Carroll, 2002). The invasion status for each county was treated as time-to-event data in which each county was assigned a '0' value on an annual basis until invasion occurred at which point a '1' was assigned.

The inclusion of time-varying predictors is a potentially useful approach for analysing invasion data given that invasive range size changes through time. The one time-dependent predictor, '*EAB pressure*', $P_{j,t}$, was calculated as:

$$P_{j,t} = 1 - \prod_{i}^{n_{t-1}} \left(1 - \beta e^{-\alpha d_{i,j}}\right),\qquad(2)$$

where $P_{j,t}$ is the probability of county j becoming invaded from any previously invaded county i at time t, β was 0.94, α was 0.06, d is distance from county i to county j and n includes all invaded counties as of time $t − 1$. Values for dispersal kernel parameters (α and β) were previously estimated in an effort to reconstruct county level spread of EAB across a smaller geographic distribution in the eastern USA (Kovacs et al., 2010). Distances between counties in Equation 2 were calculated as described above. Similar models have been used to estimate propagule pressure and/or spread for EAB (Kovacs et al., 2010; Muirhead et al., 2006; Orlova-Bienkowskaja & Bieńkowski, 2018).

Additional county-level predictors included density of ash trees (m^3 of *Fraxinus* spp. per ha of forested land; '*AshVolDen*'), density of non-ash trees ('*NonAshVolDen*'), human population density per county area in 2010 (individuals per km^2; '*HumPop2010*'), and two predictors derived from monthly temperature and precipitation data (see below). Tree volumes were estimated from USDA Forest Service Forest Inventory and Analysis (FIA) plot data. Data were extracted using the FIA EVALidator (v. 1.8.0.00; https://apps.fs.usda.gov/Evalidator/evalidator.jsp) and covered survey periods from 2000 to 2012. Forested land was defined as land greater than 1 acre in size and stocked at least 10% by forest trees of any size, or formerly having such tree cover, and not currently developed for non-forest uses (https://www.nrs.fs.fed.us/fia/data-tools/state-reports/glossary/). Counties ($n = 197$, 6.3%) that did not contain forested land were assigned '0' for ash and non-ash tree volume. Estimates for human population density per county were obtained from the USA census (https://www2.census.gov/programs-surveys/popest/datasets/2010-2017/counties/totals/).

Monthly climate normals for minimum temperature (°C), maximum temperature (°C) and precipitation (mm) were obtained for the period 1981–2010 from PRISM at a 4 km × 4 km resolution raster across the contiguous USA (PRISM, 2019) such that each grid cell in the raster contained 36 data points. We then scaled ([x − mean]/*SD*) each of the 36 climate variables and conducted a principal components analysis (PCA) at the grid cell level. Rotated principal components for each grid cell of the raster were aggregated to the county level by averaging values for all cells whose centroids

occurred within a given county boundary. This approach reduced dimensionality and collinearity of multiple potential predictors into two values ('*PC1*' and '*PC2*'); Haynes, Bjørnstad, Allstadt, and Liebhold (2013) used an equivalent approach, fitting PCA scores in a regression framework to quantify climatic effects on landscape dynamics of invasive forest insects. The first and second principal components explained 59.5% and 22.6%, respectively, of the variation in climate variables (Figure S3.1a). Minimum and maximum monthly temperatures had high loadings on the first component whereas precipitation had high loadings on the second (Figure S3.2b). Detailed descriptions (Table S1) and county level maps (Figure S4) of each predictor are provided in Supporting Information.

Non-significant (*p* < 0.05) terms were removed and the final model was used to estimate risk of invasion on an annual basis from 2019 to 2030 across the contiguous USA. For each county, annual invasion status was determined using a random draw from a Bernoulli distribution parametrized with the predicted probability of invasion according to our final Cox proportional hazards model. Thus, a new probability was predicted for each year × county combination as *EAB pressure* was updated with changes in the predicted invaded range. We ran 1,000 simulations and invasion risk was taken as the number of simulations resulting in invasion/1,000 on an annual basis. For all results, point estimates are expressed as *M* ± *SE* unless stated otherwise.

3 | RESULTS

3.1 | Radial range expansion

Note that results in this section include sub-county level data aggregated to the county level (1997–2003) along with those based on county-level USDA APHIS data (2002–2018). Fitting a piecewise regression model to assess changes in the ERR with time (1997–2018) indicated that shifts in spread rates occurred at three time points: 2002, 2012 and 2015 (Figure 2a). The range of EAB expanded at 14 km/year from 1997 to 2002, 31 km/year from 2002 to 2012, 56 km/year from 2012 to 2015 and 35 km/year from 2015 onwards (Figure 2a). Thus, from 2015 onwards, in accordance with observed patterns in the number of counties invaded per year (Figure 3; see below), the invasion appeared to have entered the saturation phase.

When analysing ERR from 1997 to 2014 (i.e. before saturation), a biphasic piecewise regression provided a superior fit (R^2 > 0.99) to a linear model (indicative of type 1 expansion) and nonlinear model (indicative of type 3 expansion), demonstrating that the invasion of EAB has most closely resembled a type 2 range expansion (Figure S5). Analysing the incremental increases in the radius per year further elucidated this pattern (Figure 2b). On average, annual increments in spread were approximately 11 km/year until 2002, followed by an increase to an average of 37 km/year from 2003 to 2014. Average increases were 43 km/year from 2015 to 2018; however, the largest single-year increase occurred in 2014 (58 km) and was followed by a decrease in each year to 31 km in 2018 (Figure 2b).
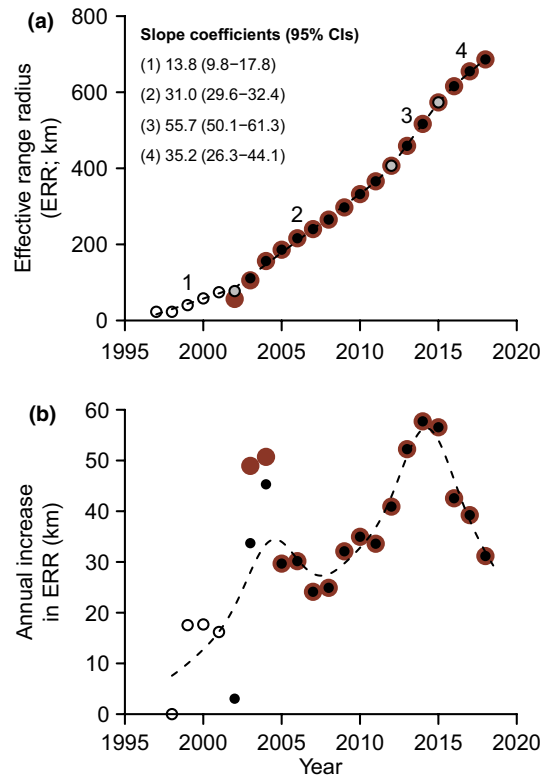

FIGURE 2 Patterns of historical emerald ash borer spread in the USA according to county-level invasion data from Siegert et al. (2014; white circles) and United States Department of Agriculture, Animal and Plant Health Inspection Service (red circles). Years 2002–2004 included some data from Siegert et al. (2014) because county invasion status was recorded as the earliest year reported between the two data sources (see main text). Grey circles indicate changes in spread rates identified by piecewise regression. White, black and grey circles were analysed, whereas red circles are provided for comparison only. (a) Effective range radius ($\text{ERR} = \sqrt{\text{Area invaded}/\pi}$) as a function of time (1997–2018). Dashed lines are linear models for each interval of time (1–4) between breakpoints (grey dots). (b) Annual increase in ERR as a function of time. For example, the increase in the radius from 2002 to 2003 was ~35 km and was assigned a time value of 2003. Generalized additive model (GAM) statistics (dashed line) for the term *s*(time): edf = 5.97, refdf = 7.09, *F* = 6.74, *p* = 0.0008; deviance explained = 84.6%

3.2 | Invasion of adjoining and isolated counties

Note that results in this section and all subsequent sections were derived solely from county-level USDA APHIS data. EAB had invaded 1,041 counties as of 2018, with six initial counties identified as invaded in 2002. From 2003 onwards, 65 ± 10 counties have been invaded per year (range: 16–134 counties; Figure 3a). Of those counties, 50 ± 9 per year were adjoining. After 2002, the lowest number of newly invaded adjoining counties in a given year was six, occurring in 2003 (Figure 3b). The number of newly invaded adjoining counties increased nonlinearly to a maximum of 115 in 2016. In 2017 and 2018, however, the number of newly invaded adjoining counties declined to 88 and 62, respectively. An average of 14 ± 2 isolated counties became invaded each year from 2003 to 2018,
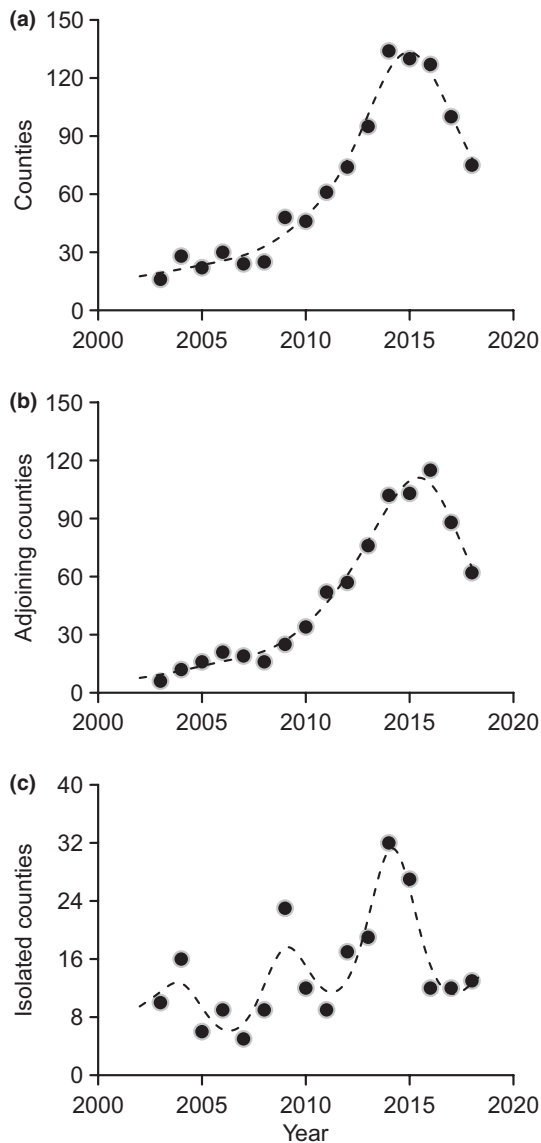
FIGURE 3 Numbers of counties invaded by emerald ash borer in the USA from 2003 to 2018 according to data from United States Department of Agriculture, Animal and Plant Health Inspection Service. Dashed lines in all panels are from generalized additive models (GAMs). (a) Number of counties that became invaded per year as a function of time. GAM statistics for the term s(time): edf = 4.74, refdf = 5.75, F = 60.82, p < 0.0001; deviance explained = 98.4%). (b) Same as in (a), but only adjoining counties are depicted. GAM statistics for the term s(time): edf = 5.14, refdf = 6.16, F = 57.38, p < 0.0001; deviance explained = 98.7%. (c) Same as in (a), but only isolated counties are depicted. GAM statistics for the term s(time): edf = 7.64, refdf = 8.51, F = 4.84, p = 0.0217; deviance explained = 81.5%

FIGURE 4 Spread distances by emerald ash borer in the USA at the county level from 2003 to 2018 according to data from United States Department of Agriculture, Animal and Plant Health Inspection Service. (a) Relative frequency of distances spread, (b) relative frequency of long-distance spread to isolated counties and (c) long-distance spread distances as a function of time (2003–2018); gneralized additive model (GAM) statistics (dashed line) for the term s(time) in panel (c): edf = 5.62, refdf = 6.75, F = 1.52, p = 0.17; deviance explained = 6.0%. Note that x-axes in panels (a) and (b) exclude 62 (6% of all data) and 2 (1% of long-distance jumps) observations to display patterns at shorter distances where the majority of spread occurred

totalling 231 jumps (Figure 3c). The lowest and highest numbers of newly invaded, isolated counties were five, occurring in 2007, and 32, occurring in 2014.

The average distance between newly invaded counties and the closest invaded county was 28 ± 2 km (Figure 4a), although we caution that this distance is largely determined by our random point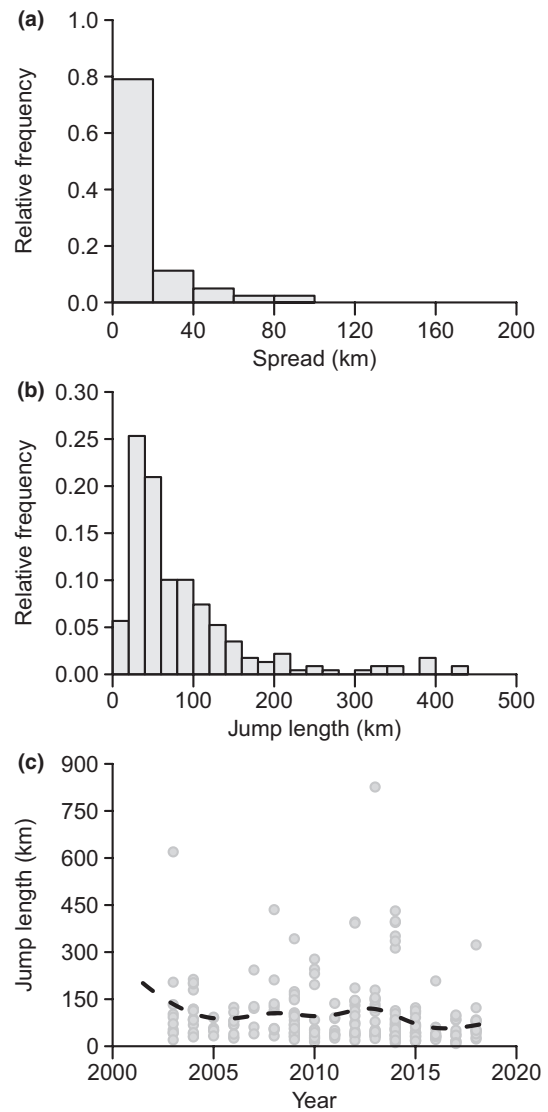 sampling procedure used to estimate distances between adjoining counties. Long-distance jumps into isolated counties averaged 93 ± 7 km (95% CI: 80–106; Figure 4b) but distances jumped did not change significantly through time (Figure 4c). The farthest jump to date by EAB was made in 2013 when the beetle invaded Boulder County, Colorado (Figure 1), ~800 km from the nearest previously invaded county (Platte County, MI) and ~1,700 km away from Wayne County, MI. Otherwise, 2%, 6%, 10% and 29% of jumps have surpassed 400, 300, 200 and 100 km, respectively (Figure 4b).

Expected lengths of long-distance jumps, L (Equation 1), over- or under-estimated observed jump distances (93 km) depending on the data used to estimate c. Using county-level data to estimate spread rates from 1997 to 2002 (Figure 2a) resulted in predicted long-distance jumps of 138 km (95% CI 98–178), or 45 km farther than observed. Using sub-county level data and regressing ERR on time from 1997 to 2002 indicated that radial expansion occurred at 4.7 km/year (slope: 4.74 ± 0.85, $t_4 = 5.56$, $p = 0.0051$; 95% CI:

TABLE 1 Summary statistics from a Cox proportional hazards model predicting time-to-invasion, indicative of risk of invasion, by emerald ash borer at the county level across the contiguous USA. Model was developed using county-level invasion data from United States Department of Agriculture, Animal and Plant Health Inspection Service (2002–2018). Detailed variable descriptions are provided in Table S1

Predictor	Estimate	SE	Z	p	Hazard ratio (95% CI[a])
(a) Full model (AIC: 13,244)					
EAB pressure	4.05	0.10	39.49	<0.0001	60 (49–74)
HumPop2010[b]	0.22	0.02	9.23	<0.0001	1.25 (1.19–1.31)
AshVolDen[b]	0.11	0.03	3.49	0.0005	1.11 (1.05–1.18)
NonAshVolDen[b]	0.37	0.04	8.56	<0.0001	1.45 (1.33–1.57)
PC1	−0.05	0.01	−4.17	<0.0001	0.95 (0.93–0.98)
PC2	0.01	0.03	0.35	0.72	1.01 (0.95–1.07)
(b) Reduced model (AIC: 13,242)					
EAB pressure	4.10	0.10	39.67	<0.0001	60 (49–74)
HumPop2010[b]	0.22	0.02	9.57	<0.0001	1.25 (1.20–1.31)
AshVolDen[b]	0.11	0.03	3.51	0.0005	1.11 (1.05–1.18)
NonAshVolDen[b]	0.37	0.04	9.21	<0.0001	1.45 (1.34–1.57)
PC1	−0.04	0.01	−4.16	<0.0001	0.95 (0.93–0.98)

[a]Changes in expected hazards. For example, in model (a) and holding all else equal, a one unit increase in ln-transformed human population density was associated with a 1.25× (i.e. 25%) increase in the expected hazard, taken here as an estimate for the risk of invasion.
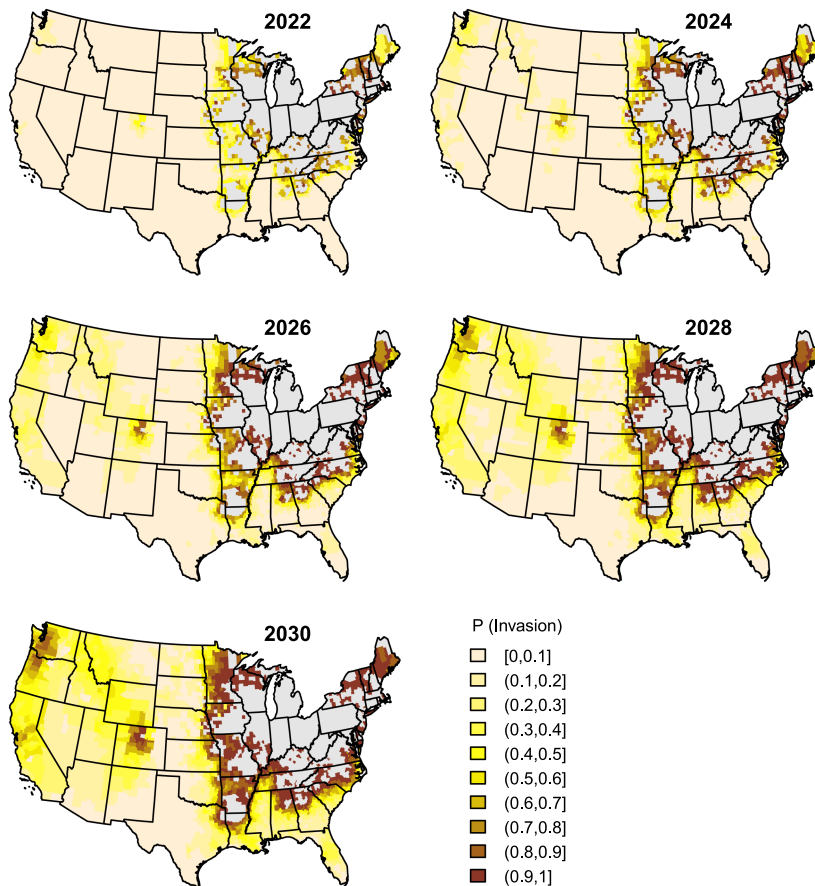[b]ln-transformed.

FIGURE 5 Predicted invasion risk for emerald ash borer at 2-year increments from 2022 to 2030 in the USA. Probability of invasion for each county was estimated on an annual basis using the model in Table 1b

2.4–7.1). Substituting the estimated slope coefficient and associated confidence limits as c in Equation 1 predicted jump distances of 47 km/year (95% CI: 24–71), or 46 km shorter than observed jump distances. Thus, county-level data predicted jump distances >90 km farther than sub-county level data.

3.3 | Risk of invasion at the county level

Analyses of time-to-invasion data using a Cox proportional hazards model identified *EAB pressure* as the most significant predictor. Indeed, spatially proximate propagules were substantially more important for predicting invasion risk ($Z = 39.49$) than other predictors we considered ($Z \leq 9.23$; Table 1a). In addition to *EAB pressure*, human population density was positively correlated with risk of invasion (Table 1). Forest composition also appeared important, as counties with higher volumes of ash and non-ash hosts were more likely to become invaded. *PC1*, which had high loadings from temperature, was negatively associated with time-to-invasion. *PC2*, which had high loadings from precipitation, was positively associated with time-to-invasion but this relationship was not statistically significant (Table 1a). The model with *PC2* removed (Table 1b) was used to forecast risk of invasion and indicated that, outside of continued range expansion in the eastern United States, areas surrounding Boulder County and heavily populated areas of northwestern Washington were the most at risk for future invasion (Figure 5).

4 | DISCUSSION

Effective management of biological invasions relies on knowledge of spread rates and the factors that govern them (Liebhold & Tobin, 2008). Quantifying patterns of range expansion by EAB indicated that the invasion has proceeded through establishment and expansion phases (Shigesada & Kawasaki, 1997), similar to invasions by other forest insects in North America (Liebhold & Tobin, 2006). The invasion, which has been characterized by exceptionally frequent long-distance jumps (Figure 4b,c), now appears to be reaching the onset of the saturation phase, at least for the eastern USA, indicated by decreases in both incremental spread (Figure 2b) and the number of newly invaded counties (Figure 3a) per year from 2015 onwards. Slowing invasion rates may be due to exhaustion of high risk counties, geographical constraints from the Atlantic coast, and/or constraints from less suitable habitat to the south where ash species are less common (MacFarlane & Meyer, 2005) and temperatures are warmer (Liang & Fei, 2014). However, there remain large areas of suitable habitat in North America that have not yet been invaded (Figure 5) and accelerating spread rates at the sub-county level may still occur.

There was considerable variability in the distances of annual increments of spread (Figure 2b). We attribute slowing spread in recent years to saturation in the eastern USA, but decreases in incremental spread from 2002 to 2004 (Figure 2b) might also indicate positive effects of quarantines on ash firewood and nursery stock coupled with increased outreach following the beetle's discovery in 2002. Slowing spread in the early part of the invasion could have also resulted from the 2008 economic recession inhibiting travel, changes in travel costs, weather or other factors. However, spread rates in 2002–2004 may have also been artificially heightened due to intense survey efforts immediately following the initial detection, which could have unearthed several satellite populations that were established several years prior to detection (Figure 2b).

Observed jump distances were also quite variable (Figure 4b,c) and comparing predicted versus observed jump lengths provided mixed results. Predicted lengths were influenced by the scale of data used to estimate parameter c in Equation 1: use of sub-county level data underestimated distances, whereas use of county-level data overestimated distances. Shigesada et al. (1995) assumed constant jump distances, which—given the inherent variability of spread (Melbourne & Hastings, 2009) and variability in jump distances observed here (Figure 4c)—could limit the utility of Equation 1 for forecasting invader spread rates. Moreover, there were several jumps beyond 100 km (Figure 4b), and use of sub-county level data would fail to predict such events. Coupling data collected at an equivalent scale—the county level for the EAB invasion—with models developed by Shigesada et al. (1995), however, could produce conservative estimates of long-distance jump lengths for a variety of organisms, including wood borers, early in an invasion. This approach could inform trapping and delimitation surveys, and when qualitatively combined with other factors that influence county invasion risk (Table 1), could help municipalities anticipate and prepare for invader arrival.

The positive effects of host (*Fraxinus* spp.) and non-host tree densities on invasion risk (Table 1) suggest that the availability of ash resources in rural forests or density of tree cover might affect population growth and/or dispersal of EAB. Previous work has implicated ash density in facilitating spread (Prasad et al., 2010) and stand-level investigations suggest that beetles prefer to disperse to areas with high densities of ash phloem (Mercader, Siegert, Liebhold, & McCullough, 2011). The finding that non-ash tree density facilitates spread may be attributable to preference of beetles to disperse into or across forested areas and/or increased risk of firewood movement between forested areas (e.g. campground to campground movement).

In addition to rural forests, urban forests (e.g. structure and composition) can mediate invasion dynamics (Colunga-Garcia, Haack, & Adelaja, 2009; Colunga-Garcia, Haack, Magarey, & Margosian, 2010; Paap, Burgess, & Wingfield, 2017) and certainly played an important role in facilitating invasion of some counties. For example, ash in Boulder County, CO only exists in urban plantings. Urban forest data are becoming more available (Koch, Ambrose, Yemshanov, Wiseman, & Cowett, 2018), and future forecasts of EAB dynamics and other pests will likely be improved by their consideration. We note, however, that proximity to invaded areas is the main driver of this invasion (Table 1), and thus, despite the absence of rural ash, some counties in Colorado are at relatively high risk (Figure 5). Several counties in the Pacific Northwest are at elevated risk due to relatively high densities of

rural ash, a cooler climate, and high human population densities. Conversely, some counties in the southern USA are at a relatively lower risk owing to warmer temperatures and/or lower densities of humans despite having substantial volumes of *Fraxinus* spp. in their rural forests.

Several important drivers underlying patterns of range expansion by EAB are not fully understood. Establishments of sub-county and county level satellite populations are presumably facilitated by movement of firewood and nursery stock (Cappaert, McCullough, Poland, & Siegert, 2005), but prominence of satellite populations might also be due to humans planting ash species in urban forests as well as the increased detectability of beetle populations in urban versus natural forests. The transition from the establishment phase into the expansion phase may have been a function of increased prevalence of EAB in domestic invasion pathways, perhaps after ash trees are noticeably affected. That is, dead or moribund trees are presumably more likely to be cut and distributed as firewood. Lastly, some of our findings and forecasts might have been influenced by the availability and inclusion of comparable invasion data from Canada. Cold temperatures can reduce population growth (Macquarrie, Cooke, & Saint-Amant, 2019) and warmer temperatures might inhibit spread (Table 1; Figure 5). Indeed, mechanistic understandings of how temperature-mediated survival (Crosthwaite, Sobek, Lyons, Bernards, & Sinclair, 2011) and flight (Fahrner, Lelito, & Aukema, 2015), among other factors, influence spread are needed to improve forecasts.

Comparing observed range expansion with predictions from theoretical models, in conjunction with spread forecasts, could help in planning and justifying management efforts. For example, type 2 range expansion typically results when isolated populations are founded following long-distance dispersal events that (a) originate from the periphery of the range and (b) travel only moderate distances (Shigesada et al., 1995). Thus, these findings indicate the continued importance of early detection of range expansion events and management on the periphery of the range to slow spread. Early detection and local eradication of satellite populations would yield considerable economic benefits (Kovacs et al., 2011), but lack of sensitive trapping techniques, a major focus of ongoing research (Poland, Petrice, & Ciaramitaro, 2019), renders this approach impractical to implement at a continental scale at present. Nonetheless, surveys and quarantines remain the most common landscape-level management tactics, and enhanced survey efforts could be justified in high risk counties such as those predicted in Colorado and Washington (Figure 5). Following detection, however, an integrated pest management program combining insecticide treatments, girdled trap trees and biological control can inhibit population growth and reduce the spread of impacts (McCullough, 2019).

AUTHORS' CONTRIBUTIONS

S.F.W. conceived the idea, organized and analysed the data, and drafted the first version of the manuscript; S.F. and A.M.L. provided substantial input on analyses, interpretation of results, and writing of subsequent drafts. All authors have approved this version of the manuscript for publication.

DATA AVAILABILITY STATEMENT

Data are available via the Purdue University Research Repository (PURR) https://doi.org/10.4231/D6R9-VD88 (Ward, Fei, & Liebhold, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.