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INVASION NOTE

Spread of the emerald ash borer, *Agrilus planipennis*, in the Front Range region of Colorado

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Abstract Until it was discovered in Boulder, Colorado in 2013, the invaded range of the emerald ash borer, *Agrilus planipennis*, in the Western Hemisphere was entirely limited to natural and urban forests of eastern North America. Subsequently, this species has expanded its range through much of the Colorado Front Range region, utilizing non-native ash, *Fraxinus* spp. These host trees are widely planted there in urban settings but natural forests containing ash are lacking in the region. Here we use survey data to quantify emerald ash borer regional spread across the Colorado Front Range as well as its local spread in the city of Longmont, Colorado. Across the region, spread rate was estimated at 3.9 km/yr, but within Longmont the rate was only 0.25 km/yr. These rates of spread are lower than what has been reported from comparable spatial scales in eastern North America and the slower spread may reflect reduced host resource availability, successful implementation of management, or differences in environmental conditions.

Keywords Biological invasion · Beetle · *Fraxinus* · Urban forest · Radial spread rate

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Introduction

While most non-native forest insects have little or no known impacts, invasions by a few species have had substantial impacts on forest ecosystem services across large spatial scales (Brockerhoff and Liebhold 2017; Fei et al. 2019; Liebhold et al. 2023). While both natural areas and managed forests may be impacted, many forest insect invasions cause considerable loss of resources in urban forests (Buenrostro and Hufbauer 2022; Raum et al. 2023). The emerald ash borer (EAB), *Agrilus planipennis*, is an example of a non-native insect that causes high levels of host tree mortality resulting in severe impacts in both natural and urban forests (Poland and McCullough 2006; Herms and McCullough 2014). Across most of the species' native range in east Asia, it is not a common insect and larval feeding is largely limited to phloem of dying ash (*Fraxinus* species) that are native there (Liu Et al. 2003). In contrast, most North American ash species exhibit little resistance, so beetles can colonize and kill otherwise healthy hosts.

Since populations of EAB were initially discovered near Detroit, Michigan in 2002 (Siegert et al 2014), it has rapidly spread across a large fraction of eastern North America and is still expanding its range (Ward et al. 2020). Initial populations typically remain unnoticed for several years, but once emerald ash borer is discovered in a locality, most forest overstory ash is typically killed during the following few years (Klooster et al. 2014; Morin et al. 2017). A similar pattern has also been observed among urban trees and the economic impact of this rapid extirpation of urban ash is substantial (Kovaks et al. 2010; Sadof et al. 2023).

During the first ten years after emerald ash borer was initially discovered in Michigan, its invaded range in the Western Hemisphere was entirely limited to eastern North America. Then in rapid succession, it was discovered in Kansas City, Missouri in 2012 then Boulder, Colorado in 2013 (Alexander et al. 2020). More recently in 2022 a population was discovered in Forest Grove, Oregon. Infested firewood and nursery stock are both known pathways by which this insect is transported long distances, sometimes resulting in the establishment of satellite populations (Herms and McCullough 2014). While there has been success in eradicating isolated populations of several invading insect species, including bark and woodboring beetles such as the Asian Longhorned beetle (Branco et al. 2022), eradication of newly discovered satellite EAB populations is generally not considered practical and no longer attempted, in part due to an inability to detect and delimit low-density populations (Liu 2018; McCullough 2020).

Over the next 20 years, EAB is anticipated to spread into several western US cities where ash is widely planted in urban areas (Ward et al. 2020). The spread of EAB in Colorado's Front Range urban corridor (Fig. 1) can serve as a model for how EAB may behave in other western cities. This region was originally dominated by largely treeless prairie ecosystems but over the last 100 years, urban land use has expanded outward from several population centers, the largest of these being the Denver metropolitan area (Drummond et al. 2019). Across much of this urbanized land area there has been widespread planting and irrigation of ornamental trees; in many urban and residential areas, ash represents ca. 25% of these plantings (Alexander et al. 2020). These are mostly green ash, *Fraxinus pennsylvanica,* and white ash, *Fraxinus americana*. Both species are native to the eastern USA but non-native in Colorado, and both species are highly preferred EAB hosts (Rebek et al. 2008). Aside from a relatively small number of invasive *Fraxinus,* mostly growing in riparian habitats, the ash resource for EAB is entirely planted and, unlike eastern North American cities, there is no background matrix of ash growing in adjacent forests.

Our objective here is to characterize the historical spread of EAB through the Front Range Urban Corridor of Colorado. We quantify rates of spread over a ten-year period from the time of initial discovery in 2013 through 2022. We also quantify localized EAB spread in the Front Range city of Longmont, Colorado. We analyze these data to compute rates of spread and compare these rates to those observed elsewhere.

Methods

Historical spread among municipalities

Since EAB was initially discovered in Boulder, Colorado in 2013, this insect has been the focus of a large, multi-agency coordinated effort to monitor and manage this problem (Alexander et al. 2020). These efforts include conducting inventories of urban ash trees but also education of municipal foresters and arborists on how to identify the symptoms of EAB-infested trees and recognize EAB life-stages. Surveys conducted annually by municipal foresters and reports from professional arborists have been compiled annually by the Colorado State Forest Service and the year of first discovery has been reported by municipality (https://csfs.colostate.edu/forest-management/emerald-ash-borer) (Fig. 1).

We estimated the radial rate of spread of EAB within the Front Range urban corridor by taking records of first discovery and regressing distance from the epicenter (Boulder) as a function of years since 2013 (when EAB was initially discovered in Boulder). This "distance regression" is a common method for estimating radial rates of range expansion (Gilbert et al. 2010). Distances from the centroid of

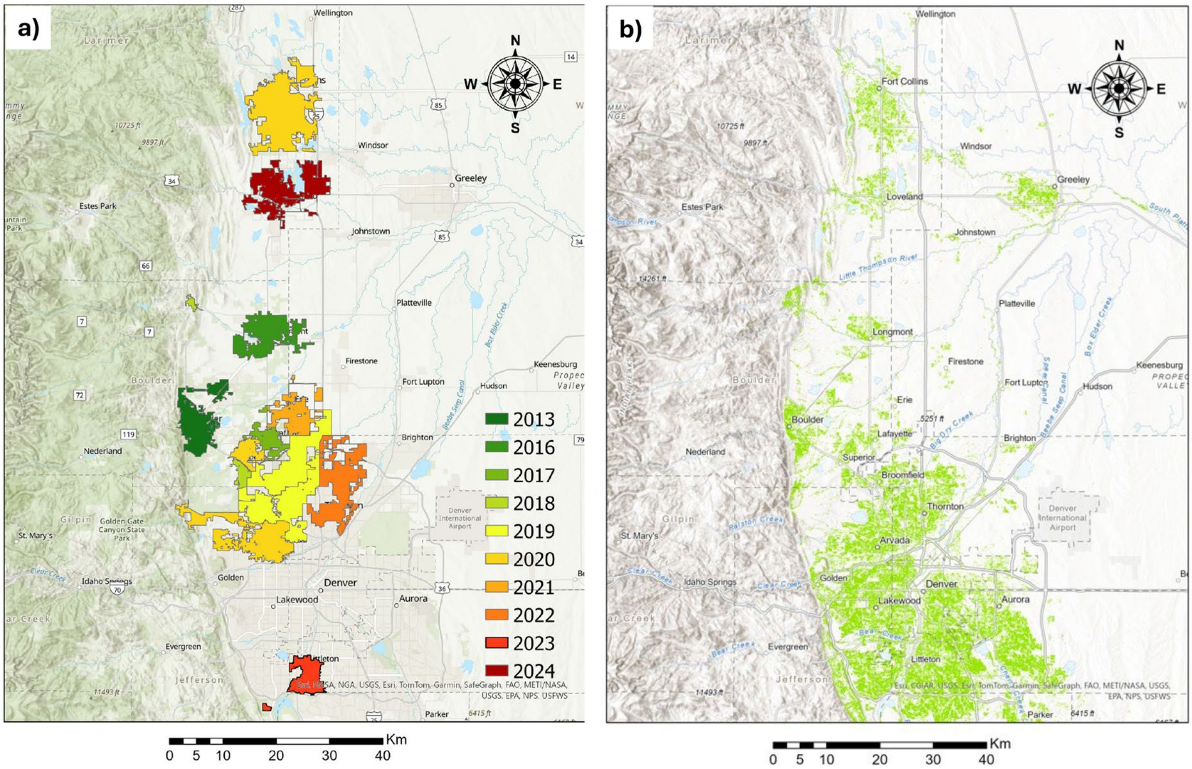

Fig. 1 Historical spread of the emerald ash borer among municipalities in the Colorado Front Range urban corridor; **a** year of first detection by municipality (compiled by the Colorado State Forest Service); **b** distribution of urban tree canopy (from US Forest Service Tree Cover Dataset derived from the US National Geological Survey National Land Cover Database)

each invaded municipality to the centroid of Boulder were calculated using ArcGIS. The radial rate of spread was estimated as the slope of the estimated regression equation.

Historical spread within a municipality

To quantify local EAB spread, we analyzed the historical spread of infested trees identified during surveys within the city of Longmont, Colorado. These surveys were conducted annually by initially scouting for EAB-infested trees via "windshield surveys" conducted by driving all major and minor arterial roads in late summer and searching for superficial signs of EAB colonization in trees (dieback, sloughing bark, mortality). In city blocks where superficial symptoms were observed, additional surveys were conducted by foot also during late summer. During these surveys, the spatial location of every ash was recorded using the Avenza Maps software (https://www.avenza.com/avenza-maps) running on an Apple iPad tablet computer. In addition to spatial coordinates, the condition of each tree was recorded as: "live" (living trees with no sign of damage), "damaged" (living trees with dieback or defects but no signs of EAB), "infested" (live trees with signs of EAB such as galleries or emergence holes), "dead" (dead trees with no symptoms of EAB) and "dead infested" (dead trees with EAB galleries or emergence holes). While it was possible to directly access trees facing roadways or alleys and inspect them, access was constrained for trees in backyards of residences and other fenced areas; while binoculars made it possible to visually confirm the presence of EAB symptoms in these trees, we acknowledge that some symptomatic trees were likely missed. Throughout the annual surveys, care was taken to distinguish symptoms of EAB from damage caused by the lilac ash borer, *Podosesia syringae* (Lepidoptera: Sesiidae), ash bark beetles, *Hylesinus spp.* (Coleoptera: Curculionidae), the redheaded ash borer, *Neoclytus acuminatus* (Coleoptera: Cerambycidae), and the banded ash borer, *Neoclytus caprea*, (Coleoptera: Cerambycidae) (Cranshaw 2019).

Spatially referenced survey data collected using the Avenza software was imported to ArcGIS for further analysis. A matrix of 100 × 100 m cells was overlaid with the survey data. For each year, every cell containing either an ash coded as "infested" or "dead infested" was classified as invaded while all other cells were classified as uninvaded. These data were then used to calculate the annual area of Longmont that was invaded for each year. We then regressed the square root of the annual invaded area from 2015 to 2022 vs. year and used the estimated slope as our estimate of the radial rate of range expansion (Gilbert and Liebhold 2010).

Results

Historical spread among municipalities

Following its initial discovery in Boulder, Colorado in 2013, reproducing EAB populations have been discovered in 14 other municipalities in the Front Range Urban Corridor (Fig. 1). In 2023, populations were also discovered in Carbondale, CO which is 179 km west-southwest of Boulder. Because Carbondale is not within the Front Range Urban Corridor, we excluded it from our analysis. Linear regression analysis of distance as a function of time yielded an estimate (regression slope) of the radial rate of spread of 3.92 km/yr (SE = 1.24) (Fig. 2a).

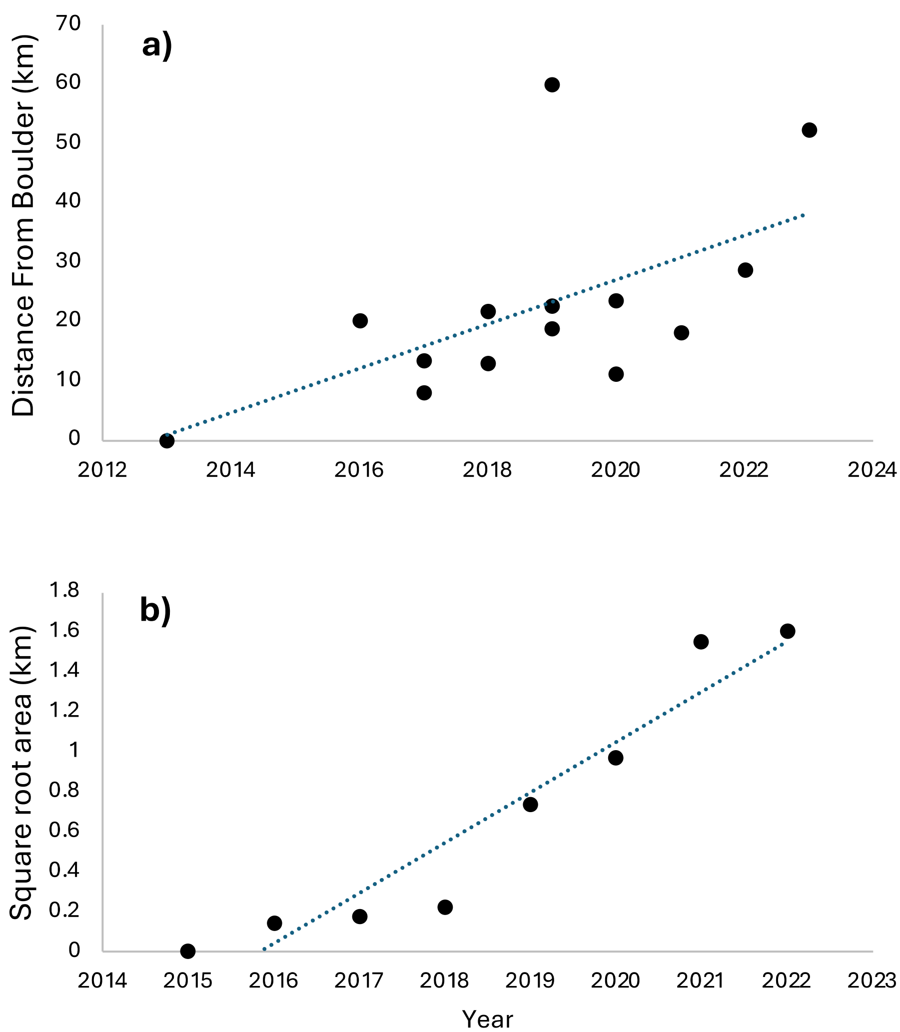

Fig. 2 Estimation of radial rate of spread from emerald ash borer discovery data (radial rate of spread estimated as slope of regression line); **a** linear regression of distance vs. time based on municipalities within the Front Range urban corridor; **b** linear regression of square root of invaded area vs. time based on 100 m cells within the City of Longmont, Colorado

To date, reproducing EAB populations have not been found in the city of Denver.

Historical spread within a municipality

The first discovery of EAB in the city of Longmont, CO was made in 2016 (Fig. 3). The discovery was based on the presence of a few infested trees in a residential area near the corner of 9th Ave. and Hover St. in the western portion of Longmont. Over subsequent years, most of the spread was into contiguous residential areas to the North though three satellite populations formed to the east, south and southwest. By 2022, EAB infested trees were found in 258 100 × 100 m cells reaching a cumulative area of 1.6 km^2. Regression of the square root area on time yielded an estimated radial rate of range expansion of 0.25 km/yr (SE = 0.031) (Fig. 2b).

Discussion

The rate of EAB spread among municipalities (3.92 km/yr) was over 10 times that of its

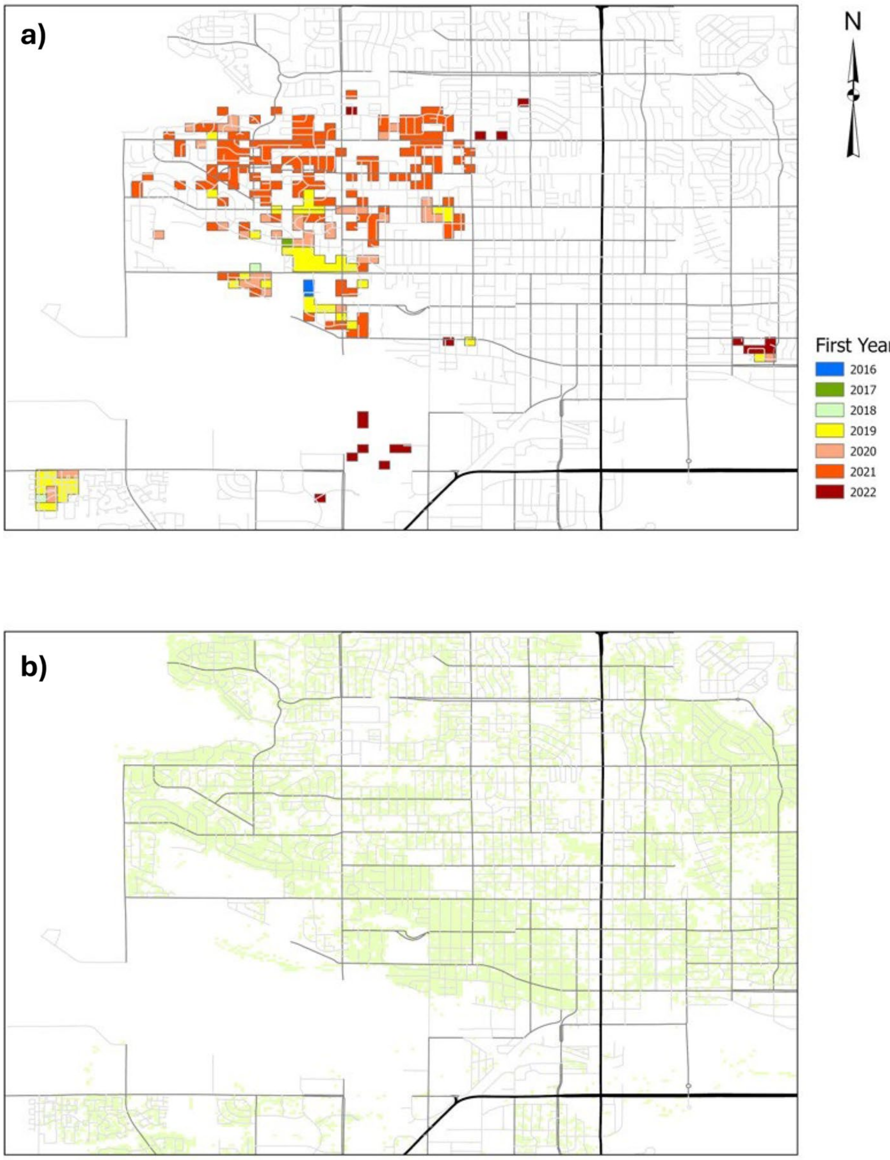

Fig. 3 Spread of emerald ash borer in Longmont, Colorado 2016–2022; **a** shaded areas are 100 × 100 m grid cells shaded to indicate the earliest date that EAB-infested trees were found within the cell; **b** distribution of urban canopy (from US Forest Service Tree Cover Dataset derived from the US National Geological Survey National Land Cover Database)

intra-municipality spread (0.25 km/yr). This inconsistency can be explained by the scales over which they were measured and the scale of at which different types of dispersal occur. Even higher spread rates ranging from 14 to 56 km/yr were recorded by Ward et al. (2020), who used county-level data to quantify EAB spread across a much larger area of the entire eastern USA. Previous studies with other non-native organisms have often found that spread rates in a given species may vary across spatial scales (Maack et al. 2007; Pyšek et al. 2008; Liebhold et al. 2020). The spread of many species is driven by a combination of both short-distance dispersal (resulting from natural movement) and long-distance dispersal (caused by anthropogenic movement of life stages) (Wilson et al. 2009). The result is some form of "fat-tailed" dispersal function that creates a pattern of spread in which long-distance dispersal results in colonization of satellite populations that grow and eventually coalesce with the continuously expanding invasion front (Shigesada et al. 1995; Kot et al. 1996). As a result, local spread rates are dominated by the influence of natural dispersal and is typically slower than spread across larger spatial scales that is dominated by human-aided dispersal.

Mercader et al. (2016) estimated spread rates of 1.2–1.7 km/yr and 0.4–0.7 km/yr in two forested portions of a 400 km^2 region (roughly the same spatial scale as our intra-municipality sampling). The slower spreading population had more recently established and they concluded, based on these and previous results, that initial spread of EAB is slow, but as more satellite populations are formed (through human-aided dispersal) that spread rates increase. The spread rate at their recently founded population was only slightly higher than the 0.25 km/yr spread rate that we observed in Longmont, Colorado. Presumably, the Longmont population was also relatively young, and its slow rate of spread may be explained in part by the fact that only a few satellite populations had formed (Fig. 3). Siegert et al. (2014) used dendrochronological techniques to reconstruct early spread of EAB from its initial epicenter in southeastern Michigan and they found that after a period of equilibration, spread proceeded across an area of roughly 100 × 100 km (comparable to our inter-municipality scale) at 13 km year. This is much faster than the 3.6 km/yr spread rate observed here in the Colorado Front range. Visual interpretation of Fig. 2b is suggestive of a sigmoidal (accelerating) pattern of spread with slower spread prior to 2017. Nevertheless, the linear portion of the graph (2017 onward) still indicates a much slower rate of spread than documented by Siegert et al. (2014).

In general, spread in the Front Range reported here is slightly slower than reported in the above studies from eastern North America. The reasons for this slower spread are not clearly identifiable but there are several possibilities. First, is that native ash is completely absent from the Front Range area. Aside from a small amount of invasive ash growing in riparian areas, ash is limited to horticultural plantings which comprise a highly fragmented resource for EAB (Figs. 1b, 3b). Habitat fragmentation is well-known to limit the spread of non-native species (With 2002; Kinezaki et al. 2003) and the lack of a continuous background matrix of wild ash in the Front Range means that the EAB habitat is more fragmented, especially at large spatial scales. Second, EAB populations in the Front Range have been managed relatively aggressively since it was first discovered there in 2013. In particular, a large fraction of residential and street trees has been treated with insecticides and there have been several releases of EAB parasitoids (Alexander et al. 2020; Morris et al. 2023); both empirical and theoretical studies indicate that both practices may contribute to decreasing EAB spread (McCullough 2020; Bushaj et al. 2021). Finally, environmental conditions in the Front Range are very different from Michigan and other regions of eastern North America; for example, xeric conditions may affect EAB population growth, either directly or indirectly through effects on host trees.

During the next 25 years, EAB is expected to establish in many western cities (Ward et al. 2020). Spread rates reported here may be of use in the timing and preparation of EAB management plans in those areas. It is possible that slower spread rates in western urban regions may create new opportunities for managing EAB that are not possible in portions of eastern North America where the rate of spread is faster.

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Data availability All data supporting the findings of this study are available within the paper.

Declarations

Conflict of interests The authors have no relevant financial or non-financial interests to disclose.

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