BUYING TIME: PRELIMINARY ASSESMENT OF THE POTENTIAL ROLE OF BIOCONTROL

IN THE RECOVERY OF NATIVE FOREST VEGETATION FOLLOWING THE INVASION OF

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by

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Abstract: Introduced forest pests have become one of the major threats to forest ecosystems in North America. Once the spread phase is underway, biological control is one of the few environmentally acceptable and sustainable practices available for the management of destructive invasive pests in natural ecosystems. Assessing the impact of a biocontrol program progresses from evaluating the establishment of biocontrol agents, to control of the target pest, to impacts on the affected organism, and ultimately, to the indirect impacts that biocontrol may have on the whole community. In our study, we assessed the recovery of forest vegetation following the mortality of overstory ash trees caused by the emerald ash borer (EAB) invasion and ongoing management of EAB using biological control. We collected data on the forest structure and composition of stands affected by this pest and where biocontrol agents were released or not (biocontrol and no-biocontrol plots). We then used a multilevel modeling framework to evaluate the potential indirect effects of a biocontrol agent on native tree seedling forest regeneration. We found that the impacts of biocontrol on ash saplings had community-level effects by protecting native seedlings from invasive and weedy saplings. Our results showed a higher number of ash saplings with increasing numbers of the dominant EAB biocontrol agent *T. planipennisi*, while the number of invasive and weedy saplings was negatively associated with number of ash saplings. Density of native seedlings was negatively associated with invasive and weedy saplings. As disturbance events produce gaps in the canopy, the protection of ash saplings by the biocontrol agent may help native recruitment during forest transition by supporting the growth of native hardwood seedlings over invasive and weedy saplings. We found that evaluating the efficacy of the ash biocontrol program will need to include varied ash size classes and the community dynamics of the co-occurring species.

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Introduction

Ash (*Fraxinus* spp.) trees grow in a variety of habitats contributing to the species diversity in key niches of North American forests (Gleason & Cronquist 1991). Ash trees also host a unique array of birds, mammals, and at least 98 species of invertebrates are closely associated or dependent on ash (Martin *et al.* 1951; Wagner & Todd 2016; Jennings *et al.* 2017). USDA Forest Service Forest Inventory and Analysis (FIA) data showed that in 2003, the United States timberlands had over 7.5 billion ash trees (Nowak *et al.* 2003). Ash were present in the Midwest and northeast on 32% of all forested land; of these 78% of these were on private property, 17% on state and local land, and 5% on federal land (Desantis *et al.* 2013). In 2008, there were an estimated 4.3 billion saplings between 2.5 – 12.6cm diameter at breast height (DBH) in the Midwest and northeast (Desantis *et al.* 2013). Ash is also a common ornamental species which has been widely planted in North American cities to replace the loss of elm in urban forests (Federal Register 2003). From FIA surveys in the 1980's until 2009, ash (>2.5cm DBH) volume increased 80% in the Great Lakes region, totaling ~427 million m^3 in 2008 (MacFarlane & Meyer 2005; Pugh *et al.* 2011; Desantis *et al.* 2013).

Michigan, our study region, had nearly 700 million ash trees that comprised 4.6% of the total forest basal area (Nowak *et al.* 2003). There are 16 species of ash (*Fraxinus* spp.) in North America, five of which can be found in Michigan (MacFarlane & Meyer 2005; Desantis *et al.* 2013; USDA NRCS 2017). The most common species is white ash (*F. americana*), which grows in mixed upland hardwood forests. Green ash (*F. pennsylvanica*) tolerates both mesic and hydric soils and has the largest distribution (Kennedy 1990; Gucker 2005). Blue ash (*F. quadrangulata*) occupies calcium-rich upland sites, while both black ash (*F. nigra*) and pumpkin ash (*F. profunda*) can be dominant in hydric soils (Kennedy 1990; Gleason & Cronquist 1991; Harlow *et al.* 1991; Gucker 2005; MacFarlane & Meyer 2005; Desantis *et al.* 2013; USDA NRCS 2017).

Currently, one of the major challenges facing North American forests are invasive forest pests (Lovett *et al.* 2016). In recent decades, the increase in new species introductions, mainly associated with an increase in global trade, have exacerbated the frequency and impact of invasive pest outbreaks (Niemeli & Mattson 1996; Work *et al.* 2005; Aukema *et al.* 2010). Outbreaks of forest pests can decimate forests and, in some instances, locally eliminated tree species (e.g., Busby & Canham 2011), or substantially change forest ecosystems (e.g., Chapin *et al.* 2000; Lovett *et al.* 2006; Moser *et al.* 2009; Kovacs *et al.* 2010; Morin *et al.* 2017). Gypsy moth (*Lymantria dispar)* and Asian longhorned beetle (*Anoplophora glabripennis)* are examples of generalist pests that attack an array of tree species, while pests such as chestnut blight (*Cryphonectria parasitica)*, hemlock woolly adelgid (*Adelgis tsugae*), Dutch elm disease (*Ophiostonza novo-ulmi*), and beech scale (*Cryptococcus fagisuga*) target specific tree species (Gavin & Peart 1993; Paillet 2002; Sharov *et al.* 2002; Smith *et al.* 2009; Dix *et al.* 2010; Potter *et al.* 2011). For instance, Dutch elm disease killed ~200 million elms (*Ulmus* spp.) in the 20th century, and currently reduces the lifespan of elm in forests, limiting its ascension into the forest canopy (Barnes 1976; Hubbes 1999; Kashian & Witter 2011). And, invasive insect pests like gypsy moth (*Lymantria dispar* (L.)) can weaken trees and make them more prone to secondary infections (Muzika *et al.* 2000; Davidson *et al.* 2001).

Healthy ash trees were occasionally infested by native species including clearwing borers (*Podoseria* spp.) and carpenter worms (*Prionoxystus* spp.), and stressed trees were colonized by cerambycids (*Neoclytus* spp.) and bark beetles (*Hylesinus aculeatus* (Say)) (Johnson & Lyons 1976; Langor & Hergert 1993; Burr & Mccullough 2014). However, in 2002, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) (emerald ash borer, EAB), a phloem-feeding beetle that attacks ash trees in Asia, was identified as the cause of ash tree mortality in southeast

Michigan and nearby Ontario (Haack *et al.* 2002; Cappaert *et al.* 2005; Herms & McCullough 2014). While Asian species of ash are relatively resistant to EAB (Liu et al. 2003; Williams, *et al.* 2005; Eyles *et al.* 2007; Rebek et al. 2008), most North American ash species show little resistance to this pest, and most overstory ash trees die within six years of initial detection (Anulewicz *et al.* 2008; Gandhi & Herms 2010; Kashian & Witter 2011; Knight *et al.* 2013; Klooster *et al.* 2014; Jennings *et al.* 2017; Spei & Kashian 2017).

Although EAB was first discovered near Detroit, Michigan in June 2002, dendrochronological reconstruction traces EAB back to 1997 in the city of Canton in southeastern Michigan (Siegert *et al.* 2014). Morin *et al.* (2017) show the rapid spread of EAB by county in Michigan and other eastern states. In response to EAB's discovery in Michigan, the Department of Agriculture imposed a state quarantine on July 16th, 2002, restricting the movement of ash nursery trees, logs, and other ash products from six southeast counties with known EAB infestations. Although a federal quarantine on ash materials was first imposed on October 14th, 2003 by USDA APHIS (Animal and Plant Health Inspection Service), and an EAB-eradication program was implemented, this destructive beetle continues to spread throughout the U.S. and Canada (Federal Register 2003; Morin *et al.* 2017). EAB is now known in 30 states, Washington D.C., and two Canadian provinces (USDA-APHIS-PPQ 2017).

EAB adults feed on ash foliage during the summer but the major damage is from the larvae feeding on the phloem (Haack *et al.* 2002, 2015; Cappaert *et al.* 2005; Smith 2006). Mating begins soon after emergence, and the females can lay up to 200 eggs (average ~70) on the bark of ash trees, initially attacking larger overstory trees with rough, textured bark (Cappaert *et al.* 2005; Wei *et al.* 2007; Anulewicz *et al.* 2008; Rutledge & Keena 2012, Poland *et al*. 2015). The newly hatched larvae burrow through the outer bark to feed on phloem and outer sapwood,

creating serpentine or elongate galleries. At high densities, the larval feeding results in girdling and death of the trees. By fall in southern Michigan, immature larvae overwinter in their galleries, often requiring a second year of larval development before reaching the adult stage, whereas mature larvae chew pupation chambers in the outer sapwood or bark, and begin emerging as adults in mid to late May (Cappaert *et al.* 2005; for review on EAB biology see Haack *et al.* 2015).

EAB dispersal in North America has been rapid because of human-assisted transport and the flight capabilities of EAB adults. Humans are the primary cause of long-range EAB spread due to the transport of EAB-infested nursery stock, firewood, lumber, and other wood products (Federal Register 2003; Prasad *et al.* 2010). Adult EAB females fly 0.8km on average in a day, with exceptional cases (<1%) traveling >4km (Taylor *et al.* 2004). The life history of EAB is similar to bronze birch borer (*A. anxius* Gory) (Herms *et al.* 2004), which can travel up to 10-20km per year (Federal Register 2003). Early-stage EAB infestation of ash trees can be hard to detect (McCullough & Roberts 2002; Cappaert et al. 2005), taking up to 10 years (Poland & McCullough 2006)**,** because of the low numbers of individuals and relatively small size and coloration of the adults (7.0-13mm long) (Siegert *et al.* 2014). Consequently, new EAB infestations are often discovered when people investigate the cause of dead or declining ash trees in an area. To monitor the spread of EAB for quarantine boundaries, regulatory agencies have developed, and continue to test various types of EAB-detection traps. However, these are relatively inefficient at detecting early EAB infestations, when population densities are low (McCullough *et al*. 2011, Poland 2011, Abell *et al.* 2015).

Land managers estimate EAB has killed hundreds of millions of ash trees in North America (Abell *et al*. 2016, Duan *et al*. 2017, Jennings *et al.* 2017). From 2004 to 2009, ash volume in

southeast Michigan decreased by nearly 75% (Pugh *et al.* 2011). Using forest inventory data from timberlands in the United States, the potential undiscounted cost of losing 7.5 billion ash trees (Nowak *et al.* 2003) to EAB in non-urban forests was estimated at more than $282 billion and $20-60 billion in the urban forests (Federal Register 2003), making EAB the most economically devastating insect pest in North American history (Herms & McCullough 2014).

When an introduced species becomes established and causes widespread economic or ecological damage, it is considered an invasive pest and eradication may be attempted (United Nations 1992; Sanderson *et al.* 2012). If efforts to eradicate are unsuccessful, biological control is often used to suppress pest population densities (Stiling & Cornelissen 2005). As EAB continued spreading in North America during the last decades, regulatory agencies transitioned from efforts to eradicate EAB to pest management (USDA-APHIS 2015). To date, EAB management in North America involves the use of systemic insecticides to protect high value trees in urban forests (Sadof *et al.* 2017) and biological control in forested ecosystems (USDA-APHIS/ARS/FS 2016).

Biological control is based on the "natural enemy release hypothesis" in which introduced species become pests due to separation from their co-evolved natural enemy complex (Keane & Crawley 2002; Mitchell & Power 2003; Duan *et al.* 2017). By introducing specialized natural enemies from a pest's native range to its invaded range, successful and self-sustaining pest control can be achieved (for reviews see Clausen 1978; Van den Bosch *et al.* 1982; Bauer *et al.* 2014, 2015). Assessing the impact of a biocontrol program progresses from evaluating natural enemies for establishment, to control of the target pest, to the impact on the affected organism, and ultimately, to the indirect impact that the biocontrol agent may have on the whole community (Denslow & Antonio 2005; Stiling & Cornelissen 2005; Lovett et al. 2006).

To improve ash tree survival in the forested ecosystems of North America, researchers have been developing a biological control program for EAB. Early research revealed a low diversity and prevalence of insect natural enemies compared to closely related native species in the genus *Agrilus* (for reviews see Taylor *et al.* 2012; Bauer *et al.* 2014). In Asia, insect natural enemy surveys resulted in the discovery of several specialized hymenopteran parasitoids that co-evolved with EAB and suppress its population densities below a threshold that allowed for the survival and reproduction of native and some exotic ash species (Liu *et al.* 2003, 2007; Duan *et al.* 2012b; Wang *et al.* 2016).

Parasitoids of EAB from Asia are the basis of a biocontrol program for management of EAB in North American forests. This program started in southern Michigan in 2007 after USDA APHIS issued environmental release permits for three EAB-parasitoid species from China: the egg parasitoid *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae), the larval endoparasitoid *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae), and the larval ectoparasitoid *Spathius agrili* Yang (Hymenoptera: Braconidae) (Federal Register 2007; Bauer *et al*. 2014). After the parasitoids were recovered from EAB sampled at Michigan field sites in 2008, the USDA EAB Biocontrol Program began, and APHIS began mass-rearing the parasitoids for release in ash stands infested with EAB. Release of *S. agrili* was later restricted to areas south of the 40th parallel due to lack of survival in northern states, and a similar EAB larval ectoparasitoid, *S. galinae* Belokobylskij & Strazanac (Hymenoptera: Braconidae) from the Russian Far East, was approved in 2015 for release north of the 40th parallel (Duan *et al.* 2014, Federal Register 2015; USDA-APHIS/ARS/FS 2016). To date, the establishment of both *T. planipennisi* and *O. agrili* have been confirmed in Michigan and several other states (Bauer *et al.* 2015). Ongoing biocontrol research of EAB in North America has focused primarily on

understanding parasitoid biology, host specificity, parasitoid interactions with its host and other parasitoids, development of parasitoid rearing, release and recovery methods, estimating stage-specific impacts of parasitoids and other mortality factors on EAB population dynamics, and impacts on ash survival (Duan et al. 2013b, 2014, 2015, 2017; Abell et al. 2012, 2014, 2015, 2016; Bauer et al. 2014, 2015; Davidson & Rieske 2016; Johnson et al. 2016; USDA-APHIS/ARS/FS 2016; Parisio et al. 2017).

Generally, mature, overstory ash trees died within five to six years of the first EAB invasion (Cappaert *et al.* 2005; Poland & McCullough 2006; Mercader *et al.* 2011; Knight *et al.* 2013; Burr & Mccullough 2014), which may make the remnant non-dominant ash an important transitional resource for forest recovery (Kashian 2016; Duan *et al.* 2017). In the aftermath forests of southern Michigan, where EAB biocontrol began, these enduring ash seedling, sapling, and basal sprouts have survived (Kashian 2016; Duan *et al.* 2017).

White ash, *F. americana*, is abundant in Michigan and many eastern North American forests (Schlesinger 1990; Kashian & Witter 2011). Ash seedlings tolerate very low light conditions and can survive with as little as 3% of full sunlight (Schlesinger 1990), which has allowed for the establishment of a robust seedling bank of up to 20,000 seedling per hectare prior to the EAB invasion (Kashian & Witter 2011). The loss of mature ash means that there are virtually no new ash seeds, thereby creating a remaining cohort of orphaned ash seedlings and saplings (Klooster et al. 2014). Kashian & Witter (2011) studied this orphan cohort of ash seedlings, which they believed would endure for a decade or more and could possibly grow into the canopy layer if EAB populations are kept low. The high mortality rates of the mature overstory ash caused by EAB is not paralleled among seedling and saplings that are less than 2.5cm DBH (Kashian & Witter 2011). Abell *et al.* (2012) found that *T. planipennisi* had higher

parasitism in thin-barked, small-diameter ash trees, which is likely correlated with its relatively short ovipositor (Duan & Oppel 2012). Thus, when these seedlings and saplings grow in response to the death of mature trees, they are temporally protected by this biocontrol agent (Duan *et al.* 2017).

The EAB invasion also affects the entire plant community, as canopy gaps, caused by death of overstory ash trees, trigger the succession process. Forest succession will then reflect the composition of the advance regeneration layer and of the seeds available for germination (Rejmanek 1989; Baraloto *et al.* 2005; González-Muñoz *et al.* 2014). In forest ecosystems, the majority of seeds originate locally (Muller-Landau *et al.* 2008; Zhao *et al.* 2016) and are correlated with the basal area of nearby trees (Greene & Johnson 2004), while some propagules come from the surrounding landscape *(*Jasper *et al.* 2008). If the surrounding areas are largely intact, native species will account for the majority of the seeds reaching a site (Lundgren et al. 2004; Mosher 2009). However, as the surrounding landscape becomes more human-altered, invasive propagules constitute a larger proportion of those seeds (With 2002; González-Moreno *et al.* 2014).

Besides propagule availability, the successful establishment of invasive plant species in a new location often depends on the higher level of resources, mainly light, associated with disturbances (With 2002; Huston 2004; Stachowicz & Tilman 2005). Moreover, disturbance is frequently necessary for invasive plant species to penetrate native ecosystems (With 2002; Lundgren *et al.* 2004; Pavlovic & Leicht-Young 2011; Simberloff *et al.* 2012), and it is often in disturbed habitats that invasive plants can outcompete native species (Von Holle *et al.* 2003; Hausman *et al.* 2010; Brym *et al.* 2014), altering natural ecosystem recovery (Hobbs & Huenneke 1992; Martin & Marks 2006; Brewer & Bailey 2014). In particular, Davis *et al.* (2017)

observed that forests with EAB damage were more susceptible to invasive plants than those that did not suffer that disturbance. And, early EAB quarantine efforts that cut mature ash trees, causing the creation of forest gaps and higher light levels, showed an increased in the likelihood of plant invasions (Hausman *et al.* 2010).

In our study, we investigated the impacts of recently introduced EAB biocontrol agents on ash sapling densities, and forest vegetation (both native and introduced), in the vicinity of the EAB-invasion epicenter in southeast Michigan, USA (Haack *et al.* 2002; Siegert *et al.* 2014; Poland & McCullough 2006). We collected and compiled data on the forest structure and composition of stands in this region, and analyzed the data as a function of biocontrol release levels. We hypothesized that if an abundant ash seedling bank exists, and it rapidly responds to the canopy opening (Schlesinger 1990), the resulting ash sapling layer, if protected from EAB, could then shade the stand and potentially curtail the success by invasive species (Fig. 1a). To test this hypothesis we studied the relationship between the release of biocontrol and native tree seedling populations, in particular, we investigated three dynamics: i) Does parasitoid release affect ash sapling density? ii) What is the relationship between ash saplings and invasive and weedy saplings? And, iii) Does invasive and weedy sapling density affect native seedling density? In this region, where >99% of overstory ash trees have died by 2009 (Klooster *et al.* 2014), we expected EAB biocontrol might slow the mortality of ash seedlings and saplings reducing then the rate of colonization by invasive and weedy saplings, thereby providing transitional time for other native and more shade tolerant species to establish and recruit (Fig. 1).

Methods

 Study sites: In 2014, we sampled forest composition at sites of varying distance from parasitoid release sites in southeastern Michigan, USA. A total of 21 vegetation sites were selected and surveyed (Fig. 2). The vegetation sites were classified as a release site if the parasitoids were released <1km away (Appendix 1). The 14 vegetation control sites were between 4.1km and 20.5km to the nearest parasitoid release site. The 7 vegetation release sites were chosen in 2014 at random from 22 parasitoid release locations within the counties of Ingham, Jackson, Livingston, Oakland, and Washtenaw (Mapbiocontrol 2017). The parasitoids were released in wooded plots >40 acres, >100m from a road, and would not be harvested or developed for at least five years after release, which prompted the selection of parks and recreation areas managed by the state, county, city or township (see Appendix 2 for plot information).

 Biocontrol releases: The EAB parasitoid release data was obtained at mapbiocontrol.org, a geospatial framework for biocontrol information (Mapbiocontrol 2017). At our seven biocontrol sites, there were 44 discrete release events with a sum of 14,065 individual releases that took place between 2007 and 2012 (Appendix 3). At the release plots, the relative proportions of *O. agrili*, *S. agrili,* and *T. planipennisi* was 19%, 13%, and 68%, respectively (Appendix 3). All 7 parasitoid-release plots received variable treatment for release (species released, numbers of parasitoids and years released). When the parasitoids were first released in 2007, there were still living canopy ash, however, as time went on the newer plots had far less live mature ash. At CRPK, LPRFLT, and SL-SLW parasitoids were released at peak EAB densities & ash canopy death occurred within a year or two, leaving gaps in which ash seedlings & saplings grew rapidly. At the other parasitoid-release plots, KS, DHMPK, PNKSL, WLPLK,

virtually all overstory ash trees had been killed by EAB at the time of release in 2011. While these sites were chosen for parasitoid release because of their large number of ash saplings, these vegetation plots were on average 361m from the parasitoid release sites in order to be centered around a dead gap tree. The release plots (SL-SLW and CRPK), each received two species, release numbers were very low, and parasitoid establishment has not been confirmed. Both *O. agrili* and *T. planipennisi* were confirmed to have established at LPFRLT, *T. planipennisi* was confirmed to have established at PNKSL, WLPLK, and the establishment of *S. agrili* has not been confirmed (Duan *et al.* 2013a; Abell *et al.* 2014; LSB unpublished data).

Vegetation sampling: To investigate the successional process at both the control and release vegetation sites, two 20x20m plots were set up at each site. CRPK was the exception, with only one vegetation plot. Plots were centered around a large dead standing tree, usually an ash tree. All living woody species >10cm DBH were classified as trees and identified to species level in the 400m² plot. We measured the DBH in cm of all the trees in the plot to calculate the plot's basal area. We established four 2x10m sapling transects, totaling 80m² per plot where saplings (>1m in height and <10cm DBH) were counted. We also set up four 1x10m groundcover and seedling transects, totaling 40m² per plot. Within each 1m², groundcover was quantified as percent cover. The groundcover plants were identified to species level when possible. The seedlings of woody plants (<1m tall) were counted and identified to species within the same groundcover transects. All plot measures were estimated per m^2 unit area, and plot-level averages and standard deviations were used in the analyses (Appendix 4).

Environmental and land cover data: We measured the light and moisture levels at each plot when vegetation was surveyed (Appendix 5). Light was measured every meter radiating along the cardinal axes from the central dead tree. This was repeated 3x, totaling 120 readings

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per plot. Photosynthetically active radiation (PAR) was measured using LightScout Quantum

Light 6 Sensor Bar and the LightScout Light Sensor Reader from Spectrum Technologies,

Plainfield, IL, USA. Soil moisture was measured every meter radiating along the cardinal axes

from the central dead tree, with a total of 40 moisture readings per plot. Volumetric water

content (VMC) was measured using Fieldscout-TDR 300 Soil Moisture Meter from Spectrum

Technologies, Plainfield, IL, USA. To determine the percent forested area surrounding each plot,

we used available land cover data from 2002, using ArcGIS 10.3 we estimated the percent of

forested land within 1km of the study sites and total land area was calculated by subtracting the

area covered by water from the total area (Michigan Geographic Data Library 2014; Appendix

5).

   Statistical analysis: To evaluate the relationship between native seedlings and the release of

parasitoids, we first carried out extensive exploratory data analysis and then developed a

multilevel, or hierarchical, model where estimates from a submodel were used as predictors in

subsequent models. First, parasitoid release information (number of released *T. planipennisi*, as

this is the most successful parasitoid establishing and spreading [Duan *et al.* 2013a, 2017]) was

used to analyze ash sapling density, then invasive and weedy sapling density was analyzed as a

function of the estimated ash sapling densities, and we finished by using estimates of invasive

and weedy sapling densities to analyze the native tree seedling data (Fig. 1b). This multilevel

approach allowed for the sharing of information across the data sets (Clark 2005), potentially

better informing the dynamics taking place in these plots. We describe below the model that was

best supported by the data (based on deviance information criterion, (DIC); (Spiegelhalter *et al.*

2002), and that addressed our research questions. We included some additional explanatory

variables (e.g., forest cover around the plots, basal area in the plots), but other variables (e.g., soil

moisture, light, total releases, distance to release) when included did not improve the fit of the model, and we opted to exclude them in our final analysis.

We first estimated the abundance of ash saplings, *AshSaplings*, as a function of the percent of forest cover (*Forest cover*) around the plots within a 1km radius. We used forest cover as a proxy for source of propagules determining the strength of the seedling bank growing into saplings. We also estimated ash sapling density as a function of the number of the *T. planipennisi* parasitoids released. Because these two variables were correlated, *r*: 0.66, we orthogonalized the number of released parasitoids with respect to forest cover, and used the residuals ($\varepsilon_{release}$) in the analysis. This approach allowed us to make a better assessment of the independent effect of the biocontrol treatment on ash sapling density once the strength of the source of propagules, the major driver of sapling density, was accounted for. The likelihood for the average density of ash saplings in plot *i*, was:

$$AshSaplings_i \sim Poisson(Ash_i)$$

and process model:

$$\ln(Ash_i) = \alpha_1 + \alpha_2 Forest\ cover_i + \alpha_3 \varepsilon_{release\ i}$$

The density of invasive and weedy saplings, *InvWeedyS,* was analyzed as a function of the estimated density of ash saplings (*Ash*), the main native competitor after disturbance. In addition, the percentage of forest cover within 1km of the vegetation plots was used here again as a proxy for sources of propagules (Chytrý *et al.* 2008; González-Moreno *et al.* 2013), but in this case assuming that areas with higher forest cover are likely to have fewer invasive and weedy saplings, likelihood:

$$InvWeedyS_i \sim Poisson(IW_i)$$

and process model:

$$\ln(IW_i) = \beta_1 + \beta_2 Ash_i + \beta_3 Forest\ cover_i$$

The average density of native woody seedlings, *NativeSeedlings$_i$*, was then analyzed as a function of the basal area of the stand (*BA*) to reflect local sources of seeds (Ilisson & Chen 2009), and the estimated density of invasive and weedy saplings (*IW*) that could be competing with the native vegetation, likelihood:

$$NativeSeedlings_i \sim Normal(Native_i, NSvar_i)$$

and process model:

$$Native_i = \gamma_1 + \gamma_2 BA_i + \alpha \gamma_3 IW_i$$

The variances associated with each plot, *NSvar$_i$*, were estimates from our data. Due to the multilevel structure of the model we followed a Bayesian approach in the estimation of the parameters (Gelman & Hill 2007). Parameters were estimated from non-informative distributions, α_*, β_*, $\gamma_* \sim Normal(0,10000)$. The model was run in OpenBugs (Thomas *et al.* 2006; see Appendix 6 for code), and three chains were run simultaneously to assess convergence. Parameters posterior means, variances and 95% credible intervals, were calculated after convergence, thinning every 100th iteration. Parameters associated with the covariates were considered statistically significant if the 95% credible interval (CI) around their means did not overlap with zero.

Results

In total, we surveyed 41 plots at 21 sites, which included 688 trees, 3,826 saplings, 19,583 seedlings, and 12,961 distinct recordings for groundcover (see Appendix 3 for detailed data of each plot). All parameter estimates from the analysis are reported in Table 1.

Results from the ash sapling submodel: Increase in percent forest cover around the plots was associated with a higher number of ash saplings (α_2 parameter was positive and statistically significant; Table 1). This variable has the strongest impact on ash sapling densities (Fig. 3). The number of released parasitoids was also statistically significant and positively associated with higher densities of ash saplings (α_3 parameter; Table 1, Fig. 3)

Results from the invasive and weedy sapling submodel: The abundance of invasive and weedy sapling was negatively associated with the increasing number of ash saplings, which had the strongest effect, and was positively associated with increasing forest cover around the plots (parameters β_2 and β_3 were statistically significant; Table 1, Fig. 3).

Results from the native seedlings submodel: Increases in plot basal area was significantly associated with a higher number of native seedlings (parameter γ_2; Table 1, Fig. 3) and had the largest effect. The density of invasive and weedy saplings was associated with a lower number of native seedlings, and the effect was statistically significant (parameter γ_3; Table1, Fig. 3).

Discussion

In this study, we carried out an analysis that linked EAB biocontrol with the recruitment dynamics taking place after EAB killed the canopy ash trees. Moreover, we assessed the delayed impact of biocontrol on the entire plant community. Our analyses showed a positive association between the release of one parasitoid species, *T. planipennisi*, and the density of ash saplings. We also documented negative associations between ash saplings, and invasive and weedy plant saplings, and between these invasive and weedy saplings and other species of native seedlings. Our results suggest that the biocontrol agents are protecting ash saplings, which are likely out-shading invasive and weedy saplings, and thus, buying time to more shade tolerant, slower growing native species to recruit into these sites. This illustrates a secondary positive community-level benefit of EAB biocontrol in these forests.

Do biocontrol agents affect ash sapling density?

Following the implementation of biocontrol as a management tool for invasive species, it may take several years before the impacts or recovery of the affected species can be realized (Duan *et al.* 2017). In the case of trees, which have a long life cycle, a comparatively long lag time is needed before impacts are known (Huenneke 1983). In our study system, the biocontrol program for EAB in North America is still in the early phases, and work continues on the foreign exploration for additional EAB biocontrol agents in Asia, rearing and releasing the approved parasitoids, assessing the establishment and spread of each introduced EAB parasitoid species in different regions and in different ash species and size classes, and assessing the effects of these parasitoids on EAB population dynamics and interactions with native natural enemies (for review see Bauer *et al.* 2015). More recently, at long-term biocontrol study sites in southern Michigan where EAB biocontrol agents were first released, researchers found that one species of

introduced parasitoid, *T. planipennisi*, is now the dominant natural enemy of EAB larvae in young ash trees and saplings, which are growing in large numbers in forest gaps after EAB decimated the overstory ash trees (Duan *et al.* 2013a, 2015, 2017).

Release of the EAB biocontrol agents began in 2007 at some of our biocontrol release plots, and over 14,000 parasitoids were released during a six-year period (Mapbiocontrol 2017; Appendix 2). While *S. agrili* (~13% of the released parasitoids) did not establish in Michigan, *O. agrili* and *T. planipennisi* did (Duan *et al.* 2012a, 2013b, 2015; Abell *et al.* 2014). Although parasitoid prevalence in some ash trees was as high as 35% for *O. agrili* and >90% for *T. planipennisi*, the mature ash trees still experienced high mortality (Duan *et al*. 2017). EAB was discovered in Livingston, Oakland, and Washtenaw counties in 2002, and in Ingham, Jackson counties between 2003 and 2004 (Morin *et al.* 2017). From first detection of EAB, it takes 5 to 6 years for the larvae to kill most overstory ash (Knight *et al.* 2013). In Michigan, parasitoids were first released in 2007 during peak EAB densities, and most ash died within one or two years after the parasitoids were released (LSB unpublished data). However, younger, thin-barked ash trees and saplings growing at these release sites seem to be protected by the dominant biocontrol agent *T. planipennisi*, a small parasitoid with a short ovipositor that parasitizes EAB larvae in ash trees <10cm DBH (Liu et al. 2003, 2007;Wang *et al.* 2007; Duan & Oppel 2012; Abell *et al.* 2012; Duan *et al.* 2017). Our results illustrate that this is likely the case in our study sites, as a higher density of ash saplings was associated with higher release numbers of *T. planipennisi* (Fig. 3).

This relationship was maintained after we controlled for the percent of forest cover around the plots, our proxy for the source of ash propagules that would subsequently grow into the seedling layer. And, as we sampled in areas with a canopy opening, we were able to document the seedling transition into a sapling layer in response to higher light levels. It would

have been at this stage that the biocontrol agent *T. planipennisi* became most effective in protecting ash, as saplings have relatively thin bark. Previous work in this system found biocontrol can reduce EAB infestation in saplings (2.5-8 cm DBH) by over 50% (Duan *et al.* 2017), ensuring a healthier sapling layer. To protect more mature ash in the U.S., researchers have studied and gained approval to introduce *S. galinae*, a larger parasitoid with a longer ovipositor, which may be useful in protecting ash trees as they reach larger size classes, with thicker bark (Abell *et al.* 2012; Belokobylskij *et al.* 2012; Duan *et al.* 2014; Federal Register 2015; USDA-APHIS-PPQ 2015). Moreover, ash can still reproduce at small sizes (8cm DBH) (Schlesinger 1990) and produce large number of seeds during mast years (Kashian 2016). This might ensure that under the influence of biocontrol agents, ash populations will not entirely disappear because of EAB.

What is the relationship between ash saplings and invasive and weedy saplings?

The study sites were surrounded by agricultural, developed and other forested areas. Therefore, the likelihood of invasive plant species rapidly colonizing an area after a disturbance was relatively high. Still, one woody species that can rapidly take over after an opening in the forest canopy is *F. americana*, white ash. White ash seedling densities have been observed as high as 20,000 per hectare (Kashian & Witter 2011), and post-EAB basal sprouts are a significant source of ash regeneration in *F. pennsylvanica*, green ash (Kashian 2016). Thus, even if adult trees succumb to the EAB, Klooster et al. (2014) observed a >99% mortality rate of overstory ash in Michigan, seedlings can rapidly grow into the sapling layer and, if protected by biocontrol, shade the ground vegetation. Our results revealed that this could be the case at our study sites, where

we found a negative association between ash saplings and the abundance of invasive and weedy saplings, unveiling a potential beneficial effect of biocontrol on the entire community.

Unexpectedly, we also documented a positive association of forest cover around the study sites and the incidence of invasive and weedy saplings. We had hypothesized that higher forest percent cover around our sites, which ranged between 25-90%, would be linked to a decrease in invasive species propagules. Invasive plant species are not common in forest interiors (Yates *et al.* 2004; Flory & Clay 2009; Mosher *et al.* 2009). However, our results illustrate an opposite trend emphasizing the importance of assessing the risk of plant invasion not only at the site, habitat characteristics level, but also within the context of the historical landscape (Vilà & Ibáñez 2011). In our study area, forests have been under considerable human influence for almost two centuries, which has led to them being highly fragmented and having a large edge to area ratio (Dickmann & Leefers 2003), creating conditions where invasive and weedy species thrive (Vilà & Ibáñez 2011). Consequently, the availability of propagules from introduced species is likely to be widespread in the region.

Does invasive and weedy sapling density affect native seedling density?
One of the indirect effects a pest outbreak may have is the creation of optimal conditions for the establishment of harmful species. The low light conditions characteristic of closed canopy forests and the lack of propagules are thought to buffer mature native forests from invasive plants (Hutchinson & Vankat 1997; Ohlemüller *et al.* 2006; Mosher *et al.* 2009; Pavlovic & Leicht-Young 2011). It is mostly after disturbance events that invasive species are able to establish populations large enough to negatively affect the native community (Lookwood *et al.* 2007; Pavlovic & Leicht-Young 2011; Ruckli *et al.* 2014). Our study showed this trend, as we reported

a negative association between invasive and weedy saplings, and native seedlings. This is due to some of the traits that prevail among invasive and weedy species (i.e., fast growing rates when resources are plentiful) which confer greater competitive ability to these species over natives in disturbed forest areas where light is not limiting (Levine *et al.* 2003; Richards *et al.* 2006; Blumenthal & Hufbauer 2007; Closset-Kopp *et al.* 2011). Numerous studies have documented the strong competition between native and exotic plants (see review by Levine *et al.* 2003). As invasive seedlings outgrow native seedlings, they are able to control the resources which may help them dominate future forest composition (Blumenthal & Hufbauer 2007).

The understory vegetation response to disturbance mostly follows the direct regeneration hypothesis (DRH), which posits that tree communities will regenerate from existing seedlings to pre-disturbance levels within decades (Yih *et al.* 1991). The resiliency of the DRH is based on the regeneration capacity of trees which is proportional to basal area (Ilisson & Chen 2009). Our analysis supports this hypothesis, we found a very strong effect of adult trees basal area on the density of seedlings from woody species (Fig. 3). However, under highly modified contemporary landscapes the availability of propagules from introduced harmful species increases with the level of development and roads around remnant vegetation patches (Vilà & Ibáñez 2011). Thus, a site with a high basal area may still be threatened by the establishment of invasive plant species taking over after a disturbance event.

This study provides a linkage between vegetative community assessment and an invasive insect biocontrol program. We found that biocontrol protection on ash saplings could have secondary effects that protect native seedling recovery from invasive and weedy saplings. Our results indicate that after a disturbance event, biocontrol efforts can facilitate forest recovery by buying time for the native community to recruit while reducing the threat of invasive and weedy

species. We found that the efficacy of the EAB biocontrol program could not be solely evaluated using the effect it had on parasitism levels or protecting mature ash trees, but should also include other ash size classes and the community dynamics of the adjacent species.

Table 2. Posterior means and 95% credible intervals (CI) for all the parameters included in the analysis. Coefficients associated with the explanatory variables that were statistically significant (95%CI did not include zero) are shown in bold.

Parameter		Mean±SD	95% CI	
Ash saplings submodel:				
α_1	intercept	-0.382±0.002	-0.385	-0.377
α_2	forest cover	**0.406±0.003**	**0.398**	**0.412**
α_3	number of parasitoids released	**0.001736±0.0000019**	**0.001734**	**-0.001737**
Invasive and weedy sapling submodel:				
β_1	intercept	0.8999±0.00015	0.8996	0.9002
β_2	ash saplings	**-1.506±0.005**	**-1.512**	**-1.492**
β_3	forest cover	**0.2737±0.0015**	**0.2715**	**0.2753**
Native seedlings submodel:				
γ_1	intercept	1.97±0.19	-2.31	-1.64
γ_2	basal area	**3830±3.62**	**3822**	**3835**
γ_3	invasive and weedy saplings	**-4.95±0.05**	**-5.04**	**-4.86**

Figure 1. a) Visual representation of the forest transition with and without biocontrol. This graphic outlines the hypothesis that as gaps are created from the loss of mature ash trees, EAB biocontrol agents, mainly *T. planipennisi* an introduced EAB natural enemy, can protect ash saplings, buying time for native seedlings to grow and fill gaps (left pathway). Without the influence of the EAB biocontrol program, ash do not survive long enough to allow the native community to recruit, resulting in invasive and weedy saplings taking over (right pathway). b) Graphical representation of analysis testing the hypothesis, with positive and negative signs indicating our original expectations.

Figure 2. Map of Michigan showing the location of our 21 vegetative study sites. Insert shows the five Michigan counties where the release and control vegetation plots were located (colored dots in the map). The star indicates the location of Canton, MI, the EAB-invasion epicenter in North America (Siegert *et al.* 2014).

Figure 3. Posterior parameter means (+95%CI) of each of the parameters included in the analyses. Parameters have been standardized (i.e., multiplied by the covariate mean) to assess their influence. Coefficients that were statistically significant (95%CI did not overlap with zero) are indicated by an asterisk. Note: symbols are larger than the 95% CIs.

Figure 1.

Figure 2.

25
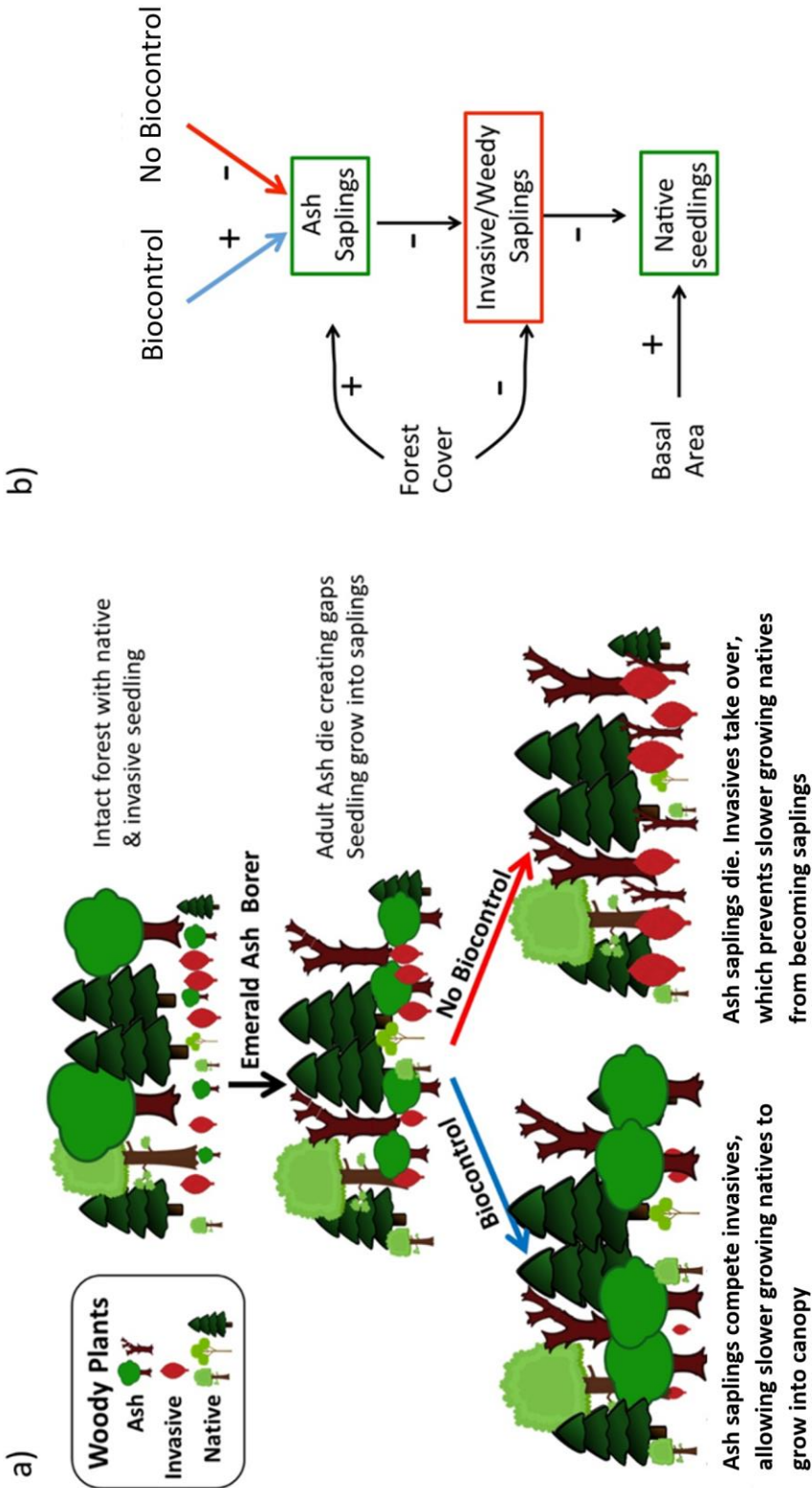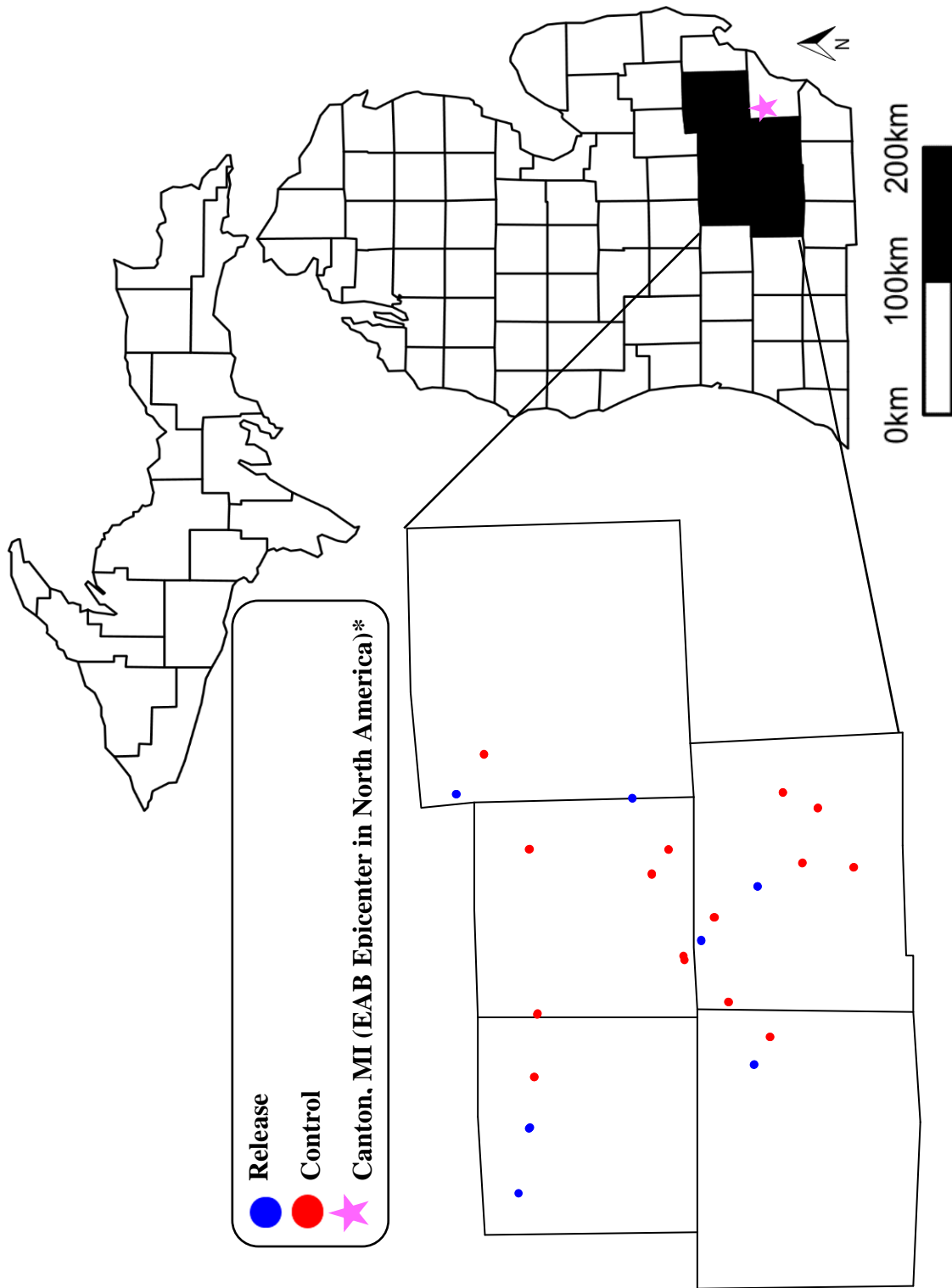
Figure 3.
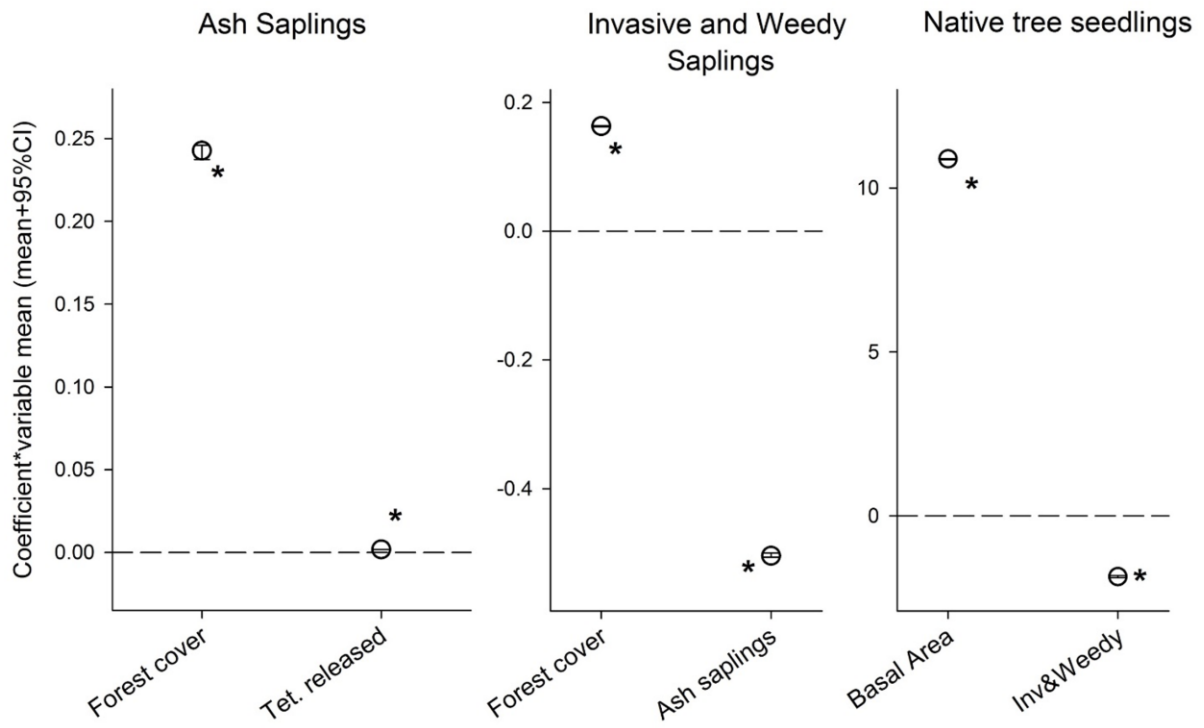
Appendix 1: Parasitoid release information for each study plot: plot name; distance from a biocontrol release site; if defined as a parasitoid-release plot or control plot; total number of female parasitoids released (*O. agrili, S. agrili, T. planipennisi*); and, total number of female *T. planipennisi* released. Note: Because *T. planipennisi*, the dominant EAB-biocontrol agent established in this region, was not released at or near plot SL-SLW, these plots were considered non-release control plots for the final analysis.

Plot name	Distance from Release Site (m)	Release within 1km (1=yes release plot, 0=control plot)	Total biocontrol insects released	Total female *T. planipennisi* released
BRIa	10821	0	0	0
BRIb	11006	0	0	0
CALa	8082	0	0	0
CALb	8008	0	0	0
CRPK	564	1	573	300*
DHMPKa	46	1	3084	2534**
DHMPKb	69	1	3084	2534**
GEOa	5429	0	0	0
GEOb	5058	0	0	0
GREa	11865	0	0	0
GREb	11787	0	0	0
HURa	7403	0	0	0
HURb	7355	0	0	0
KSa	444	1	1994	1447***
KSb	403	1	1994	1447***
LPRFLTa	13	1	4410	3454****
LPRFLTb	222	1	4410	3454****
PNKSLa	936	1	1400	713**
PNKSLb	809	1	1400	713**
RADa	17086	0	0	0

RADb	17101	0	0	0
REDa	20140	0	0	0
REDb	19944	0	0	0
RIZa	16357	0	0	0
RIZb	16253	0	0	0
RODa	17654	0	0	0
RODb	17555	0	0	0
SCAa	17452	0	0	0
SCAb	17560	0	0	0
SCIa	8987	0	0	0
SCIb	9085	0	0	0
SL, SLWa	281	0	812	0
SL, SLWb	205	0	812	0
STIa	1884	0	0	0
STIb	2025	0	0	0
WATa	5482	0	0	0
WATb	5517	0	0	0
WILa	9027	0	0	0
WILb	9012	0	0	0
WLPLKa	110	1	1792	1074**
WLPLKb	199	1	1792	1074**

*   *T. planipennisi* released in 2009
**   *T. planipennisi* released in 2011
***   *T. planipennisi* released in 2009 and 2010
**** *T. planipennisi* released in 2008 and 2009

Appendix 2: Information on vegetation study sites: name of plots (lower case letter, a and b, indicate replicate plots), forest name, land manager, and plot latitude and longitude.

Plot name	Forest Name	Land Manager	Latitude	Longitude
BRIa	Brighton State Recreation Area	Michigan Department of Natural Resources	42.501287	-83.832168

BRIb	Brighton State Recreation Area	Michigan Department of Natural Resources	42.501145	-83.834423
CALa	Calla Burr Memorial Plant Preserve	Michigan Nature Association	42.772765	-83.577278
CALb	Calla Burr Memorial Plant Preserve	Michigan Nature Association	42.772793	-83.578355
CRPK	Ralph W. Crego Park	Lansing Parks and Recreation	42.716870	-84.514143
DHMPKa	Dexter Huron Metropark	Huron-Clinton Metroparks	42.330148	-83.859518
DHMPKb	Dexter Huron Metropark	Huron-Clinton Metroparks	42.329730	-83.859760
GEOa	George Reserve	University of Michigan	42.448313	-84.016475
GEOb	George Reserve	University of Michigan	42.449970	-84.007905
GREa	Waterloo State Recreation Area	Michigan Department of Natural Resources	42.377523	-84.105953
GREb	Waterloo State Recreation Area	Michigan Department of Natural Resources	42.376417	-84.106348
HURa	Huron Meadows	Huron-Clinton Metroparks	42.473927	-83.781120
HURb	Huron Meadows	Huron-Clinton Metroparks	42.474168	-83.780630
KSa	Kensington Metropark	Huron-Clinton Metroparks	42.532887	-83.671127
KSb	Kensington Metropark	Huron-Clinton Metroparks	42.532480	-83.671987
LPRFLTa	Harris Nature Center	Meridian Township Parks and Recreation	42.699945	-84.375873
LPRFLTb	Harris Nature Center	Meridian Township Parks and Recreation	42.698285	-84.373737
PNKSLa	Pinckney State Recreation Area	Michigan Department of Natural Resources	42.421137	-83.976012
PNKSLb	Pinckney State Recreation Area	Michigan Department of Natural Resources	42.421230	-83.973828
RADa	Radrick Natural Area	University of Michigan	42.288885	-83.659352
RADb	Radrick Natural Area	University of Michigan	42.289145	-83.659073
REDa	Red Cedar River	Private Property	42.685967	-84.130560
REDb	Red Cedar River	Private Property	42.686712	-84.132885
RIZa	Rizor Memorial Nature Sanctuary	Michigan Nature Association	42.698717	-83.780013
RIZb	Rizor Memorial Nature Sanctuary	Michigan Nature Association	42.700138	-83.780542
RODa	Joan Rodman Memorial Plant Preserve	Michigan Nature Association	42.173980	-83.818548
RODb	Joan Rodman Memorial Plant Preserve	Michigan Nature Association	42.174818	-83.818992
SCAa	Scarlett Mitchell Nature Area	Ann Arbor Parks and Recreation	42.232692	-83.692945
SCAb	Scarlett Mitchell Nature Area	Ann Arbor Parks and Recreation	42.232205	-83.691803
SCIa	Scio Woods Preserve	Washtenaw County Parks and Recreation	42.257720	-83.810115
SCIb	Scio Woods Preserve	Washtenaw County Parks and Recreation	42.257133	-83.809045
SL-SLWa	Seven Lakes State Park	Michigan Department of Natural Resources	42.817112	-83.662805
SL-SLWb	Seven Lakes State Park	Michigan Department of Natural Resources	42.818143	-83.662807
STIa	Stinchfield Woods	University of Michigan	42.399235	-83.925522
STIb	Stinchfield Woods	University of Michigan	42.400750	-83.925562

WATa	Waterloo State Recreation Area	Michigan Department of Natural Resources	42.310217	-84.180520
WATb	Waterloo State Recreation Area	Michigan Department of Natural Resources	42.309372	-84.180700
WILa	Williamston Floodplain Plant Preserve	Michigan Nature Association	42.690963	-84.266045
WILb	Williamston Floodplain Plant Preserve	Michigan Nature Association	42.691817	-84.266113
WLPLKa	Waterloo State Recreation Area	Michigan Department of Natural Resources	42.335235	-84.239290
WLPLKb	Waterloo State Recreation Area	Michigan Department of Natural Resources	42.335987	-84.240015

Appendix 3: Parasitoid release numbers for the biocontrol release sites as posted on Mapbiocontrol.org, the EAB biocontrol database. The parasitoid release information is sorted by site, date, species, and the total numbers and percentages released by species.

	Site name	Date	*O. agrili*	*S. agrili*	*T. planipennisi*
1	CRPK	14-Aug-08	118	0	0
2	CRPK	23-Sep-09	0	0	300
3	CRPK	10-Jun-12	155	0	0
4	DHMPK	3-Jun-11	0	0	450
5	DHMPK	10-Jun-11	0	0	900
6	DHMPK	23-Jun-11	0	0	1083
7	DHMPK	28-Jun-11	260	50	50
8	DHMPK	11-Jul-11	140	100	51
9	KS	4-Sep-09	0	0	150
10	KS	9-Sep-09	0	0	225
11	KS	23-Jul-10	260	287	1072
12	LPRFLT	23-Jul-08	100	0	0
13	LPRFLT	10-Aug-08	100	0	0
14	LPRFLT	14-Aug-08	0	56	0
15	LPRFLT	12-Sep-08	0	0	80
16	LPRFLT	20-Sep-08	0	0	28
17	LPRFLT	27-Sep-08	0	0	35
18	LPRFLT	30-Sep-08	0	0	20
19	LPRFLT	4-Oct-08	0	0	40
20	LPRFLT	28-May-09	0	0	80
21	LPRFLT	2-Jun-09	0	0	420
22	LPRFLT	12-Jun-09	0	0	200
23	LPRFLT	15-Jun-09	0	0	200
24	LPRFLT	24-Jun-09	300	0	0
25	LPRFLT	3-Jul-09	0	0	600
26	LPRFLT	10-Jul-09	0	0	500
27	LPRFLT	17-Jul-09	0	0	700
28	LPRFLT	21-Jul-09	0	200	0
29	LPRFLT	4-Aug-09	0	0	200
30	LPRFLT	7-Aug-09	0	0	151
31	LPRFLT	21-Aug-09	0	200	0
32	LPRFLT	10-Sep-09	0	0	200
33	PNKSL	8-Jul-11	67	100	113
34	PNKSL	16-Jul-11	200	0	600
35	PNKSL	16-Aug-11	30	290	0
36	SL	22-Aug-07	0	93	0
37	SL	28-Aug-07	0	33	0
38	SL	14-Sep-07	0	45	0
39	SL	21-Jun-12	321	0	0

40	SLW	21-Jun-12	320	0	0
41	WLPLK	16-Jun-11	0	0	353
42	WLPLK	8-Jul-11	53	95	121
43	WLPLK	16-Jul-11	200	0	600
44	WLPLK	16-Aug-11	70	300	0
	Parasitoids released		**2694**	**1849**	**9522**
	Percent of total release		**19%**	**13%**	**68%**

Appendix 4: Vegetation information at each study plot for native seedlings, basal area of trees, ash saplings, invasive and weedy groundcover, and invasive and weedy saplings. All measurements are in m² and include means and standard deviation (±SD).

Plot name	Native Seedlings	Basal Area	Ash Saplings	Invasive & Weedy Groundcover	Invasive & Weedy Saplings
BRIa	8.87 ± 0.09	0.0033 ± 0.0001	0.6875 ± 0.0119	0.0225 ± 0.0010	0.1125 ± 0.0137
BRIb	1.57 ± 0.03	0.0044 ± 0.0002	0.5250 ± 0.0089	0.1298 ± 0.0017	0.1375 ± 0.0098
CALa	6.22 ± 0.04	0.0039 ± 0.0004	0.1000 ± 0.0047	0.0905 ± 0.0014	0.0000 ± 0.0001
CALb	5.40 ± 0.03	0.0019 ± 0.0001	0.3250 ± 0.0035	0.0003 ± 0.0001	0.0000 ± 0.0001
CRPK	4.17 ± 0.57	0.0013 ± 0.0001	0.0625 ± 0.0001	0.4005 ± 0.0030	1.2125 ± 0.0157
DHMPKa	9.22 ± 0.23	0.0025 ± 0.0002	3.2250 ± 0.0246	0.0273 ± 0.0005	0.0250 ± 0.0001
DHMPKb	1.17 ± 0.20	0.0041 ± 0.0004	1.3375 ± 0.0143	0.0573 ± 0.0030	0.0125 ± 0.0001
GEOa	18.0 ± 0.20	0.0012 ± 0.0001	0.1125 ± 0.0001	0.1093 ± 0.0023	0.2500 ± 0.0236
GEOb	37.55 ± 0.12	0.0037 ± 0.0002	0.0375 ± 0.0001	0.1458 ± 0.0017	0.1500 ± 0.0053
GREa	1.40 ± 0.10	0.0023 ± 0.0001	0.3875 ± 0.0111	0.1678 ± 0.0016	0.4750 ± 0.0157
GREb	0.70 ± 0.15	0.0030 ± 0.0002	0.1000 ± 0.0001	0.3460 ± 0.0031	1.8375 ± 0.0229
HURa	11.92 ± 0.11	0.0018 ± 0.0001	0.0500 ± 0.0001	0.7428 ± 0.0030	1.4875 ± 0.0173
HURb	18.90 ± 0.07	0.0037 ± 0.0003	0.0500 ± 0.0001	0.7990 ± 0.0039	1.9125 ± 0.0187
KSa	4.70 ± 0.08	0.0010 ± 0.0002	0.0750 ± 0.0001	0.8033 ± 0.0029	1.0500 ± 0.0127
KSb	10.15 ± 0.07	0.0015 ± 0.0001	0.1375 ± 0.0040	0.3413 ± 0.0022	0.5500 ± 0.0250
LPRFLTa	0.00 ± 0.0001	0.0041 ± 0.0003	0.5750 ± 0.0097	0.2530 ± 0.0021	0.2625 ± 0.0118
LPRFLTb	5.80 ± 0.08	0.0038 ± 0.0002	0.7625 ± 0.0118	0.0883 ± 0.0020	0.2375 ± 0.0135
PNKSLa	10.85 ± 0.06	0.0012 ± 0.0001	0.0000 ± 0.0001	0.1783 ± 0.0021	0.6750 ± 0.0283
PNKSLb	2.45 ± 0.07	0.0020 ± 0.0005	0.3375 ± 0.0042	0.1788 ± 0.0040	0.1125 ± 0.0094
RADa	5.20 ± 0.05	0.0016 ± 0.0001	0.0250 ± 0.0001	0.0450 ± 0.0022	0.0000 ± 0.0001
RADb	3.75 ± 0.07	0.0050 ± 0.0003	0.0625 ± 0.0001	0.1008 ± 0.0024	0.0875 ± 0.0191
REDa	5.70 ± 0.05	0.0035 ± 0.0001	0.9875 ± 0.0161	0.1260 ± 0.0014	0.0375 ± 0.0088
REDb	3.15 ± 0.04	0.0055 ± 0.0003	0.2000 ± 0.0032	0.2860 ± 0.0019	0.1250 ± 0.0298
RIZa	15.20 ± 0.04	0.0018 ± 0.0002	0.0125 ± 0.0001	0.0675 ± 0.0007	0.0000 ± 0.0001
RIZb	5.07 ± 0.04	0.0026 ± 0.0001	0.0250 ± 0.0001	0.1025 ± 0.0028	0.1125 ± 0.0068
RODa	14.12 ± 0.04	0.0022 ± 0.0002	0.0000 ± 0.0001	0.0200 ± 0.0009	0.0000 ± 0.0001
RODb	11.62 ± 0.03	0.0013 ± 0.0001	0.0000 ± 0.0001	0.0913 ± 0.0012	0.0000 ± 0.0001
SCAa	7.45 ± 0.03	0.0021 ± 0.0001	0.5750 ± 0.0123	0.1053 ± 0.0015	0.0250 ± 0.0001
SCAb	3.05 ± 0.03	0.0046 ± 0.0005	0.9500 ± 0.0096	0.2125 ± 0.0020	1.5250 ± 0.0206
SCIa	6.90 ± 0.04	0.0017 ± 0.0000	0.0500 ± 0.0072	0.2363 ± 0.0019	0.0750 ± 0.0001
SCIb	15.97 ± 0.04	0.0023 ± 0.0002	0.4625 ± 0.0163	0.0698 ± 0.0012	0.0000 ± 0.0001
SL-SLWa	3.00 ± 0.02	0.0009 ± 0.0002	0.4625 ± 0.0130	0.5310 ± 0.0034	0.5750 ± 0.0196
SL-SLWb	3.55 ± 0.02	0.0042 ± 0.0002	0.4125 ± 0.0107	0.1128 ± 0.0021	0.0250 ± 0.0001
STIa	2.72 ± 0.02	0.0031 ± 0.0002	0.0000 ± 0.0001	0.2648 ± 0.0022	0.0000 ± 0.0001

STIb	2.07 ± 0.03	0.0032 ± 0.0002	0.0625 ± 0.0001	0.0155 ± 0.0018	0.0000 ± 0.0001
WATa	3.40 ± 0.02	0.0029 ± 0.0001	0.0875 ± 0.0068	0.1993 ± 0.0026	0.6500 ± 0.0138
WATb	5.40 ± 0.03	0.0036 ± 0.0002	0.1250 ± 0.0058	0.0818 ± 0.0017	0.4375 ± 0.0131
WILa	6.25 ± 0.02	0.0009 ± 0.0000	0.2375 ± 0.0113	0.2028 ± 0.0016	0.5625 ± 0.0148
WILb	45.27 ± 0.01	0.0055 ± 0.0004	0.0625 ± 0.0144	0.1213 ± 0.0019	0.2375 ± 0.0125
WLPLKa	4.72 ± 0.06	0.0038 ± 0.0006	0.0250 ± 0.0001	0.0215 ± 0.0010	0.0125 ± 0.0001
WLPLKb	3.55 ± 0.06	0.0034 ± 0.0001	0.0250 ± 0.0001	0.1120 ± 0.0031	0.3750 ± 0.0149

Appendix 5: Invasive and weedy species. Plants were characterized as weedy species if they are native do not typically grow in closed canopy forests, but rather in more open, higher-light environments. Plants were characterized as invasive if they are not native to North America.

Scientific Name	Weedy	Invasive
Acer negundo	*	
Acer sachharinum	*	
Ailanthus altissima		*
Alliaria petiolata		*
Ampelopsis brevipedunculata		*
Berberis thunbergii		*
Celastrus orbiculatus		*
Chenopodium album	*	
Convolvulus arvensis	*	
Elaeagnus umbellata		*
Euonymus alatus		*
Frangula alnus		*
Leonurus cardiaca		*
Ligustrum vulgare		*
Lonicera maackii		*
Lonicera tatarica		*
Oxalis spp.	*	
Parthenocissus quinquefolia	*	
Phytolacca americana	*	
Plantago spp.		*

Species	Column 1	Column 2
Polygonum spp.	*	
Rhamnus cathartica		*
Rhus glabra	*	
Robinia pseudoacacia	*	
Rosa multiflora		*
Rosa spp.		*
Rubus spp.	*	
Sambucus spp.	*	
Smilax spp.	*	
Solanum spp.	*	
Solidago spp.	*	
Taraxacum officinale		*
Toxicodendron radicans	*	
Urtica spp.	*	
Vicia spp.	*	
Vinca minor		*
Vitis riparia	*	
Vitis spp.	*	

Appendix 6: Soil moisture (volumetric, %, means±SD), light (photosynthetic active radiation (PAR), means±SD), and forest cover percentage around the plot (1km radius) for each study site.

Plot name	Soil moisture	Light	Forest cover
BRIa	8.4 ± 3.3	27.4 ± 15	79%
BRIb	4.8 ± 1.8	7.6 ± 9.3	75%
CALa	16.7 ± 5.7	41.3 ± 27.5	60%
CALb	16.4 ± 3.0	86.1 ± 141.8	61%
CRPK	31.5 ± 4.9	110.5 ± 180.9	52%
DHMPKa	23.8 ± 5.1	63.3 ± 40.2	50%
DHMPKb	20.5 ± 6.6	68.6 ± 189.7	50%
GEOa	24.6 ± 5.3	177.0 ± 162.3	79%
GEOb	14.1 ± 3.2	90.1 ± 190.5	85%
GREa	16.3 ± 4.1	165.5 ± 255.7	60%
GREb	9.9 ± 2.9	20.8 ± 8.0	63%
HURa	11.7 ± 3.1	163.3 ± 146.4	72%
HURb	22.6 ± 4.1	64.1 ± 30.1	72%
KSa	37.0 ± 6.0	547.9 ± 231.5	70%
KSb	34.0 ± 5.0	131.8 ± 89.8	68%
LPRFLTa	32.0 ± 5.9	31.6 ± 11.2	55%
LPRFLTb	24.1 ± 6.3	47.0 ± 31.9	52%
PNKSLa	19.7 ± 5.1	105.8 ± 158.3	87%
PNKSLb	16.7 ± 5.3	109.2 ± 122.6	84%
RADa	10.9 ± 3.8	70.6 ± 92.4	61%
RADb	10.3 ± 3.4	12.5 ± 8.3	61%
REDa	25.5 ± 4.1	80.5 ± 88.6	32%
REDb	23.5 ± 5.7	7.7 ± 7.1	32%
RIZa	11.5 ± 2.9	89.3 ± 130.6	53%
RIZb	14.6 ± 4.8	31.4 ± 23.9	54%

RODa	33.7 ± 6.3	30.6 ± 17.6	33%
RODb	25.3 ± 6.1	25.7 ± 17.4	32%
SCAa	23.3 ± 6.2	28.6 ± 10.1	26%
SCAb	34.8 ± 3.4	24.1 ± 44.4	25%
SCIa	25.0 ± 5.5	149.0 ± 250.7	45%
SCIb	22.5 ± 4.9	18.8 ± 3.9	44%
SL-SLWa	9.5 ± 3.6	184.2 ± 141.6	56%
SL-SLWb	12.5 ± 6.8	45.5 ± 23.6	51%
STIa	27.7 ± 6.0	19.1 ± 10.8	90%
STIb	27.9 ± 2.8	21.0 ± 10.8	93%
WATa	25.4 ± 12.2	25.8 ± 34.7	78%
WATb	20.0 ± 8.9	78.5 ± 83.0	77%
WILa	16.7 ± 4.7	89.8 ± 42.7	36%
WILb	9.7 ± 2.9	55.0 ± 80.8	34%
WLPLKa	14.8 ± 5.0	86.6 ± 298.9	80%
WLPLKb	15.8 ± 4.5	28.8 ± 17.6	77%

Appendix 7: Model Code for OpenBugs 3.2.3.

```
model{
for(i in 1:41){
#estimating precisions from SD
        All_slingtau[i]<-pow(All_sling_sd[i],-2)
        FRtau[i]<-pow(FR_Sapling_sd[i],-2)
        SIWtau[i]<-pow(ScoverIW_sd[i],-2)
#adding variability around the basal area estimates
        batau[i]<-pow(ba_sd[i],-2)
        baS[i]~dnorm(ba[i],batau[i])
#likelihood for Fraxinus saplings
        FR_Sapling[i]~dpois(FRM[i]) #likelihood
        FRM[i]<-alpha[1]+alpha[2]*forest[i]+alpha[3]*Tresiduals[i] #process model
#likelihood for IW saplings
        IW_saplings[i]~dpois(IW[i]) #likelihood
        IW[i]<-beta[1]+beta[2]*FRM[i]+beta[3]*forest[i] #process model
#likelihood for all seedlings
        All_slingNoIW[i]~dnorm(AS[i],All_slingtau[i]) #likelihood
        AS[i]<-gamma[1]+gamma[2]*baS[i]+gamma[3]*IW[i] #process model
}
#priors
for(i in 1:3){alpha[i]~dnorm(0,0.0001)}
for(i in 1:3){beta[i]~dnorm(0,0.0001)}
for(i in 1:3){gamma[i]~dnorm(0,0.0001)}
}
```

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