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Natural enemies implicated in the regulation of an invasive pest: a life table analysis of the population dynamics of the emerald ash borer

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Abstract

1 The emerald ash borer *Agrilus planipennis* Fairmaire is a serious invasive forest pest of ash (*Fraxinus*) trees in North America. Life tables were constructed for both experimentally established cohorts and wild populations of *A. planipennis* on healthy host trees from 2008 to 2011 in six forests in central Michigan.

2 Life table analysis showed that the net population growth rates (R_0) for the experimental cohorts (16.0 ± 2.9) and associated wild *A. planipennis* (19.4 ± 1.9) were the highest for the first study period (2008–2009) at three Ingham Co. sites but decreased to 4.7 ± 0.9 and 4.6 ± 0.4, respectively, for the second (2009–2010) study period at the same sites. By contrast, R_0 values of both experimental cohorts (5.7 ± 2.2) and associated wild *A. planipennis* populations (11.3 ± 2.5) were intermediate in the third (2010–2011) study period at different sites in the Gratiot and Shiawassee Cos.

3 The sudden decrease in R_0 of both experimental and wild *A. planipennis* cohorts in the Ingham Co. sites corresponded with increases in parasitism by hymenopteran parasitoids *Atanycolus* spp. (native) and *Tetrastichus planipennisi* Yang (introduced), as well as an increase in woodpecker predation, indicating the role of these natural enemies in regulation of the pest's population dynamics.

Keywords Biological control, invasive, life table, net population growth rate, wood borers.

Introduction

Understanding the dynamics of insect pests and the role of various biotic factors in suppressing their population growth is critical to the development of sound pest management strategies. Life tables are widely used to study the dynamics of insect pest populations, as well as to determine the effectiveness of different biotic and abiotic factors in regulating their population dynamics (Varley *et al.*, 1973; Southwood & Henderson, 2000). By monitoring a cohort or population throughout its entire life cycle in its natural environment and recording the survivorship and/or specific mortalities at each stage (or age) group, one can construct stage-specific life tables for an insect pest and determine the role of different biotic factors in suppressing the pest population growth (Hassell, 1985; Parker, 2000). This type of life table study is particularly useful when implementing biological control programmes against invasive species, which often require critical information on impacts of particular biological control agents on target pest populations (Nielsen *et al.*, 2008; Duan *et al.*, 2010; Jennings *et al.*, 2013).

The emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) is a serious invasive forest pest that has killed tens of millions of ash (*Fraxinus*) trees in North America subsequent to its discovery in 2002 in Michigan, U.S.A., and Ontario, Canada (Cappaert *et al.*, 2005; Poland & McCullough, 2006; Kovacs *et al.*, 2010; Herms & McCullough, 2014). In most of the infested areas, emerald ash borer adults emerge from late spring to early summer (May to June) and feed on ash foliage for at least 1 week before mating and laying eggs in crevices and under bark flakes on limbs and trunks of ash trees in mid to late summer (June to August). After eclosion from the eggs, first-instar larvae chew through the bark to reach the phloem, where they feed and develop for one or two growing seasons (Cappaert *et al.*, 2005; Duan *et al.*, 2010).

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Mature fourth-instar larvae chew pupation chambers in the outer sapwood or bark in late summer or autumn and fold their bodies into a J-shaped larva, the stage in which they overwinter in an obligatory diapause (J. J. Duan, unpublished data). These J-shaped larvae are mature fourth-instars (the last larval stage), termed 'J-larvae' by Duan *et al.* (2010) but called prepupae in Chamorro *et al.* (2012). After winter, J-larvae (JLs) develop to prepupae and pupae in spring and summer, and to adults approximately 1 month later (Cappaert *et al.*, 2005; Wang *et al.*, 2010). The adults feed on ash foliage; however, tree mortality is caused by larval feeding in the phloem and cambial region of the main trunk, disrupting the transport of nutrients and water in the tree (Cappaert *et al.*, 2005; Poland & McCullough, 2006; McCullough *et al.*, 2009; Wang *et al.*, 2010).

In both its native and invaded ranges, *A. planipennis* requires one or two growing seasons to complete its life cycle, depending on climate, timing of oviposition, host tree species and health of the host tree (Liu *et al.*, 2003, 2007; Cappaert *et al.*, 2005; Wei *et al.*, 2007; Rebek *et al.*, 2008; Duan *et al.*, 2010, 2012a). In Michigan, the North American invasion epicentre for this buprestid, a majority of *A. planipennis* require two growing seasons to complete their life cycle (Cappaert *et al.*, 2005; Duan *et al.*, 2010; Siegert *et al.*, 2010; Tluczek *et al.*, 2011, Herms & McCullough, 2014). This long and variable life cycle, along with the cryptic nature of immature stages, poses challenges to the construction of life tables for wild populations of *A. planipennis*. By artificially infesting relatively healthy ash tree trunks with caged adults or laboratory-reared eggs, Duan *et al.* (2010) and Jennings *et al.* (2013) established experimental cohorts of *A. planipennis* larvae on ash trees and subsequently recorded the fate of each larva by debarking the infested tree trunks. Because each *A. planipennis* larval stage creates a feeding gallery of a distinct width under the bark and evidence of larval mortalities are often preserved inside the feeding gallery, larval stages and associated mortalities can be estimated. When the mortality and fecundity of adults and other difficult-to-measure parameters (e.g. egg mortality) are estimated separately, data collected from such experimental cohorts can be used to construct stage-specific life tables for analysis of the impact of different biotic factors on *A. planipennis* population dynamics.

In the present study, experimental cohorts were established by caging gravid adult *A. planipennis* on the trunks of healthy green ash trees (*Fraxinus pennsylvanica*). Survivorship or mortality of those larvae was observed along with the fates of naturally occurring (wild) *A. planipennis* larvae in the same trees. The biotic mortality factors observed in the present study included predation, parasitism, putative host-tree resistance, disease and intraspecific competition. The study was conducted in six forested areas of central Michigan, where one species of egg parasitoid [*Oobius agrili* Zhang and Huang (Hymen.: Encyrtidae)] and two species of larval parasitoid [*Tetrastichus planipennisi* Yang (Hymen.: Eulophidae) and *Spathius agrili* Yang (Hymen.: Braconidae)] were released as part of a biological control programme against *A. planipennis* (Bauer *et al.*, 2008; Duan *et al.*, 2010, 2012a, 2013). Using separate estimates of adult fecundity and egg mortality, we constructed life tables of both experimentally established cohorts and wild *A. planipennis* populations and compared the net population growth rates across different study sites in three study periods from 2008 to 2011.

Materials and methods

Study sites

The study was conducted at six forested sites in three southern Michigan counties: Ingham, Gratiot and Shiawassee. The latitude and longitude for each of the sites are described in Duan *et al.* (2010, 2013). Three study sites, located in Ingham Co., consist of adjacent Meridian Township parks (i) Central and Nancy Moore Parks (CP) and (ii) Legg and Harris Nature Center Parks (LP), as well as one county park (iii) William M. Burchfield Park (BF). CP and LP were approximately 5 km from each other and 32 km from BF. These three Ingham county sites were used to establish two consecutive experimental cohorts of *A. planipennis* in the early summers of 2008 and 2009, respectively. Three additional study sites, located on Michigan Department of Natural Resources lands, were used to establish a cohort of *A. planipennis* larvae in the early summer of 2010. Two of these additional sites were in Gratiot Co. and located approximately 10 km apart: (iv) Gratiot-Saginaw State Game Area (GSW) and (v) Maple River State Game Area (MRE). The remaining site was located in Shiawassee Co.: (vi) Rose Lake State Wildlife Area (RL), which was approximately 60 km from MRE, 50 km from GSW, 47 km from BF and 15 km from CP.

Each study site consisted of two forested plots (each > 10 ha), separated from each other by 1–6 km, and randomly assigned as either a parasitoid-release treatment plot or a nonrelease control plot. All study sites were early to intermediate successional stage, secondary-growth northern deciduous forests, initially dominated by green ash (*F. pennsylvanica* Marsh.). Less abundant tree species included white ash (*Fraxinus americana* L.), black ash (*Fraxinus nigra* Marsh.), maple (*Acer*), oak (*Quercus*), cherry (*Prunus*), poplar (*Populus*), black walnut (*Juglans nigra* L.), basswood (*Tilia americana* L.) and some pine (*Pinus*). Although there were notable differences in tree species composition, abundance, basal area and diameter at breast height (DBH, approximately 1.5 m above the ground) among the six study sites, these characteristics were similar between the parasitoid-release and control plots within a site. At the time the studies were initiated, symptoms of *A. planipennis* infestation (reduced canopy, woodpecker attack and epicormic growth) were observed in all study sites, particularly on mature canopy ash trees (2008 for Ingham Co. sites and 2010 for Gratiot and Shiawassee Co. sites).

Selection of trees for establishment of A. planipennis *cohorts*

Within each study plot, 5–10 healthy green ash trees (*F. pennsylvanica*) with no apparent symptoms of *A. planipennis* infestation (e.g. bark splits, adult-exit holes, epicormic growth, woodpecker feeding) were selected for cohort establishment, marked with flagging and aluminum tree tags, and their DBH measured. There were no significant differences in mean DBH of selected ash trees between parasitoid release plots (mean $\pm$ SE: 14.4 ± 0.81 cm for 2008, 11.6 ± 0.88 cm for 2009 and 12.90 ± 0.69 cm for 2010) and control plots (mean $\pm$ SE: 13.5 ± 0.84 cm for 2008, 13.6 ± 0.78 cm for 2009 and 13.6 ± 0.67 cm for 2010) in each of the three study years ($F = 0.6541$, d.f. $= 1, 23$, $P = 0.4263$ for 2008; $F = 1.86$, d.f. $= 1, 48$, $P = 0.0726$ for 2009; $F = 0.6549$,

d.f. = 1, 48, $P = 0.4254$ for 2010). The ash trees selected within each plot were separated by at least 3–10 m.

Establishment of A. planipennis *cohorts*

Using the method described in Duan *et al.* (2010), we established two consecutive cohorts of *A. planipennis* in the three Ingham Co. (BF, CP and LP) sites: one in the early summer (21 June–25 July) of 2008 and the other at the same time in 2009. Using the same method, we established an additional cohort of *A. planipennis* in the Gratiot (GWS and MRE) and Shiawassee (RL) Co. sites in the early summer (17 June–27 July) of 2010. Briefly, we placed gravid emerald ash borer females and males in cages fixed to the trunks of the selected ash trees. Adult *A. planipennis* used in the study were collected from heavily infested, urban ash trees from mid-June to mid-July in each year in East Lansing, Michigan, and fed fresh green ash (*F. pennsylvanica*) foliage in ventilated plastic 200-mL cups for approximately 1 week before use. Cages consisted of a ventilated rectangular plastic container (length 10 cm, width 7 cm, depth 4 cm) secured onto the trunk with rubber bands, with the cage opening facing the trunk. Weather stripping (width 1.5 cm, thickness 0.5 cm) was used to fill gaps between the edge of the open face of the container and the trunk surface. Cages were placed at heights ranging from 0.5 to 2.0 m above ground, with a total of four or five cages per tree. One male adult and one gravid female adult *A. planipennis* were placed in each cage and provided with a cluster of field-collected green ash foliage secured in a water-filled vial. Caged females oviposited into natural bark crevices or bark slits artificially created with a utility knife on smooth-barked trees. All *A. planipennis* adults were removed after 7–10 days, and the location of each cage was marked with weather-resistant liquid Wite-Out® (Mmix; Bic USA Inc., Shelton, Connecticut) for future reference. Foliage in each cage was not replaced during the 7–10 days caging period. All cages were removed 1 month after the beetles were removed. The number of eggs (l_0) at the start of the generation for our experimental cohorts for each site was estimated using the total number (n) of the cohort larvae observed and the egg mortality rate ($r \approx 0.30$) determined from the survey of naturally occurring eggs at those sites (Duan *et al.*, 2010, 2011): $l_0 = n/(1 - r)$.

Biological control agents released

Three introduced parasitoids (*O. agrili*, *S. agrili* and *T. planipennisi*) were released in the six study sites before or during initiation of the study. Detailed information on the number of wasps of each species released and exact time of releases are reported in Duan *et al.* (2010, 2011, 2013). Briefly, adults of each parasitoid species were released in the three Ingham Co. sites in 2008 and 2009, with approximately 100 females of each species (plus 30–40 males for *T. planipennisi* and *S. agrili*) released in 2008, and approximately 3000 females (plus 1000–2000 males) of *T. planipennisi* and 200 females and 100 males of *S. agrili* in 2009; similar numbers of parasitoids were released in the Gratiot and Shiawassee Co. sites in 2010. The parasitoid adults were released onto the lower 2 m of trunk of 4–10 ash trees distributed within 100–300 m from the centre of the release plot at each study site (Duan *et al.*, 2013).

Previous studies conducted at these sites (Duan *et al.*, 2010, 2011, 2012b, 2013) and preliminary data analyses indicated that parasitism rates were not significantly different between parasitoid release and control plots. This was either a result of the initial low established parasitoid populations in the release plots (Duan *et al.*, 2010, 2012a) or dispersal of the liberated parasitoids (such as *T. planipennisi*) to the adjacent control plots (Duan *et al.*, 2010, 2013). Additionally, the paired parasitoid release and no-release control plots at each of our study sites had similar characteristics in forest tree species composition, ash tree species, DBH and stage of *A. planipennis* infestation. In the present study, therefore, we did not focus on the comparison of *A. planipennis* population growth rates between parasitoid release and control treatments. Instead, we focused first on quantifying the relative contribution of different biotic factors including the established biological control agents (primarily *T. planipennisi*) to the apparent (stage specific) mortality of experimental and wild *A. planipennis* cohorts. We then used this information to construct stage-specific life tables for both experimental cohorts and wild populations of *A. planipennis* across the different study sites, and then compared the net population growth rate of the experimental cohorts and wild populations for each study period across different study sites.

Determining the fate of A. planipennis *cohorts*

The experimental cohorts were allowed to develop for two growing seasons before being sampled because *A. planipennis* typically requires 2 years to complete its life cycle in Michigan (Duan *et al.*, 2010). The trees containing *A. planipennis* cohorts at the Ingham Co. sites in the early summer of 2008 and 2009 were debarked in the autumn (29 September to 8 October) of 2009 and 2010, respectively. Cohort trees established for the Gratiot and Shiawassee Cos. sites in the early summer of 2010 were sampled in the autumn (18–25 October) of 2011, except for one parasitoid release plot (at MRE) where cohort trees were sampled in early spring (22–25 April) of 2012 as a result of flooding the previous autumn. Except for more woodpecker predation over the winter months, this delay in sampling likely had negligible effects on populations of *A. planipennis* and associated larval parasitoids as a result of the cold temperatures.

To determine the fate of each *A. planipennis* experimental cohort, a draw knife was used to debark each cohort tree from the ground to a height of 2.5 m. The experimental cohorts were distinguished from wild populations of *A. planipennis* based on the point of origin of each gallery. However, in approximately 20% of cases, the experimental cohorts were obscured by overlapping galleries from wild *A. planipennis* populations. We recorded data on the life stage and fate of *A. planipennisi* from both the experimental cohorts and the wild populations. Larval instar was determined based on gallery width: < 2 mm wide for L1–L2, 2–3 mm wide for L3, and > 3–4 mm for L4. The fate of each *A. planipennis* larva was assigned to one of six categories: (i) complete development (D-shaped adult emergence hole); (ii) living immature stage; (iii) killed by putative host tree defence (often encapsulated by callous tissue); (iv) died

of undetermined disease; (v) woodpecker predation (missing or partially consumed, with bark and/or sapwood damage by woodpecker feeding) (Lindell *et al.*, 2008) or (vi) parasitized (eggs, larvae, pupae, cocoons and/or pharate adults of parasitoids present).

Because parasitism was not always evident in the field, the live *A. planipennis* larvae were removed from their feeding galleries or pupation chambers using soft forceps, placed into culture plates and reared in the laboratory for 8–12 weeks to observe developing parasitoids. Parasitoid adults that emerged during laboratory rearing were identified to species (*T. planipennisi*, *Balcha indica* Mani & Kaul) or genus (*Atanycolus* spp.). Host larvae damaged in the field during tree sampling or during laboratory rearing were dissected under a stereomicroscope to look for parasitoid remains, which were identified to species for the two endoparasitoids: *T. planipennisi* (gregarious) and *Phagonophora sulcata* Westwood (solitary). Parasitism by the ectoparasitoid *Spathius* spp., however, was based on the presence of gregarious parasitoid larvae or cocoons in a gallery as a result of a lack of adult emergence in the laboratory.

Statistical analysis

Life tables were constructed by applying the general methods and column definitions described in Southwood and Henderson (2000): l_x = the number of live *A. planipennis* entering each stage; d_x = the number of *A. planipennis* dying in each stage or d_i = number of *A. planipennis* in each stage dying as a result of a specific mortality factor (i); q_x = apparent mortality (for each life stage); q_i = apparent mortality at each life stage as a result of a specific factor (i) and q = real mortality. Net reproductive rate or population growth (R_0) was calculated as the ratio of the number of individuals in a cohort at the start of generation to the number at the beginning of the previous generation.

The number of live *A. planipennis* entering each stage was estimated based on reverse calculation of the different stages of individuals observed at the sampling time. For example, the number of individuals entering the L1–L2 stage was calculated as the total number of L1–L2 individuals in the sample plus individuals (dead or alive) from all other stages (L3 to adult). Because samples were taken approximately 1.5 years after cohort creation, L1–L2 individuals of the experimental cohorts found were dead. For wild *A. planipennis* stages, however, the number of live L1–L2 and L3 individuals observed at the time of sampling (m_x) were excluded from such calculations because these young larvae were part of the current year generation (Duan *et al.*, 2010) and thus not fully exposed to parasitism and predation. We used these early life stages of wild *A. planipennis* to estimate the number of dead L1–L2 and L3 individuals that might have originated from the current year generation (d_{1x}). To adjust the number of individuals entering those earlier stages from the previous year generation of wild *A. planipennis* populations (i.e. equivalent to the generation of associated experimental cohorts), we assumed that the observed apparent mortality rate (Q_x) for L1–L2 and L3 individuals was constant for the previous year generation and the current year generation, and could be estimated as the ratio of the total number of the dead individuals observed for that stage (D_x) over the total number of the individuals (L_x) observed entering that stage (including m_x): $Q_x = D_x/L_x$. The number of individuals entering L1–L3 stages for the previous year generation (l_x) was thus estimated as $l_x = L_x - (m_x + d_{1x})$, where $d_{1x} = m_x \times Q_x$.

Because of the large variation in sample sizes (i.e. the number of larvae established in each cohort group) among different trees in each site, we pooled the experimental cohorts or the wild *A. planipennis* from different cohort trees at the same site as a sampling unit for data analysis. Life tables for both experimental cohorts and associated wild *A. planipennis* were constructed separately for each of the three study periods at each of the six study sites. Likelihood ratio chi-squared tests were used to compare development stage distributions of the experimental cohorts with the associated wild populations for each study period among different study sites. Apparent mortality (d_x/l_x) for both experimental cohorts and associated wild populations for each study period was compared across different study sites with the same chi-squared test procedure (SAS Institute Inc., 2012). An analysis of covariance (ANCOVA) with site and cohort type as covariates was carried out to detect the effect of the study time on R_0 of both experimental cohort and wild *A. planipennis* for the first two consecutive study periods in the Ingham co. sites. Separate ANCOVA with site as a covariate for each of the three study periods were also conducted to detect differences in the net reproductive growth rate (R_0) between experimental cohorts and wild *A. planipennis*.

Because of the destructive nature of our sampling, we were unable to generate our own field data for adult sex ratio and fecundity, and we used the sex ratio of 1 : 1 and a mean of 103 eggs per gravid female as reported by Wang *et al.* (2010) for these parameters in our life tables. In addition, woodpecker predation rate of both the experimental cohorts and wild larvae was not fully measured by our autumn sampling scheme. Duan *et al.* (2010) observed the number of late-instar *A. planipennis* larvae (L4 and JL) preyed upon by woodpeckers in both the autumn and the subsequent spring. Based on those observations, we estimated that woodpecker predation during the winter season (from the autumn to the spring) would result in an additional 29% mortality of overwintering late-instar larvae, and thus applied this additional mortality (from woodpecker predation) to both experimental cohorts and wild *A. planipennis* populations in life table constructions. In addition, we also applied 5% mortality to adult stages mainly as a result of pathogens (J. J. Duan, unpublished data).

Results

Life stages and survival rates of A. planipennis *cohorts*

After two growing seasons (approximately 1.5 years), all live experimental cohort individuals were either L4, JL or had emerged as adults (Fig. 1A,C,E). By contrast, wild *A. planipennis* in the cohort trees consisted of all larval stages (L1–L2, L3, L4, and JL), with a few emerged adults (Fig. 1B,D,F). The beetle life-stage distributions (relative abundance) between the experimental cohorts and associated wild *A. planipennis* stages were significantly different for all three study periods (for 2008–2009: likelihood ratio $\chi^2 = 164.42$, d.f. = 4, $P < 0.0001$; for 2009–2010: likelihood

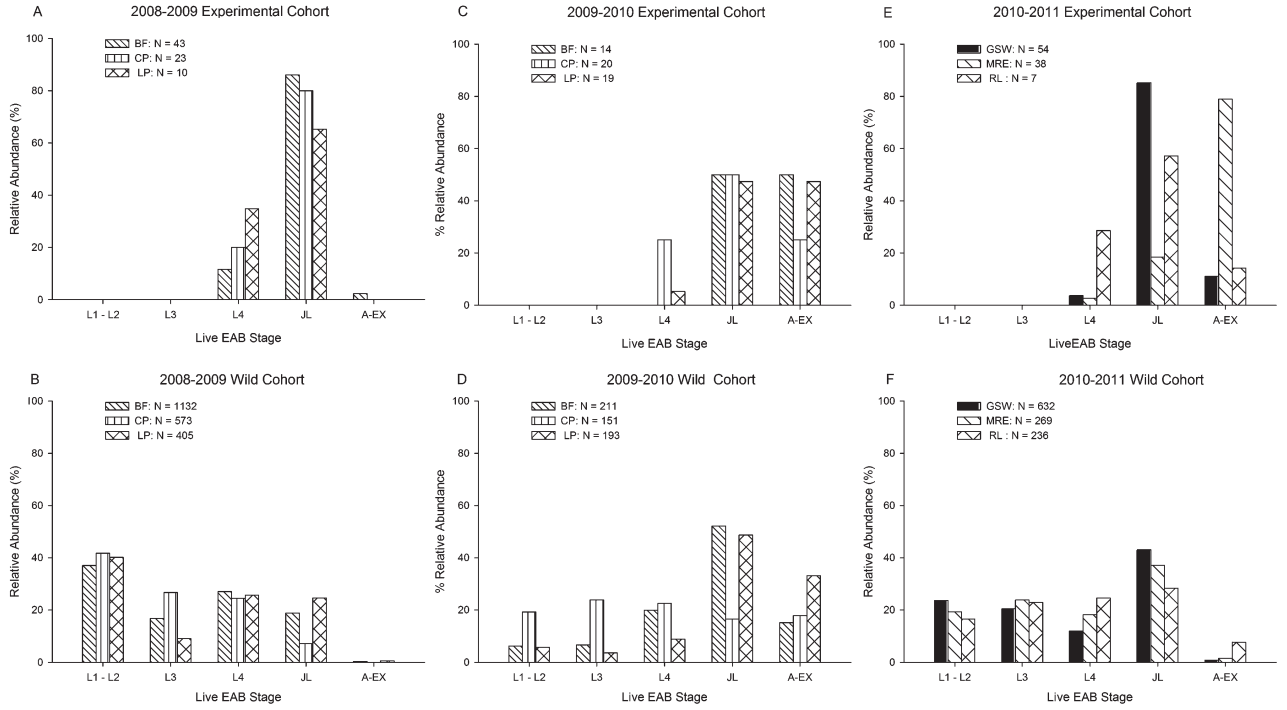

Figure 1 (A–F) Distribution of life stages of the experimental cohorts and associated wild *Agrilus planipennis* populations recovered from the sampling zone of cohort trees each year at the different study sites. Life stages of *A. planipennis*: L1–L4, first- to fourth-instar larvae; JL, J-larvae (mature fourth-instar larvae in pupation chambers); A-Ex, D-shaped emergence holes from emerged adults. EAB, emerald ash borer. For study site abbreviations, see Table 1.

ratio $\chi^2 = 26.980$, d.f. = 4, $P < 0.0001$; for 2010–2011: likelihood ratio $\chi^2 = 202.64$, d.f. = 4, $P < 0.0001$). Across all study sites, the experimental cohorts contained higher proportions of live L4 to adult stages and no L1–L2 and L3 individuals compared with the wild *A. planipennis* populations. For both experimental cohorts and associated wild *A. planipennis*, there were also significant differences in the life-stage distribution pattern among different study sites (likelihood ratio $\chi^2 = 84.71$, d.f. = 12, $P < 0.0001$ for experimental cohorts; likelihood ratio $\chi^2 = 212.46$, d.f. = 12, $P < 0.0001$ for wild cohorts) and among different study periods (experimental cohorts: likelihood ratio $\chi^2 = 37.82$, d.f. = 2, $P < 0.0001$; wild cohorts: likelihood ratio $\chi^2 = 542.55$, d.f. = 2, $P < 0.0001$). Data from these observations strongly indicated that a majority of *A. planipennis* required more than 1 year to complete one generation, although there were variations among different sites and years of study. Late-instar larvae (L4 individuals and JLs) observed in the autumn sampling originated from the previous year's generation and overlapped with early instars (L1 to L3 individuals) that originated from the current year's generation.

Survivorship of experimental *A. planipennis* cohorts ranged from 57% to 82% for the first study period (2008–2009) in the Ingham Co. sites, which is slightly lower than for associated wild *A. planipennis* populations (81–91%) (Table 1). For the second (2009–2010) study period, however, survivorship of both experimental cohorts and associated wild *A. planipennis* in the same Ingham Co. sites decreased to 12–23% and 14–29%, respectively. For the third (2010–2011) study period, survival of experimental cohorts established at the Gratiot and Shiawassee Cos. Sites ranged from 5% to 35%, which is lower than that of associated wild *A. planipennis* (34–75%).

Apparent mortality of A. planipennis *and associated biotic factors*

Throughout the study (Fig. 2), the mortality of L4 individuals and JLs was higher than for the earlier larval instars (L1–L2 and L3) for both experimental *A. planipennis* cohorts (1.0–20% versus 5.0–16% in the 2008–2009 period, 40–63% versus 13–17% in the 2009–2010 period and 56–43% versus 6.0–16% in the 2010–2011 period) and wild cohorts (6.0–27% versus 2.9–3.8% in 2008–2009, 40–70% versus 4.5–15% in 2009–2010 and 19–43% versus 5.1–8.1% in 2010–2011). No dead adults in galleries were observed in 2009 and only a few dead adults ($n = 14$) in experimental and wild cohorts were observed in galleries in 2010 and 2011, which accounted for < 1% adult mortality (relative to the number of adult exit holes observed). There were no significant differences in the apparent (stage-specific) mortality rate between the experimental cohorts and associated wild *A. planipennis* for corresponding stages in the first 2 years of the study conducted at the Ingham Co. sites ($F < 0.0001$, d.f. = 1, 18, $P = 0.9989$ for 2009; $F < 0.0171$, d.f. = 1, 22, $P = 0.8971$ for 2010). However, there was a significant difference in the apparent mortality rate between experimental cohorts and associated wild *A. planipennis* of L4 individuals in the third year of the study conducted in the Gratiot and Shiawassee Cos. sites ($F = 7.960$, d.f. = 1, 22, $P = 0.0014$ for 2011).

Table 1 Survivorship of experimentally established cohorts and associated wild *Agrilus planipennis* in Michigan study sites each autumn

Year of sampling	Study sites	Experimental cohort trees (*n*)	Diameter at breast height (cm) (mean ± SE)	Experimental cohort larvae observed (*n*)	Wild larvae observed (*n*)	Survival of experimental cohort larvae (%)[a]	Survival of wild larvae (%)[b]
2009	Burchfield (BF)	10	12.6 ± 0.9	56	1247	76.8	90.7
	Central/Moore (CP)	8	13.5 ± 1.2	23	625	56.5	80.8
	Legg/Harris (LP)	8	16.0 ± 1.3	28	501	82.1	91.3
2010	Burchfield (BF)	12	11.0 ± 0.7	61	1186	23.0	17.8
	Central/Moore (CP)	17	11.3 ± 0.6	140	530	14.3	28.4
	Legg/Harris (LP)	18	15.5 ± 1.3	160	1343	11.9	14.3
2011	Gratiot Saginaw (GSW)	18	12.3 ± 0.5	153	979	35.3	64.4
	Maple River (MRE)	20	14.7 ± 1.7	216	640	22.2	73.0
	Rose Lake (RL)	16	12.8 ± 1.0	126	690	5.0	34.0

[a]Containing only late *A. planipennis* life stages (L4 to exited adults).
[b]Containing all *A. planipennis* life stages (L1 to exited adults).

Table 2 Relative dominance of stage-specific mortalities observed in the combined *Agrilus planipennis* experimental and wild cohorts caused by different biotic factors. The Michigan field sites sampled in 2009 and 2010 were in Ingham Co. (BF, CP, LP), and those sampled in 2011 were in Gratiot and Shiawassee Cos. (GSW, MRE, RL)

Year of sampling	Stage	Dead individuals observed (*n*)	Putative host tree resistance (%)	Unknown disease (%)	Parasitized (%)	Woodpecker predation (%)
2009	L1–2	93	63	26	5	5
	L3	44	27	55	14	5
	L4	47	13	43	32	13
	J-larvae	110	4	5	2	90
	Adult	0	–	–	–	–
2010	L1–2	171	92	2	6	0
	L3	471	29	30	41	0
	L4	1031	22	12	60	6
	J-larvae	1123	1	0	0	99
	Adult	12	0	100	0	0
2011	L1–2	130	82	6	12	0
	L3	209	36	21	38	5
	L4	438	5	9	25	61
	J-larvae	443	0	1	2	97
	Adult	2	0	100	0	0

Levels of apparent mortality varied significantly among different *A. planipennis* stages ($F = 4.5503$, d.f. = 4, 18, $P = 0.0103$ in 2009; $F = 37.4423$, d.f. = 4, 22, $P < 0.0001$ in 2010; $F = 9.7713$, d.f. = 4, 22, $P = 0.0001$ in 2011) for both experimental cohorts and wild cohorts, with L4 and JL stages generally having higher levels of mortality than earlier stages (L1–L2 and L3).

Although a majority (57–94%) of early (L1–L2) and intermediate (L3) instar deaths were a result of putative host-tree resistance or unknown diseases (Table 2), very few (5–12%) dead early instars were parasitized. By contrast, 14–41% of dead L3 individuals and 25–60% of dead L4 individuals were a result of larval parasitism (Table 2). A complex of hymenopteran parasitoids, consisting of the North American natives *Atanycolus* spp., the introduced biological control agent *T. planipennisi* and others, were observed in association with primarily L4 individuals of both experimental cohorts and wild *A. planipennis* throughout the study (Table 3). *Tetrastichus planipennisi* appeared to be the most abundant parasitoid species associated with both experimental cohorts and wild *A. planipennis* (accounting for 50% of observed parasitism) in the Ingham Co. sites in the first study period (2008–2009), whereas *Atanycolus* spp. was the most abundant parasitoid in the complex in the second study period (2009–2010) in the Ingham Co. sites (accounting for 92% of all parasitism), as well as in the third study period (2010–2011) in the Gratiot and Shiawassee Cos. sites (accounting for 93% of all parasitism). Less abundant parasitoid species included *P. sulcata*, *Spathius* spp. *B. indica*, and *Eurytoma* sp. For the mature J-larvae, predation by woodpeckers was the dominant mortality factor, accounting for > 90% of the mortality (Table 3).

Life tables and net population growth rate (R_0)

Representative life tables of the experimental cohorts and the wild *A. planipennis*, for the first study period (2008–2009) from one of the three Ingham Co. sites (BF), are presented in Tables 4 and 5, respectively. These representative life tables contain details of apparent (stage-specific) mortality and associated mortality factors, real mortality and net population growth rate

Table 3 Major parasitoid taxa observed from experimental cohorts and wild *Agrilus planipennis* from cohort trees (pooled from all three sites) established in three different years

Generation	Parasitoid taxa	Number of observed or parasitized hosts			Relative abundance (%) (experimental and wild cohorts combined)
		Experimental cohorts	Wild emerald ash borer	Both types of cohorts combined	
2008–2009	Observed hosts (*n*)	107	2373	2480	(Parasitized hosts = 15)
	Atanycolus spp.	0	4	4	26.7
	Tetrastichus planipennisi	1	7	8	50
	Phasgonophora sulcata	0	0	0	0
	Spathius spp.	0	1	1	6.3
	Balcha indica	0	0	0	0
	Eurytoma sp.	0	3	3	18.7
2009–2010	Observed hosts (*n*)	361	3059	3420	(Parasitized hosts = 824)
	Atanycolus spp.	61	704	765	92.8
	Tetrastichus planipennisi	5	15	20	2.4
	Phasgonophora sulcata	2	17	19	2.3
	Spathius spp.	0	4	4	0.5
	Balcha indica	2	13	15	1.2
	Eurytoma sp.	0	1	1	0.1
2010–2011	Observed hosts (*n*)	495	2309	2804	(Parasitized hosts = 228)
	Atanycolus spp.	43	170	213	93.4
	Tetrastichus planipennisi	3	7	10	4.4
	Phasgonophora sulcata	0	4	4	1.2
	Spathius spp.	0	1	1	0.4
	Balcha indica	0	0	0	0
	Eurytoma sp.	0	0	0	0

Generations 2008–2009 and 2009–2010 were from the Ingham Co. sites, and generation 2010–2011 was from the Gratiot and Shiawassee Cos. site.

(R_0). Data from analyses of the 18 site-specific life tables showed that the mean ± SE of R_0 values for the experimental cohorts (16.0 ± 2.9) and associated wild *A. planipennis* populations (19.4 ± 1.9) were the highest for the first (2008–2009) study period at the Ingham Co. sites but decreased significantly to 4.7 ± 0.9 and 4.6 ± 0.4, respectively, for the second (2009–2010) study period at those same sites (study time effect: $F = 125.175$, d.f. = 1, 9, $P < 0.0001$; Fig. 3). The sudden, highly significant decrease in R_0 values for both experimental cohorts and wild *A. planipennis* from the first to the second study period at the Ingham Co. sites appeared to correspond to the sudden increase in parasitism by the native North American parasitoids *Atanycolus* spp. and the introduced biological control agent *T. planipennisi* (Fig. 2 and Table 3). By contrast, net population growth rate (R_0) of both the experimental cohorts (5.7 ± 2.2) and associated wild *A. planipennis* (11.3 ± 2.5) were moderate in the 2010–2011 cohort at the Gratiot and Shiawassee sites. Although there were no significant differences in R_0 between the experimental cohorts and associated wild *A. planipennis* populations for the first two (2008–2009 and 2009–2010) study periods in the Ingham Co. sites ($F = 12.09$, d.f. = 1, 2; $P = 0.0738$ for the first study period; $F = 0.0154$, d.f. = 1, 2; $P = 0.9125$ for the second study period), R_0 of the experimental cohorts was significantly lower than that of associated wild *A. planipennis* for the third (2010–2011) study period at the Gratiot and Shiawassee sites ($F = 28.80$, d.f. = 1, 2; $P = 0.0353$). In addition, there were significant differences in R_0 for both experimental cohorts and wild *A. planipennis* among different study sites for the first ($F = 23.14$, d.f. = 2, 2; $P = 0.0414$) and third study periods ($F = 18.09$, d.f. = 2, 2; $P = 0.0524$).

Discussion

Analysis of the 18 site-specific life tables showed that natural enemies, primarily the native North American parasitoids (*Atanycolus* spp.) and the introduced biological control agent *T. planipennisi*, contributed to significant decreases in the net population growth rate of *A. planipennis* in Michigan, the epicentre of the invasion. These findings suggest that biotic factors such as parasitoids and avian predators played an important role in regulating the population dynamics of the invasive pest *A. planipennis* over the course of the invasion process. This demonstrates the ecological premise for biological suppression of the invasive pest populations via a complex of natural enemies.

The results from the present study further confirmed that a majority of *A. planipennis* required more than 1 year to complete one generation in Michigan, although there were variations among different sites and years of study. In addition, experimental cohorts established from beetles caged on trees were more synchronized than cohorts from the wild populations. This was probably a result of the fact that oviposition by caged beetles occurred only during 7–10 days in early summer (late June to mid-July), whereas oviposition by wild beetles might occur for a much longer period (late June to mid-August). However, this within-season difference in oviposition periods between caged-beetles and wild adults did not appear to have affected levels of apparent larval mortality between experimental cohorts and wild *A. planipennis*.

Throughout the study, levels of the apparent mortality varied significantly among different *A. planipennis* stages for both experimental cohorts and wild cohorts. For the three study periods (2008–2009, 2009–2010 and 2010–2011), later larval

Table 4 Life table for cohorts of *Agrilus planipennis* experimentally established with caged adults in early summer of 2008 and sampled in the autumn of 2009 at the Burchfield Park (BF) in Ingham Co

Life stage[a]	l_x	m_x	d_x	d_i	Mortality factor	q_x	q_i	q
(Egg)	80	–	24	24	Infertility/parasitism by *Oobius agrili* (30%; Duan *et al.*, 2010, 2011)	0.300	0.300	0.300
L1–L2	56	0	7	7	Host tree resistance	0.125	0.125	0.088
L3	49	0	0	0	No mortality observed	0.000	0.000	0.000
L4	49	5	1	1	Undetermined disease	0.020	0.020	0.013
J-larvae	43	37	5	4	Woodpecker predation	0.116	0.093	0.050
				1	Parasitized by *Tetrastichus planipennisi*		0.023	0.013
Adult exit holes	1	1	0	0	No mortality observed	0.000	0.000	0.000
(Overwintering L4/JL-pupae)	42	–	0	0	Woodpecker predation (29%; Duan *et al.*, 2010)	0.290	0.290	0.152
(Emerging adults)	31	–	12	12	Fungal infections (5%; J. J. Duan, unpublished data)	0.050	0.050	0.019
(Females)	15	–	2	2	Female : male = 1 : 1	–	–	–
(F1 eggs)	1464	–	–	–	≈100 eggs per female in the laboratory (Wang *et al.*, 2010)	–	–	–
R_0	18.3	–	–	–	–	–	–	–

[a]Life stages in parentheses were not observed and parameters for those stages were calculated based on separate estimates from other studies (for calculations, see Materials and methods).

l_x, number of live emerald ash borer (EAB) entering each stage; m_x, number of live EAB observed at sampling time; d_x, the number of dead EAB observed in each stage; q_x, apparent (stage-specific) mortality rate (d_x/l_x,); d_i, number of EAB dying in association with specific factor observed; q_i, apparent mortality rate because of specific biotic factor (d_i/l_x); q, real mortality (d_x or d_i/l_0); R_0, net reproductive rate, calculated as the ratio of l_0 (number of eggs estimated to start the life table) divided by l_{F1} (the number of eggs produced by surviving adults).

stages of both experimental and wild cohorts had consistently higher levels of mortality than earlier larval stages. Host tree resistance and/or unknown diseases were the dominant mortality factor associated with the earlier larval instars (L1–L2 and L3). The major mortality factor for the L4 *A. planipennis* larvae appeared to be parasitism by the indigenous braconid parasitoid complex (*Atanycolus* spp.) and the introduced agent *T. planipennisi*, particularly in the second (2009–2010) and third (2010–2011) study periods. Predation by woodpeckers was the dominant mortality factor for JLs. The apparent (stage specific) mortality was similar for the experimental cohorts and wild *A. planipennis* for each larval stage in the first and second study periods established in the Ingham Co. sites. These results indicate that both experimental and wild cohorts may be comparably used to measure the stage-specific mortality rates of immature *A. planipennis* stages under these conditions, provided that adjustments are made to separate the overlapping larval generations.

However, there was a significant difference in the apparent mortality rate between experimental cohorts and associated wild *A. planipennis* of L4 individuals in the third (2010–2011) study period in the Gratiot and Shiawassee Cos. sites. The apparent mortality rate of L4 individuals from the experimental cohorts was several-fold higher than that of the corresponding stage of wild *A. planipennis* populations (Fig. 2). Although we could not determine the exact cause of this discrepancy, we speculate that most L4 individuals of the wild *A. planipennis* population at these study sites might have originated from the current year (2011) generation of possibly univoltine populations. This speculation stems from our observations of much higher proportions of live L4 individuals (15–25%) of the wild *A. planipennis* (Fig. 1) in two of the study sites (GSW and MRE), where the majority of experimental cohorts had already advanced to JL or emerged as adults (accounting for > 95% of all live stages) at the time of sampling. Because L4 individuals from the univoltine populations were likely to have shortened exposure to parasitism, diseases, predation and/or other potential sources of mortality factor (e.g. extreme weather conditions), a lower mortality rate would be expected for this group of L4 individuals than for the semi-voltine group in the experimental cohorts. It might prove difficult to accurately measure the stage-specific mortality of wild immature *A. planipennis* when the same stages of two different (semi-voltine and univoltine) populations overlap in the study sites. In these situations, the use of experimental cohorts may be a better choice for accurately measuring the stage-specific mortality rate of *A. planipennis* populations.

The invasion wave of *A. planipennis* in ash-dominated forests was described as having three main stages: the cusp, crest and core (Burr, 2012). The cusp phase occurs at newly infested sites in the first few years as *A. planipennis* populations slowly build, before their numbers rapidly increase and cause tree mortality in the crest phase. The core phase then occurs approximately 10 years after the initial infestation, by which time most ash trees have died and *A. planipennis* populations have collapsed. Host tree mortality (or depletion of host tree resources) is generally considered to be the major factor driving the invasive population of *A. planipennis* to emigrate or disperse into new areas or forests (Mercader *et al.*, 2009; Burr, 2012). Our study sites were approximately approaching the crest phase of *A. planipennisi* invasion (within 5–6 years of initial infestation). However, we observed a more than 75% decrease in the population growth rate of both experimental cohorts and wild *A. planipennisi* populations from the first (2008–2009) study period ($R_0 = 16–19$) to the second (2009–2010) period ($R_0 = 4.6–4.7$) in the three Ingham Co. study sites (Fig. 3). This sudden, highly significant

Table 5 Life table for wild *Agrilus planipennis* populations infesting cohort ash trees sampled in the autumn of 2009 at the Burchfield Park in Ingham Co

Life stage[a]	l_x	m_x	d_x	d_i	Mortality factor	q_x	q_i	q
(Egg)	891	–	267	267	Infertility/parasitism by *Oobius agrili* (30%; Duan *et al.*, 2010, 2011)	0.300	0.300	0.300
(L1–L2)	623	419	18	5	Host tree resistance	0.029	0.009	0.006
				11	Undetermined disease		0.017	0.012
				2	Wood pecker predation		0.003	0.002
(L3)	606	190	18	2	Host tree resistance	0.029	0.003	0.002
				12	Undetermined disease		0.020	0.014
				2	Parasitism by *Tetrastichus planipennisi*		0.003	0.002
				1	Parasitism by *Atanycolus* sp.		0.001	0.001
				2	Wood pecker predation		0.003	0.002
L4	588	307	12	1	Host tree resistance	0.020	0.002	0.001
				6	Undetermined disease		0.010	0.007
				1	Parasitism by *T. planipennisi*		0.002	0.001
				1	*Spathius* spp.		0.002	0.001
J-larvae	576	213	53	3	Undetermined disease	0.092	0.005	0.003
				1	Parasitism by *Atanycolus* sp.		0.002	0.001
				49	Wood pecker predation		0.085	0.055
Adult exit holes	3	3	0	0	No mortality observed	0.000	0.000	0.000
(Overwintering L4/JL-pupae)	520	–	151	151	Woodpecker predation (29%; Duan *et al.*, 2010)	0.290	0.290	0.169
(Emerging adults)	372	–	19	19	Fungal infections (5%; J. J. Duan, unpublished data)	0.050	0.050	0.021
(Females)	186	–	–	–	Female : male = 1 : 1	–	–	–
(F1 eggs)	18 609	–	–	–	≈100 eggs per female in the laboratory (Wang *et al.*, 2010)	–	–	–
R_0	20.9	–	–	–	–	–	–	–

[a]Parameters for life stages in parenthesis were either calculated based on separate estimates from other studies or re-adjusted (for L1–L2 and L3 individuals) to exclude individuals of the sampling year-generation that was equivalent to the generation of associated experimental cohorts (see Materials and methods).

l_x, number of live emerald ash borer (EAB) entering each stage; m_x, number of live EAB observed at sampling time; d_x, the number of dead EAB observed in each stage; q_x, apparent (stage-specific) mortality rate (d_x/l_x,); d_i, number of EAB dying in association with specific factor observed; q_i, apparent mortality rate because of specific biotic factor (d_i/l_x); q, real mortality (d_x or d_i/l_0); R_0, net reproductive rate, calculated as the ratio of l_0 (number of eggs estimated to start the life table) divided by l_{F1} (the number of eggs produced by surviving adults).

decrease in the net population growth rate appeared to correspond with the sudden increase in parasitism by the native North American parasitoid complex *Atanycolus* spp. and the released biological control agent *T. planipennisi*, as well as an increase in woodpecker predation. Other potential sources of mortality factors such as extreme weather (cold or hot) and climatic changes, however, may also affect the population growth and range expansion of *A. planipennis* in different regions (Liang & Fei, 2014). Such weather-related mortality would more likely affect adults or eggs and, to a lesser extent, the immature stages that live under ash tree bark and are buffered from extreme weather conditions (Vermunt *et al.*, 2012).

Although the R_0 values of *A. planipennis* in the six study sites in Michigan were still several-fold greater than one (replacement) at the end of the present study, the continued release and increased establishment of the three introduced biological control agents (Federal Register, 2007; Duan *et al.*, 2011, 2013) are likely to elevate mortality from parasitism, which may lead to significant reduction in the net population growth rate of *A. planipennis* in the earlier (cusp) phase of invasion. For example, Duan *et al.* (2013) reported a sudden increases in parasitism by *T. planipennisi* from 1–5% in 2011 (autumn sampling) to 12–21% in 2012 (autumn sampling) at these same study sites. Unfortunately, the present study missed this sudden increase in *T. planipennisi* parasitism from 2011 to 2012. However, further life table analyses of data on wild *A. planipennis* populations reported in Duan *et al.* (2013), as well as more recent samples from the same study sites, are currently in progress. Such analysis is likely to reveal the temporal and spatial patterns of the population dynamics of *A. planipennis* in its invasion process, and allow us to more accurately determine the potential efficacy of the introduced biological control agents in suppression of this invasive pest.

Life table analysis can be a powerful tool for evaluating the impact of mortality factors on the dynamics of many insect pest populations. However, the technical difficulty and labour-intensity of creating experimental cohorts for construction of appropriate life tables often prevents the use of this analytical tool to study the population dynamics of many important wood-boring insects such as the invasive *A. planipennis* (Duan *et al.*, 2010; Jennings *et al.*, 2013) and long-horned beetles (Haavik *et al.*, 2012), both of which have a long-life

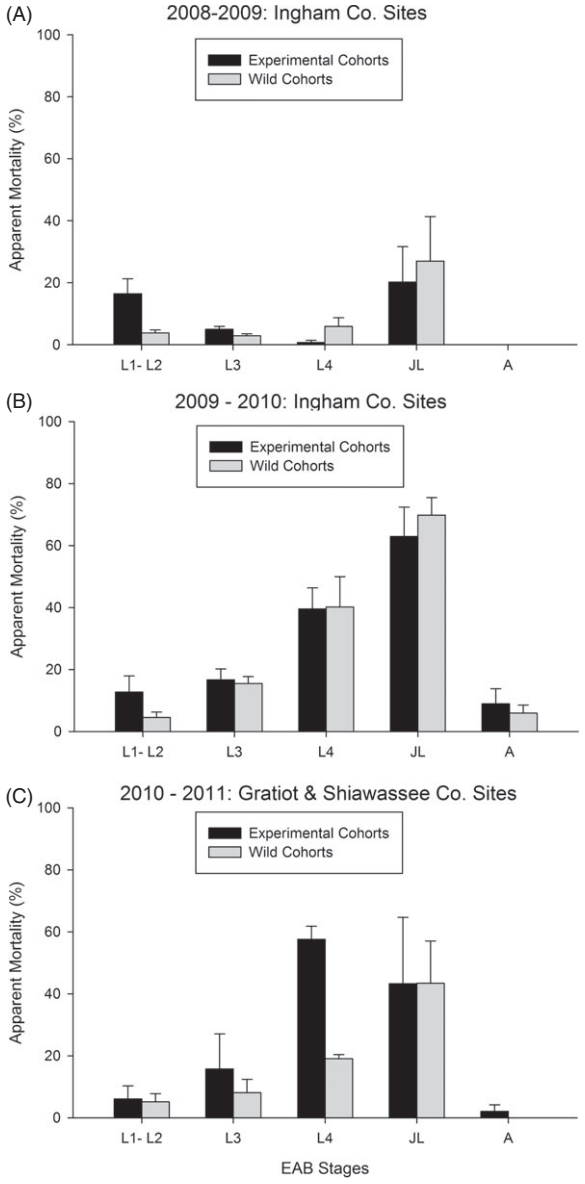

Figure 2 (A–C) Apparent mortality of experimental cohorts and associated wild *Agrilus planipennis* recovered in the sampling zone of cohort trees established across different study sites for three different study periods.

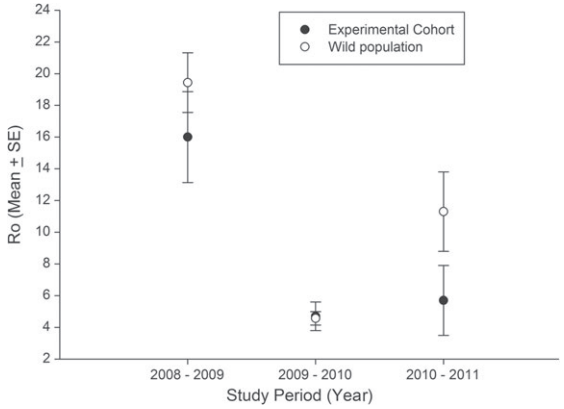

Figure 3 Net population growth rates (R_0) of experimental cohorts and associated wild *Agrilus planipennis* estimated from life tables of each generation established across different study sites in Michigan. The 2008–2009 and 2009–2010 cohorts were established in the Ingham Co. study sites, and the 2010–2011 cohorts were established in the Gratiot and Shiawassee Cos. sites.

cycle and cryptic immature stages. The present study showed that appropriate stage-specific life tables could be constructed by monitoring the galleries of wild *A. planipennis* larvae and documenting their stages and associated mortality factors (including natural enemies). The results of our life table analyses demonstrated that the outcome (R_0) from such wild population life tables could be comparable with that from the analysis of life tables for the associated experimental cohorts in some study sites (e.g. in Ingham Co. sites), where only one type of population (semi-voltine) occurred during the study. In situations where there is no mixture of semi-voltine and univoltine populations, construction of life tables may be effectively achieved with the wild *A. planipennis* population, and analyses of such life tables can provide insights into the impact of different mortality factors (including the released biocontrol agents) on the population growth of this invasive pest. In addition, the spread or invasion of *A. planipennis* in North America has involved long-distance or 'jump' dispersal associated with human-assisted movement of infested host plant materials (Cappaert *et al.*, 2005), short-distance movement in contiguous ash stands (100 m per season; Mercader *et al.*, 2009) and natural diffusive range expansion (Muirhead *et al.*, 2006; Taylor *et al.*, 2010). Considering the long distances (15–60 km) between some of our study sites (e.g. from the Ingram Co. sites to the Gratiot and Shiawassee Co. sites), the wild *A. planipennis* populations at our six study sites are probably representative of different populations across the study area. Future life-table study designs should aim initially to delineate different population boundaries and then include as many populations as possible.

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References

Bauer, L.S., Liu, H.P., Miller, D.L. & Gould, J. (2008) Developing a classical biological control program for *Agrilus planipennis* (Coleoptera: Buprestidae), an invasive ash pest in North America. *Newsletter of the*

Michigan Entomological Society, **53**, 38–39 [WWW document]. URL http://www.nrs.fs.fed.us/pubs/jrnl/2008/nrs_2008_bauer_002.pdf [accessed on 30 December 2008].

Burr, S.J. (2012) Evaluation of emerald ash borer populations and the ash resource at three stages of the invasion wave. MSc Thesis, Michigan State University.

Cappaert, D., McCullough, D.G., Poland, T.M. & Siegert, N.W. (2005) Emerald ash borer in North America: a research and regulatory challenge. *American Entomologist*, **51**, 152–165.

Chamorro, M.L., Volkovitsh, M.G., Poland, T.M., Haack, R.A. & Lingafelter, S.W. (2012) Preimaginal stages of the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae: Agrilinae): an invasive species of ash trees (*Fraxinus*). *PLoS One*, **7**, e33185.

Duan, J.J., Ulyshen, M.D., Bauer, L.S., Gould, J. & Van Driesche, R.G. (2010) Measuring the impact of biotic factors on populations of immature emerald ash borer (Coleoptera: Buprestidae). *Environmental Entomology*, **39**, 1513–1522.

Duan, J.J., Bauer, L.S., Ulyshen, M.D., Gould, J. & Van Driesche, R.G. (2011) Development of methods for the field evaluation of *Oobius agrili* (Hymenoptera: Encyrtidae) in North America, a newly introduced egg parasitoid of the emerald ash borer (Coleoptera: Buprestidae). *Biological Control*, **56**, 170–174.

Duan, J.J., Yurchenko, G. & Fuester, R.W. (2012a) Occurrence of emerald ash borer (Coleoptera: Buprestidae) and biotic factors affecting its immature stages in the Russian Far East. *Environmental Entomology*, **41**, 245–254.

Duan, J.J., Bauer, L.S., Abell, K.J. & Van Driesche, R.G. (2012b) Population responses of hymenopteran parasitoids to the emerald ash borer (Coleoptera: Buprestidae) in recently invaded areas in north central United States. *BioControl*, **57**, 199–209.

Duan, J.J., Bauer, L.S., Abell, K.J., Lelito, J. & Van Driesche, R.G. (2013) Establishment and abundance of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) in Michigan: potential for success in classical biocontrol of the invasive emerald ash borer (Coleoptera: Buprestidae). *Journal of Economic Entomology*, **106**, 1145–1154.

Federal Register (2007) Availability of an environmental assessment for the proposed release of three parasitoids for the biological control of the emerald ash borer (*Agrilus planipennis*) in the continental United States. *Federal Register*, **72**, 28947–28948 [Docket No. APHIS-2007-006] [WWW document]. URL http://www.regulations.gov/#!docketDetail;D=APHIS-2007-0060 [accessed on 30 August 2007].

Haavik, L., Coleman, T.W., Flint, M.L., Venette, R.C. & Seybold, S.J. (2012) *Agrilus auroguttatus* exit hole distributions on *Quercus agrifolia* boles and a sampling method to estimate their density on individual trees. *Canadian Entomologist*, **144**, 1–12.

Hassell, M.P. (1985) Insect natural enemies as regulating factors. *Journal of Animal Ecology*, **54**, 323–334.

Herms, D.A. & McCullough, D.G. (2014) Emerald ash borer invasion of North America: history, biology, ecology, impact and management. *Annual Review of Entomology*, **59**, 13–30.

Jennings, D.E., Gould, J.R., Vandenberg, J.D., Duan, J.J. & Shrewsbury, P.M. (2013) Quantifying the impact of woodpecker predation on population dynamics of the emerald ash borer (*Agrilus planipennis*). *PLoS One*, **8**, e83491.

Kovacs, F.K., Haight, R.G., McCullough, D.G., Mercader, R.J., Siegert, N.W. & Leibhold, A.M. (2010) Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecological Economics*, **69**, 569–578.

Liang, L. & Fei, S. (2014) Divergence of the potential invasion range of emerald ash borer and its host distribution in North America under climate change. *Climatic Change*, **122**, 735–746.

Lindell, C.A., McCullough, D.G., Cappaert, D., Apostolou, N.M. & Roth, M.B. (2008) Factors influencing woodpecker predation on emerald ash borer. *American Midwest Naturalist*, **159**, 434–444.

Liu, H.P., Bauer, L.S., Gao, R.T., Zhao, T.H., Petrice, T.R. & Haack, R.A. (2003) Exploratory survey for the emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae), and its natural enemies in China. *The Great Lakes Entomologist*, **36**, 191–204.

Liu, H.P., Bauer, L.S., Miller, D.L. *et al.* (2007) Seasonal abundance of *Agrilus planipennis* (Coleoptera: Buprestidae) and its natural enemies *Oobius agrili* (Hymenoptera: Encyrtidae) and *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) in China. *Biological Control*, **42**, 61–71.

McCullough, D.G., Poland, T.M. & Cappaert, D. (2009) Attraction of the emerald ash borer to ash trees stressed by girdling, herbicide treatment, or wounding. *Canadian Journal of Forest Research*, **39**, 1331–1345.

Mercader, R., Siegert, N.W., Liebhold, A.M. & McCullough, D.G. (2009) Dispersal of the emerald ash borer, *Agrilus planipennis* , in newly colonized sites. *Agricultural and Forest Entomology*, **11**, 421–424.

Muirhead, J.R., Leung, B., Overdijk, C.V., Kelly, D.W., Nandakumar, K., Marchant, K.R. & MacIssac, H.J. (2006) Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. *Diversity and Distributions*, **12**, 71–79.

Nielsen, A.L., Hamilton, G.C. & Matadha, D. (2008) Developmental rate estimation and life table analysis for *Halyomorpha halys* (Hemiptera: Pentatomidae). *Environmental Entomology*, **37**, 348–355.

Parker, I.M. (2000) Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecological Applications*, **10**, 726–743.

Poland, T.M. & McCullough, D.G. (2006) Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry*, **104**, 118–124.

Rebek, E.J., Herms, D.A. & Smitley, D.R. (2008) Interspecific variation in resistance to emerald ash borer (Coleoptera: Buprestidae) among North American and Asian ash (*Fraxinus* spp.). *Environmental Entomology*, **37**, 242–246.

SAS Institute Inc. (2012) *JMP Pro 10.0.1 Introductory Guide*. SAS Institute Inc., Cary, North Carolina.

Siegert, N.W., McCullough, D.G., Williams, D.W., Fraser, I. & Poland, T.M. (2010) Dispersal of *Agrilus planipennis* (Coleoptera: Buprestidae) from discrete epicenters in two outlier sites. *Environmental Entomology*, **39**, 253–265.

Southwood, R. & Henderson, P.A. (2000) *Ecological Methods*, 3rd edn. Blackwell Science, U.K.

Taylor, R.A.J., Bauer, L.S., Poland, T.M. & Windell, K.N. (2010) Flight performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a flight mill and in free flight. *Journal of Insect Behavior*, **23**, 128–148.

Tluczek, A.R., McCullough, D.G. & Poland, T.M. (2011) Influence of host stress on emerald ash borer (coleoptera: buprestidae) adult density, development, and distribution in *Fraxinus pennsylvanica* trees. *Environmental Entomology*, **40**, 357–366.

Varley, G.C., Gradwell, G.R. & Hassell, P.M. (1973) *Insect Population Ecology, an Analytical Approach*. Blackwell, U.K.

Vermunt, B., Cuddington, K., Sobek-Swant, S. & Crosthwaite, J. (2012) Cold temperature and emerald ash borer: modelling the minimum under-bark temperature of ash trees in Canada. *Ecological Modelling*, **235–236**, 19–25.

Wang, X.Y., Yang, Z.Q., Gould, J.R., Zhang, Y.N. & Liu, G.J. (2010) The biology and ecology of the emerald ash borer, *Agrilus planipennis*, in China. *Journal of Insect Science*, **10**, 1–23.

Wei, X., Wu, Y., Reardon, R., Sun, T.H., Lu, M. & Sun, J.H. (2007) Biology and damage traits of emerald ash borer (*Agrilus planipennis* Fairmaire) in China. *Insect Science*, **14**, 367–373.

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