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Article

Coleopteran Communities Associated with Forests Invaded by Emerald Ash Borer

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Abstract: Extensive ash mortality caused by the non-native emerald ash borer alters canopy structure and creates inputs of coarse woody debris as dead and dying ash fall to the forest floor; this affects habitat heterogeneity; resource availability; and exposure to predation and parasitism. As EAB-induced (emerald ash borer-induced) disturbance progresses the native arthropod associates of these forests may be irreversibly altered through loss of habitat; changing abiotic conditions and altered trophic interactions. We documented coleopteran communities associated with EAB-disturbed forests in a one-year study to evaluate the nature of these changes. Arthropods were collected via ethanol-baited traps on five sites with varying levels of EAB-induced ash mortality from May to September; captured beetles were identified to the family level and assigned to feeding guilds (herbivore; fungivore; xylophage; saprophage; predator; or parasite). Over 11,700 Coleoptera were identified in 57 families. In spite of their abundance; herbivores comprised a relatively small portion of coleopteran family richness (8 of 57 families). Conversely, coleopteran fungivore richness was high (23 families), and fungivore abundance was low. Herbivores and fungivores were more abundant at sites where ash decline was most evident. The predatory Trogossitidae and Cleridae were positively correlated with ash decline, suggesting a positive numerical response to the increased prey base associated with EAB invasion. Ash forests are changing, and a deeper understanding of arthropod community responses will facilitate restoration.

Keywords: *Fraxinus*; invasive species; trophic guild; natural enemies

1. Introduction

Invasions by non-native invasive species pose significant threats to forest ecosystem function [1] and native biodiversity [2,3], and have widespread economic impacts [4,5]. Ash (*Fraxinus* spp.) are a consistent component of hardwood forests throughout the United States [6,7]; their prevalence and persistence is threatened by the emerald ash borer (EAB, *Agrilus planipennis* Fairmaire, Coleoptera: Buprestidae). Since its discovery near Detroit, MI in 2002 [8], EAB has spread rapidly through much of the eastern contiguous United States and southeastern Canada [9] inflicting extensive ash mortality in invaded regions. Larvae feed on phloem beneath the bark, forming serpentine galleries and destroying the vascular tissue, disrupting translocation of water and nutrients to the canopy, ultimately girdling the tree [10,11]. The majority of EAB-induced ash mortality (>85%) occurs within 3–5 years of the initial invasion [12,13]. All North American *Fraxinus* species are susceptible to attack and EAB readily colonizes healthy trees [10].

The direct effects of EAB invasion include altered forest structure due to rapid ash mortality, with subsequent alterations in ash-associated communities [14–18]. The indirect effects of rapid and broad scale tree mortality include increased gap formation which alters light penetration to the forest floor, accumulation of coarse woody debris, and qualitative and quantitative alterations in litter inputs

causing shifting temperature and moisture regimes on the forest floor [19,20]. Such changes associated with EAB-induced ash mortality is affecting arthropod community associates of these invaded forests. In particular, changes at the soil-surface interface via increased leaf litter and coarse woody debris inputs can influence the abundance and distribution of soil biota [21,22]. Coleopterans, in particular the Carabidae, are well documented indicators of disturbance [23,24], and have been shown to respond to EAB-induced changes [25,26].

We sought to gain a broader understanding of the extent to which EAB-induced ash mortality might affect arthropod community associates, and focus here on aerial Coleoptera. We evaluated the extent to which coleopteran abundance and richness are affected by widespread changes in forest structure associated with the EAB invasion, and further considered these changes in relation to trophic guilds. We hypothesized that EAB-induced changes in forest composition and structure will lead to guild-specific changes in coleopteran communities. Specifically, we expected that xylophage, saprophage, and fungivore abundance and overall richness would increase in response to increases in habitat caused by inputs due to EAB disturbance.

2. Materials and Methods

2.1. Study Sites

Five study sites were established in mixed mesophytic forests in north-central Kentucky along the forefront of the expanding EAB invasion [27], in Anderson, Fayette, Henry, Shelby, and Spencer counties. Ash thrive on the moist and fertile soils that predominate in this region [28,29], and were historically a significant component of these forests [25]. At the onset of the study EAB was present at the Anderson, Henry, and Shelby sites (initially reported in November 2011, October 2009, and May 2009, respectively). EAB was first detected at the Fayette and Spencer sites in 2014, but there were little to no signs of EAB-induced stress.

At each site, 0.04 ha circular whole plots, situated ≥ 50 m apart, were placed in contiguous forests in blocks of three, with three blocks at each site, for a total of 45 plots across all five sites [27]. Ash canopy dieback was visually assessed by a single observer and each tree assigned a crown dieback value from 0% (healthy) to 100% (dead). When split or sloughing bark, larval galleries, or adult exit holes were evident, dieback was attributed to EAB. Our sites represented the full spectrum of forest disturbance associated with the EAB invasion, including pre-invasion at Fayette and Spencer (newly detected; <17% ash canopy dieback, <2% ash mortality), peak invasion at Shelby (EAB populations high; 25–30% ash canopy dieback, ~10% ash mortality), and post-invasion forests at Henry and Anderson (EAB populations low; >55% canopy dieback, 19–50% ash mortality) [27].

2.2. Arthropod Monitoring

Native coleopteran communities in the sub-canopy strata were monitored using 12-unit Lindgren multi-funnel traps (one per plot, $N = 45$) from 20 May to 12 September 2014. Traps were suspended over an ash branch (~4 m) and fitted with two 50 mL vials of 70% ethanol, a commonly used lure for xylophagous insects [30–32], hung from the funnel edge, and with a dichlorvos strip (2×5 cm²) (American Vanguard Corporation Chemical Corp., Los Angeles, CA, USA) placed in each trap bottom. Traps were monitored every 7–14 days; contents were removed and stored in 70% EtOH in resealable plastic bags, and lures were replenished. In the laboratory samples were sorted to order [33]; Coleoptera were sorted and identified to family using available keys [33–36], counted, and assigned to trophic guilds based on larval feeding habits, including herbivore, saprophage, fungivore, xylophage, predator, or parasite [37]. We used family-level identifications, which are deemed taxonomically sufficient when undertaking a study of this nature [38,39]. This approach provides a good estimate of invertebrate populations within a given community when using a given sampling method, and has been utilized in a number of invertebrate studies [39–43]. Ordinarily the Coleoptera are trophically diverse, but more or less trophically uniform within families [37,44], which allows classifying families into feeding guilds

that exploit resources in a similar manner [45]. In our study, the carrion feeders, including the Silphidae, some Staphylinidae (e.g., *Aleochara* spp.), some Histeridae, some Nitidulidae (e.g., *Nitidulia* spp.), and some Leiodidae, were responding to the decaying trap contents rather than the ethanol lure, which resulted in excessive fluctuations in abundance, and so were excluded from additional analyses.

2.3. Analysis

We used assessments of ash mortality from Davidson and Rieske [27] and also evaluated ash canopies for decline, ranging from low (Fayette) to high (Henry), to assess the influence of ash decline on coleopteran abundance and richness. The abundance of aerial coleopterans was evaluated with funnel traps (total no. trapped). Richness (total no. families captured) and evenness (E_{var}) [46] was derived by site. Diversity indices were not derived because of data gaps caused by intermittent difficulties in accessing monitoring sites. Data were tested for normality (PROC UNIVARIATE) and transformed when necessary. Significance was determined at $\alpha = 0.05$ unless stated otherwise. All analyses were performed using SAS (v9.3, SAS Campus Drive Cary, NC, USA) [47].

Overall coleopteran abundance and cumulative richness by site were analyzed using a repeated measure mixed linear model (PROC MIXED), with sample interval as the repeated measure and individual plots (traps) as subjects. The difference of least squares (Least Squares Means) was used to separate means for these population parameters. Coleopteran feeding guild abundance and richness summed over the 16-week sampling period were analyzed using a generalized linear mixed model (PROC GLM) to compare guild \times site interactions. Feeding guild abundance was transformed using a square root transformation for total counts and arcsine transformation for percent abundance. Feeding guild abundance (absolute and percent) was compared across all sites where the difference of least squares was used to separate means and post-hoc analysis was performed using pairwise T-Comparisons if differences arose. A chi squared analysis was used to determine differences in trophic guild abundance across sites. Correlations between the predator guild and ash canopy decline were evaluated (PROC CORR).

3. Results

3.1. Study Sites

Across our study sites, ash composition ranged from 12–26% for stems >2.5 cm diameter. EAB-induced ash mortality ranged from 0–50% and was highly correlated with EAB abundance [27]. Ash canopy dieback ranged from a low of ~7% at our least-disturbed, most recently invaded site to a high of 74% at our most degraded site (Table 1).

Table 1. Ash canopy dieback and coleopteran abundance at five sites in north-central Kentucky used to evaluate the coleopteran community associated emerald ash borer-induced ash decline. Means followed by the same letter do not differ ($\alpha = 0.05$).

Site	Location (Lat., Long.)	Sample Intervals (Site Visits)	<i>Fraxinus</i> spp. Canopy Dieback (Mean % (s.e.))	Coleoptera Abundance ¹	Coleoptera Evenness ²
Henry	38.56572, 85.14665	14	73.9 (4.6) a	1.30 (0.07) b	0.27 (0.01) a
Anderson	32.00857, 84.95980	13	56.9 (1.9) b	1.53 (0.07) ab	0.23 (0.01) a
Shelby	38.27980, 85.36258	16	27.4 (3.9) c	1.64 (0.06) a	0.27 (0.01) a
Spencer	38.02163, 85.27577	6	16.2 (2.8) cd	1.49 (0.11) ab	0.11 (0.01) b
Fayette	37.89653, 84.39270	10	7.4 (3.0) d	1.27 (0.08) b	0.17 (0.02) ab

$F_{3,350} = 58.6; p < 0.001$ $F_{4,527} = 2.1; p < 0.02$ $F_{4,14} = 35.0; p < 0.01$

¹ Number of individuals per day (LS-means \pm s.e.) captured in ethanol-baited funnel traps. Means separation on transformed data. ² Evenness index: $E_{var} = 1 - \frac{2}{\pi} \arctan\left\{\frac{\sum_{s=1}^S (\ln(x_s) - \sum_{t=1}^S \ln(x_t)/S)^2}{S}\right\}$.

3.2. Arthropods

Funnel traps yielded 16,455 arthropods, including 11,786 coleopterans (>71%) representing 57 families, excluding carrion feeders (Table A1). Elateridae was the most abundant family (Figure 1), with 16% of the total, followed by the Curculionidae and Staphylinidae (13 and 12%, respectively); these three families comprised nearly 41% of the coleopterans captured. The next most abundant families were the Ptilodactylidae (9%), the Latridiidae (9%), and the Histeridae (8%); collectively they comprised almost 27% of the total coleopterans.

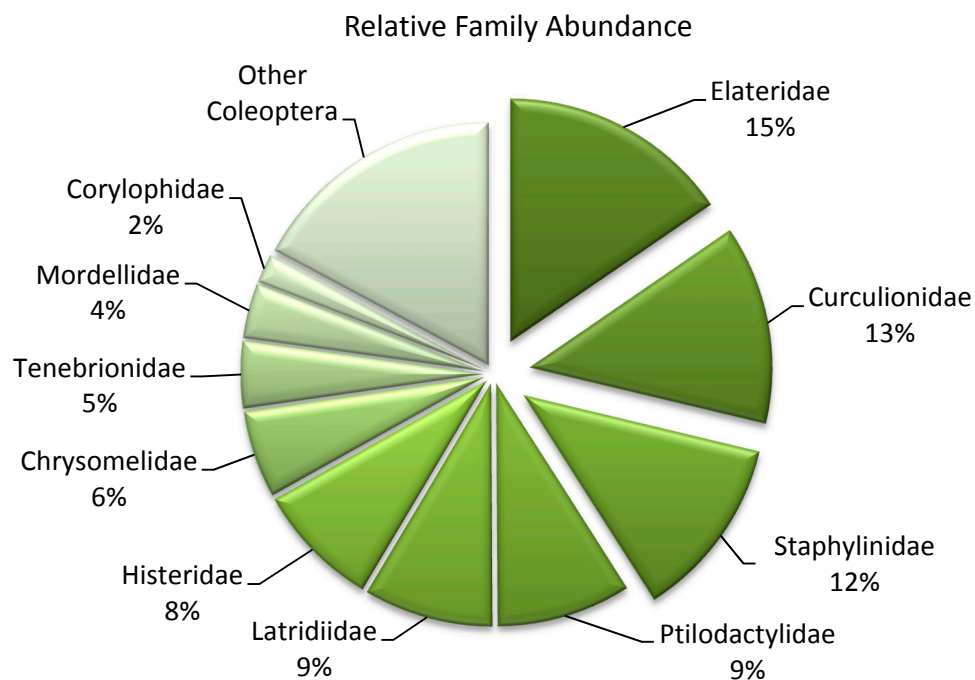


Figure 1. Relative abundance of the 10 numerically dominant coleopteran families found in forests associated with emerald ash borer-induced ash mortality.

Coleopteran abundance (Table 1), but not cumulative family richness (Figure 2) differed significantly among study sites; both tended to be lowest in pre-(Fayette) and post-disturbed (Henry) sites, and greatest at the site typifying peak invasion (Shelby). Henry, Anderson, and Shelby had the highest coleopteran evenness, and Spencer had the lowest (Table 1).

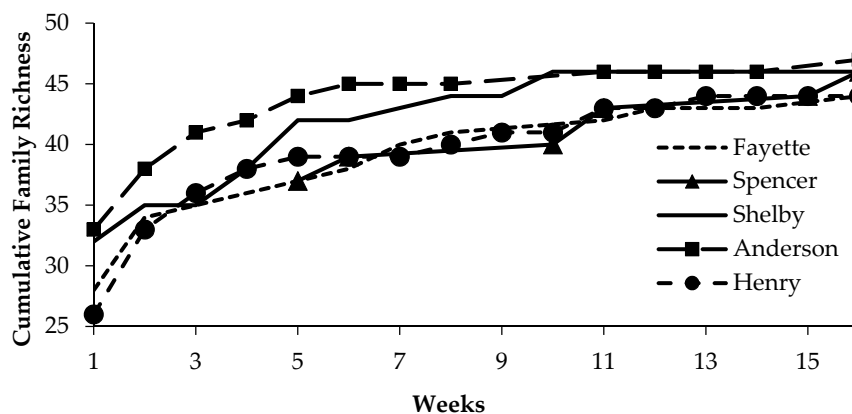


Figure 2. Cumulative coleopteran family richness at five forested sites in north central Kentucky varying in levels of EAB-induced (Emerald Ash Borer-induced) disturbance.

Coleopteran abundance was greatest among herbivores (4207 individuals, 36%) (Table 2), comprised primarily of the Elateridae, which feed on flowers, nectar, pollen, and rotting fruit [35].

Table 2. Relative abundance and richness of Coleopteran feeding guilds sampled from five sites affected by emerald ash borer ash decline.

Trophic Guild	Coleopteran Family-Level	
	Abundance (%)	Richness (%)
Herbivore	36	14
Fungivore	17	40
Predator	26	19
Xylophage	10	12
Saprophage	10	10
Parasite	<1	5
Unidentified	<1	–
Total	100	100

However, in spite of their abundance, herbivores comprised only 14% of total family richness (8 families). In contrast, coleopteran fungivore richness was highest at 40% (23 families), in spite of the fact that abundance was relatively low (2082 individuals, 17%) (Table 2; Figure 3).

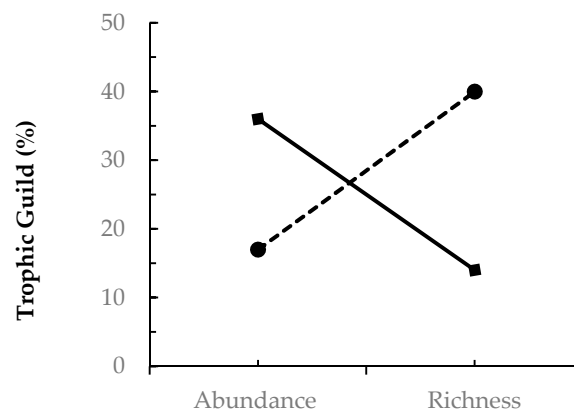


Figure 3. Relationship between relative herbivore (◆—◆) and fungivore (●-●) abundance and richness among coleopterans sampled from EAB-impacted (Emerald Ash Borer-impacted) forests.

Fungivores were dominated by the Latridiidae (Figure 1), which typically feed on the reproductive structures of fungi and are commonly found in plant debris [35]. Predators comprised 26% of the total (3050 individuals) and 19% of the coleopteran family richness (11 families) (Table 2). Predators consisted primarily of the Staphylinidae (Figure 1), which are generalists, and the Histeridae, which has one subfamily associated with bark beetle (Curculionidae) galleries, and another subfamily that feeds principally on fly and beetle larvae associated with dung [35]. Saprophages and xylophages made up ~10% of the abundance, and similarly 10 and 12% of coleopteran family richness, and consisted primarily of Ptilodactylidae and Scolytines (Figure 1; Table 2).

Trophic guild abundance across sites varied ($\chi^2 = 1045.6$; $df = 20$; $p < 0.0001$) (Figure 4). Herbivore and saprophage abundance was greatest at Shelby (Figure 4a,b), which represented the greatest EAB activity, reflected in EAB intercept trap catch [27], among the five sites. Fungivore abundance (Figure 4c) was positively correlated with ash decline and was greatest at Shelby, Anderson, and Henry, where disturbance caused by the EAB invasion was more advanced, and lowest at Fayette and Spencer, where EAB-related disturbance was minimal. Xylophages were most abundant at Spencer (Figure 4d), again representing relatively early stages of EAB invasion. Predator abundance (Figure 4e) was lowest

at Fayette and Henry, representing both pre- and post-EAB invasion and highest at the sites where the invasion is nearer its peak. Parasite abundance (Figure 4f) was similar across all sites.

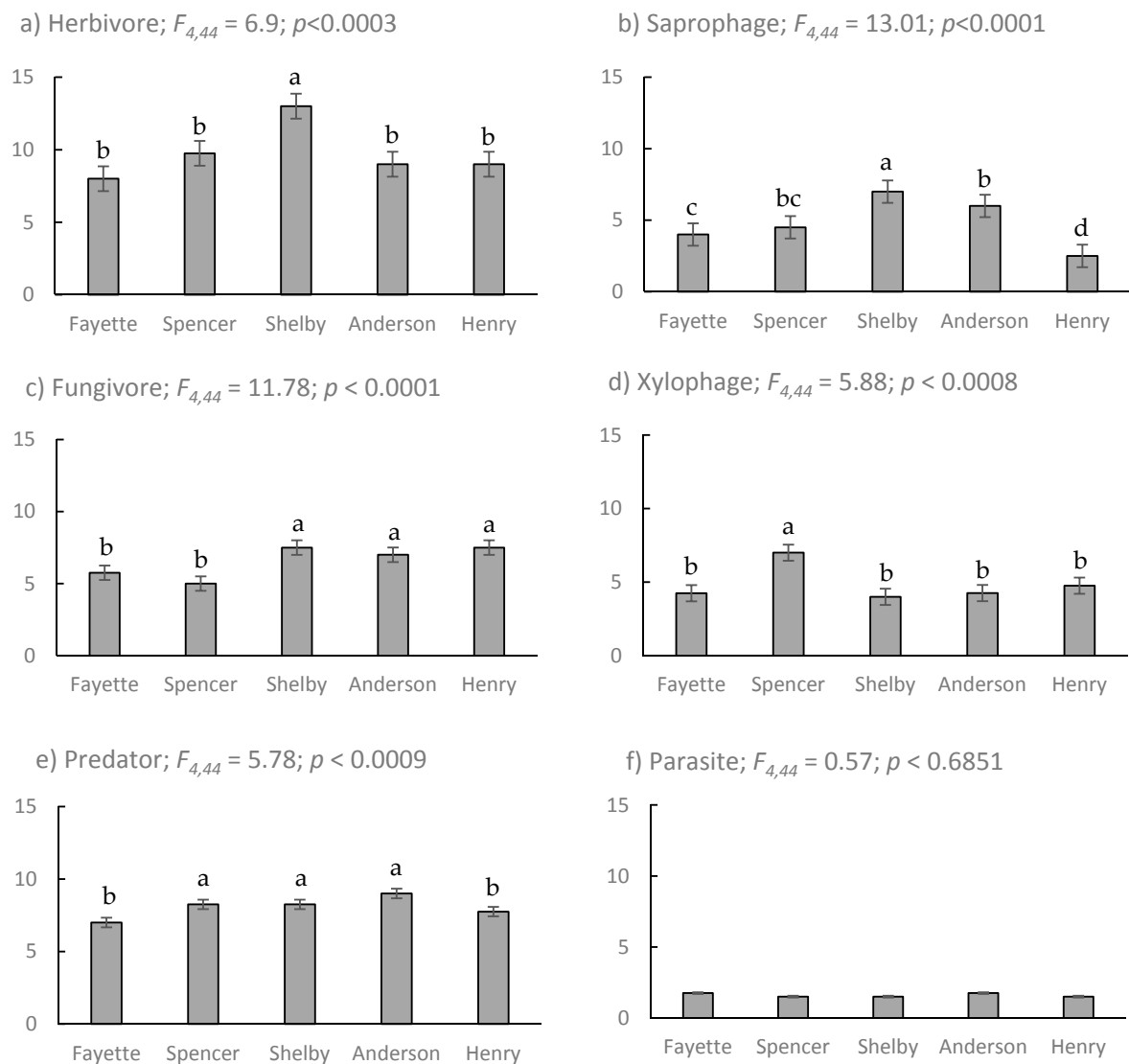


Figure 4. Coleopteran feeding guild abundance at five forested sites in north central Kentucky, including (a) herbivores, (b) saprophages, (c) fungivores, (d) xylophages, (e) predators, and (f) parasitoids. Means followed by the same letter do not differ ($\alpha = 0.05$).

Among the predators, Trogossitidae and Cleridae abundance (7% and 5% of total predator abundance, respectively) were positively correlated ($\alpha < 0.1$) with ash decline (Figure 5).

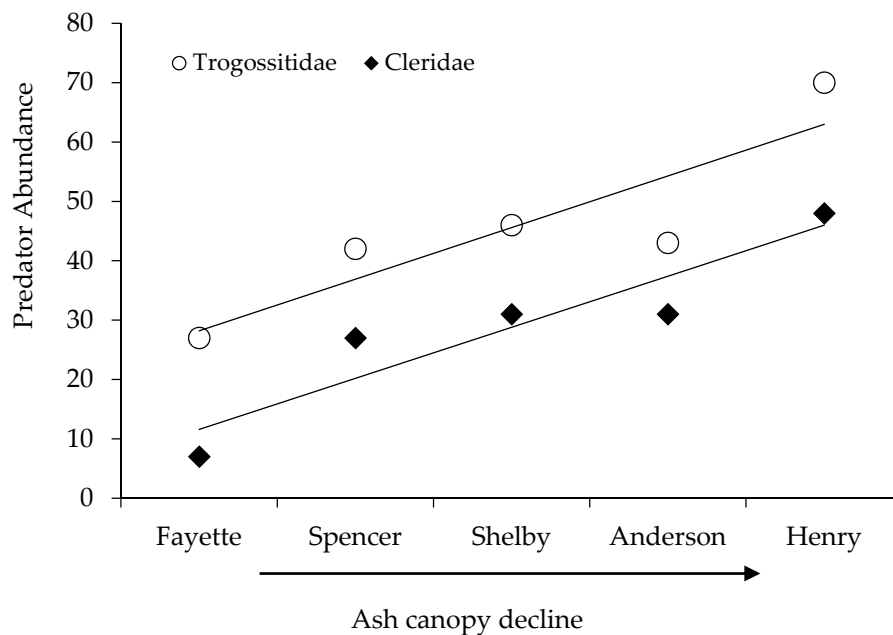


Figure 5. Relationship between *Fraxinus* canopy decline and abundance of two coleopteran predators: the Trogossitidae (Trogossitid abundance = $8.7 \times$ canopy decline (%) + 19.5, $R^2 = 0.71$, $p = 0.07$) and the Cleridae (Clerid abundance = $8.6 \times$ canopy decline (%) + 3, $R^2 = 0.74$, $p = 0.06$).

4. Discussion

Changes in structure, composition, and succession [14–18], alterations in light availability to the forest floor [19,20], and inputs of coarse woody debris associated with forest disturbance create and eliminate habitats [14–17,21,22,25], and affect resource availability and trophic relationships. Ash-dominated forests in the wake of the EAB invasion are expecting a loss of overall arthropod richness and are facing cascading ecological impacts and altered ecosystem processes. Of the 282 native arthropods associated with ash, 43 are monophagous; nine of these monophages are coleopterans [24]. Undoubtedly, these ash specialists will be negatively affected and may experience localized extirpation. We found discernible differences in aerial coleopteran communities associated with EAB-disturbed forests. The increase in abundance and cumulative richness of coleopteran associates where EAB activity density was at its greatest may be attributable to increases in habitat availability due to newly forming snags and coarse woody debris, and to volatile emissions from dying trees [30,31,48,49]. These resources are relatively transient, and as they decline we can anticipate a corresponding decline in coleopteran taxa reliant on their persistence. Contrary to expectations, coleopteran family evenness was highest in sites more heavily disturbed by EAB, where these transient resources would be most plentiful.

We found coleopteran abundance to be greatest among herbivores, comprised primarily of the Elateridae, which feed on flowers, nectar, pollen, and rotting fruit [35]. The Latridiidae, which feed on fungal reproductive structures and are common in plant debris [35], were the dominant fungivore family. The increase in fungivore richness that we observed may be a response to an increase in availability of these types of resources as ash decline progresses. Predators comprised 26% of the total trap catch, and consisted primarily of the Staphylinidae, which are generalist predators, and the Histeridae, which has one subfamily most commonly associated with bark beetle (Curculionidae) galleries [35,36]. Among the predators, Trogossitidae and Cleridae were positively correlated with ash decline. Trogossitids consisted of 228 individuals of primarily *Tenebroides* sp.; these are bark-gnawing beetles found beneath the bark of dead trees and are associated with wood-boring beetles [35]. Clerids (144 individuals) consisted primarily of *Enoclerus* sp.; these checkered beetles are associated with dead wood, and are often found predating larval Curculionidae, Cerambycidae, and Buprestidae [35].

Interestingly, the parasitic Passandridae, comprised entirely of *Catogenus rufus* (Fabricius), were consistently present in low numbers, regardless of the extent of forest disturbance (Figure 4f). *Catogenus rufus* has been found as both larvae and adults in EAB galleries from dead ash in EAB-invaded forests [27]; it was present in low numbers across sites and appeared unaffected by the stage of the EAB invasion or by the corresponding decline in ash canopies. Its presence at all sites in similar abundance suggests that it utilizes a variety of wood-boring hosts and is not demonstrating a numerical response to the EAB invasion in these forests, though it may still be utilizing EAB as a resource. *Tenebroides*, *Enoclerus* and *Catogenus* spp. have been documented in association with EAB larvae and pupae near the epicenter of the EAB invasion in North America [50], suggesting that they may be playing a role in population dynamics of this aggressive invader.

Our use of family level identifications in the evaluation of aerial coleopteran communities could be viewed as a limitation of this study. However, “taxonomic sufficiency” (sensu Ellis 1985 [38]) recognizes that, within a community, changes at the species level are often reflected at coarser taxonomic levels. The use of coarser taxonomic identifications reduces the inputs associated with large scale community level studies [40–42,51,52]. Family level richness is a good predictor of species richness for a variety of taxa, including butterflies [51]. Family level identifications of benthic fauna are appropriate for calculating stream quality indices [53–56] and multivariate analyses of community data [54], and can reliably detect moderate ecosystem impacts [57]. Identifications beyond the family level may not yield much more information and may not be cost effective [58]. Targeting coarser taxonomic resolution, rather than insisting upon species level identification for woody plant surveys, significantly reduces costs of field work [52]. Clearly, accepting coarser taxonomic sufficiency provides us with an effective approach to conduct rapid studies on ephemeral systems such as ours, as well as larger landscape scale studies over longer periods of time to answer broad questions regarding arthropod community responses to change. However, findings must be treated with caution, as not all members within a family are trophically equivalent (e.g., Formicidae) [58,59], leading to potentially misleading conclusions [60].

We compare the assemblage of aerial coleopterans in forest plots with no apparent EAB to the assemblage associated with the projected post-EAB community [17], which allows projections about long-term effects of ash loss on aerial coleopterans. Our comparative approach does not describe unforeseen alterations in successional trajectories independent of the EAB invasion, nor does it compare the ecological histories of the communities within these distinct forests, but it does provide a means of estimating potential long-term changes in arthropod community structure as a result of EAB-induced ash mortality (see [42,43]).

5. Conclusions

Endemic aerial coleopterans are readily utilizing the influx of resources provided by the EAB invasion. Collectively, our data suggest that native predators and parasites are being recruited to forests impacted by EAB, and that these native natural enemies may be a viable component of post-invasion EAB population dynamics in eastern North American forests.

Unprotected ash are devastated by the emerald ash borer. Following depletion of the ash resources, EAB populations sharply decline [61], greatly reducing the pest pressure on regenerating seedlings and saplings. The decline in pest pressure increases the chance of continued survival of young ash in North American forests [62], providing essential resources for ash specialists.

Ash forests are changing, and a deeper understanding of how arthropod communities and trophic guilds are responding will contribute to more proficient monitoring and protection.

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Author Contributions: M.B.S. and L.K.R. conceived and designed this experiment; M.B.S. performed the experiments and analyzed the data as partial requirements for a master degree; M.B.S. and L.K.R. wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Coleopteran family abundance at five forested sites in north central Kentucky with trophic guild designations including; herbivores (H), fungivores (F), predators (P), saprophages (S), xylophages (X), and parasitoids (Pa).

Coleopteran Families	Trophic Guilds	Abundance					Total
		Fayette	Spencer	Shelby	Anderson	Henry	
Elateridae	H	205	345	678	353	240	1821
Chrysomelidae	H	127	176	272	56	55	686
Curculionidae	H	81	127	154	99	113	574
Tenebrionidae	H	94	83	142	54	154	527
Mordellidae	H	48	103	148	75	59	433
Scarabaeidae	H	20	24	20	23	23	110
Phalacridae	H	2	5	26	6	12	51
Attelabidae	H	0	0	2	0	3	5
Latridiidae	F	141	33	274	230	340	1018
Corylophidae	F	21	2	73	41	94	231
Ptinidae	F	16	47	38	36	13	150
Eucnemidae	F	16	50	33	39	8	146
Erotylidae	F	14	14	8	16	17	69
Mycetophagidae	F	22	5	16	6	10	59
Tetratomidae	F	3	12	7	21	15	58
Nitidulidae	F	7	13	11	11	13	55
Cerylonidae	F	15	4	8	13	7	47
Zopheridae	F	6	10	5	13	5	39
Silvanidae	F	1	22	1	6	7	37
Melandyriidae	F	5	11	10	6	4	36
Synchroidae	F	4	4	6	9	9	32
Endomychidae	F	7	1	6	4	4	22
Leiodidae	F	5	2	3	8	4	22
Cryptophagidae	F	0	1	4	3	0	8
Laemophloeidae	F	3	1	1	2	1	8
Anthribidae	F	4	1	0	1	0	6
Cucujidae	F	0	0	1	1	0	2
Pyrochoidae	F	0	0	1	0	1	2
Sphindidae	F	0	0	1	1	0	2
Throscidae	F	0	1	0	0	1	2
Salpingidae	F	1	0	0	0	0	1
Staphylinidae	P	225	224	356	443	192	1440
Histeridae	P	188	316	141	204	136	985
Trogossitidae	P	27	42	46	43	70	228
Carabidae	P	16	20	63	43	34	176
Cleridae	P	7	27	31	31	48	144
Lampyridae	P	3	14	14	13	4	48
Coccinellidae	P	5	7	4	0	2	18
Melyridae	P	1	0	1	0	4	6
Cantharidae	P	0	2	1	0	0	3
Hydrophilidae	P	0	1	0	0	0	1
Lycidae	P	0	0	0	1	0	1
Ptilodactylidae	S	139	131	480	266	40	1056
Dermestidae	S	7	26	1	6	7	47
Monotomidae	S	2	6	0	0	0	8
Scirtidae	S	0	1	0	3	0	4
Hybosoridae	S	2	0	0	1	0	3
Silphidae	S						0

Table A1. Cont.

Coleopteran Families	Trophic Guilds	Abundance					
		Fayette	Spencer	Shelby	Anderson	Henry	Total
Scolytinae	X	168	465	107	117	134	991
Scraptiidae	X	1	1	8	24	53	87
Cerambycidae	X	6	13	12	19	24	74
Bostrichidae	X	1	5	2	0	3	11
Buprestidae	X	0	0	2	2	5	9
Lucanidae	X	0	0	0	1	0	1
Lymexylidae	X	0	0	0	1	0	1
Passandridae	Pa	21	13	14	16	14	78
Rhipiceridae	Pa	1	0	0	1	2	4
Bothrideridae	Pa	0	3	0	0	0	3
Unidentified	–	33	22	9	21	15	100
Total		1721	2436	3241	2389	1999	11,786

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