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Downed Coarse Woody Debris Dynamics in Ash (*Fraxinus* spp.) Stands Invaded by Emerald Ash Borer (*Agrilus planipennis* Fairmaire)

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Abstract: Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) has had major ecological impacts in forests of eastern North America. In 2008 and 2012, we characterized dynamics of downed coarse woody debris (DCWD) in southeastern Michigan, USA near the epicenter of the invasion, where the mortality of white (*Fraxinus americana* L.), green (*F. pennsylvanica* Marshall), and black (*F. nigra* Marshall) ash exceeded 99% by 2009. Percentage of fallen dead ash trees and volume of ash DCWD on the forest floor increased by 76% and 53%, respectively, from 2008 to 2012. Ash and non-ash fell non-randomly to the east and southeast, conforming to prevailing winds. More ash fell by snapping along the bole than by uprooting. By 2012, however, only 31% of ash snags had fallen, indicating that DCWD will increase substantially, especially if it accelerates from the rate of 3.5% per year documented during the study period. Decay of ash DCWD increased over time, with most categorized as minimally decayed (decay classes 1 and 2) in 2008 and more decayed (decay classes 2 and 3) in 2012. As the range of EAB expands, similar patterns of DCWD dynamics are expected in response to extensive ash mortality.

Keywords: *Agrilus planipennis*; ash; coarse woody debris; emerald ash borer; *Fraxinus*

1. Introduction

Above and belowground woody debris is a critical biological and structural component of forest ecosystems [1,2]. Through both standing material as snags and fallen material as logs, above-ground coarse woody debris (CWD) provides many ecological functions in terrestrial and aquatic ecosystems, including organic matter inputs; nutrient cycling; soil moisture retention; a habitat for vertebrate, invertebrate, and fungal species; micro-sites for plant regeneration; and altered fire behavior [3–9]. Depending on the disturbance rate, tree species, and rate of decomposition, CWD can impact forest ecosystem patterns and processes from decades to centuries [10,11].

Input and accumulation of CWD in forests is highly dynamic due to variation in the intensity and frequency of abiotic and biotic disturbances (e.g., fire, windstorms, ice-storms, and native and non-native insects and diseases) [12,13]. Consequently, tree death can occur on spatial scales that vary from individual to landscape levels, and time scales that vary from annually to 500 or more years [14–16]. Small-scale gap formation provides a slow but consistent input of CWD, whereas sudden large-scale ecosystem disturbances provide an infrequent but high input of CWD [14,17–19]. At the smallest spatial scale, tree death results in the formation of snags, with branches and stems breaking and falling at different rates [20]. CWD is also created when live trees fall, for example, during storms and/or under the weight of other falling trees. This results in a rich diversity of the type and volume of CWD inputs to the forest floor [20,21], which has major implications for nutrient cycling, successional pathways, and community dynamics, especially for organisms that depend upon dead and decaying wood for some part of their life cycles [6,9,22,23].

Alien insects and pathogens that kill trees provide a major input of CWD to forest ecosystems [24–26]. During the last century, alien insects and pathogens caused widespread tree mortality in North American forests, including hemlock woolly adelgid (*Adelges tsugae* Annand), as well as the chestnut blight (*Cryphonectria parasitica* (Murrill)), white pine blister rust *(Cronartium ribicola* J.C. Fisch.), Dutch elm disease (*Ophiostoma ulmi* (Buismann) Nannf.) pathogens, and beech bark disease (a complex of the scale insect *Cryptococcus fagisuga* Lindinger and *Neonectria* spp. fungi) [26–29]. Conversion of living trees to CWD by alien species at landscape scales within a relatively short time-frame represents a novel disturbance because these ecosystems have not previously experienced similar historical disturbance events. The impact on forests is patchy and confined to one or a few tree species in otherwise heterogeneous communities, and regeneration of the impacted species is typically limited by the alien invader. All of these factors interact to alter patterns of accumulation and decomposition of CWD. Despite the major ecological consequences of non-native insects and pathogens, only a few studies have quantified the effects of alien species on patterns of CWD accumulation and subsequent impacts on ecological processes [30,31].

Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) is the most damaging alien insect that has established in North American forests [32]. Introduced from eastern Asia, EAB attacks ash (*Fraxinus* spp.) [32], and to a lesser degree, white fringetree (*Chionanthus virginicus* L.) [33]. Since its first detection in North America in 2002 in southeast Michigan, USA, EAB has caused the widespread mortality of ash in invaded forests [34–37]. For example, Klooster et al. [35] observed >99% mortality of ash with stem diameters greater than 2.5 cm and a cessation of new seedling regeneration in southeastern Michigan near the epicenter of the invasion. Many North American ash tend to be abundant canopy trees in heterogeneous landscapes, and hence a major decline of ash, waves of tree mortality, and CWD formation will continue as EAB spreads across the landscape [31].

To better understand the dynamics of DCWD in response to tree mortality caused by alien species, we quantified the formation and accumulation of DCWD in forests in the Upper Huron River watershed in southeastern Michigan, where rates of ash decline and mortality were previously documented [35,38,39]. These forests are near the epicenter of the EAB invasion [40], and thus have been impacted longer than any other in North America. Our research objectives were to: (1) quantify the current volume (m^3 ha^{-1}) and species of DCWD (as fallen trees or logs); (2) assess whether the change in the rate of input of DCWD to the forest floor corresponded with the rate of change of ash mortality; (3) determine whether there were any differences in the pattern of accumulation of DCWD between ash and non-ash tree species; (4) assess the manner of treefall (broken or uprooted) and the height of broken stumps; and (5) assess the spatial patterns of DCWD accumulation (i.e., the general direction of treefall within these forest stands). Results from this study may contribute to the prediction and management of CWD dynamics (e.g., which ash species will fall first and when) in response to EAB-induced ash mortality in North America.

2. Materials and Methods

2.1. Study Sites

The study was conducted in a subset of 16 forested stands randomly selected from 38 stands previously established and characterized in the Livingston, Oakland, and Washtenaw counties in the Upper Huron River watershed in southeastern Michigan [35,38,39,41]. The 16 stands represented a gradient of percentage ash mortality that decreased with the distance (25–45 km) from the presumed epicenter of EAB infestation in the township of Canton, Michigan, USA [38–40] and were located in the Highland, Island Lake, Pontiac, and Proud Lake State Recreation Areas, and Hudson Mills, Indian Springs, and Kensington Metro Parks (Table S1, Figure S1). The soils are Hapludalfs with loamy to clay and sandy texture [42]. Average annual temperature was 8.7–12.1 °C, average annual precipitation was 69–121 cm, and average annual snowfall was 66–241 cm from 1997–2017 near Detroit, Michigan, USA [43]. The forest overstory consisted of oak (*Quercus* spp.), maple (*Acer* spp.), basswood (*Tilia* spp.), cherry (*Prunus* spp.), elm (*Ulmus* spp.), and tamarack (*Larix* spp.) [38]. Ash was once abundant in these forests [38,39]. The density and basal area of ash ranged from 32.9 to 461.1 stems ha^{-1} and 2.8 to 14.5 m^2 ha^{-1}, respectively, in these stands in 2005 prior to significant treefall [39]. However, across all stands sampled, the mortality of ash with stem diameters greater than 2.5 cm exceeded 95% by 2008 and 99% by 2009 [35]. Detailed information about these stands, including overstory and understory species composition, soil conditions, and patterns of ash mortality, can be found in Smith [38], Klooster et al. [35], and Smith et al. [39].

Within each stand, we utilized a previously established transect that consisted of three 0.1 ha replicate circular plots, each with a radius of 18 m. When established, transects were oriented along a randomly selected compass heading between 0–90°, and plots contained at least two mature ash trees with stem diameters greater than 10 cm. Within a transect, the replicate plots were separated by ~80 m from their centers [35,38,39]. Each transect was previously classified according to soil moisture class as xeric, mesic, or hydric, in which white ash (*Fraxinus americana* L.), green ash (*Fraxinus pennsylvanica* Marsh.), or black ash (*Fraxinus nigra* Marsh.) was the most common ash species, respectively [35,38,39]. The formation and accumulation of DCWD was quantified in 48 circular plots within the 16 transects (three xeric, eight mesic, and five hydric).

2.2. Sampling of Downed Coarse Woody Debris

Percentage mortality of ash was monitored in each plot annually from 2004–2013 [35,38,39]. Sampling was conducted during the summers of 2008 and 2012 to assess temporal patterns of treefall and accumulation of DCWD. All ash trees with stem diameters $\geq$10 cm were cataloged in each plot as either standing or fallen. We sampled DCWD (i.e., logs which included boles and branches) rather than standing coarse woody debris (i.e., snags). To be considered DCWD, each piece had to meet the following criteria [as modified from the USDA Forest Service Forest Inventory Analysis (FIA) guidelines]: (1) diameter at the small end $\geq$7.6 cm; (2) length $\geq$ 1 m; and (3) distance above the forest floor $\leq$ 0.5 m (i.e., leaning snags and suspended woody debris were excluded) [44]. If a log had a diameter <7.6 cm at the small end, the diameter and length measurements (at least 1 m long) were taken from where the end diameter met the above requirements. If the bole was broken, each piece was independently assessed. Measurements of DCWD were taken using a dbh-tape for diameters and a logger tape measure for the length. Diameters and lengths were measured at the end of each intact side with the size criteria as described previously. Portions of DCWD that extended outside of the plot were excluded from the study (i.e., only the portions within the plots that met the above criteria were measured).

All sections of DCWD were categorized according to decay class using a 1–5 decay stage scale adapted from the USDA Forest Service FIA guidelines [44] as follows: Class 1—recently fallen CWD with intact bark, sound wood, and no decay; Class 2—mostly intact bark and wood (cannot be pulled apart by hand), but with softer sapwood and early signs of decay; Class 3—bark in advanced stage of decay (but present), sapwood can be pulled apart by hand, but heartwood is sound and can maintain its own weight; Class 4—bark and sapwood decayed, heartwood beginning to decay, the log cannot support its own weight, but maintains its shape; and Class 5—bark, sapwood, and heartwood has decayed, loss of structural integrity, and the log is incorporated into the forest floor. Based on these decay class descriptions, tree species were identified for DCWD in classes 1–3, but it was not possible to identify species for DCWD in classes 4–5. Therefore, DCWD was categorized as either known (to genus or species level) or unknown, and further as ash or non-ash. Fallen trees were categorized based on whether they uprooted or snapped along the trunk. Heights of broken stumps were measured at the highest point using a logger tape measure. Azimuth (degrees) was measured by pointing a compass towards either the top of the tree or smaller end of the piece of DCWD to assess the direction of fall.

2.3. Statistical Analyses

Percentage of fallen (versus standing) ash was calculated at the plot level for trees with stems $\geq$ 10 cm in diameter in 2008 and 2012. The year at which 90% ash mortality was reached at the transect level was identified, and the number of years since 90% ash mortality was determined for each transect in 2008 and 2012. Volume (m^3) of DCWD was calculated using the formula for a frustum cone:

$$V = \frac{\pi l}{3}\left(R^2 + Rr + r^2\right) \quad (1)$$

where r is the small radius, R is the large radius, and l is the length of the log [45,46]. Volumes of total DCWD, non-ash DCWD, and ash DCWD were calculated separately to assess patterns of woody debris accumulation from EAB-induced ash mortality.

Separate repeated measures analysis of variance (RMANOVA) tests were used to compare: (1) the percentage of ash trees that had fallen; (2) the volume of non-ash DCWD; (3) the volume of total DCWD; and (4) the volume of ash DCWD across the three habitat types based on soil moisture conditions (xeric, mesic, and hydric) from 2008 to 2012 using the package 'car' [47] in R version 3.7.1 [48]. All four response variables were calculated at the plot level and then averaged across the three replicate plots in each transect, which was the unit of replication in this study. Volume data were then multiplied by 10 to express values on a per hectare basis. All data were checked for statistical assumptions of normality and homogeneity of variance. Volume data for total DCWD and non-ash DCWD did not meet assumptions of normality and were rank transformed [49]. Predictor variables for the four ANOVA models were soil moisture class (xeric, mesic, or hydric) as a fixed factor, transect as a random factor, and year (2008 or 2012) as a repeated factor. Tukey's pairwise comparisons were used to evaluate mean separation following a significant F-test. Data are reported as mean $\pm$ standard error. At the stand level, the relationship between the percentage of ash trees that had fallen and the number of years since occurrence of 90% ash mortality was characterized by regression analysis.

Chi-square analyses were used to determine whether ash DCWD decay class or the method of treefall (broken or uprooted) were influenced by ash species (*F. americana*, *F. pennsylvanica*, or *F. nigra*), soil moisture class (xeric, mesic, or hydric), or year (2008 or 2012; assessed for decay class only). All percentage data met assumptions of equal variances. Only decay classes 1-3 were included in the analyses to ensure the accurate identification of ash species. Kruskal-Wallis tests were used to compare the heights of broken ash stumps (pooled across years) by species (*F. americana*, *F. pennsylvanica*, or *F. nigra*) and by soil moisture class (xeric, mesic, or hydric). Chi-square and Kruskal-Wallis analyses were completed using the package 'stats' in *R* version 3.7.1 [48].

For the treefall data, all analyses were performed at the transect level by taking an average of azimuth or angles of fallen trees from the three plots. Transects that had <3 fallen trees were excluded from the analyses [2008: N (transects) = 8 for ash and N = 12 for non-ash; 2012: N = 12 for ash and N = 12 for non-ash trees]. We performed analyses of uniformity to test the null hypothesis that there was no mean sample direction of treefall (based on the averages of angles of fallen trees) for ash and non-ash species. Rayleigh z analysis was used, which is a likelihood ratio test for uniformity within the von Mises distribution family [50,51]. Angular data were first transformed into polar coordinates (sine and cosine) to place them in a Cartesian space before conducting the Rayleigh *z* tests. Watson U^2 non-parametric tests were conducted to compare the directions of treefall between: (1) ash and non-ash trees within each year; and (2) across years for the same tree-type (2008 and 2012) [50]. Rose Diagrams were used to plot frequency distributions of the angles of individual fallen trees (rather than individual transects) in circular histograms [52].

3. Results

Across all stands, the overall mortality of ash with stems $\geq$ 10 cm in diameter was 99.5 $\pm$ 0.3% in 2008 and 99.6 $\pm$ 0.4% in 2012, with 90% mortality reached in three stands in 2006, in eight stands in 2007, and in the remaining five stands in 2008. The density of standing dead ash decreased from 123.8 $\pm$ 13.6 trees ha^{-1} in 2008 to 98.5 $\pm$ 12.3 trees ha^{-1} in 2012, while the density of fallen dead ash increased from 11.3 $\pm$ 2.1 to 39.2 $\pm$ 5.7 trees ha^{-1} in 2008 and 2012, respectively. The percentage of dead ash trees that had fallen increased from 7.6 $\pm$ 1.0% in 2008 to 30.7 $\pm$ 3.3% in 2012 ($F_{1,4}$ = 105.9; P < 0.001), with no differences among soil moisture classes ($F_{2,4}$ = 0.08; p = 0.776). At the stand (transect) level, the percentage of dead ash that fell increased 3.5% per year after ash mortality reached 90% (Figure 1; percentage of ash fallen = 2.81 + 3.53 $\times$ years; $F_{1,30}$ = 57.4; R^2 = 0.65; p < 0.001).

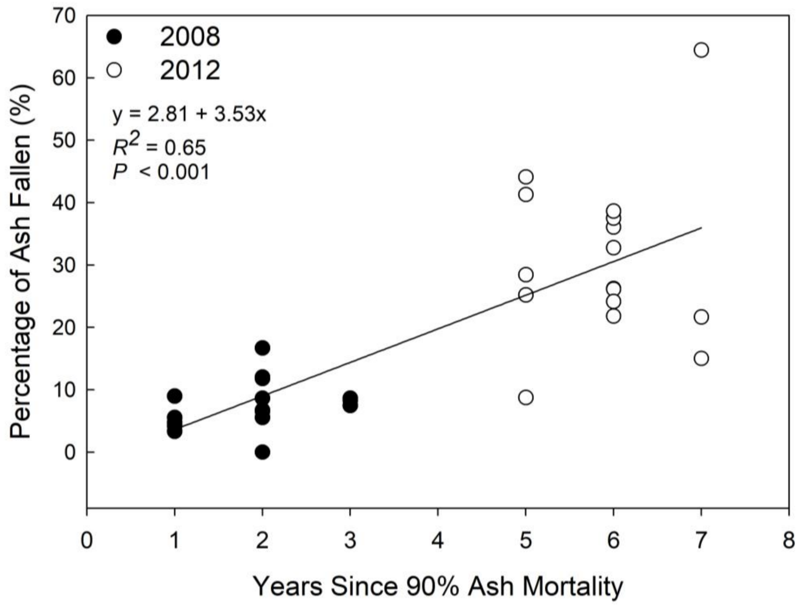

Figure 1. Relationship between the percentage of dead ash (*Fraxinus* spp.) that had fallen and the number of years since the occurrence of 90% ash mortality in 16 forest stands sampled in 2008 (open circles) and in 2012 (closed circles) in the Upper Huron River watershed in southeastern Michigan, USA. Stands reached 90% ash mortality in 2006, 2007, or 2008.

A higher percentage of ash trees fell to the forest floor by snapping along the bole (62.5 $\pm$ 4.4%) than by uprooting (37.4 $\pm$ 4.4%) (Figure 2A; χ^2 = 26.2; p = 0.010). A higher percentage of *F. americana* fell to the forest floor by breaking than by uprooting, as compared to *F. pennsylvanica* or *F. nigra* (Figure 2B; χ^2 = 17.1; P = 0.020). The method of ash treefall was not influenced by soil moisture class (χ^2 = 11.3; P = 0.788). Average stump height of broken ash trees was 2.5 $\pm$ 0.4 m and was not influenced by species (χ^2 = 5.50; P = 0.064) or by soil moisture class (χ^2 = 1.58; P = 0.452).

Ash and non-ash trees fell in a non-random manner in 2008 (ash: Rayleigh z = 4.602, 0.02 > P > 0.01; non-ash: z = 11.875, P < 0.001) and 2012 (ash: z = 9.063, P < 0.001; non-ash: z = 9.79, P < 0.001), indicating a distinct direction of treefall towards the east and southeast (Figure 3). Watson U^2 tests suggested that there were no differences in the direction of treefall between ash and non-ash trees in 2008 (U^2 = 0.06,

$P > 0.05$) and 2012 ($U^2 = 0.05$, $P > 0.05$). Similarly, there were no differences in the direction of treefall between 2008 and 2012 for ash ($U^2 = 0.102$, $P > 0.05$) and non-ash ($U^2 = 0.111$, $P > 0.05$).

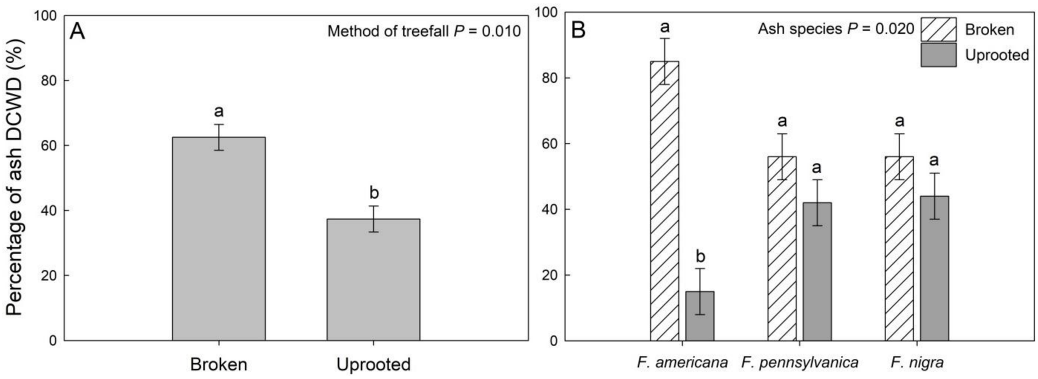

Figure 2. Average percentage (±SE) of downed coarse woody debris (DCWD) by method of treefall (broken or uprooted) (**A**) and by ash species (white ash, *Fraxinus americana* L.; green ash, *Fraxinus pennsylvanica* Marsh.; and black ash, *Fraxinus nigra* Marsh.) that fell to the forest floor by breaking (white bars) or uprooting (gray bars); (**B**) in 16 forest stands in the Upper Huron River watershed in southeastern Michigan, USA. Different letters indicate a significant difference at $\alpha = 0.05$.

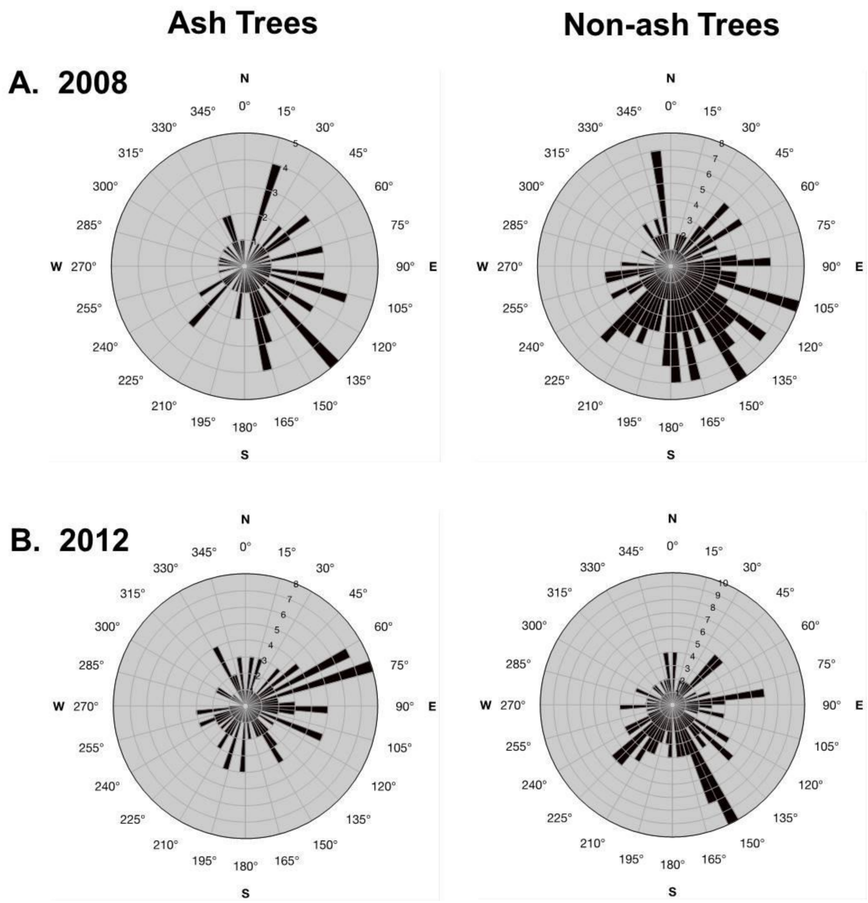

Figure 3. Average azimuth (angles) of the direction of fall for ash (left) and non-ash (right) trees in 2008 (**A**) and 2012 (**B**) in 16 forest stands in the Upper Huron River watershed in southeastern Michigan, USA. The numbers within the circles refer to frequency distribution of the angles of individual trees. Analyses were performed at the transect-level with transects that had <3 fallen trees excluded (2008: N (transects) = 8 for ash and N = 12 for non-ash; 2012: N = 12 for ash and N = 12 for non-ash trees).

Ash species comprised 17% and 27% of the total volume of DCWD sampled in 2008 and 2012, respectively (Table 1). Other tree species comprised 27% in 2008 and 11% in 2012, and DCWD classified as 'unknown' comprised 56% in 2008 and 62% in 2012 (Table 1). From 2008 to 2012, ash trees that had fallen increased the volume of ash DCWD by 53% ($F_{1,10}$ = 15.1; P = 0.003) (Table 2). Average volume of ash DCWD was 17.2 ± 3.3 m^3 ha^{-1} (range of 0.18–45.2 m^3 ha^{-1}) in 2008 and 36.6 ± 4.1 m^3 ha^{-1} (range of 29.5–56.4 m^3 ha^{-1}) in 2012 (Table 2). Volume of ash DCWD was higher in wetter (hydric and mesic) stands than in xeric stands ($F_{1,10}$ = 4.3; P = 0.043).

Table 1. Average ± SE volume (m^3 ha^{-1}) and percentage of downed coarse woody debris (DCWD) by tree species in 2008 and 2012 in 16 forest stands in the Upper Huron River watershed in southeastern Michigan, USA.

Tree Species	2008		2012	
	Volume (m^3 ha^{-1})	Percentage of Total DCWD	Volume (m^3 ha^{-1})	Percentage of Total DCWD
Acer spp.	16.8 ± 16.1	16.5	4.5 ± 1.6	7.1
Fraxinus pennsylvanica Marsh.	9.3 ± 2.9	9.1	7.9 ± 2.1	11.4
Fraxinus nigra Marsh.	4.6 ± 1.7	4.5	7.1 ± 3.1	10.3
Fraxinus americana L.	3.5 ± 1.7	3.4	2.8 ± 1.7	5.5
Populus deltoides Bartr. ex Marsh.	5.8 ± 5.8	5.6	0.2 ± 0.1	0.3
Quercus spp.	2.5 ± 1.9	2.8	1.1 ± 0.6	1.7
Prunus serotina Ehrh.	0.5 ± 0.3	0.5	0.4 ± 0.3	0.5
Larix spp.	0.8 ± 0.8	0.8	0.0	0.0
Tilia americana L.	0.3 ± 0.1	0.3	0.3 ± 0.1	0.4
Ulmus spp.	0.2 ± 0.1	0.2	0.1 ± 0.1	0.1
Carya spp.	0.0	0.0	0.2 ± 0.1	0.3
Sassafras albidum (Nutt.) Nees	0.1 ± 0.1	0.05	0.1 ± 0.1	0.2
Fagus grandifolia Ehrh.	0.1 ± 0.1	0.1	0.0	0.0
Betula spp.	0.1 ± 0.1	0.05	0.0	0.0
Carpinus caroliniana Walt.	0.1 ± 0.1	0.3	0.0	0.0
Unknown	56.9 ± 10.3	55.8	39.8 ± 9.4	62.2

Table 2. Patterns of downed coarse woody debris (DCWD) sampled in 2008 and 2012 in 16 forest stands in the Upper Huron River watershed in southeastern Michigan, USA for the percentage of ash trees that had fallen, volume of ash DCWD (m^3 ha^{-1}), volume of non-ash DCWD (m^3 ha^{-1}), and volume of total (ash and non-ash) DCWD (m^3 ha^{-1}) by year (2008 and 2012). Data are expressed as mean ± SE, with percentage of total DCWD in parentheses. Comparisons were made across years, with means followed by different letters being significantly different at α = 0.05.

	Year	
	2008	2012
Percentage of ash trees that had fallen	7.6 ± 1.0 a	30.7 ± 3.3 b
Volume of ash DCWD (m^3 ha^{-1})	17.2 ± 3.3 a (17.0%)	36.6 ± 4.1 b (27.2%)
Volume of non-ash DCWD (m^3 ha^{-1})	90.3 ± 24.2 a (83.0%)	68.3 ± 10.1 a (72.8%)
Volume of total DCWD (m^3 ha^{-1})	106.7 ± 26.0 a (100%)	93.5 ± 12.3 a (100%)

Volume of non-ash DCWD did not change from 2008 to 2012 (Table 2; $F_{1,12}$ = 0.15; P = 0.701), and did not differ across soil moisture classes ($F_{2,12}$ = 1.2; P = 0.310). Moreover, volume of total (ash and non-ash) DCWD also did not change over time (Table 2; $F_{1,12}$ = 2.2; P = 0.158), or differ across soil moisture classes ($F_{2,12}$ = 0.8; P = 0.437).

In 2008, higher percentages of ash DCWD were characterized as decay classes 1 and 2, but in 2012, higher percentages of ash DCWD were characterized as decay classes 2 and 3 (Figure 4; χ^2 = 83.1; P = 0.004). Decay classes of ash DCWD did not vary by ash species (P ranged from 0.143–0.837) or by soil moisture class (χ^2 = 58.3; P = 0.076).

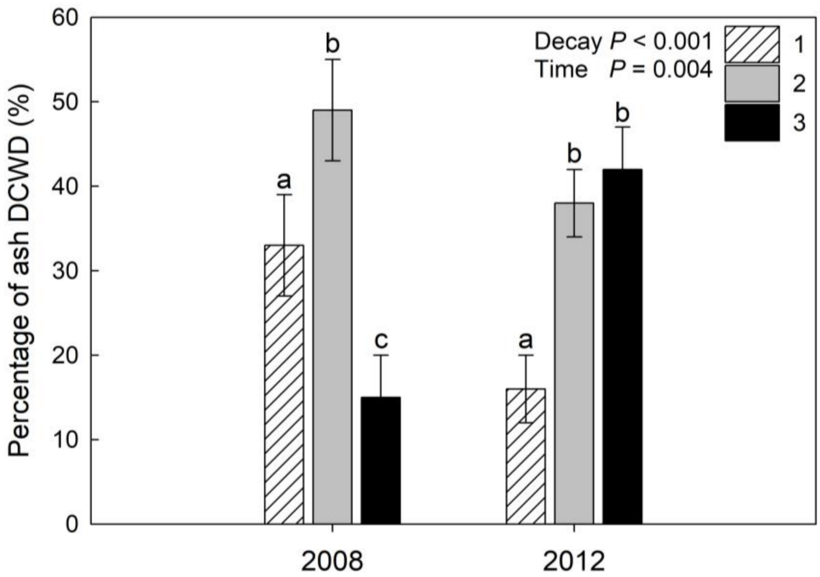

Figure 4. Average percentage (±SE) of downed coarse woody debris (DCWD) that was ash by year (2008 and 2012) for decay classes 1 (white bars), 2 (gray bars), and 3 (black bars) in 16 forest stands in the Upper Huron River watershed in southeastern Michigan, USA. Different letters indicate a significant difference at $\alpha = 0.05$.

4. Discussion

By 2009, ash mortality exceeded 99% in forests in the Upper Huron River watershed of SE Michigan near where EAB first established in North America [35]. By 2008, 8% of dead ash trees greater than 10 cm dbh had fallen, which increased to 31% by 2012. Temporal dynamics of ash and non-ash DCWD in these forests revealed the following patterns: (1) over the time-frame of our study, dead ash trees fell at a rate of 3.5% per year once stands reached 90% ash mortality; (2) dead ash trees fell primarily by snapping along the bole and to a lesser degree by uprooting; (3) ash and non-ash trees fell mostly towards the east and southeast in the direction of prevailing winds; (4) volume of ash DCWD increased nearly two-fold from 2008 to 2012, while volume of non-ash and total DCWD did not change; and (5) majority of ash DCWD was characterized as minimally decayed in 2008, with degree of decay increasing over time. To our knowledge, this is the first study that has investigated temporal dynamics of CWD accumulation following extensive tree mortality from an invasive insect.

Mortality of ash trees with stem diameters $\geq$ 10 cm reached 90% in 2006, 2007, or 2008 in the stands we sampled, but most dead trees were still standing or leaning as snags in 2008, with only 8% of trees having fallen. Once ash mortality reached 90% in a stand, the percentage of dead ash that fell and became DCWD increased at a rate of 3.5% per year through 2012. Volume of ash DCWD doubled from 2008 to 2012, increasing by 19 m^3 ha^{-1} in these stands. Volume of non-ash DCWD did not change over the four years of this study, which indicates that the increase in ash DCWD resulted from EAB-induced ash mortality, rather than another disturbance such as ice or wind that would have affected a broader diversity of tree species. By 2012, however, only 31% of ash snags had fallen to the forest floor, which indicates that the volume added to these forests by EAB-induced ash mortality will increase substantially in the years following this study. Higham et al. [31] observed faster rates of treefall in Ohio forests during earlier stages of EAB invasion, with 60–80% of the standing dead ash falling to the forest floor within six to seven years after ash mortality had reached only 25%. In the stands we sampled, ash mortality had already reached 40% by 2004 [35,39].

The magnitude of the pulse of ash DCWD accumulation that we observed from 2008 to 2012 was not enough to significantly increase the total volume of DCWD (combined ash and non-ash) at our study sites. A trend for a decline in the volume of non-ash species may have contributed to this pattern, although the difference between the two years sampled was not statistically significant.

As a basis of comparison, the volume of DCWD measured in southern Ohio forests prior to the EAB invasion averaged 42.0 $\pm$ 5.1 m^3 ha^{-1}, with ash species comprising 7.6 $\pm$ 2.5 m^3 ha^{-1} of the total [53]. This is less than half the total volume of DCWD that we observed in 2008 and 2012, but the percentage of DCWD that was ash (18%) in the Ohio forests was very similar to what we observed in Michigan in 2008 (17%). By 2012, the volume of ash DCWD in our study sites had more than doubled.

Only a few studies have investigated the accumulation of DCWD from tree mortality caused by alien insects. Higham et al. [31] found that the volume of DCWD in forests experiencing early stages of EAB-induced ash mortality ($\geq$ 25%) averaged 60.3 m^3 ha^{-1}, and was positively correlated with ash basal area. They did not differentiate between total volume of ash and non-ash DCWD, but ash comprised a higher proportion of the total volume of minimally decayed DCWD (decay class 1) in sites with a higher ash mortality. In forests of a similar composition [54], but much more advanced ash mortality, we observed that substantially lower percentages of dead ash had fallen, but higher volumes of total DCWD, when compared to Higham et al. [31].

Mortality of American beech (*Fagus grandifolia* Ehrh.) caused by beech bark disease resulted in DCWD accumulation of 13 and 38 m^3 ha^{-1} in maturing and old growth northern hardwood forests, respectively, in New York [46]. These values are comparable to the volume of ash DCWD observed in this study (17.2 m^3 ha^{-1} in 2008 and 36.6 m^3 ha^{-1} in 2012), although tree mortality from EAB has occurred faster and more recently than from beech bark disease, which has existed in North America since the early 1900s [55]. Although extensive mortality of hemlock (*Tsuga* spp.) caused by hemlock woolly adelgid (HWA) has occurred in eastern North America since its introduction in the 1950s, studies have generally reported percentage cover but not volume of DCWD on the forest floor [56–58]. A manipulative experiment designed to investigate the effects of HWA-induced tree mortality and preemptive management via logging [59] found that trees girdled to simulate early stages of decline and mortality by HWA were still standing after four years [60]. By year five, carbon inputs from hemlock DCWD in the girdled treatment were >three-fold higher than in the logging treatment, and >two-fold higher than in the treatment meant to simulate two decades post-HWA disturbance [61].

Ash species comprised 17% and 27% of the total volume of DCWD measured in 2008 and 2012, respectively, for this study, although most could not be confidently identified to species due to the loss of bark and decomposition. Nearly 25% of ash DCWD was determined to be decay class 1 and over 40% was categorized as decay class 2, indicating that this pool of downed wood was still intact with sound structural integrity (class 2 has early stages of decay, but heartwood is still sound), attached branches, and the absence of invading roots [44,62]. Based on ash decay class transition models [63], this suggests there was a pulse of ash DCWD accumulation on the forest floor approximately five years prior to this study. We observed a shift in the percentage of ash DCWD from decay classes 1 and 2 in 2008 to decay classes 2 and 3 in 2012, as decomposition progressed over time. Many biotic and abiotic factors contribute to the rate of woody debris decomposition, which can take up to several decades or longer depending on species-specific factors and site-specific conditions [1,62,64–66], although ash is considered to have a low resistance to decay [45]. We observed a similar progression of ash decay irrespective of ash species or soil moisture class.

Ash and non-ash trees fell primarily to the east and southeast, which conforms to prevailing winds, with no effects of tree species, year, or soil moisture class. Over 60% of ash trees fell to the forest floor by snapping along the bole at an average of 2.5 m above the ground with the rest uprooting. Understanding how ash trees fall and in which direction will contribute to the management of dead ash trees in urban and recreational landscapes where standing snags may pose safety hazards. Among species, this pattern of treefall was driven by *F. americana*, with over 80% of trees snapping, while similar percentages of *F. pennsylvanica* and *F. nigra* fell by snapping and uprooting. Method of treefall did not differ by soil moisture class, suggesting that other species-specific properties may have contributed to this pattern of treefall. Snags (i.e., standing dead trees) create habitat for a variety of forest species [1,67–71]. When they snap, the litter and soil layers are minimally disturbed beyond the point of impact. Trees that uproot, however, result in a patchy formation of pit-and-mound topography, which can have long-term effects on community dynamics by altering patterns of nutrient cycling, standing water, and the physical and chemical properties of the soil through mixing of the litter and soil layers, exposing the root mass, and adding fine and coarse woody debris to the forest floor [72–74].

Altered patterns of DCWD formation and accumulation from tree mortality caused by alien insects and pathogens indirectly affect plant and animal populations in forests. As a fundamental structural component, DCWD increases habitat complexity [75] and provides resources for wildlife such as food, habitat, and sites for sprouting, breeding, and overwintering [1,70,76]. DCWD acts as refugia for species including ground-dwelling invertebrates [77,78], amphibians and reptiles [79], and small mammals [80]. The accumulation and decomposition of ash DCWD caused by EAB-induced ash mortality impacted the abundance, diversity, and community composition of ground-dwelling invertebrates [81–84]. Because the distribution of ash species is widespread in North America [85], the pulse of ash DCWD resulting from ash mortality will have widespread ecological impacts on the flora and fauna of forests as EAB continues to expand its range.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/9/4/191/s1, Figure S1: Location of transects within the Upper Huron River watershed in southeastern Michigan, USA. From bottom-left to top-right, parks include Hudson Mills MetroPark (red), Island Lake State Recreation Area (purple), Kensington MetroPark (blue), Proud Lake State Recreation Area (green), Highland State Recreation Area (pink), Pontiac State Recreation Area (brown), and Indian Springs MetroPark (orange), Table S1: GPS coordinates and additional information for transects within the Upper Huron River watershed in southeastern Michigan, USA. For this study, 16 transects were selected from 38 transects previously established and characterized by Smith [38], Klooster et al. [35], and Smith et al. [39].

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