

Review

Responses of Ground-Dwelling Invertebrates to Gap Formation and Accumulation of Woody Debris from Invasive Species, Wind, and Salvage Logging

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Abstract: Natural and anthropogenic disturbances alter canopy structure, understory vegetation, amount of woody debris, and the litter and soil layers in forest ecosystems. These environmental changes impact forest communities, including ground-dwelling invertebrates that are key regulators of ecosystem processes. Variation in frequency, intensity, duration, and spatial scale of disturbances affect the magnitude of these environmental changes and how forest communities and ecosystems are impacted over time. We propose conceptual models that describe the dynamic temporal effects of disturbance caused by invasive insects, wind, and salvage logging on canopy gap formation and accumulation of coarse woody debris (CWD), and their impacts on ground-dwelling invertebrate communities. In the context of this framework, predictions are generated and their implications for ground-dwelling invertebrate communities are discussed.

Keywords: arthropods; disturbance; emerald ash borer; exotic species; tornado

1. Disturbance in Forest Ecosystems

Disturbances are inherently variable events that generate spatial and temporal heterogeneity in forest ecosystems by altering habitat structure, energy and nutrient flow, and species composition, thereby shaping long-term patterns in community dynamics and ecosystem processes [1–4]. In forest ecosystems, disturbances are natural (e.g., fire, wind, floods, ice, insect and disease outbreaks) or anthropogenic (e.g., invasive species, forest management practices, land-use change) [5–9]. Natural and anthropogenic disturbances impact forest communities directly through tree mortality and indirectly through changes in resource availability, habitat structure, competitive interactions, and ecosystem processes [10,11]. Disturbance events can be characterized by properties including type, intensity, frequency, severity, extent, and duration [1,12,13] that determine their impact on forest structure and function. These events range on a continuum from small-scale, low intensity, frequent disturbances affecting individual trees to large-scale, high intensity, infrequent disturbances affecting entire stands [3]. Depending on their nature, the effects of disturbance on forest communities and ecosystems can have major ecological and economic impacts [14–16].

Establishment and spread of invasive species is a significant driver of anthropogenic environmental change, and has been identified as a threat to natural ecosystems, second only to habitat destruction [17–19]. The frequency of biological invasions continues to increase worldwide [20,21], causing unprecedented economic impacts while threatening native habitat, biodiversity, and ecosystem services [11,17,22–24]. Moreover, invasive species are capable of modifying as well as creating new disturbances with potentially novel combinations of properties [5,9].

Climate change may result in unexpected ecological and economic impacts in forest ecosystems due to altered disturbance regimes [25]. Patterns of forest disturbance and their effects on communities are influenced by climate change by means of altered disturbance properties [26]. For example, climate change is predicted to increase the intensity and frequency of strong storms that can cause extensive stand-replacing disturbance in forests [25,26]. This likely would affect land management decisions by increasing pressures to salvage timber in order to recover economic losses, perhaps with effects that counter conservation objectives such as retaining structural legacies created by natural disturbances.

Disturbances maintain local and landscape heterogeneity through the creation and spatial arrangement of biological legacies [2,27,28], which have been defined as “organisms, organically derived structures, and organically produced patterns” remaining in the disturbed patch [29]. Such legacies include living residual trees, snags, newly downed boles and existing woody debris, tip-up mounds and pits from fallen trees, intact ground-level understory vegetation, advanced regeneration, and patches of undisturbed forest [2,27,30]. Anthropogenic disturbances alone or in combination with natural disturbances may deplete these structural features [29], resulting in altered or exacerbated effects on community and ecosystem dynamics [31]. Natural and anthropogenic disturbances often result in tree mortality, which creates biological legacies that include altered canopy structure and accumulation of woody debris on the forest floor. Outbreaks of invasive insects and strong winds are two disturbances that cause tree mortality in forest ecosystems [3,9,32–36], and affect millions of hectares of forest globally [37]. These agents form canopy gaps and alter the amount of CWD on the forest floor, which has the potential to affect populations of ground-dwelling invertebrates.

Responses of ground-dwelling invertebrates to natural and anthropogenic disturbances have implications for ecosystem services, including decomposition, nutrient cycling, and maintenance of soil structure [38–43]. Invertebrates respond quickly to changes in forest structure and microclimate such as soil moisture [44], leaf litter [45], and vegetation cover [46]. Because of this, several taxa, including ground beetles, spiders, ants, and springtails, have been used as biological indicators [47–50]. High taxonomic and functional diversity of ground-dwelling invertebrate communities makes them a fundamental component of the forest ecosystem, and their sensitivity to environmental change makes them useful for detecting and characterizing forest responses to disturbance [51].

Formation of canopy gaps of varying sizes is a consequence of disturbances that cause tree mortality. Gaps alter the forest floor environment by increasing light availability, altering soil temperature and moisture regimes, stimulating understory vegetation regeneration and growth, and decreasing leaf litter moisture and depth [52–58]. The magnitude of differences on the forest floor environment between a gap and the surrounding undisturbed forest is determined by local (gap size, shape, orientation, structure, and amount of edge) and landscape (gap isolation, number of gaps, and forest structure) characteristics [46,59]. Canopy gaps and their associated environmental changes on the forest floor impact the abundance, diversity, and distribution of ground-dwelling invertebrates, including insects and spiders [46,53,60–64].

Woody debris accumulates on the forest floor as trees fall including fine woody debris (FWD; stems and small branches <10 cm in diameter at the large end) and coarse woody debris (CWD; logs and large branches ≥10 cm in diameter at the large end). Downed CWD is a fundamental structural component that increases habitat complexity in forests [65] and provides resources for flora and fauna, including nutrients, habitat, and sites for sprouting, breeding, and overwintering [66–68]. As CWD decays over time, the communities utilizing this resource change with the physical and chemical properties of the wood [67,69,70]. During early stages of decay when the bark is still firmly attached, CWD primarily regulates abiotic conditions at the soil surface for ground-dwelling invertebrates [67,71,72], whereas nutrients and habitat become abundant following fungal and insect colonization as decay progresses [67,69]. Because wood decomposition occurs on timescales of 50–200 years [67,69,73], the effects of downed woody debris on ground-dwelling invertebrate communities can be long-lasting [67,69,73].

Canopy gaps consistently influence the structure of invertebrate communities [53,60,74,75], as do the presence and amount of CWD [76–79], suggesting that both are key structural features in forests. Formation of canopy gaps and accumulation of CWD may have interacting effects on ground-dwelling invertebrate communities due to their differing impacts on the forest floor environment. Isolating the individual effects of canopy gaps and CWD on ground-dwelling invertebrates after natural and anthropogenic disturbances is a challenge because these two factors are often intricately linked. Dynamic patterns of effects of canopy gap formation and CWD accumulation may shift the relative importance of these factors over time, altering the impacts on ground-dwelling invertebrate community structure and function.

2. Temporal Responses of Forests to Disturbance

Effects of disturbances on canopy gap formation and accumulation of CWD on forest communities change over time. The spatial and temporal scales at which these changes occur are ultimately determined by the properties of the disturbance event. Here, we develop conceptual models of dynamic effects of disturbances caused by invasive insects, wind, and salvage logging on canopy gaps and downed CWD, and their implications for ground-dwelling invertebrate communities (Table 1).

Table 1. Descriptions of the predicted impacts of canopy gap formation, accumulation and removal of coarse woody debris (CWD), and soil disturbance caused by invasive insect-induced tree mortality, wind, and intensive salvage logging after natural disturbance on ground-dwelling invertebrate communities. When these factors are predicted to have the greatest impact on invertebrates is indicated by early and late.

Disturbance Agent	Canopy Gaps	Coarse Woody Debris		Soil
		Accumulation	Removal	
Invasive Insects	High, Early	High, Late	–	Minimal
Wind	High, Early	High, Early	–	Minimal to Moderate
Salvage Logging	High, Early	–	High, Early	High

2.1. Invasive Insects

In eastern deciduous forests of North America, gap-phase dynamics caused by native insects such as wood-boring beetles result in the formation of small-scale canopy gaps that are unevenly distributed throughout the stand, as most tree species exist in diverse communities. However, populations of native insects such as spruce budworm (*Choristoneura fumiferana* [Clem.]) [80,81] and forest tent caterpillar (*Malacosoma disstria* Hbn.) [82,83] can cause large-scale tree mortality during outbreak years. Tree mortality caused by invasive insect species such as gypsy moth (*Lymantria dispar* L.), hemlock woolly adelgid (*Adelges tsugae* Annand), beech scale (*Cryptococcus fagisuga* Lind.), and emerald ash borer (*Agrilus planipennis* Fairmaire) can produce more spatially extensive patterns of gap formation in forests [9,18,84].

Emerald ash borer (EAB) has killed hundreds of millions of ash trees (*Fraxinus* spp.) in eastern North America since its accidental introduction from southeast Asia [85]. Ash tree mortality causes widespread, nearly simultaneous formation of canopy gaps in forests [86,87], owing to the low resistance of North American ash species to EAB [88]. The speed, synchrony, and specificity of ash mortality differs from gap-phase dynamics caused by other forest insects. EAB-induced ash mortality increases both the frequency of canopy gaps as ash trees die (Figure 1A) and the accumulation of ash CWD as trees fall (Figure 1B) [78,89]. Our model predicts that this pattern of tree mortality has an inverse temporal relationship in the effect sizes of canopy gaps and accumulation of ash CWD on ground-dwelling invertebrate communities (Table 1), as the effects of canopy gaps diminish with canopy closure, while the effects of ash CWD are predicted to increase and change over time as trees fall and decompose [60].

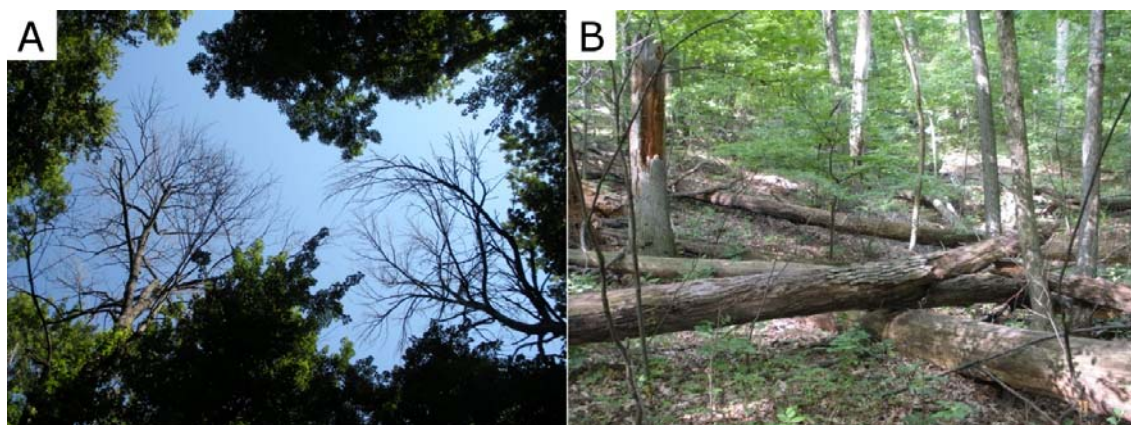


Figure 1. Canopy gaps created by the death of ash trees during early stages of ash mortality (A) and the accumulation of CWD on the forest floor during late stages of ash mortality (B).

Based on this conceptual model, canopy gaps are predicted to have their greatest impact on ground-dwelling invertebrates soon after they form, with these effects dissipating over time as growth from suppressed understory trees and surrounding canopy trees close the gaps. Gaps are presumably at their maximum size soon after tree death, and gaps created by EAB-induced tree mortality averaged 18.8% (± 1.8) to 26.5% (± 2.0) canopy openness [53,89]. Growth from understory and canopy trees closed the gaps, decreasing their canopy openness to 1–10% during late stages of ash mortality [78,90].

Accumulation of ash CWD is predicted to have the greatest effects on ground-dwelling invertebrates during late stages of EAB-induced ash mortality. Ash trees fall relatively quickly after they are killed by EAB but can remain standing for several years. Thus, rate of CWD accumulation above background levels is initially low. An average of 2.2% cover of downed CWD was observed in forests experiencing early stages of ash mortality [91]. However, as more ash trees fall, larger volumes of CWD accumulate on the forest floor. In forests experiencing late stages of ash mortality, an average of 19.3% cover of downed CWD was observed [90]. Hence, our model predicts that rate and volume of ash CWD accumulation increase as gaps caused by ash mortality close.

Studies investigating the impacts of ash mortality caused by EAB on ground-dwelling invertebrates support these predicted effects of canopy gaps and CWD. During early stages of ash mortality, decreased invertebrate richness and diversity was reported in canopy gaps, owing to the decreased activity-abundances of harvestmen, scarab beetles, camel crickets, and springtails [60]. Activity-abundance of ground beetles initially was lower in canopy gaps, but these effects were ephemeral, suggesting some degree of resilience to small-scale canopy gaps [53,89]. During late stages of ash mortality, higher densities of ground-dwelling invertebrates were observed near ash CWD, including earthworms, spiders, harvestmen, isopods, millipedes, beetles, and springtails [78]. Further investigation revealed increased activity-abundance, evenness, and diversity of invertebrates near recently fallen than more decayed ash CWD [90].

Effects of tree mortality caused by other invasive insects on ground-dwelling invertebrates were more variable. Early stages of eastern hemlock (*Tsuga canadensis* (L.)) mortality from hemlock woolly adelgid (HWA) increased ant activity-abundance and species richness [92], which is consistent with predictions of the model. Sackett et al. [93] reported altered composition of spider and beetle assemblages in stands where hemlock were experimentally girdled to emulate gaps created by HWA-induced tree mortality compared to undisturbed hemlock stands, but CWD accumulation was not investigated. To our knowledge, effects of late stages of hemlock mortality on invertebrates have not been investigated. Decline and mortality of American beech (*Fagus grandifolia* (Ehrh.)) from beech bark disease [a complex of beech scale and the fungal species (*Nectria coccinae* var *faginata* Lohman, Watson and Ayers)] had no clear impacts on ground-dwelling invertebrates [94]. However, information on the size of gaps created by beech mortality was not reported, nor was the amount

of CWD on the forest floor [94], which limits the ability to compare these patterns to predictions of the model.

2.2. Wind

Tree mortality can occur at small scales (tens of meters or less) from windthrow or large scales (thousands of hectares) from intense storms such as tornados, downbursts, derechos, and hurricanes [8,36,62,95]. When trees are felled by wind, canopy gaps form and CWD accumulates simultaneously (Figure 2A). Therefore, a negative temporal relationship is predicted for the effect sizes of both gaps and CWD on ground-dwelling invertebrate communities [60], with the greatest impacts occurring immediately after the wind storm and then decreasing over time (Table 1).

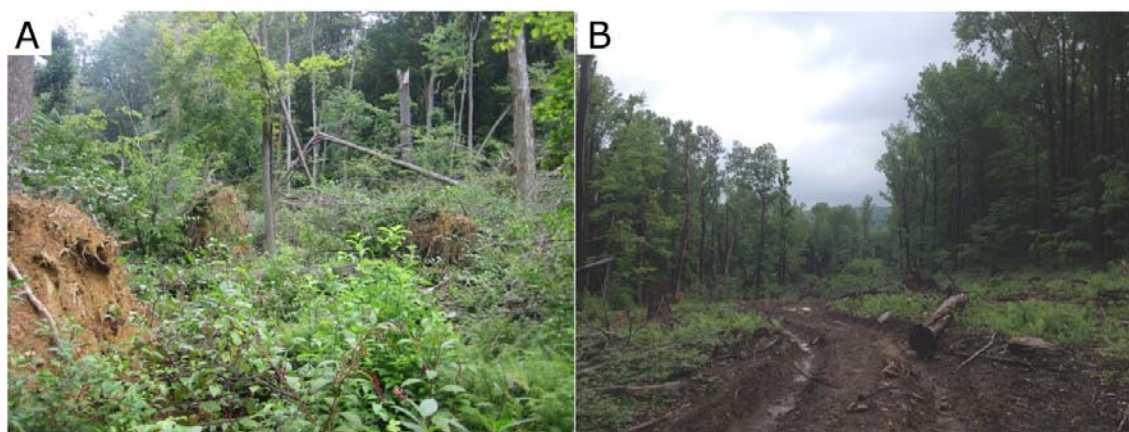


Figure 2. Forest disturbance caused by strong winds from a tornado (A) followed by salvage logging (B).

Severe wind storms generally fell a high proportion of canopy trees forming large, patchy gaps, although some trees lose only branches and remain standing [96]. Tipped trees form pits and mounds that mix organic and mineral layers, expose rocks and roots, and create distinct microsites that differ from neighboring undisturbed soil [97–101]. Trees fall nearly simultaneously and often in the same direction, resulting in accumulation of CWD of different species, types, and sizes [36,96]. The probability that a tree will fall is influenced by species-specific characteristics (size, root and canopy structure, wood strength, and prior insect or disease infestation) and abiotic site factors (local topography and soil properties) [2,36].

Studies investigating the impacts of wind disturbance on ground-dwelling invertebrate communities generally reported initial impacts of canopy gaps and accumulation of CWD, but the long-term impacts of wind storms are understudied. Richardson et al. [74] reported lower ground-dwelling invertebrate diversity and biomass in canopy gaps owing to decreased activity-abundance of large predators and detritivores, but found no effects of woody debris following a manipulative experiment designed to emulate hurricane disturbance. Similarly, Greenberg and Forrest [52] observed lower invertebrate biomass and activity-abundances of millipedes, centipedes, spiders, and ground beetles in canopy gaps created by Hurricane Opal than in undisturbed forest. In the year following a tornado, invertebrate activity-abundance was higher, diversity was lower, and community composition was altered in windthrow gaps compared to nearby undisturbed forest, but these differences disappeared by year three [102]. Activity-abundances of millipedes (Spirobolidae), spiders, harvestmen, ants, ground beetles, bark beetles, featherwing beetles, and rove beetles were higher in canopy gaps, but were lower for centipedes, millipedes (Julidae), earth-boring dung beetles, and small dung beetles. Windthrow gaps were characterized by increased growth of understory vegetation as well as high volume of downed CWD [102], making it difficult to determine which factors had the greatest impact on ground-dwelling invertebrates.

2.3. Salvage Logging

Salvage logging, or post-disturbance logging, is the practice of harvesting commercially valuable standing and downed damaged, dying, and dead trees, as well as undamaged living trees from forest stands following natural disturbance [29,30,103] to recover economic losses [104], prevent subsequent insect or disease outbreaks, and reduce the risk of fire [30,36]. Salvage logging tends to remove biological legacies created by natural disturbances [30], although effects vary widely based on the harvesting methods [30,105] and site-specific conditions such as soil type and water content [105,106]. Removal of biological legacies simplifies stand structure, decreases habitat connectivity, and influences patterns of forest recovery [29,30].

Intensive and extensive salvage logging increases the size of canopy gaps by removing undamaged living trees as well as downed timber (Figure 2B). Therefore, the greatest effect of canopy gap formation on ground-dwelling invertebrate communities is predicted to occur soon after the logging operation when gap size is at its maximum (Table 1). Moreover, removal of living and dead trees significantly reduces the amount of CWD, leaving forests depauperate in the diversity of sizes, types, and decay classes characteristic of undisturbed or naturally disturbed forests [27,107–109]. Hence, we predict that the greatest effects of CWD accumulation on invertebrates occur soon after natural disturbance (e.g., wind), while the effects of CWD removal are predicted to be greatest soon after the logging operation (Table 1).

Ground-based salvage logging methods that use heavy machinery, roads, and skid trails for timber removal increase erosion and compaction of organic and mineral soil layers [110,111]. Following salvage operations, increased bulk density has been detected 15–60 cm below the soil surface [110,112–115] with changes to soil structure that decreased aeration, porosity, water infiltration and retention, gas exchange, and root growth [103,105,106,112,116–118]. Soil erosion and compaction are predicted to have the greatest effects on ground-dwelling invertebrates immediately after the salvaging operation (Table 1), and relax slowly over time as the organic layer accumulates and compaction decreases.

Studies investigating the impacts of salvage logging on ground-dwelling invertebrates reported taxon-specific responses. Greenberg and Forrest [119] observed higher activity-abundance of harvestmen and ants in salvaged gaps than in intact windthrow gaps created by Hurricane Opal. Urbanovičová et al. [120,121] observed increased dominance of springtails and mites in salvaged gaps after wind disturbance in spruce forest, resulting in lower arthropod evenness and diversity. Thorn et al. [75] found that the formation of canopy gaps was the most important factor structuring ground beetle and epigeal spider assemblages after experimentally decoupling the effects of gaps and forest floor microhabitats created by windthrow and salvage logging. Activity-abundance and species richness of spiders was higher in windthrow gaps, while ground beetles were more abundant under closed canopy [75]. In gaps created by a tornado, activity-abundance of ground-dwelling invertebrates was lower one year and higher two years after salvage logging compared to adjacent unsalvaged windthrow gaps [102]. Snails and slugs, true dung beetles, and crickets were more abundant, while two families of millipedes and three families of Collembola were less abundant in salvaged gaps [102]. Invertebrate communities showed resilience in windthrow gaps, which had similar composition to those in the undisturbed neighboring deciduous forest, whereas invertebrate communities in salvage logged gaps were distinctly different [102], highlighting the importance of biological legacies such as downed CWD following disturbance.

Responses of ground beetle assemblages to salvage logging have been studied extensively. Species richness and diversity of ground beetles were higher in salvaged gaps following severe wind disturbance (>70% tree mortality) [61], and activity-abundance was higher in salvaged gaps following wildfire [122]. Koivula and Spence [123] reported increased activity-abundance and species richness with increasing salvage logging intensity (low: 23–30% timber removed, moderate: 40–50%, and high: 60–70%) following wildfire compared to unsalvaged patches. Activity-abundance, richness, and (or) diversity of ground beetles often increases because open-habitat and generalist species quickly colonize the disturbed patch, while the presence of forest species decline more slowly. Perhaps retention of

biological legacies in salvaged areas would support long-term populations of forest ground beetle species in these disturbed areas.

3. Conclusions

Natural disturbances are essential to the structure and function of ecosystems and contribute to the maintenance of biodiversity [2,10]. We proposed conceptual models describing temporal relationships in the effect sizes of disturbance from invasive insect-induced tree mortality, wind storms, and salvage logging on canopy gap formation, accumulation (and removal) of CWD, and soil disturbance, and their effects on ground-dwelling invertebrate communities. Responses to EAB-induced ash mortality supported predictions of the first conceptual model of an inverse temporal relationship in the effect sizes of canopy gaps and CWD accumulation, but responses to tree mortality caused by other invasive insects were inconsistent and understudied. The initial effects of canopy gaps and CWD caused by wind storms and salvage logging predicted by the second and third conceptual models were generally supported, but we are not aware of data that can test predictions of longer-term impacts on ground-dwelling invertebrate communities. These models provide a conceptual framework that can interpret results of existing studies and enlighten the design of future experiments.

This review highlights key knowledge gaps in understanding the temporal effects of natural and anthropogenic disturbances on ground-dwelling invertebrate communities. Most studies have investigated the initial short-term effects of disturbance events, but longer-term studies are under-represented in the literature. Moreover, effects of soil disturbance following salvage logging were not quantitatively assessed in most studies, and thus are confounded with impacts of decreased volumes of CWD. Combined effects of canopy and ground-level factors need to be experimentally decoupled in order to assess their individual effect sizes on ground-dwelling invertebrate communities, as well as other forest flora and fauna.

Forest ecosystems are innately dynamic, which complicates land management decisions made following small- and large-scale disturbances to achieve economic and ecological objectives. Ecologically sustainable forestry practices based on natural disturbance regimes and processes of forest stand development are intended to provide economically valuable resources while maintaining ecosystem integrity [104,124–126]. The combined, interacting impacts of natural disturbance followed quickly by salvage logging may decrease the capacity of forest ecosystems to recover [29,30]. Potential ecological impacts of salvage logging can be mitigated by employing alternative lower-impact harvesting methods such as timber removal by cable or helicopter. Moreover, incorporating biological legacies into management plans by selectively retaining downed and standing woody debris as well as patches of undisturbed forest within the landscape can help maintain structural complexity and provide habitat [27,30,127] for forest species including ground-dwelling invertebrates.

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