Impacts of Exotic Pests on Forest Ecosystems

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Contributor: Qinfeng Guo, Kevin M. Potter, Hai Ren, Peixia Zhang

Pests (e.g., insects, pathogens) affect forest communities through complex interactions with plants, other animals, and the environment. While the effects of exotic (non-native) pests on trees received broad attention and were extensively studied, fewer studies addressed the ecosystem-level consequences of these effects. Related studies so far mostly only targeted a very few dominant pests (e.g., hemlock woolly adelgid—HWA, beech bark disease—BBD, and spongy moth—SM) and were limited to aspects of the complex situation such as (1) pests' direct physical disturbance to forest ecosystems, (2) altered geochemical elements of soils, water, and air (e.g., excretion), and (3) feedback effects from the alteration of ecosystems on plants, native insects, and present and future pest invasions. New studies also show that, in general, planted forests appear to be more prone to exotic pest invasions and thus suffer greater impacts than natural forests. Integrated studies are critically needed in the future to address (1) direct/indirect interactions of pests with ecosystem elements, (2) both short- and long-term effects, and (3) feedback effects. The implications of the new findings and corresponding management strategies are discussed.

Keywords: climate change ; diseases ; forest health ; indirect effects ; insects ; invasion ; pathogens

1. Biotic Effects

1.1. Direct Effects

Using a 4-year field experiment, Wilson et al. [1] found that the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) and elongated hemlock scale (*Fiorinia externa* Ferris) can significantly alter the foliar chemistry of eastern hemlock (*Tsuga canadensis* (L.) Carrière), although the effects from the two pest species are also very different. High tree mortality caused by insect herbivory can open up the canopy and increase light and temperature on the forest floor [2]. Massive pest infestations can greatly affect overall forest health, leading to reduced ecosystem primary and net productivity, carbon sequestration, and aboveground carbon storage (biomass), but increased decomposition rate (**Table 1**, **Figure 1**) [3][4].

Table 1. Examples of exotic pests posing significant impacts on ecosystem functions and processes.

Source	Forest Pests	Community	Ecosystem-Level Impacts	Study Type
Avila et al. [5]	*Phytophthora cinnamomi*	*Quercus suber*	Altered biogeochemical cycles, soil respiration, and nutrient availability.	Field
Anderson-Teixeira et al. [3]	All pests on 66 plots	Oaks forests, Hemlock forests, ash forests	Reduced biomass and carbon storage.	Field
Bergemann et al. [6]	*Phytophthora ramorum*	*Notholithocarpus densiflorus* forest	Reduction in the hyphal abundance of ectomycorrhizal fungi from soil thus affecting decomposition, nutrient acquisition, and ecosystem succession.	Field
Bjelke et al. [7]	*Phytophthora alni*	Alder trees (*Alnus* spp.)	Reduced soil nitrogen, shade, and river/stream bank stability, changes in food webs of both terrestrial and aquatic.	Field
Block et al. [8]	Hemlock woolly adelgid	Hemlock forests	Decrease N retention.	Field
Brantley et al. [9]	Hemlock woolly adelgid	Hemlock forests	Reduced annual forest transpiration (E_t); species replaced by deciduous species may increase forest E_t but reduce stream discharge.	Field

Source	Forest Pests	Community	Ecosystem-Level Impacts	Study Type
Cameron et al. [10]	**Terrestrial invertebrate invaders**	**Terrestrial ecosystems (general)**	**Single invaders increased soil nitrogen pools, while multiple species did not.**	**Review**
Crowley et al. [11]	**Beech bark disease, hemlock woolly adelgid (*Adelges tsugae*), sudden oak death**	**Tree species replacement**	**NPP lower, net C loss (first 100 years), total N lower.**	**Simulation**
De la Fuente and Beck [12]	**Pine wood nematode**	**Coniferous forests**	**Disrupt the coherence and functionality of protected area networks.**	**Field**
Edburg et al. [13]	**Bark beetle**	**Lodgepole pine forests**	**Reduced plant C-uptake and GPP, increased decomposition and nutrient loss; effects are time (stage)-dependent.**	**Conceptual**
Ellison et al. [14]	**Hemlock woolly adelgid**	**Hemlock (*T. canadensis*) forests**	**Reset successional sequences, homogenized biological diversity at landscape scales, altered hydrological dynamics, and changed forest stands from carbon sinks into carbon sources.**	**Review**
Hogg and Daane [15]	***Cheiracanthium mildei* L. (spider)**	**Oak woodland Vineyards**	**Cascading negative cross-trophic effects that ultimately reduce ecosystem service.**	**Field**
Ignace et al. [16]	**Hemlock woolly adelgid, elongate hemlock scale (*Fiorinia externa*)**	**Hemlock (*T. canadenis*) forests**	**Dramatic increases in soil respiration; decrease in soil organic layer mass and in the C:N of the remaining organic material; and decline in soil organic layer C storage.**	**Field**
I-M-Arnold et al. [17]	**Winter moth and mottled umber**	**Deciduous oak forests**	**Increased soil C and N levels but reduced C:N ratio.**	**Field**
Jenkins et al. [2]	**Hemlock woolly adelgid**	**Eastern hemlock (*Tsuga canadensis*) forests**	**Light availability to the understory and seedling regeneration both increased. Net N mineralization, nitrification, and N turnover increased. Inorganic N availability and nitrification rates increased dramatically, leading to nitrate leaching.**	**Field**
Knoepp et al. [18]	**Hemlock woolly adelgid**	**Hemlock (*T. canadensis*) forests**	**During the 4-year study, litterfall composition changed, hemlock plots had cooler spring soil temperatures, greater surface soil and forest floor total C than hardwood plots.**	**Field**
Kristensen et al. [19]	**Geometrid moth**	**Birch forests**	**Lower foliar C, higher soil C-accumulation, reduced C:N of mineralization.**	**Microcosm experiment**
Letheren et al. [20]	**Hemlock woolly adelgid**	**Hemlock (*T. canadensis*) forests**	**Negative impacts on the diversity and stability of ecosystems.**	**Review**
Lovett et al. [21]	**Spongy moth (*Lymantria dispar*), hemlock woolly adelgid, beech bark disease, Asian long-horned beetle**	**Oak forests, beech forests, hemlock forests, sugar maple forests, white ash forests**	**Reduction in productivity, disruption of nutrient cycles, and reduction in seed production.**	**Field**
Milligan et al. [22]	**Soil-nesting invasive ant (*Pheidole megacephala*)**	***Acacia drepanolobium* saplings**	**Reduced carbon fixation and storage.**	**Field**
Nisbet et al. [23]	**Emerald ash borer**	**Ash trees (riparian forests)**	**Reductions in high-quality leaf litter, large canopy openings.**	**Review and synthesis**

Source	Forest Pests	Community	Ecosystem-Level Impacts	Study Type
Seidl et al. [24]	Five detrimental alien pests	Forests in Europe	Projected to significantly reduce the long-term C storage potential of European forests.	Simulation/modeling
Wilson et al. [1]	Hemlock woolly adelgid, hemlock scale (*Fiorinia externa*)	Hemlock (*T. canadensis*) forests	Lower above/belowground biomass ratios, more needle loss, impacted the concentrations of primary metabolites, increased free amino acids local, reduction in starch, and manipulation of nitrogen pools.	Field

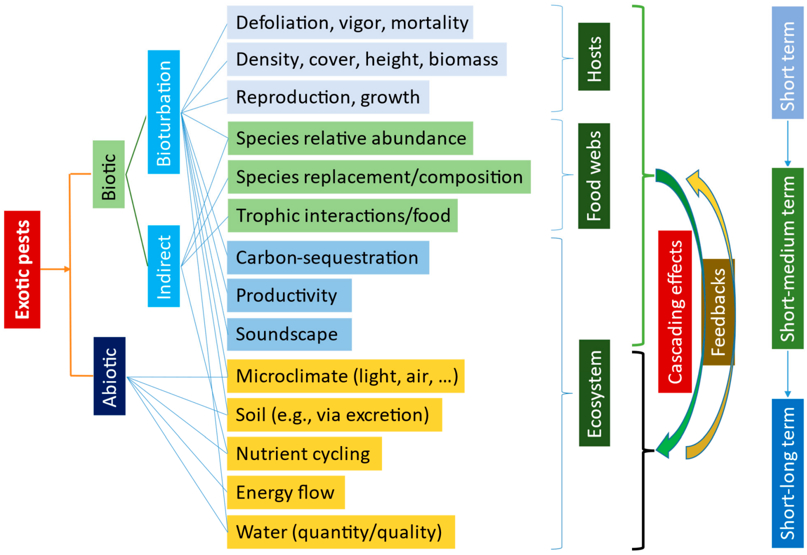

Figure 1. Examples of how exotic pests may initiate short-medium-long-term effects on community- and ecosystem-level patterns and processes. Impacts of exotic pests on ecosystems can both be direct and indirect (e.g., pest-induced changes in trees at the individual, population, and community levels), which could eventually lead to landscape-level changes (Lázaro-Lobo and Ervin 2021). Feedback effects could be found at all organization levels, although varying time legs may also exist.

Mounting evidence shows that nonnative pest invasion can cause profound cascading and cross-trophic effects on food webs and many other ecosystem processes [15][23]. For example, modified hemlock foliar chemistry by the hemlock woolly adelgid [1] will affect other component plant species and associated herbivory activities and the entire ecosystem's chemical profile. Additionally, avian community composition could be altered by HWA infestation because it causes high mortality of the hemlock trees that birds rely on [25]. Numerous specialist arthropod species dependent on ash (*Fraxinus*) may be extirpated because of the decimation of this host species by the invasive emerald ash borer (EAB, *Agrilus planipennis* Fairmaire) [26][27][28].

Existing evidence shows that, in general, planted forests appear to be more vulnerable to pest invasions than natural forests, possibly due to their lower biodiversity [29][30][31]. For example, planted poplar trees (*Populus* spp.) in China were seriously damaged by the star beetle and Chinese red pine (*Pinus massoniana* Lamb.) was seriously affected by pine wood nematode (*Bursaphelenchus xylophilus)*, as evidenced by extensive tree death in these plantations e.g., [32].

In addition to the direct effects on host trees, exotic pests can also pose direct (and indirect) effects on native insects, especially pollinators, through various and sometimes complex interactions, including competition and predation. For example, a recent meta-analysis by Debnam et al. [33] shows that exotic pollinators can displace native insect and bird pollinators in certain cases, but their direct effects on native pollinators can be context-dependent, ranging from mutualism to antagonism.

1.2. Indirect Effects

A problematic indirect effect of insect and disease infestation is an "invasional meltdown," during which the mortality of native tree hosts facilitates the invasion of non-native plants [26]. For example, forests experiencing high levels of ash mortality because of EAB infestations in Michigan and Ohio experienced increased growth of invasive woody shrubs, such as multiflora rose (*Rosa multiflora* Thunb.), Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder), and autumn olive (*Elaeagnus umbellata* Thunb.) [28][34]. In Hawaii, rapid ʻŌhiʻa death (ROD), a recently discovered wilt disease of the widespread endemic *Metrosideros polymorpha* Gaudich. caused by the fungal pathogens *Ceratocystis lukuohia* and *C.*

huliohia [35][36], may cause dramatic increases in non-native tree dominance in Hawaiian forests that are intensified by feral ungulate disturbance and competition with non-native plants in the understory [37]. In a reversal of these dynamics, the introduction of exotic plants could lead to the arrival of associated exotic pests that can affect ecosystems in different ways, such as altering forest succession and leading to species replacement [38].

2. Abiotic Effects

2.1. Direct Effects

There is abundant evidence that the loss of trees can directly and negatively affect water availability [39][40]. Some exotic pests cause direct disturbances on the soil surface through their movements and migration. Some build nests (large and small) or drill holes in the ground that affect soil structure and nutrients, as well as forest carbon dynamics. For example, soil nesting near tree roots by invasive ants was found to reduce carbon fixation and storage of *Acacia drepanolobium* Harms ex Sjöstedt saplings in Kenya, suggesting that direct interactions between invasive ants and plant roots in other ecosystems may strongly influence carbon fixation and storage [22]. Additionally, Warren et al. [41] found evidence that *Brachyponera chinensis* Emery, an invasive ant species in eastern North American forests, does not provide the seed dispersal services of the native ant that it replaces, potentially shifting ecological dynamics in these forests. Meanwhile, the feeding and burrowing behaviors of invasive earthworms in eastern North American forests, including at least three pheretimoid "jumping worm" species, reduce carbon storage in the forest floor, redistribute soil nutrients, and change basic soil properties, such as bulk density and soil pH, all causing substantial impacts on ecosystem functions and cascading effects on forest organisms [42].

2.2. Indirect Effects

Indirect geochemical and geophysical impacts from exotic pests on forest ecosystems include altering water and energy cycling, such as interception, runoff, storage, and recharge that subsequently influence surface albedo, evaporation, and transpiration [9]. Altered vegetation structure, including canopy height and density, will affect light penetration and wind speed [13]. A good example of indirect effects from exotic pests is the effects of losing eastern hemlock (due to HWA), a keystone species in the Southern Appalachian Mountains of the United States, on nitrogen (N) dynamics (mostly declining N retention except where N availability is high). Furthermore, pest and forest management through chemical use (i.e., in pest control) can definitely affect water, soil, and overall habitat quality [43].

The loss of trees caused by exotic pests can negatively and indirectly affect water quality [39][40]. For example, high tree mortality may increase nitrogen mineralization and nitrification and nitrate leaching to groundwater and/or surface waters [2][9][44]. In riparian ecosystems, the loss of riparian species can affect nutrient subsidies to rivers and streams. For example, ash leaves rapidly decompose, and therefore likely release nutrients relatively quickly when they fall into or near streams [17]. The loss of ash to EAB may, in some cases, shift to greater proportions of leaf litter from species, such as oaks (*Quercus*), that take longer to decompose, and therefore alter the timing of nutrient inputs into aquatic systems.

The effects of exotic pests on trees and water can negatively and indirectly affect soil conditions. For example, exotic pests may increase soil C and N levels but reduce C:N ratio e.g., [17]. An altered soil moisture regime can then affect the diversity and activity of soil microorganisms [19][45].

Canopy herbivory and frass deposition from native insects can affect soil nutrient dynamics [46] and nutrient cycling [2], but invasions from nonnative pests could substantially enhance such effects, causing much greater damage to the extent that the hosting ecosystem may not be sustainable over the long term [3].

Meanwhile, the loss of ash to EAB may indirectly affect forest soil chemistry, given that decomposed ash litter can contribute significantly to nutrient availability [47].

3. Short- vs. Long-Term Effects

Exotic pests can indeed pose many short- (days-years) and long-term (decades–centuries) impacts on trees and forest ecosystems [48][49]. They first affect their hosts (trees) and the hosts' predators and competitors, mutualists, and other animals, at the individual scale (short-term), population scale (mid-term), and community/ecosystem scale (long-term).

Intuitively and most evidently, immediate short-term effects from nonnative pests would include those from pest activities, such as feeding (herbivory) and nesting on hosting plants (trees). Most early studies first focused on morphological changes in trees (leaves, flowers, stems, and roots) and tree mortality [50]. Subsequent studies then investigated changes in surroundings (e.g., lights) and forest composition [51].

The medium-to-long-term effects of exotic pest invasions are usually associated with cross-trophic and cascading consequences, which usually occur after tree species composition is affected, thus forest structure and dynamics (e.g., water and nutrient uptake) are altered (**Figure 1**). First, the mortality of the host trees, and then subsequently the resulting canopy gaps, may eventually change the forest tree species composition, which will later affect the animal and soil microbial species composition.

For example, a modified foliar chemical profile by the hemlock woolly adelgid [1] may have post chronic long-term effects on the forest ecosystem (both above and belowground), although time lags may exist [16] (**Figure 1**).

4. Climate Change May Enhance the Impacts of Pests on Forest Ecosystems

Vertical (elevational) and horizontal (latitudinal) tree migration forms novel communities and food webs [52]. Hosts and pests may not keep the same pace to track climate change (e.g., time lags, host-jumping, host expansion, and food web mismatch may occur). Climate change could increase the chances of new pest invasions and outbreaks and exacerbate the impacts of existing insect and disease infestations on forest ecosystem functions. For example, increases in temperatures could reduce generation time and improve overwintering survival for the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), thus increasing its impacts on forest ecosystems mostly through high tree mortality [53]. In another example, Seidl, Klonner, Rammer, Essl, Moreno, Neumann and Dullinger [24] observed that climate change in Europe allows for the wider spread of existing exotic pests and pathogens on the continent, resulting in extensive impacts on carbon stocks.

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