

Impacts of Exotic Pests on Forest Ecosystems: An Update

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Abstract: 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. We discuss the implications of the new findings and corresponding management strategies.

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

1. Background

Forests, natural and planted, host a large portion of global biodiversity. Forests play critical roles in human well-being, ecosystem functioning (e.g., nutrient and carbon cycling), and ecosystem services [1,2]. Yet, invading exotic (non-native) pests (insects, pathogens) are growing problems that interrupt major biogeochemical processes and energy flow in forest ecosystems (Figure 1). They can pose many short- and long-term impacts [1,3,4] through the novel and complex interactions with coexisting species with varying character and intensity over both space and time [5,6] and landscape structure (e.g., fragmentation) [7]. The consequences of such novel interactions are mostly negative. These pests affect forest ecosystems through biotic and abiotic interactions with plants, other animals, and the environment that occur at individual, population, and community levels. Such interactions can then be both direct and indirect. Biotic (within and cross trophic) interactions are mainly through altering species composition and their relative abundance of plants (hosts) and other animals (e.g., their competitors and predators) (Figure 2).

Most previous studies regarding exotic forest pest invasions focused on community-level consequences [8], such as how pests directly affect host plants [9–12]. The community-level effects of exotic pests (effects on trees) received extensive attention [13], but studies on ecosystem-level consequences lagged behind [3,14]. The main reason could be because the effects of exotic pests on biogeochemical processes may be mostly indirect and more difficult to detect, that is, through changes in tree communities due to pest damage. While this may be partly true, pests could also directly affect soils, water, and microclimates [15]. Abiotic interactions between pests and their hosting forest ecosystems are relatively less



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studied. The interactions between the two include (1) physical disturbance to the habitats, and (2) altered geochemical elements of soils, water, and air (e.g., excretion).



Figure 1. An example of impacts of a forest pest: infested hemlock trees by a hemlock woolly adelgid (*Adelges tsugae*) that killed many trees in the Linville Gorge area of the Great Smoky Mountains, North Carolina (Pisgah National Forest) (Photo by Steve Norman, USDA Forest Service). From <https://forestthreats.org/products/photos-and-videos/photos/hemlock-woolly-adelgid/image> (accessed on 1 February 2023).

Economic costs due to exotic pest invasion are massive and are also closely linked to related ecological impacts and threats, including losses of species, weakened ecosystem functioning, and reduced productivity, wood/timber, food, and fiber [1,3]. Managing exotic pest infestations include searching for biocontrol agents and developing pest-resistant genotypes for native trees, which are often expensive, take a long time, and have unexpected indirect costs or consequences [16–18]. To develop efficient management strategies and priorities, we need to better understand the relative impacts of pest invasions on various forest ecosystem properties.

While there are already several comprehensive reviews regarding the impacts of exotic pests on forests at the community level [1], comparable reviews or syntheses that focus on the ecosystem level are lacking [3]. We particularly need an update of related knowledge based on recent research progress. Here, we review the most recent relevant literature (mostly in the past decade). We outline the review based on recent findings as follows:

- (1) Examining the direct and indirect biotic vs. abiotic effects of pests on forest ecosystems, followed by an assessment of short- and long-term impacts and feedback;
- (2) Assessing and discussing how climate change and major disturbances may facilitate such effects;

- (3) Proposing future research perspectives with a list of urgent questions and tasks for current and future studies;
- (4) Recommending corresponding management strategies following new research findings.

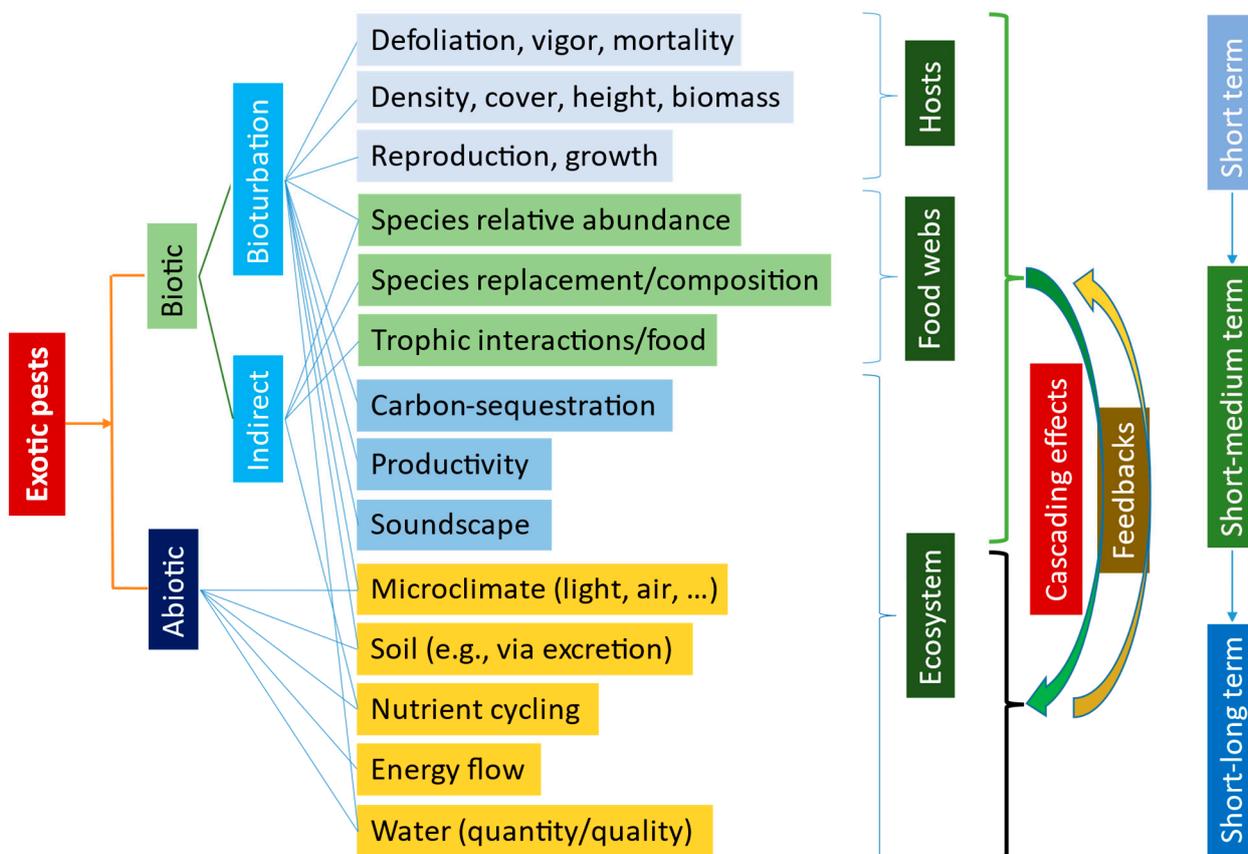


Figure 2. Examples of how exotic pests may initiate short-medium-long-term effects on community- and ecosystem-level patterns and processes. Impacts of exotic pests on ecosystems can both be direct and indirect (e.g., pest-induced changes in trees at the individual, population, and community levels), 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.

We shall point out that, here in this review (update), the term “exotic pests” includes both foreign and domestic (internally introduced) non-native insects and pathogens (diseases). In our literature search, we used Google Scholar and keywords such as “exotic pest”, “forest”, “ecosystem”, “soil”, “water”, and “biogeochemical”. However, due to the large number and variation in keywords and terms used in related studies, our search was in no way exhaustive. For example, some studies use biomass, carbon storage, or carbon stocks interchangeably. Additionally, some terms such as “productivity” and “biomass” were used at both community- and ecosystem-level studies. For these reasons, we made every effort to only include literature that uses “ecosystem” in its strict sense.

Most earlier studies never targeted both biotic and abiotic effects or both direct and indirect effects. However, in the real world, all these effects are likely to be significant and interrelated at the same time. Therefore, following the findings from previous studies, we also describe these effects separately for clarity and for convenience.

2. Biotic Effects

2.1. Direct Effects

Using a 4-year field experiment, Wilson et al. [19] 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 [20]. 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 2) [2,21].

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. [22]	<i>Phytophthora cinnamomi</i>	<i>Quercus suber</i>	Altered biogeochemical cycles, soil respiration, and nutrient availability.	Field
Anderson-Teixeira et al. [2]	All pests on 66 plots	Oaks forests, Hemlock forests, ash forests	Reduced biomass and carbon storage.	Field
Bergemann et al. [23]	<i>Phytophthora ramorum</i>	<i>Notholithocarpus densiflorus</i> forest	Reduction in the hyphal abundance of ectomycorrhizal fungi from soil thus affecting decomposition, nutrient acquisition, and ecosystem succession.	Field
Bjelke et al. [24]	<i>Phytophthora alni</i>	Alder trees (<i>Alnus</i> spp.)	Reduced soil nitrogen, shade, and river/stream bank stability, changes in food webs of both terrestrial and aquatic.	Field
Block et al. [25]	Hemlock woolly adelgid	Hemlock forests	Decrease N retention.	Field
Brantley et al. [26]	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
Cameron et al. [27]	Terrestrial invertebrate invaders	Terrestrial ecosystems (general)	Single invaders increased soil nitrogen pools, while multiple species did not.	Review
Crowley et al. [13]	Beech bark disease, hemlock woolly adelgid (<i>Adelges tsugae</i>), sudden oak death	Tree species replacement	NPP lower, net C loss (first 100 years), total N lower.	Simulation
De la Fuente and Beck [28]	Pine wood nematode	Coniferous forests	Disrupt the coherence and functionality of protected area networks.	Field
Edburg et al. [29]	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. [30]	Hemlock woolly adelgid	Hemlock (<i>T. canadensis</i>) 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 [31]	<i>Cheiracanthium mildei</i> L. (spider)	Oak woodland Vineyards	Cascading negative cross-trophic effects that ultimately reduce ecosystem service.	Field
Ignace et al. [32]	Hemlock woolly adelgid, elongate hemlock scale (<i>Fiorinia externa</i>)	Hemlock (<i>T. canadensis</i>) 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. [33]	Winter moth and mottled umber	Deciduous oak forests	Increased soil C and N levels but reduced C:N ratio.	Field

Table 1. Cont.

Source	Forest Pests	Community	Ecosystem-Level Impacts	Study Type
Jenkins et al. [20]	Hemlock woolly adelgid	Eastern hemlock (<i>Tsuga canadensis</i>) 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. [34]	Hemlock woolly adelgid	Hemlock (<i>T. canadensis</i>) 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. [15]	Geometrid moth	Birch forests	Lower foliar C, higher soil C-accumulation, reduced C:N of mineralization.	Microcosm experiment
Letheren et al. [35]	Hemlock woolly adelgid	Hemlock (<i>T. canadensis</i>) forests	Negative impacts on the diversity and stability of ecosystems.	Review
Lovett et al. [36]	Spongy moth (<i>Lymantria dispar</i>), 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. [37]	Soil-nesting invasive ant (<i>Pheidole megacephala</i>)	<i>Acacia drepanolobium</i> saplings	Reduced carbon fixation and storage.	Field
Nisbet et al. [38]	Emerald ash borer	Ash trees (riparian forests)	Reductions in high-quality leaf litter, large canopy openings.	Review and synthesis
Seidl et al. [39]	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. [19]	Hemlock woolly adelgid, hemlock scale (<i>Fiorinia externa</i>)	Hemlock (<i>T. canadensis</i>) 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

Mounting evidence shows that nonnative pest invasion can cause profound cascading and cross-trophic effects on food webs and many other ecosystem processes [31,38]. For example, modified hemlock foliar chemistry by the hemlock woolly adelgid [19] 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 [40]. 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) [4,41,42].

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 [43–45]. 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., [46].

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. [47] 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.

2.2. 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 [4]. 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.) [42,48]. In Hawaii, rapid ‘Ōhi‘a death (ROD), a recently discovered wilt disease of the widespread endemic *Metrosideros polymorpha* Gaudich. caused by the fungal pathogens *Ceratocystis lukuohia* and *C. huliohia* [49,50], 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 [51]. 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 [52].

3. Abiotic Effects

3.1. Direct Effects

There is abundant evidence that the loss of trees can directly and negatively affect water availability [53,54]. 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 [37]. Additionally, Warren et al. [55] 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 [56].

3.2. 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 [26]. Altered vegetation structure, including canopy height and density, will affect light penetration and wind speed [29]. 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 [57].

The loss of trees caused by exotic pests can negatively and indirectly affect water quality [53,54]. For example, high tree mortality may increase nitrogen mineralization and nitrification and nitrate leaching to groundwater and/or surface waters [20,26,58]. 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 [33]. 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., [33]. An altered soil moisture regime can then affect the diversity and activity of soil microorganisms [14,15].

Canopy herbivory and frass deposition from native insects can affect soil nutrient dynamics [59] and nutrient cycling [20], 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 [2].

Meanwhile, the loss of ash to EAB may indirectly affect forest soil chemistry, given that decomposed ash litter can contribute significantly to nutrient availability [60].

4. Feedback Effects

Clearly, most of the direct and indirect effects of exotic pests on plants and ecosystems are intertwined; that is, both direct and indirect processes are at work at the same time. However, one of the major information and knowledge gaps in related research fields is the extent of feedback effects on forest ecosystems associated with exotic pest infestation. For example, reduced forest productivity, among other factors resulting from exotic pest infestation, will in turn affect future exotic pest invasion and the activity of pests that are currently present (Figure 2). Exotic pest infestation could also eventually disrupt the connectivity of conservation networks [26].

There are a few new theoretical and promising studies that address these complex feedback effects. For example, Dietze and Matthes [61] proposed an ecophysiological framework for modeling the impact of pests and pathogens on forest ecosystems that could better predict pests' impacts under varying global change scenarios.

5. 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 [1,3]. 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 [62]. Subsequent studies then investigated changes in surroundings (e.g., lights) and forest composition [5].

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 2). 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 [19] may have post chronic long-term effects on the forest ecosystem (both above and belowground), although time lags may exist [32] (Figure 2).

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

Vertical (elevational) and horizontal (latitudinal) tree migration forms novel communities and food webs [63]. 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 [64]. In another example, Seidl, Klöner, Rammer, Essl, Moreno, Neumann and Dullinger [39] 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.

7. Perspectives on Future Ecosystem-Level Research

While most previous studies focused on how pests affect hosting plants and plant communities, work to understand ecosystem-level effects lags behind. We make the following recommendations on related research (see also Box 1):

- (1) More rigorous studies are needed to examine exotic pests' direct and indirect impacts on native insect species, especially those that provide key ecosystem functions necessary to maintain healthy ecosystems;
- (2) Large-scale studies are needed to examine regional, latitudinal, and elevational variations of ecosystem consequences due to exotic pest infestation;
- (3) Wherever possible, long-term studies that are newly initiated or are based on ongoing research (especially short-term projects) are needed to continue to detect chronic changes at the ecosystem level. Because invasion impacts can be highly context-dependent, the most helpful studies would include repeated observations and experiments at multiple sites that differ in the abundance of invertebrate invasive species [27];
- (4) More research to delineate exotic pests' native ranges is critical for developing more effective biocontrol and management policies and practices [65];
- (5) Pre-invasion assessments of new exotic pests and risk assessments of potential invasion and impact are needed to facilitate threat assessment and management of exotic pests/pathogens [66–69];
- (6) Future research should assess the feedback effects of altered soil and microbial communities due to exotic pest invasion on further pest and plant invasions;
- (7) We need to study whether affected ecosystems can recover to pre-invasion status, and if so, how fast, assuming the target pest can be successfully eradicated. Similarly, if the target pest cannot be eradicated, we need to better understand how cycles of pest infestation are related to regeneration of the host species;
- (8) Better and constantly improved models and tools are needed to predict the spread of invasive forest insects and diseases [70];
- (9) We need a better understanding of how exotic pest infestations directly and indirectly affect the services provided by forest ecosystems.

8. Urgent Tasks for Ecosystem-Level Management

Effective ecosystem-level management of species invasions, such as by exotic pests, needs complete and constantly updated baseline information on those pests. We make the following suggestions for immediate efforts:

- (1) In some regions and for some habitats, complete baseline information on exotic pests (e.g., the number of species, species identities, abundance, and distribution) is still lacking. Contributing to this is the difficulty of systematically monitoring the presence of exotic pests when their detection typically requires field surveys across broad scales, over which the pests may be spreading at a relatively high rate. Such information/knowledge gaps could be filled by enhanced efforts and

investments in field surveys, inventories, and timely assessments at all levels (i.e., local, regional, national, and international), in addition to the wider incorporation of citizen science participation;

- (2) Many of the impacts from exotic pests are due to the fact that many such pests escape their natural enemies in their native habitats and many hosts in invaded regions never developed resistance and adaptations (if they ever can) [71]. Therefore, more efforts are needed to identify natural enemies that can be used in biological control;
- (3) For many exotic pests, basic research is urgently needed to investigate the species' invasiveness, life history, genetics, dispersal mechanisms, and mutualism mechanisms [72];
- (4) The impact of invasive species research can be extended through large-scale citizen science activities and public education on exotic pests, including those targeted at inventorying species and monitoring their effects, among other efforts [73];
- (5) The introduction and spread of exotic pests can be interrupted by improving and implementing rules and regulations and strengthening quarantine law enforcement;
- (6) Closer collaborations in data and information sharing around the world should be performed [74].

Most importantly, what we learned from this review is that while most existing management tools only focus on one or two aspects of the pest impacts, new and comprehensive strategies must consider the extremely complex nature of the interactions of target pests with their hosts, other pests, potential new invaders (both plants and animals), and their physical environment. New management plans in particular need to consider both direct and indirect interactions and feedback effects that interrelate at the same time and at the same place.

Managing exotic pest invasions cannot be separated from managing other major forest disturbances, such as climate change (and associated sea-level rise), fire, severe storm events, and flooding, among others [1,75]. However, with the advances of new technologies, there are new nature-friendly technologies to curb pest spread. For example, nanotechnology was developed to produce pesticides and insecticides using bio-conjugated nanoparticles. This technology would facilitate remote sensing in precision pest monitoring and provide green and efficient alternatives for the management of insect pests in various ecosystems [76]. New genetics-based mosquito control technologies [77] also have potential to be used to control exotic pests in the forests (Box 1).

Box 1. Key questions for future research

- (1) Whether and/or to what level may an infested forest ecosystem recover if the exotic pest can be eradicated? Are there any concrete successful examples?
- (2) What exotic pests may be enhanced or hindered by projected climate change, and how?
- (3) How do we better deal with multiple stresses including pest infestation, fire, and drought, at the same time?
- (4) How can advances in new technologies such as remote sensing, genetics, artificial intelligence (AI), and machine learning assist in prevention and pest management?

9. Conclusions

In general, most findings regarding the impacts of exotic pests are still largely limited to population and community levels, i.e., how pests affect their host trees. Thus, available data and evidence, to a large extent, limit our ability to better document ecosystem-level consequences in forest ecosystems due to exotic pest invasion. There is also a high uncertainty in predicting future pest invasions. The reasons include the unpredictable effects of (1) non-native plants as potential new hosts for exotic pests [78], (2) novel invaders associated with global change (e.g., climate and land use changes), as well as (3) feedback effects [3,79]. Relative to and based on findings from community-level research, future efforts should include more ecosystem-level and more comprehensive investigations. In

addition, future studies at population and community levels should consider or at least make some predictions about possible consequential ecosystem-level consequences. To minimize further possible negative impacts from exotic pests on forest health, it will be important to avoid new introductions (including back introductions) and to practice early detection/eradication under adaptive and integrated management [35,80–82].

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