Review

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Review

Forest Resistance to Insects and Pathogens

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Abstract

Forests provide biodiversity to the planet and other forest ecosystem services – the essential benefits of humans from forests. The resilience of forest ecosystems and individual trees to stressors has always interested scientists and practitioners. Scientists have focused on the mechanisms of tree resistance. Practitioners have sought ways to reduce forest productivity losses. This work aimed to review the modern knowledge regarding forest ecosystem resilience, forest health, tree resistance, mutual adaptations of plants and phytophagous insects, and breeding trees for disease resistance. As a case study, the resistance of European ash (*Fraxinus excelsior* L.) to ash dieback and emerald ash borer *Agrilus planipennis Fairmaire*, 1888 (Coleoptera: Buprestidae): mechanisms, evidence, and future perspectives is presented. Breeding tree species for resistance to pests should play an important role in preventing their spread. Since each tree species is susceptible to some pests and resistant to others, to ensure maximum resilience, it is advisable to create mixed-age and multi-species stands, despite potential productivity losses.

Keywords: forest health; host and habitat preferences; tree tolerance; phenological synchrony; plant–herbivore interaction

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1. Introduction

According to the latest Global Forest Resources Assessment (GFRA 2025) from the UN Food and Agriculture Organization (FAO), forests cover about 32% of the Earth's land area (approximately 4.14 billion hectares) [1]. Forests provide biodiversity to the planet and other forest ecosystem services – the essential benefits of humans from forests. The main groups of forest ecosystem services are provisioning (food, timber, fuel), regulating (climate regulation, air and water cleaning, flood control, pollination), supporting (soil formation, nutrient cycling, carbon storage, habitats, biodiversity maintenance), and cultural (spiritual value, aesthetic beauty, recreation) [2,3].

The resilience of ecosystems and individual trees to stressors has always interested scientists and practitioners. Scientists have focused on the mechanisms by which var-ious factors influence tree health and growth, tree resistance, and the adaptations of insects and pathogens to overcome it [4–11]. Practitioners have sought ways to reduce forest productivity losses. Since many stressors (hurricanes, droughts) are difficult to control, the main focus has been on finding ways to "combat" insects and, to a lesser extent, pathogens [12,13].

As knowledge of forest ecosystem services has evolved, it has become clear that direct control of forest phytophagous insects and pathogens is insufficient to ensure the resilience of forest ecosystems. Therefore, efforts should be directed towards preventing those stressors that can be prevented, mitigating the effects of unavoidable stressors, and identifying and selecting tree species and forms that are resistant to certain factors, most often pathogens.

This work aimed to review the modern knowledge regarding forest ecosystem resilience, forest health, tree resistance, mutual adaptations of trees and phytophagous insects, and breeding trees for disease resistance.

2. Materials and Methods

To collect and review publications related to the subject of this paper, a comprehensive literature search was conducted using the databases Web of Science, Scopus, and Google Scholar. The following keywords and their combinations were used: "forest resilience", "tree defense", "resistance", "tolerance", "herbivory". Mainly peer-reviewed papers, book chapters, written in English from the last 10 years, were included.

3. Results

3.1. Resilience of the Forest Ecosystem

The concept of resilience of a forest ecosystem characterizes its ability to resist disturbance while maintaining its structure and functions [14]. The complexity of the horizontal and vertical structure, the diversity of niches for a large number of plant, animal, and fungal species, and their functions (e.g., phytophages, entomophages, and detritivores among insects, nitrogen-fixing and nitrifying bacteria, etc.), the diversity of intra- and interspecific relationships, and their responses to natural and anthropogenic factors contribute to forest ecosystem resilience [15]. Resilience includes three main aspects – adaptability, resistance, and recovery [14]. This approach is also applicable for urban forests [16]. Adaptability is the capacity of species and the ecosystem to adjust to ongoing changes through genetic diversity, behavioral changes, shifting ranges, or altering behaviors of species; the capacity to reorganize and persist for ecosystems. Resistance shows how the forest can withstand the factor without great changes. Recovery shows how quickly a forest restores its health after disturbance. Recovery time can range from a few years (in boreal forests) to centuries (in tropical forests) [14].

3.2. Paul Manion's Concept of Forest Health

According to Paul Manion's concept of forest health [17], every ecosystem is influenced by a variety of stressors and characterized by a baseline mortality (normal tree death) at which it remains a sustainable system. P. Manion identifies three groups of factors influencing the health condition of the forest:

- long-term factors that create the prerequisites for the deterioration or improvement of forest health (predisposing factors): climate, forest site conditions, tree genotype, chronic exposure to low-concentration air pollutants;
- short-term factors that initiate negative changes in the forest health (inciting factors): short-term stresses of abiotic (frost, drought), biotic (insects, pathogens), and anthropogenic impact (industrial emissions);
- factors that accompany the forest weakening (contributing factors): bark beetle outbreaks, epiphytoty, etc. [17].

For hundreds of years, the forests have adapted to many natural factors, including phytophagous insects and pathogens [12,18]. However, against the rapid climate change and the increased negative impact of anthropogenic factors [19–22], forests do not have time to adequately respond to the sudden increase in the spread and development of biotic factors, and lose stability [23–25].

Many impacts of natural factors (lowering of groundwater levels, hurricanes, fires), and especially the impact of anthropogenic factors (technogenic pollution, intensive thinning, clear felling on a neighboring site) lead to both direct and indirect death of trees, because they change the

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microclimate and worsen the conditions for tree growth, promote the penetration of pathogens through wounds, attraction bark beetles to the volatiles of damaged trees, and attraction defoliating insects to lay eggs in sparse and sharply illuminated parts of the crowns and quickly develop there [26–28].

The resistance of an individual tree is maintained due to genotype features, health, and environmental traits (in particular, soil richness, humidity, and illumination) [9,18,29]. These traits depend on tree species composition, age, relative density of stocking, horizontal and vertical structure of the forest, presence of seedlings, shrubs, and grasses. and create the microclimate, availability of nutrients for trees, and conditions for maturation feeding of entomophages [12,29].

3.3. Phytophagous Insects

Insects predominate in species diversity and biomass in many ecosystems on Earth [12]. From a human perspective, insects are largely considered pests or potential pests [11], although they include not only herbivores but also carnivores, detritivores, omnivores, and others [12]. Insects in forest ecosystems represent diverse trophic niches and play several different ecological roles. Herbivorous insects are primary consumers, transferring energy from producers (plants) to higher trophic levels. The net primary productivity of a forest can be increased due to the activity of phytophagous insects. Carnivorous insects prey on other insects, sometimes controlling prey populations, maintaining balance in ecosystems. Detritivorous insects (decomposers) feed on dead and decaying organic matter (detritus), promoting nutrient recycling back into the soil, which is necessary for tree growth. Insects influence herbivory, predation, decomposition, pollination, seed dispersal, forest regeneration, tree species composition and forest structure, microclimate, nutrient cycling, tree health, and productivity [29,30].

Herbivorous insects feed on leaves, sap, pollen, nectar, or wood; therefore, some herbivorous insects become pests of trees when they increase in numbers in certain stands and during years with favorable weather conditions [12,18]. Although herbivorous insects comprise more than 40% of forest insect species [31], several dozen species can significantly impact forest health, and the role of individual species and ecological groups has changed over the past decades [25,32]. The areas of oak defoliator outbreaks have decreased, and the frequency and duration of outbreaks have decreased [32]. Foliage pests with an open lifestyle and gnawing mouthparts have been replaced by species with a hidden lifestyle (leaf miners), gallmakers, and sucking insects [12].

The role of bark beetles, especially multivoltine ones (*Ips typographus, Ips acuminatus*), has increased [24,33], as well as stem pests of other taxa from the orders Coleoptera, Lepidoptera, and Hymenoptera [12]. These insects typically colonize trees weakened by other factors (herbivorous insects, drought, fire, air pollution), and then increase their numbers dramatically, becoming capable of successfully attacking relatively healthy trees. Stem pests are characterized by physiological and/or technical damage. The physiological damage of stem pests is manifested in their ability to colonize more or less weakened trees, damage trees during adult feeding, and act as pathogen vectors [33,34]. Bluestain fungi, carried by bark beetles [35–37], have been the most studied. These fungi help overcome the host tree's defense mechanisms and accelerate its death [7,11]. Bluestain fungi rapidly degrade phenolic compounds in spruce bark, increasing the attractiveness and accessibility of the phloem to beetles [38,39]. These fungi can also synthesize components of bark beetle aggregation pheromones, confirming their long-term coevolution [40]. The technical damage of stem pests can affect both living trees and forest products. It is assessed by the width and depth of their tunnels, the sapwood surface occupied by the tunnels, and the colonized portion of the trunk. Overall damage is evaluated based on physiological and technical damage, the number of generations per year, and the prevalence of the insect (the percentage of trees colonized) [33]. Outbreaks of phytophagous insects do not occur everywhere. Insects inhabit regions and planted areas with the most favorable climate and microclimate, the presence of preferred host plants as a food source, feeding sites, breeding sites, over-wintering areas, and diapause, and protection from adverse environmental factors and entomophages [5,12,18]. Trees of each age are more vulnerable to some factors and less so to others.

For pine trees aged 1-3 years, damage to roots by *Melolontha* sp. larvae and other organs by *Hylobius abietis* is dangerous. Between 7 and 20 years of age, *Aradus cinnamomeus* becomes increasingly important, and from 10 years onward, *Neodiprion sertifer* becomes more important. In mature forests, *Diprion pini*, *Panolis flammae*, *Bupalus piniarius*, *Dendrolimus pini*, as well as bark beetles, jewel beetles, and longhorn beetles, become increasingly important. The composition and role of pathogens also change with tree age: from *Melampsora pinitorqua* in the first years of life to wood-destroying fungi in mature forest [5,12,18]. Each phytophagous insect primarily inhabits forest plots dominated by its preferred host trees. Each phytophagous insect prefers specific forest site types and relative stocking densities. Taking into account preferences for forest site types, host trees, forest age, and relative stocking densities, a scoring system was developed for these forest characteristics for the most common oak and pine defoliators [18], as well as for some other phytophagous insects, such as *Aradus cinnamomeus* and pine bark beetles, for the plain part of Ukraine [26]. It allows for calculating the risk of outbreaks of these pests for each forest subcompartment, as well as the total potential outbreak area for the entire forest area or forestry district, using the forest management database.

Classic insect outbreaks, characterized by cyclical population dynamics of eruptive type [41], recur with a certain frequency, intensity, duration, and intervals between periods of population growth. An analysis of long-term dynamics of pine and oak defoliator outbreaks in Ukraine allowed us to calculate average values for these parameters. It turned out that outbreaks of these insects are most frequent, intense, and long-lasting in the southern and eastern regions [18]. A comparison of individual insect species revealed that outbreaks of species that overwinter as eggs are the most frequent, intense, and long-lasting. This is explained by the fact that in temperate climates, the coincidence of larval hatching and budburst of the host tree is especially significant [42,47]. If the eggs hatch when the bud is closed, the larva starves or migrates to a less favorable host tree. If the eggs hatch when the bud is just beginning to open, the larva receives the most favorable food – a leafy shoot that is beginning to develop, and its tissues are rich in nitrogen. If the eggs hatch much later than the bud has opened, the larva is forced to feed on a leaf containing less nitrogen and more protective substances. A comparison of the phenological characteristics of defoliating insect populations and data on the timing of foliage development in 1978-1998 showed that in eastern Ukraine (Kharkiv Region, Ukraine), the ratio of egg hatch and budburst dates is more often favorable for the development of *Tortrix viridana* caterpillars than in the west of the country (Lviv Region, Ukraine) [18]. However, analysis of data for 2002–2025 showed a shift in oak budburst and *Tortrix viridana* hatching in Kharkiv region to earlier dates, with a tendency of earlier bud-flushing than egg-hatching [32].

3.4. R.H. Painter's Factors of Plant Resistance

R.H. Painter described plant traits that allow them to resist insect attacks [48].

He called them antixenosis (non-preference/avoidance), antibiosis (harm to the insect), and tolerance (plant recovery/less damage despite infestation).

Antixenosis and antibiosis are examples of true resistance where the plant actively deters or harms the pest. Antixenosis (non-preference) is expressed by insects' rejection of resistant plant forms for colonization, feeding, egg laying, and development. Antixenosis can occur due to the presence of repellent substances in plants or their morphological features.

Antibiosis manifests as a direct negative impact on insects' nutritional and developmental processes through the actions of plants. Antibiosis results in increased insect mortality, digestive disorders, decreased feeding activity and harmfulness, prolonged development, the formation of small and underdeveloped insects, and decreased female fertility.

Tolerance is the ability of trees to regenerate damaged organs and only slightly reduce their current height growth. Some trees form callus and heal the wounds caused by damage.

Even with complete temporary defoliation, deciduous trees usually survive, although their growth is reduced [12].

For example, according to our observations, the horse chestnut leaf miner *Cameraria ohridella* Deschka & Dimić, 1986 (Lepidoptera: Gracillariidae) has caused almost 100% defoliation of chestnut trees *Aesculus hippocastanum* L. in Kharkiv's urban stands (49.98° N, 36.25° E) annually since 2007. The black ash sawfly *Tomostethus nigritus* (Fabricius, 1804) (Hymenoptera: Tenthredinidae) in Molodezhny Park has been annually damaging ash trees *Fraxinus excelsior* L. by 70–100 % since 2002. However, in the past period, only a few chestnut trees have died, and ash tree mortality has increased only since 2023, following the infestation of the emerald ash borer *Agrilus planipennis* Fairmaire, 1888 (Coleoptera: Buprestidae) [49].

Conifers are generally less resilient to insect damage. They recover damaged tissue more slowly, and growth drops sharply if even part of the needles are destroyed [12].

In contrast to antibiosis and antixenosis, "escape" is a form of "ecological resistance" where a plant avoids pests by timing its life cycle (e.g., early maturity) or growing in places where pest numbers are low, effectively escaping infestation [50]. "Escape" is the lack of coincidence of vulnerable plant phenophases and the harmful stage of phytophagous insect. It may also be called "phenological resistance" because it is manifested due to the asynchrony of critical plant phases and the period of insect damage. Thus, seeds of specimens that show signs of resistance germinate quickly and have increased germination energy. At different phenological stages, the levels of defense compounds, physical barriers (waxes), or physiological tolerance to stressors vary [51,52].

A plant's growth stage (phenology) influences its susceptibility or resistance to pests and pathogens, often involving timing, resource allocation (monoterpenes, phenolics, etc.), and seasonal changes where plants might develop stronger defenses as they mature or shift their timing to avoid peak pest pressure.

Advancing spring phenology (earlier green-up) can mismatch plant defenses with pest activity, altering vulnerability and requiring new management approaches. In the example above, climate change, along with other factors, has led to a reduction in the risk of *Tortrix viridana* outbreaks [32].

In a multifactorial growth chamber experiment, the influence of spring phenology on a plant pathogen (oak powdery mildew *Erysiphe alphitoides*) was studied, as well as the influence of spring phenology and pathogen infestation on the spread of two multivoltine phytophages (the oak leaf miner *Tischeria ekebladella* and the aphid *Tuberculatus annulatus*) on *Quercus robur* at the beginning, middle, and end of the growing season. Oak powdery mildew infestation levels were consistently high on late-phenological plants. The leaf miner preferred late-phenological plants and healthy seedlings, while the aphid's preferences changed throughout the growing season [53].

3.5. Mutual Adaptations of Plants and Phytophagous Insects

For centuries, plants and their phytophagous insect have co-evolved. Plants have developed adaptations to minimize consumption by insects, and insects have developed adaptations to avoid or tolerate tree defenses [14,16,54].

Active defense of trees against insects can be achieved through changes in the structure of the bark, leaves, and other tissues (physical defense), the synthesis of protective substances (chemical defense), and constitutive (preformed resin) and inducible (traumatic resin ducts) [10].

Examples of physical defense include trichomes on the leaf surface, spines and thorns on shoots, changes in bark texture, and an increase in the number of specialized sclerenchyma cells. Such changes prevent phytophages from feeding and/or penetrating the tree to bore tunnels [15,55,56].

Chemical defense of plants against herbivores is provided by monoterpenes, sesquiterpenes, diterpenes, soluble phenolics like flavonoids, and stilbenes [15,55]. Tolerance is manifested in accelerated growth, increased intensity of photosynthesis, additional branching, and carbon storage in the roots [57].

Insects also adapt to overcome tree resistance. They select a tree and a site on it where they can lay eggs relatively safely (external adaptations). Insects with sucking mouthparts and an open lifestyle are more vulnerable to the tree's chemical defenses, while xylophages, carpophages, conophages, and leaf miners are also vulnerable to physical defenses.

Insect strategies for overcoming plant defense mechanisms are considered extrinsic or intrinsic, depending on whether they are used before or after feeding on plant tissue. Examples of extrinsic insect strategies include host selection for feeding and egg laying, while examples of intrinsic strategies include tasting and avoidance, excretion (removal of ingested toxic substances from the gut), detoxification (chemical conversion and conjugation of toxic substances), and sequestration (using toxic substances for protection or pheromone production) [11]. In a comprehensive review, these authors categorize plant defense traits against insects according to four levels of organization. These include: mode of action (plant-side), temporal sequence (interaction between plant and insect), effective dose (insect-side), and ecological function (tritrophic interactions). Mode of action (plant-side) includes chemical traits (providing toxic effect), physical traits (providing a mechanical barrier), and or both modes.

Temporal sequence (interaction between plant and insect) determines whether the protection element exists before or after the insect attack. Constitutive defense always exists even in the absence of an insect attack [6]. Thus, phenolic metabolites are immediately released from the polyphenolic cells of the phloem when feeding begins. The resin ducts always contain oleoresin - a source of terpenes [58,59]. Stony cells function as physical barriers [60–64]. Induced defense is mobilized in response to an insect attack. Examples are the formation of traumatic resin ducts in the wood of coniferous species and the hypersensitive reaction of leaves. Effective dose (insect-side) assumes an optimal combination of physical and chemical protection [58].

Tritrophic interactions present ecological functions [54]. Tritrophic interactions are indirect defenses: attracting third trophic level organisms (carnivores/parasitoids) to control herbivores, involving chemical signals like jasmonic acid that trigger responses like releasing volatile organic compounds (VOCs) or extrafloral nectar (EFN). These interactions involve species of three trophic levels: producers, a primary consumer (the phytophagous insect), and its natural enemy. The tree benefits from the phytophagous insect being attacked by its natural enemy [54,65].

Such interactions were used in experiments using methyl jasmonate to protect trees from biotic stressors, particularly Picea sp. against Ceratocystis polonica, a bark beetle-associated fungus [66] and bark beetles [67,68], Fraxinus sp. against emerald ash borer [63,64]. A meta-analysis of 120 relevant papers has shown that methyl jasmonate significantly reduces tree damage caused by biotic stressors but lowers tree growth [69].

3.6. A Case Study: Resistance of European Ash (Fraxinus excelsior) to Ash Dieback (ADB) and Emerald Ash Borer (EAB): Mechanisms, Evidence, and Future Perspectives

Forest resistance to insects and pathogens arises from interactions among host genotype, physiological condition, associated microbiota, and environmental context. Host defence responses and host developmental stage are major factors influencing the outcome of microbial and insect infection challenges in forest trees. The host microbiome is increasingly recognised as an extension of the host phenotype, contributing to defence, stress tolerance and nutrient cycling [70]. Emerging infectious diseases and invasive pests rarely eliminate an entire host population; instead, they leave a fraction of surviving individuals. These survivors are critical for the long-term persistence, adaptive evolution and recovery of affected tree species.

In long-lived forest trees, resistance rarely implies complete immunity; instead, it is expressed as reduced susceptibility, delayed damage progression, or enhanced survival under sustained biotic pressure. European ash (*Fraxinus excelsior* L.) provides a representative case study for illustrating general principles of forest resistance within the broader framework of tree–insect–pathogen interactions.

Ash dieback (ADB), caused by the invasive fungus *Hymenoscyphus fraxineus*, has severely affected ash populations throughout Europe. Despite high infection pressure, long-term monitoring consistently reveals a small proportion of trees that remain healthy or only moderately affected. This resistance is heritable and polygenic, involving phenological traits, stem and bark defence responses, and variation in secondary metabolites [71,72]. Such surviving individuals are essential for natural selection processes and for resistance-based forest management.

The emerald ash borer (*Agrilus planipennis* Fairmaire, 1888) represents an additional and novel stressor for European ash. Although F. excelsior lacks a shared evolutionary history with this beetle, comparative studies among ash species indicate that resistance to wood-boring insects is mediated by constitutive phloem chemistry, induced defences, and anatomical traits limiting larval performance.

The westward expansion of EAB from its invasion front in eastern Europe poses an additional and potentially catastrophic threat to already weakened ash populations. Understanding resistance and tolerance mechanisms to both ADB and EAB is therefore essential for developing effective conservation, breeding and management strategies [71,72].

Natural resistance and tolerance to ADB: Long-term field surveys across Europe demonstrate that a small but consistent proportion of European ash trees remain healthy or only weakly affected despite prolonged exposure to high infection pressure of H. fraxineus. The frequency of such trees is typically estimated at 1–5%, although higher values have been reported locally. Importantly, reduced susceptibility to ADB is under moderate to strong genetic control and is heritable, providing a basis for both natural selection and resistance breeding. Resistance and tolerance to ADB are complex, polygenic traits involving phenological, physiological, morphological, phytochemical and molecular mechanisms [73–76]. Defence responses in bark and stem tissues appear particularly important, as lesion length following artificial stem inoculation correlates well with crown damage observed in the field. At the same time, foliar-level resistance and tolerance mechanisms, including restriction of fungal growth from leaves into shoots, may also contribute but remain less well understood [72,77].

Molecular and chemical mechanisms of ADB resistance: Advances in genomics and transcriptomics have enabled the identification of single nucleotide polymorphisms (SNPs) and candidate genes associated with reduced ADB susceptibility. These genes are often involved in pathogen recognition, signal transduction, cell wall modification and defence regulation. However, most molecular markers identified so far require validation across multiple populations and environmental conditions before operational application in breeding programmes [75,76,78]. Metabolomic studies have revealed that variation in specialised metabolites, including phenolics and iridoid glycosides, is associated with ADB resistance [79]. Interestingly, lower levels of certain iridoid glycosides have been linked to increased resistance, suggesting trade-offs among defence pathways. Such trade-offs may have important consequences for interactions with in-sect herbivores, including EAB.

Resistance of ash to EAB: Knowledge of the resistance of European ash to EAB is still limited, largely because the beetle has only recently begun to invade Europe. In contrast, extensive research in North America and Asia has demonstrated strong interspecific and intraspecific variation in EAB resistance among ash species. Coevolved Asian ash species, such as *Fraxinus mandshurica*, show substantially higher resistance than naïve North American species. Partial resistance to EAB has been linked to phloem chemistry, defence-related proteins and induced responses. Whether similar intraspecific variation exists within European ash populations remained uncertain until recently [80,81].

At the molecular level, increasing attention has also been paid to the biology of EAB itself. Studies on the beetle's genome and transcriptome have demonstrated that A. *planipennis* possesses a conserved and functional RNA interference (RNAi) machinery, including key components such as Dicer-2, Argonaute-2, and R2D2 [80]. Experimental gene knockdown via double-stranded RNA injection confirms that RNAi pathways are active in this species. Although RNAi-based control strategies are not yet applicable at the forest scale, these findings provide valuable insight into beetle physiology and host–pest interactions and may inform future targeted or integrated pest management approaches.

Cross-resistance between ADB and EAB: Experimental evidence has now demonstrated cross-resistance between ADB and EAB in European ash. Gossner et al. [81] showed that grafted *F. excelsior* genotypes resistant to ADB supported significantly lower EAB larval performance than susceptible

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genotypes. Differences in beetle performance were associated with constitutive variation in phloem chemical profiles, providing mechanistic evidence that defence chemistry can confer resistance to antagonists from different taxonomic kingdoms. These findings have important implications for ash conservation and breeding, suggesting that selection for ADB resistance may simultaneously reduce vulnerability to EAB.

Climate change and combined ash stressors: Resistance and tolerance to ADB and EAB must be considered in the context of climate change. Drought stress may reduce tree vigour and compromise defence-related pathways, potentially increasing susceptibility to secondary pests such as EAB. Interactions among abiotic stress, fungal pathogens and insect pests are therefore likely to intensify under future climate scenarios.

Another important but still underexplored dimension of ash resistance is the role of host-associated microbial communities. Fungi also may contribute to disease suppression, competitive exclusion of pathogens, or modulation of host defence responses. Network-based analyses of microbiomes and metabolite profiles in resistant vs susceptible ash trees give promising opportunities to identify functionally important microbial taxa and metabolites. Integrating microbiome data with host genomics and metabolomics may substantially improve understanding of resistance mechanisms and open new ways for biocontrol or resilience-based management.

Perspectives: The potential recovery of ash populations in Europe will further depend on the extent of gene flow among populations and on how disease pressure alters competitive interactions within forest ecosystems. Genetic markers enabling paternity assignment and detection of selection signatures in natural stands can support adaptive management of infected forests. However, the development and validation of robust marker sets require coordinated, large-scale sampling and phenotyping efforts across Europe, highlighting the importance of international collaboration. Most analytical tools are already available; the main challenge lies in integration and translation into practical conservation, breeding and policy solutions. Coordinated European efforts are essential to mitigate ash decline and preserve this keystone species.

3.7. Breeding Trees for Disease Resistance

Tree breeding is typically accomplished by selecting specimens with desired traits from plantations, selecting or crossing them, and testing the resulting progeny. This process is repeated to increase the expression of the desired traits in each breeding generation. Improving tree resistance to diseases and pests involves studying the relationship between the tree and the pathogen, their genetics, and the environmental conditions favorable for infection. However, selecting trees resistant to various pathogens is a complex task. Unlike most crops, forest trees live for decades and even become parents to the next generation. Therefore, the goal of resistance breeding is to create tree populations that are adapted to local conditions and possess sufficient genetic diversity to survive and thrive under the influence of potential abiotic and biotic factors [82].

Tree breeding should contribute to biodiversity conservation, improve ecosystem services, and maintain global carbon sequestration. Therefore, forest tree breeding requires combining advanced genetic technologies and ecological understanding to ensure that the resulting clones and hybrids can thrive in environments with unpredictable changes in various factors [83,84].

4. Conclusions

Climate change and increasing anthropogenic pressure are already having negative impacts on forest ecosystems, due to groundwater level lowering, increased drought frequency, expanding ranges of non-native pests and pathogens, and disruption of the synchronic development of species at different trophic levels. Trees' natural defense mechanisms can prevent pest and disease attacks and/or mitigate their impacts.

Breeding tree species for resistance to pests should play an important role in preventing their spread. Specimens resistant to native pests have evolved over centuries in natural populations and have been developed by scientists using selective breeding or genetic engineering. However, trees resistant to non-native pathogens are not yet available. In the event of a threat from the spread of a non-native pest or pathogen, one possible solution is to change the tree species composition. Since each tree species is susceptible to some pests and resistant to others, to ensure maximum resilience, it is advisable to create mixed-age and multi-species stands, despite potential productivity losses.

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