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Restoring forests in a changing world: the ash dieback crisis

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Abstract

Invasive tree pests and pathogens are increasingly threatening global forest health. While restoration aims to recover degraded or destroyed ecosystems, these biotic agents question the feasibility of restoring ecosystem structure, function, and stability to a historical baseline. This paper uses ash dieback (*Hymenoscyphus fraxineus*) as a case example to review the difficulty of restoring ash woodlands under complex interactions between the pathogen, host, changing environment, and the society. It reviews the history of the spread of ash dieback disease, its ecological impact, the climate-pathogen interactions, how scientific communities respond to the tree health issue, and how the society adapts to the crisis. The difficulty of early disease detection and disease control are the most important impediments of restoration actions. Under persistent disturbance regimes, restoration should adopt a dynamical view of the ecosystems, carefully making risk adaptation plans, and monitor the long-term dynamics of biodiversity, nutrient cycles, and other ecosystem functions of interest. With continuous global change, risk management becomes increasingly important for restoration and rewilding activities.

1. Restoration in the context of tree pests and pathogens

Invasive tree pests and pathogens accumulate rapidly around the globe, with emerging forest diseases doubling every approximately 11 years (Gougherty, 2023). While forest functions as the most important terrestrial carbon sink, as well as biodiversity shelters, these biotic agents can substantially change its landscape. Some striking examples include Dutch Elm Disease (*Ophiostoma novo-ulmi*), ash dieback (*Hymenoscyphus fraxineus*), Pine wood nematode (Bursaphelenchus xylophilus), and chestnut blight (*Cryphonectria parasitica*). Widespread and damaging insects and disease outbreaks could cause long-term deterioration of forest ecosystem services, which is unfortunately under-researched (Boyd et al., 2013). As international transport and trade—key drivers of invasive species' spreading—continues to grow, it is uncertain how these invasive species will affect the forests and whether it may impede our agenda on nature restoration, climate net zero, and biodiversity net gain.

While restoration aims to recover degraded or destroyed ecosystems, insect and disease outbreaks introduce novel disturbances that challenge woodland management efforts. These agents are often difficult to detect at first, and the symptoms they cause on trees can be confounded with abiotic stress such as drought and excessive heat (Carroll and Boa, 2024). After a latent period, they could spread quickly across the woods and even at a continental scale before the society responds to them. Forest restoration projects should thus embed in the context that forest ecosystems may undergo alternative shifts in a short timeframe, and may consistently change due to changing climate–insect and climate–pathogen interactions.

Current restoration strategies use a static view that requires assessment of multi-faceted complexity (structure, functioning and stability) of ecosystems as a reference or baseline state (Moreno-Mateos et al., 2020). However, a compositional shift of forest ecosystems may happen easily, and its historical structure and functions could be impossible to recover. Tree pests and pathogens are good examples where traditional restoration and nature recovery approaches may no longer be effective. Unfortunately, there are limited reviews on applying a dynamic view of ecological restoration under such a changing context. This paper aims to use ash dieback as an example to demonstrate why forest recovery should embed in a changing context, and what this case study implies for restorations and rewilding in the next decade.

2. Ash dieback

Ash dieback is a fatal disease caused by an ascomycete fungus (*Hymenoscyphus fraxineus*) on the European ash tree (*Fraxinus excelsior L.*). Ash is an important deciduous tree throughout Europe. It occurs in 64% of European territories and has a long history as a hedgerow and street tree in many European countries (Thomas, 2016). Ash also forms many temperate woodlands, dominating with Acer campestre and Mercurialis perennis on bare-rich soils of lowland Britain, and with Sorbus aucuparia and Mercurialis perennis in cooler and wetter conditions (Thomas, 2016). These ash woodlands provide shelters for 953 associated species, including 12 birds, 28 mammals, 58 bryophytes, 68 fungi, 239 invertebrates and 548 lichens (Mitchell et al., 2014). 44 of them are obligated to ash, including 11 fungi, 29 invertebrates and 4 lichens (Mitchell et al., 2014). Ash also has a unique role in the ecosystem functioning of the woodlands, with its higher litter degradability and faster decomposition and nutrient cycling than other tree species (Mitchell et al., 2014).

Ash dieback has profoundly affected European forest health for decades. The disease was first reported in 1992 in Poland, accompanied with trees dying in large numbers (Przybył, 2002). However, the dieback fungus H. fraxineus may already have been present in Poland since the 1960s (Sønstebø et al., 2017). At the early infection stages, the disease is difficult to detect and can be misidentified as other physical stress. The pathogen quickly spread across continental Europe before its anamorph being identified in 2006 (Kowalski, 2006). It has now affected the majority of the native range of ash trees, being reported in the British Isles since 2012 (Woodward and Boa, 2013). The result of infection is often extensive crown damage and ash tree loss, with a maximum mortality of ~70% in woodlands and ~82% for naturally regenerated saplings (Coker et al., 2018). The actual mortality varies substantially, primarily depending on genotypes, and also affected by tree stage, local climate, woodland density, and a number of other factors. Susceptible trees die quickly after infection, and even old trees would succumb after a few years of infection. But around 1–5% of ash trees may have disease tolerance, with most of its crown remaining to be healthy.

Nowadays, ash trees have reached a critical survival probability of 0.51 after 30 years of infection, with a great variation among regions (0.20 – 0.86) (George et al., 2022). An overall defoliation will likely reach 50% by 2030 according to a modelling forecast (George et al., 2022). Despite scientific efforts of two decades, we are still on the way to identify effective methods to rescue the ash population, and potential ecological impacts from the loss of ash. One research direction is to understand how the environment interacts with the pathogen life cycle. Early experimental study suggested that H. fraxineus grows best at ~20°C, and it could hardly survive the hot water treatment of diseased ash tissues at 36 °C (Hauptman et al., 2013). This aligns well with a woodland study in southeast France, which reported that high summer temperature could stress the pathogen living in tree tissues, thus reducing the disease severity in the following year (Grosdidier et al., 2018). Although the European climate is mostly suitable for pathogen development, the summer heatwave with a temperature record at 40°C would perhaps alleviate the disease impact by killing the fungus. Spring and summer rainfall are important for the fungus to produce enough ascospores to initiate new infections (Marçais et al., 2023). This explains why disease severity is higher at moist sites. Under the global climate change scenario, it is predicted that ash dieback disease will expand the range poleward, while at the same time the crisis would alleviate in southern and occidental Europe (Goberville et al., 2016).

Another area of interest is breeding resistant trees. A genome-wide association study identified 3,149 single nucleotide polymorphisms (SNPs) that are associated with the level of health deterioration, providing the genomic basis of the disease resistance (Stocks et al. 2019). Based on the specified heritability mechanism, a modelling research predicted that the proportion of initial resistant ash has a large effect on population size after 100 years, indicating the viability of an ash selective breeding programme (Evans, 2019). In many sites, nature selection on resistant ash has already been in progress, as ash dieback lowers the tree reproductive performance by reduced flower formation and pollen viability (Eisen et al., 2024). It is also important that ash trees resistant to the dieback fungus should also be resistant to other stresses to survive in a changing world, such as Emerald Ash Borer (*Agrilus lanipennis*), a destructive insect that attacks ash trees and causes massive tree mortality. Fortunately, resistant ash was found to also perform better against the A. planipennis, thus the promotion of resistant genotypes also helped to control the Emerald Ash Borer-caused ash loss (Gossner et al., 2023).

Finally, ash dieback disease may indirectly cause associated species loss, and a profound change of nutrient cycles. Invertebrates, lichens, and bryophytes are particularly at risk from ash population loss. In Sweden, 52 species (4 fungi, 3 bryophytes, 43 invertebrates and 2 lichens) use ash as the only substrate (Hultberg et al., 2020). Of all 483 species associated with ash, 260 are invertebrates (211 beetles, 30 butterflies, etc.), 87 are lichens, and 71 are bryophytes (Hultberg et al., 2020). Ground flora communities would also be affected by the loss of ash dominance, including five ash associated species of conservation status (Mitchell et al., 2016).

3. Society’s response to ash dieback

The spread of ash dieback disease was facilitated by international transport and trade of Fraxinus material. Although the European and Mediterranean Plant Protection Organization (EPPO) included H. fraxineus on its alert list, actions on stopping the trade of plant material were generally too late and were ineffective (EPPO, 2023). In the UK, H. fraxineus is believed to have arrived in the early 2000s on infected planting stock from continental Europe, although the disease was first reported in 2012. Prior to the report year, British publics were largely unaware of the severity and symptoms of the disease, which may explain why it went unreporeted (Carroll and Boa, 2024). In 2012, the detection of H. fraxineus attracted intensive media attention, with 825 national newspaper articles published on this tree health issue between late 2012 and 31 December 2015 (Fellenor et al., 2019). The Woodland Trust called for a ban on importing ash timber, which finally came into legal force as an EU plant health regulation in 2020. However, these legal actions were too late to prevent the disease spreading further across the UK and Ireland.

Nowadays, recovery of ash woodlands relies on conservative approaches: to let the disease progress naturally and accelerate the natural selection process to increase the proportion of resistant trees in the next generation. Meanwhile, projects that monitor tree health are being initiated in sites with ash woodlands. The Royal Botanic Gardens, Kew, holds a large collection of ash seeds through the UK National Tree Seed Project, and is continuously finding candidate genes that are possible for breeding trees resistant to ash dieback and ash borer. Hybridisation among ash species is also being explored as an alternative tree planting solution.

4. Conclusion and implications

The UN defines ecosystem restoration to be assisting in the recovery of degraded or destroyed ecosystems, or to conserve ecosystems that are still intact. It published ten principles for orienting restoration activities towards a shared vision that maximises the biodiversity net gain, ecosystem health and integrity, human health and wellbeing globally (UN, 2021). Under persistent disturbances like tree pests and pathogens, ecosystem degradation could be irreversible. Complex interactions among pathogens, tree hosts, environment, and society could have unprecedented impact that may persist for several decades. It is likely that restoration should allow itself to live with the crises, prioritising restoration goals in a changing world, with continuous monitoring of biodiversity, nutrient dynamics, and tree health. Doing so might be seen as a response, in ecological management practices, to calls from researchers to 'stay with the trouble' (Haraway, 2020) and to acknowledge and work with unexpected forms of life emerging from capitalist ruins (Tsing, 2015).

While restoration may have many options (e.g. the use of pesticides, sanitary felling, breeding resistant trees for the battle of tree pathogens), the actual strategy should take a dynamic view, recognising the potential impact on forest biodiversity, ecosystem functioning, societal concerns, and human well-being. These principles are important for risk adaptation in a nature recovery process. Restorations failed to consider these principles include large-scale monoculture plantings or applying pesticides in a top-down approach. As an example, in the 20th century, China has initiated the largest reforestation program in the world to combat expanding desertification, decrease water and soil erosion, prevent sandstorms, and shelter agriculture land. Unfortunately, large-scale planting of fast-growing poplar (*Populus spp.*) promoted the spread of Asian longhorned beetle (*Anoplophora glabripennis*), a fatal insect that can tunnel into the tree's wood and eventually cause the tree's death (Carter et al., 2009). Therefore, tree pests and disease outbreaks provide a valuable example on the complex reality of recovering woodland health, as the disease is difficult to detect at the early stage, and is impossible to prevent once it has been established in a woodland. The presence of such a crisis may question restoration efforts that fails to adopt a dynamic view of ecosystems, and will, hopefully, advance the integration of risk adaptation strategies in restoration policies. Rather than seek to preserve static ecological communities, which in many cases may be impossible, ash dieback highlights the need to explore and implement alternative ecological management strategies. Rewilding and certain forms of regenerative agriculture, which entail more complex and dynamic approaches and an open-ended disposition towards the ecological communities of the future (Perino et al., 2019; Prior and Ward, 2016), may offer guiding principles for such strategies.

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