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Review Article

Site-specific factors influencing *Hymenoscyphus fraxineus* spore dispersal: the role of understorey vegetation and slope steepness in ash dieback spread

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Abstract

Ash dieback (ADB), caused by *Hymenoscyphus fraxineus*, is a severe threat to *Fraxinus excelsior* populations across Europe, with spore dispersal playing a critical role in disease progression. While broad-scale environmental drivers of spore dispersal are well studied, site-specific factors remain underexplored. This review uniquely explores how understorey and slope steepness influence the dispersal, deposition, and development of *H. fraxineus* spores, along with stand management strategies reported to impact ADB disease progression. The dense understorey vegetation creates microclimatic conditions favouring spore development and retention through increased humidity, reduced airflow, and light accessibility, while also potentially modifying transmission dynamics. Slope steepness may affect spore dynamics through gravity-driven movements of infected ash rachises, and microclimatic variation associated with slope aspect. Understanding these site-specific effects can enhance disease management strategies aimed at conserving tolerant individuals and preserving the genetic basis of tolerance for future *Fraxineus excelsior* generations. The review also identifies knowledge gaps and highlights the need for empirical research on context-specific management strategies across diverse forest landscapes.

Keywords: ash dieback; *Hymenoscyphus fraxineus*; life cycle; site-specific characteristic; slope aspects; spore; understorey presence

Introduction

An invasive pathogen, *Hymenoscyphus fraxineus*, causing ADB disease has been endangering the population of *Fraxinus excelsior* across Europe (Coker *et al.*, 2019) and the United Kingdom (Clark and Webber, 2017). The impact of ADB disease has led to widespread tree mortality, severely causing stand disruptions (Madsen *et al.*, 2021), ecological (Pautasso *et al.*, 2013) and economic (Hill *et al.*, 2019) losses. While substantial research has explored broad-scale disease determinants, including weather conditions (Timmermann *et al.*, 2017), environmental drivers (Chumanová *et al.*, 2019), genetics (Harper *et al.*, 2016; Stocks *et al.*, 2017), silvicultural practices (Skovsgaard *et al.*, 2017), microbial communities (Griffiths *et al.*, 2020) and biology of the pathogen (Gross *et al.*, 2014), the studies on the influence of site-specific factors remains comparatively understudied. Emerging evidence suggests that local environmental heterogeneity may

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influence *H. fraxineus* spore production, dispersal, and infection success. Dense understorey vegetation can alter the microclimate by increasing humidity and reducing airflow (Combes, 2022) and serving as a physical barrier (Forestry Commission and Natural England, 2019), while slope can affect spore deposition through gravitational forces through the transport of leaf litter (Du *et al.*, 2019), rain intensity (Madden, 1997), air humidity (Geiger *et al.*, 2009), and surface materials (Miura *et al.*, 2002). These factors are likely to contribute to spatial variability in infection pressure and disease severity, yet have not been systematically reviewed in relation to ADB epidemiology.

The importance of appropriate forestry practices and site conditions were reported as important factors in preserving ash trees showing fewer ADB symptoms and retaining those individuals withstanding the disease in all phases of stand development (Skovsgaard *et al.*, 2010; Langer *et al.*, 2022). Felling all ash trees without considering their health status is to be avoided because tolerant genotypes will be lost according to recommendations by Skovsgaard *et al.* (2017), and subsequently, the loss of ash would lead to a loss in the forest ecosystem (Mitchell *et al.*, 2014). Havrdova *et al.* (2017) reported that ash density is associated with an increase in ash dieback symptoms found in tree crown and stem collars, which was also reported by Grosdidier *et al.* (2020) that forest stands with low ash density had less severe signs of ADB. Despite the potential importance of the site-specific characteristics in the context of ADB severity, they remain underexplored.

Thus, this review aims to address the knowledge gap on the impact of the understorey vegetation and slope steepness on the development *of H. fraxineus* spores, along with stand management strategies impacting the ADB disease progression. Addressing these aspects may offer new perspectives for disease monitoring, risk assessment, and refining management strategies to prevent further losses of ash trees and preserve the tolerant genes in the forests.

Biology of *Hymenoscyphus fraxineus*

H. fraxineus is an invasive fungal pathogen, as described by Kowalski (2006), with taxonomy classified in class *Leotiomycetes*, order *Helotiales*, genus *Hymenoscyphus*. Originating from Asia (Japan, Korea, China), and Russia (Marčiulynienė *et al.*, 2018). In Europe, ash dieback has emerged over the last 20 years, but symptoms of *H. fraxineus* were first observed in the early 1990s in Poland (Przybył, 2002). Known at that time as *Chalara fraxinea*, it was first described as an anamorph and named *Chalara fraxinea* (Kowalski, 2006). ADB disease was first discovered in the United Kingdom, in February 2012 during a routine inspection of a nursery in Buckinghamshire (Rowley, 2012) (Sansford, 2013), although there is evidence of its presence may date back to the early 1990s (Wylder *et al.*, 2018). According to a study conducted by (George *et al.*, 2022), the spread of the pathogen has substantially increased over the 30 years of infection, with a 0.51 survival probability value.

Life cycle

As a pleiomorphic heterothallic fungus (Gross *et al.*, 2012), *H. fraxineus* completes its entire sexual life cycle on ash leaves during the growing season (Gross *et al.*, 2014). The fungus invades the rachices and petioles tissues where it persists latently until leaf senescence (Kirisits and Cech, 2009; Gross *et al.*, 2014). The sexual phase takes place during the summer when fruiting bodies (apothecia) mature (Kirisits and Cech, 2009). The mature apothecia develop on infected fallen leaves and petioles from previous years (Kowalski and Holdenrieder, 2009). Once the apothecia are fully developed, ascospores are discharged and germinate on living leaves and invade the vascular tissue and woody parts of ash trees (Cleary *et al.*, 2013). The asexual (anamorph) phase of the *H. fraxineus* life cycle involves the production of prolific asexual spores via phialides that develop on the pseudosclerotial layer at low temperatures in the autumn and winter (Gross *et al.*, 2014). According to a study by Fones *et al.* (2016) conidia were found to infect seedlings. However, the primary infection is almost certainly caused by the sexual spores (Gross *et al.*, 2014) further experimental validation is required (Enderle *et al.*, 2019).

Observations on the apothecia and ascospore dispersal were reported from May (Mansfield *et al.*, 2018) until late October (Kirisits and Cech, 2009). with the maximum sporulation period during the summer months outlining the key role of temperature in the apothecia development from mid-June until early September (Chandelier *et al.*, 2014) and Grosdidier *et al.* (2018) indicated that sporulation variability is linked to weather conditions. Ascospores are released from the apothecia (Gross *et al.*, 2014) and further develop on the leaf and rachises of ash trees. Furthermore, the apothecia of *H. fraxineus* occurs almost exclusively on the previous year's *Fraxinus* petioles and leaflet veins in the leaf litter (Kirisits and Cech, 2009). Timmermann *et al.* (2011) found that the deposition of putative ascospores of *H. fraxineus* during the period 29 July and 12 August, mainly occurred between 6 and 8 a.m. with a distinctive peak around 7 a.m. *In vitro* experiments revealed that a high percentage of *H. fraxineus* ascospores germinate under specific conditions. Up to 93% germinated within 48 h in the presence of sterile water droplets in laboratory conditions fluctuating between 15 and 21˚C (Mansfield *et al.*, 2018), up to 91% in a Petri dish with sterile water agar after 68 h at 20˚C (Brühwiler and Sieber, 2021) and ~85–96% on malt extract agar after 67 h at 20˚C (Schlegel *et al.*, 2016). According to Chandelier *et al.* (2014) spore density was found to be consistently higher at 0.5m than at 3 m from the ground, which could be explained by the proximity of the primary source of the infected leaf litter on the forest floor. Additionally, the density of the spores was found to influence the development and severity of ash dieback symptoms, including necrotic lesions on leaflets and rachises, wilting of shoots, crown dieback, and the formation of stem lesions (Combes, 2022; Hietala *et al.*, 2022). This can be attributed to the genus *Hymenoscyphus*, order *Helotiales*, where some of the growth development stages for the species alter from endophytic to pathogenic individuals when a specific threshold of the endophytes is reached (Cross *et al.*, 2017).

Environmental characteristics influencing ADB spread

The widespread distribution of *H. fraxineus* demonstrates its ability to tolerate different environmental conditions – from Asia to Europe (Combes *et al.*, 2024).

Environmental factors such as leaf wetness and humidity are critical for apothecia development and ascospore viability (Gross *et al.*, 2012; Hietala *et al.*, 2013). High humidity favours pathogen growth, whereas extreme temperatures (>30°C) reduce it (Hauptman *et al.*, 2013; Grosdidier *et al.*, 2018). The fungus survives unfavourable conditions in a melanized pseudosclerotial layer on rachises, allowing it to persist for years (Kirisits, 2015).

Soil moisture and humidity

Soil moisture (Marçais *et al.*, 2016) and air humidity (Havrdova *et al.*, 2017) were reported as one of the critical factors impacting the ADB disease severity, along with increased humidity (Chumanová *et al.*, 2019), site moisture (Grosdidier *et al.*, 2020), temperature (Grosdidier *et al.*, 2018), elevation, precipitation and wind speed (Chumanová *et al.*, 2019; Burns *et al.*, 2022). Studies suggested that increased severity of ADB was reported at moist sites and humid areas (Chumanová *et al.*, 2019). The latter is supported by the finding that higher relative humidity, leaf moisture and wetness were positively associated with aerial ascospores density (Combes *et al.*, 2024). Similarly, in Japan, an increased quantity of apothecia were observed in shady and humid areas compared to dry and sunny sites (Inoue *et al.*, 2019). The correlation between a site flood risk index and the density of apothecia was also statistically proven by Grosdidier. *et al.* (2018) outlining site conditions favouring the pathogen.

Temperature

Outlined as a critical factor for the distribution of species and ecosystems processes (Lembrechts *et al.*, 2020; Bennett *et al.*, 2021; Ismaeel *et al.*, 2024), temperature has also been found to differ across the forest types with different impacts (Barbier *et al.*, 2008; von Arx *et al.*, 2012; Ismaeel *et al.*, 2024) and on understorey (Brooks and Kyker-Snowman, 2008; Landuyt *et al.*, 2019; Balandier *et al.*, 2022). *Hymenoscyphus fraxineus* growth is optimal at around 20°C (Kowalski and Bartnik, 2010), apothecia development at 10˚C mean daily temperature (Combes, 2022) with the growth rate declining at higher temperatures (Grosdidier. *et al.*, 2018), and very little growth occurring at 30˚C (Hauptman *et al.*, 2013). A study by Havrdova *et al.* (2017) reported a positive relationship between the extent of ash dieback and the mean annual temperature range, while other studies reported that shoot mortality was observed at extremely high temperatures (Marçais *et al.*, 2023). Thus, it is reasonable to expect that warm temperatures, and not extreme, would be conducive for the pathogen development. Moreover, if unfavourable conditions are present, the pathogen persists at the pseudosclerotial layer consisting of melanized wall (Gross *et al.*, 2014) formed as a thin black stromatic layer on the surface of the rachices and veins (Baral and Bemmann, 2014) until environmental factors become more conducive. That said, the development of a pseudosclerotial layer allows the fungus to survive and reproduce apothecia for up to 5 years (Kirisits, 2015).

Precipitation

A study by Chumanová *et al.* (2019) demonstrated a positive relationship between the mean annual precipitation and disease severity. This is in accordance with findings by (Havrdova *et al.*, 2017; Marçais *et al.*, 2023). That said, leaf moisture was described by Burns *et al.* (2022) as more important than rainfall for the spore emotion, which, according to t Timmermann *et al.* (2011) and Hietala *et al.* (2013), could be attributed to the role of humid air that supports the process of the maturity and germination of *H. fraxineus* spores.

Wind

As a wind-dispersed pathogen (Kowalski and Holdenrieder, 2009), wind is another important factor in the spread and colonization of *H. fraxineus* spores (Chumanová *et al.*, 2019). The wind can impact spore dispersal, transporting ascospores to different areas (Orton *et al.*, 2018). At the same time most ascospores are likely deposited within 50 meters (Chandelier *et al.*, 2014) of an infected ash stand, whereas estimation of a long-distance areal dispersal reported of 30-70 km per year (Børja *et al.*, 2017). Based on the literature, wind factor also plays a role in influencing microclimate and disease suitability conditions. According to the findings by Chumanová *et al.* (2019), windy locations were reported as less suitable areas for ash dieback. The explanation of the results is attributed to the wind velocity reported to impact foliage, resulting in lower leaf moisture availability, inhibiting the process of spore germination, deposition and infection. Additionally, windy sites could reduce the level of air humidity through increasing evaporation processes (Kim *et al.*, 2014).

Site-specific characteristics influencing ADB severity

Influence of understorey vegetation on microclimate and H. fraxineus spore dispersal

The influence of the site characteristics on apothecia development and spore dispersal were reported as significant (Chandelier *et al.*, 2014; Dvořák *et al.*, 2023). One such factor has been found to be the understorey (Skovsgaard *et al.*, 2017). The role of the understorey in modifying microclimate (Combes, 2022), serving as a physical barrier (Rodríguez-Rodríguez *et al.*, 2023) and pathogen dynamics (Landuyt *et al.*, 2019), which increases the infection pressure in the affected areas. Reduced light in dense stands, influenced by canopy closure and stand management (Kerr, 2004; Ahlberg, 2014) can suppress understorey growth (Philippe *et al.* (2022). Nevertheless, denser understorey vegetation was found to reduce light penetration (De Pauw *et al.*, 2022), maximal temperatures and airflow (Balandier *et al.*, 2022) along with providing higher humidity near-surface (Pickering *et al.*, 2021) influencing environmental conditions and favouring fungal spore development (O'Hanlon-Manners and Kotanen, 2004). Additionally, where understorey is present, it moderates temperature extremes: maximum temperatures are lower and minimum temperatures higher compared to open areas (Philippe *et al.*, 2022). This buffering effect could be explained by the slower heat exchange due to the structural complexity of the understorey (Combes, 2022), providing favourable conditions for pathogen development. Airflow is also modulated by the understorey layer, with studies confirming that denser understorey reduces both horizontal and vertical wind speeds (Mahaffee *et al.*, 2023). Several tunnel and field studies on the wind (Finnigan, 2000; Dupont and Brunet, 2008) confirmed that heterogeneous surface elements absorbed kinetic energy from airflow, especially within the lower layers (<2 m). The latter is a critical height, according to Chandelier *et al.* (2014), where *H. fraxineus* spore density was found to be consistently higher. Such reduced airflow limits the uplift and dispersal of ascospores, effectively decreasing the distance of spore travel (Chandelier *et al.*, 2014). In fact, in sheltered sites with low wind speeds, no ascospores were detected beyond 25 m from the source (Chandelier *et al.*, 2014), whereas high wind speeds can inhibit fungal development altogether (Chumanová *et al.*, 2019). The physical barrier effect could be, therefore, explained by the limited spore trajectories that *H. fraxineus* spore have within a denser understorey vegetation.

Humidity near the forest floor, enhanced by understorey cover (Pickering *et al.*, 2021; Combes, 2022), creates favourable conditions for apothecia formation and spore germination (Dvořák *et al.*, 2016). Increased humidity and moderate temperatures during the peak understorey growth period in summer (Augusto *et al.*, 2003; Timmermann *et al.*, 2011; Hietala *et al.*, 2013) synergistically promote *H. fraxineus* infection pressure. The latter could be explained by the timing of the highest growth of understorey vegetation found during the summer period (Augusto *et al.*, 2003), which corresponds with the period of maximum apothecia development of *H. fraxineus* (Hietala *et al.*, 2013), combined with the recorded maximum mean daily temperatures (Timmermann *et al.*, 2011) lead to favourable conditions for pathogen development.

Importantly, the understorey itself may act as a pathogen reservoir Landuyt *et al.* (2019). For example, canopy gaps caused by ash dieback are often colonised by grasses and other species that maintain high humidity, potentially suppressing ash regeneration and altering pathogen dynamics (Jochner-Oette *et al.*, 2021). Landuyt *et al.* (2019) emphasised that understorey vegetation can facilitate pathogen persistence and spread by maintaining suitable microhabitats.

Evidence on the protective or exacerbating effects of understorey vegetation remains mixed. Some studies suggest that an understorey of conifers or broadleaved species can slightly reduce ash dieback severity, possibly due to more stable microclimatic conditions or a physical barrier effect (Skovsgaard *et al.*, 2017; Forestry Commission and Natural England, 2019). Conversely, denser understorey layers have also been linked to conditions that favour spore development and pathogen establishment, as observed in other forest pathogens like *Phytophthora ramorum* (Meentemeyer *et al.*, 2008). As illustrated in Figure 1, the denser understorey layer (A and B) at 1 m (serving as a physical barrier) is likely to favour pathogen development within the denser understorey layer that creates conducive conditions for fungal development, whereas (C and D) demonstrate plots with no presence of understorey layer were the favourable microclimate in A and B is missing, potentially with improved airflow and humidity levels. That said, the role of dense understorey on ADB severity still remains to be studied and statistically confirmed. Moreover, the dual role of understorey in modulating *H. fraxineus* dynamics, acting as a physical barrier to spore dispersal by altering airflow and limiting spore trajectories, yet simultaneously creating microclimatic conditions, through increased humidity and moderated temperatures (Combes, 2022), favouring pathogen development and possessing the risk of collar lesions and secondary infection such as *Armillaria* spp (Marçais *et al.*, 2016). This highlights the importance of considering understorey composition and structure in forest management strategies designed to mitigate ash dieback. It is important to note that management practices are likely to be influenced by the DBH size of trees (Dieler *et al.*, 2017) and, therefore, play a co-founding effect in the relationship between the impact of understorey and dispersal of *H. fraxineus* spores.

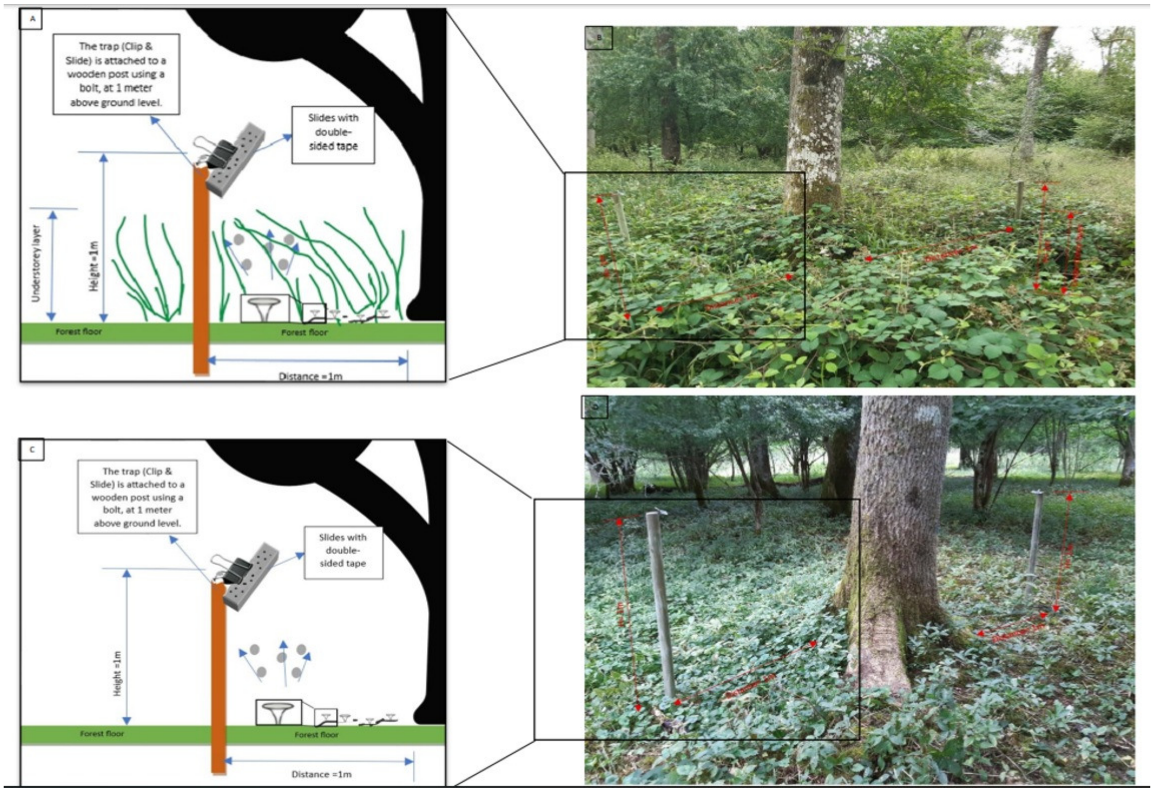

Figure 1. Spore traps to explore the effect of understorey on ADB development demonstrating: A) Design of spore trap with wooden posts positions in a plot with understorey layer; B) *In situ* representation of the passive spore traps at the plot with presence of dense understorey layer; C) Design of spore trap with wooden posts positions in plot with no presence of understorey layer; D) *In situ* representation of the passive spore traps at plot with no presence of dense understorey layer (Source: (C and D) Raykova (2023) and (A and C) unpublished data by Raykova, A (2019))

Host density and Forest stand management

Ash trees of all ages were reported to have different progression of the dieback regardless of the stand history (Pastirčáková *et al.*, 2020), with smaller, younger trees being the most susceptible (Klesse *et al.* 2021; Madsen *et al.*, 2021). ADB disease quickly develops on small trees in comparison to other tree-size groups, perhaps due to the shorter distance between the spore of the fungus on the forest floor and the crown, which could expedite the disease in smaller trees (Timmermann *et al.*, 2017). On the contrary, ADB disease was found to develop more slowly in mature trees, which could be attributed to the fungus requiring more time to navigate the intricate network of branches and vascular tissues in larger trees Lonsdale (2013). Additionally, the density of *Fraxineus excelsior* was reported by Skovsgaard *et al.* (2017) and Grosdidier *et al.* (2020) as an important factor for ADB disease progression. In their study, Grosdidier *et al.* (2020) demonstrated that the progression of ADB disease was significantly reduced when the host density of ash was low. These findings were in accordance with the results published by Skovsgaard *et al.* (2017) that mixed stands tend to be less damaged than pure stands. In addition, Grosdidier *et al.* (2020) reported that the spore production depended mainly on the ash density, which the authors explained by the disease etiology. Similarly, Chumanová *et al.* (2019) report that higher stocking density increases the humidity levels, which favours disease progression.

As previously mentioned, the influence of site-specific management practices may be indirectly influencing ADB progression by factors such as DBH (Dieler *et al.*, 2017). Thus, silviculture practices need to be modified based on the circumstances, including stand age and composition, taking into account ecological and economic benefits (Skovsgaard *et al.*, 2017; Short and Hawe, 2018). Several management practices have been evaluated to mitigate the impact of ADB (Bakys *et al.*, 2013; Skovsgaard *et al.*, 2017; Larger *et al.* 2022). These include reducing ash density in infected stands, removing infected material, promoting mixed-species compositions, and avoiding heavy thinning or clear-felling, which may serve as an additional stressor. Maintaining a diverse canopy structure can buffer microclimatic extremes; however, dense canopies have also been associated with higher humidity, enhancing conditions for pathogen sporulation (de Groot *et al.*, 2022; Greiser *et al.*, 2024). Additionally, forest canopies have been reported to influence the microclimate (Greiser *et al.*, 2024). The closed forest canopy was found to have a significant correlation with higher leaf damage by fungus (de Groot *et al.*, 2022). The closed canopy creates less variable temperature and increases soil moisture (Greiser *et al.*, 2024), which favours fungal spore development of *H. fraxineus* (Skovsgaard *et al.*, 2017; Combes, 2022) and increases inoculum concentration (Hietala *et al.*, 2013). The immediate effect of the created opportunities for pathogen development subsequently supports the proven relationship between the inoculum concentration produced on the infected rachises and the observed damage score (Grosdidier *et al.*, 2018; Combes, 2022), enhancing the possibilities for ADB progression in such areas. An experiment by Combes (2022) investigating the proportion of rachises in the leaf litter colonised by the pathogen revealed that the higher ascospore density would increase the probability of disease infection on ash foliage. Thus, according to Combes (2022), the higher leaf invasion by *H. fraxineus* on ash would increase the probability of disease infection.

Slope aspect and its influence on H. fraxineus spore dispersal and ADB progression

Slope and gravity effect on spore accumulation

Slope gradient and aspect can influence air humidity (Geiger *et al.*, 2009), soil climate (moisture and temperature) (Apaydin *et al.*, 2011), microclimate and microbial activity (Shang and Liu, 2024), vegetation (Nadal-Romero *et al.*, 2014), soil characteristics (Conforti *et al.*, 2016), and the spread of plant pathogens (Cardillo *et al.*, 2018). Similarly, a statistical model created by Havrdova *et al.* (2017) found a suite of variables, among which was the SD (standard deviation) of slope to impact *H. fraxineus* distribution at a medium scale. Gravity-driven processes (Figure 2) on sloping terrain facilitate the downslope (Ancey, 2012) movement and accumulation of leaf litter, including rachises infected with *H. fraxineus.* Ancey (2012) described this process, where leaf litter can exceed the binding forces of the slope surface and accumulate in lower areas. This process increases the local inoculum load, enhancing infection risk at the base of slopes. The relationship between rachis accumulation and disease severity has been demonstrated by Grosdidier *et al.* (2018), who found that higher densities of infected rachises in the litter layer correlated with more severe disease symptoms. This is in agreement with a study conducted by Havrdova *et al.* (2017), where analysis found that slope significantly impacted ADB severity. These findings correspond well with the gravity theory explained by Ancey (2012) and the interconnection between slope gradient and spore dispersal, therefore anticipating that areas at the bottom of slopes, where infected material accumulates, can act as hotspots for pathogen development and spore production. Additionally, rain can further redistribute spores downslope (Du *et al.*, 2019), compounding the risk of infection in lower-lying areas.

Furthermore, *H. fraxineus* is a heterothallic fungus requiring the meeting of two compatible mating types on rachises to complete its life cycle and produce ascospores (Gross *et al.*, 2014). Higher concentrations of rachises in downslope areas likely increase the probability of mating encounters and subsequent apothecia formation, thereby elevating inoculum pressure and infection risk (Cross *et al.*, 2017).

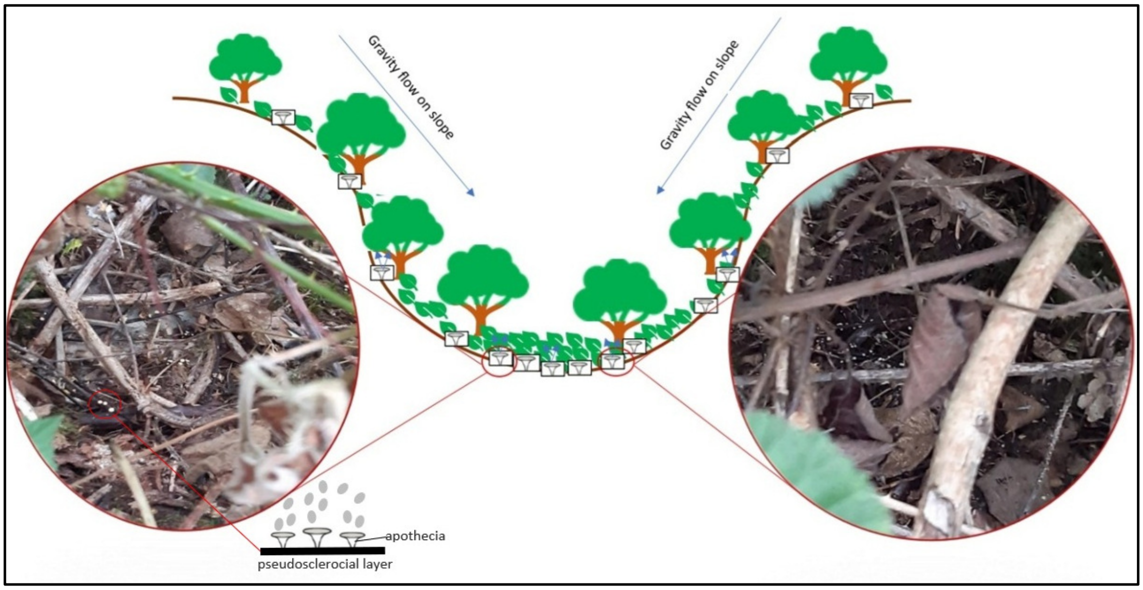

Figure 2. Longitudinal and cross-section representation of leaf litter flow on the slope through gravity with visualisations of the pseudosclerotial layer and apothecia of *H. fraxineus* (Source image: Raykova, 2020; unpublished data)

Slope aspect effects on microclimate and pathogen development

The slope aspect-related determinants of forest vegetation, microclimate, fungal communities, and soil properties were reported to be significant (Gilliam *et al.*, 2014). The slope aspect was found to modulate microclimate by influencing solar radiation, air temperature, soil moisture, and humidity, all of which are critical factors for pathogen development. North-facing slopes typically receive less direct sunlight, leading to cooler temperatures and higher humidity (Small and McCarthy, 2003; Chu *et al.*, 2016). These conditions can favour the development and survival of *H. fraxineus* spores, as high humidity and moist litter promote the development of apothecia and spore release (Grosdidier *et al.*, 2020). In contrast, south-facing slopes generally receive more sunlight, resulting in higher temperatures and lower moisture levels (Read, 1968; Leuschner and Lendzion, 2009). Such conditions may limit the ability of the pathogen to germinate and infect ash tissues. Moreover, studies have found lower disease prevalence on south-facing slopes compared to north-facing ones (Read, 1968; Lione *et al.*, 2024), likely reflecting less favourable microclimates for *H. fraxineus* sporulation.

Research studies confirmed the presence of *H. fraxineus* DNA in forest soil (Fones *et al.*, 2016; Böhm *et al.*, 2024), suggesting that soil acts not only as a reservoir, but may also influence pathogen persistence and potential reinfection routes. Böhm *et al.* (2024) further highlighted that pathogen load in soil may exacerbate host susceptibility by promoting stem necrosis, thereby increasing susceptibility to secondary pathogens such as *Armillaria* spp (Chandelier *et al.*, 2016). Crucially, soil pH is a well-established determinant of microbial community structure (Yang *et al.*, 2017), and these communities play a pivotal role in driving leaf litter decomposition processes (Yuan *et al.*, 2024). Given that *H. fraxineus* relies on infected rachises in the litter layer for the development of apothecia and subsequent ascospore release, the decomposition rate of this material directly influences the duration of spore production potential. The slope aspect significantly influences soil pH, with north-facing slopes typically exhibiting more acidic conditions compared to the less acidic or slightly alkaline soils found on south-facing slopes (Chu *et al.*, 2016; Wei *et al.*, 2021). Acidic soils, often associated with reduced microbial diversity and activity, retain moisture for longer periods and support slower organic matter decomposition (Chu *et al.*, 2016), potentially extending the persistence of viable infected rachises. This prolonged substrate availability may sustain local inoculum pressure by allowing apothecia to develop over multiple seasons (Laubray *et al.*, 2024). Conversely, the faster decomposition rates facilitated by more alkaline soils on south-facing slopes may reduce the lifespan of rachises and the window for spore production, as hypothesised by Turczański *et al.* (2020), who observed lower ADB severity in more acidic environments. These findings may support the hypothesis that soil pH, via its influence on microbial activity and litter decomposition, indirectly regulates the availability of the sporulating substrate, thereby modulating *H. fraxineus* epidemiology. This highlights the importance of incorporating appropriate and site-specific topographical variables into ash dieback management strategies.

Collectively, these findings highlight that slope aspect and steepness, through their influence on microclimate, moisture, and litter accumulation, play a critical role in shaping the local risk of spore dispersal and infection by *H. fraxineus*. North-facing slopes with higher moisture, cooler temperatures, and accumulated infected litter present a greater risk of ash dieback development. This aligns with the broader hypothesis that factors such as understorey vegetation and terrain could modify the microclimate and serve as physical barriers, potentially influencing spore dispersal and infection risk.

In summary, the reviewed studies (Table S1) highlight the need for context-specific management strategies that consider stand composition, host density, and spatial configuration. Evidence suggests that high tree density and closed canopy conditions promote microclimates conducive to *H. fraxineus* sporulation and infection (Hietala *et al.*, 2013; Grosdidier *et al.*, 2020), while fragmented or low-density stands can significantly reduce disease severity. However, poorly designed interventions may disrupt soil processes and alter moisture regimes in ways that unintentionally favour pathogen development (Dannenmann *et al.*, 2007; Sundqvist *et al.*, 2014). Therefore, stand-level ADB mitigation requires an integrated approach, including balancing host density, DBH distribution, and microclimatic regulation to suppress inoculum build-up and preserve tolerant individuals. Tailoring management to landscape and stand-specific conditions is crucial for minimising disease impact while maintaining ecosystem function and genetic resilience (Short and Hawe, 2018).

Conclusions

This review highlights the critical role of site-specific factors and the influence of dense understorey and slope aspects on modulating microclimatic conditions that affect the development and dispersal of *H. fraxineus*. Dense understorey layers promote elevated humidity and reduced airflow, conditions that enhance spore retention and pathogen persistence. Similarly, slope aspects influence local soil moisture, temperature, and acidity, with north-facing slopes offering more conducive conditions for fungal development than the south-facing slope.

Notably, the review highlights that these environmental and site-specific characteristics interact in a complex manner. Stand structure, including host density, DBH distribution, and canopy closure, influence disease severity. High-density stands impact microclimatic conditions and provide greater leaf rachises that favour pathogen development, while silvicultural practice associated with identifying individuals exhibiting tolerance, favouring them with well-considered thinning, and removing severely damaged trees will improve airflow, tree individual vitality, and reduce humidity, thereby limiting disease progression. Additionally, stands dominated by small size ash trees should be avoided due to the high susceptibility to ADB disease.

Given the complex interplay between biotic and abiotic factors, forest disease management strategies should incorporate site-specific characteristics and silvicultural interventions to assist in promoting tolerant ash individuals. Integrating these considerations can enhance efforts to suppress inoculum pressure, reduce host susceptibility, and conserve genetically tolerant *Fraxinus excelsior* individuals for long-term population resilience.

Authors' Contributions

The author declares the ownership of the review paper.

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Conflict of Interests

The author declares no conflicts of interest related to this article.

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