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Dieback of riparian alder caused by the *Phytophthora alni* complex: projected consequences for stream ecosystems

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Summary

1. Alder trees (*Alnus* spp.) are key nitrogen fixing riparian species in the northern hemisphere. They contribute to several ecosystem services such as, input of nutrient rich leaf litter into stream food webs, stabilization of banks, provision of habitat for terrestrial and aquatic organisms, and nitrogen dynamics at local and landscape scales.

2. Recently, substantial declines in alder stands have occurred along streams in Europe and North America. A major driver has been the invasive oomycete pathogen *Phytophthora alni* species complex, which can spread rapidly along stream networks.

3. This review synthesizes information on the pathogen, processes of spread and infection, and its impacts on alder. We further address the potential ecosystem-level and management consequences of the decline of alder, and highlight research needs.

4. The alder dieback caused by *P. alni* is associated with reductions in shade and quality and quantity of leaf litter. A decline in the structural integrity of branches and roots further threatens bank stability. Stream banks dominated by other tree species or no trees at all will result in ecosystem-level changes both above and below the waterline.

5. The *P. alni* taxonomic complex includes different species with varying phenotypes. An improved understanding of their environmental tolerance, virulence, and evolution, along with the processes regulating the spread and impacts of the pathogen, would assist in identification of the riparian and stream systems most vulnerable not only to invasion but also to the heaviest disease outbreaks and ecosystem-level impacts.

6. Within the P. alni complex, the highly pathogenic hybrid species *P. x alni* is favoured by mild winters and warm, but not excessively hot summer temperatures suggesting possible changes in distribution and level of impact under future global climate change.

Introduction

During the past decades, an increase in outbreaks of invasive fungal and fungal-like diseases has severely affected native plant and animal species and ecosystems worldwide (Fisher *et al.*, 2012). Freshwater ecosystems are particularly vulnerable to species invasions, due to the ease with which organisms, including pathogens, can spread along stream and river corridors as a result of their inherent connectivity (Richardson *et al.*, 2007; Leuven *et al.*, 2009). Examples of rapidly expanding pathogens in freshwaters include the crayfish plague *Aphanomyces astaci*, a major cause of the ongoing decline of the native Noble Crayfish *Astacus astacus* in Europe (Alderman, 1996, Holdich *et al.*, 2009), and the chytrid *Batrachochytrium dendrobatidis*, a zoosporic fungus contributing to massive declines in amphibian species worldwide (Stuart *et al.*, 2004; Cheng *et al.*, 2011). However, not only aquatic organisms, but also those living along streams and rivers are vulnerable to pathogens that spread along river corridors, with riparian plants being particularly at risk (Cotruvo *et al.*, 2004, Richardson *et al.*, 2007).

During the 1990s, declines of riparian alder trees (*Alnus glutinosa* and *A. incana*) were noticed in several European regions (Brasier, Rose & Gibbs, 1995; Brasier, Cooke & Duncan, 1999; Brasier *et al.*, 2004). Fungal pathologists pinpointed the novel Oomycete *Phytophthora alni* sensu lato *(P. alni* hereafter) as the cause, a hybrid species complex of unclear origin which has recently been described as composed of three species *P. x alni, P. x multiformis*, *P. uniformis* (Husson *et al.*, 2015). Nitrogen-fixing alder trees (*Alnus* spp.) have a number of attributes (Box 1) which make them a key riparian species in Europe, and across large parts of North America and Asia (Malanson, 1993; Govaerts & Frodin, 1998). Most significantly, alder species produce high quality, nitrogen rich leaf litter, which enters stream food webs during autumn abscission as a result of decomposition mediated by microbes and invertebrate detritivores (Handa *et al.*, 2014), and their presence can affect wider nitrogen dynamics (Box 1). Additionally, alder trees are tolerant of wet habitats, and are characterised by an extensive root structure that both stabilizes banks (Morgan & Rickson, 1995), and provides habitat for fish (especially fry) and other organisms (Flory & Milner, 1999; Erős, Botta-Dukát & Grossman, 2003; Brauns *et al.*, 2007). These and other qualities underpin the key roles that alder species play in the ecology of freshwater ecosystems, especially across Mediterranean, temperate and boreal regions of the northern hemisphere, and in the delivery of ecosystem services related to nutrient cycling, ecosystem productivity, and recreational and aesthetic values (Box 1).

The sickening and dieback of alder stands following infection by *P. alni* thus has strong potential to have major knock-on effects on running water ecosystems, given the prominence of alder as a component of riparian vegetation across the northern hemisphere, and the importance of its plant litter in the functioning of aquatic food webs (Piccolo & Wipfli, 2002). However, to date, the effects of *P. alni* have mainly been assessed and reviewed with the host tree in focus (Brasier *et al.*, 2004; Claessens *et al.*, 2010; Aguayo *et al.*, 2014), with little consideration given to the potentially cascading effects on aquatic ecosystems associated with impacted riparian strips.

This review begins with an overview of the pathogen, including its history and characteristics, processes of spread and infection, impacts on alder and known associations with environmental variables including river water conditions. Then, we discuss the implications of the loss of alder from stream riparian vegetation for the structure and function of stream ecosystems themselves, including potential impacts on stream morphology, diversity, and the functioning of stream food-webs. Finally we highlight knowledge gaps and give suggestions of future research and management directions, with a focus on disentangling the linkages between the environment and the level of impact of the pathogen on alder and the wider stream ecosystem.

Phytophthora alni: a novel pathogen of alder trees

Phytophthora alni is a novel pathogen complex arising from within a genus of Oomycota that is well-known for a number of devastating plant diseases, which together cause large economic damage worldwide, especially in crop cultivation (Box 2). *P. alni* was first observed infecting alder trees in the UK in 1993 (Gibbs, 1995), and subsequently has been reported from several European countries and a large number of river systems across the continent (Table 1, Fig. 1.). The pathogen originated from a hybridization event, possibly in a plant nursery (Brasier *et al.*,, 1999). Initially, several different variants of the pathogen were described, which were later designated into three different subspecies, *P. alni* subsp. *alni*, *uniformis* and *multiformis* (Brasier *et al.*, 2004), recently formally described as species (Husson *et al.*, 2015). The phylogenetic relationships among the subspecies and the identity of the parent species have been debated. It has been suggested that the species *P.* x *alni* may be a hybrid of the other two species (Ioos *et al.*, 2006); and that *P. uniformis* may have been introduced to Europe from North America (Aguayo *et al.*, 2013). Studies have shown that the species display somewhat different properties, including their degree of frost tolerance and pathogenicity (Brasier & Kirk, 2001; Černý, Filipová & Strnadová, 2012). For example, *P.* x *alni* is more pathogenic than *P. uniformis* and *P.* x *multiformis,* and whereas *P.* x *alni* is regarded frost sensitive, *P. uniformis* is normally isolated from cold regions such as central Sweden or Alaska.

Pathways of spread, symptoms of the disease, and present impacts on alder

The mechanisms underlying the rapid expansion of *P. alni* throughout Europe are poorly understood. The planting of alder trees from infected nurseries is often pinpointed as the initial pathway for the introduction of *P. alni* into new regions (Jung *et al.*, 2007). Human activities like fish farming, where fish along with substantial quantities of water are moved between catchments, are also believed to be a disease vector (Jung *et al.*, 2007). Other authors point to the movement of cattle between river systems (Redondo *et al.*, 2015). Once present in an area, swimming zoospores of *P. alni* can disperse from infected roots, which can lead to rapid spread through riverine networks (Jung & Blaschke, 2004), and the worst infections are often observed in trees immediately bordering stream banks (Gibbs, Lipscombe & Peace, 1999). Infection also appears to be exacerbated after flood periods, when trees are stressed and flood-damage to roots and stems may be substantial (Strnadová *et al.*, 2010), although high levels of disease incidence have also been found in non-flooded forest stands (Jung & Blaschke, 2004)

Infection of *P. alni* on alder is typically observed initially as crown dieback, with the remaining leaves becoming smaller and yellowish (Fig 2). In contrast, cone production in infected trees is often higher than that of healthy trees. The pathogen typically infects the tree through the roots and at the lower part of the stem (Lonsdale, 2003). Thus, bleeding cankers are often observed at the base of the stem or in between coarse roots (Černý & Strnadová, 2010; Redondo *et al.*, 2015) (Fig 3). Infected trees seem to be able to survive up to ten years while gradually losing vitality, although recovery may sometimes occur, especially when cold conditions suppress the pathogen (Jung & Blaschke, 2004; Jung *et al.*, 2007). *P. alni* only survives in soil for less than one year in the absence of host tissue (Jung & Blaschke, 2004), and Elegbede *et al.* (2010) showed that recently dead trees (1-3 years) produced very little inoculum.

The magnitude of the decline in alder stands attributable to *P. alni* can be very high, especially near river systems. In Sweden, for instance, a recent survey showed that 28% of ca. 168 alder stands investigated were infected by *P. alni*, with 45% of the trees in the infected stands showing symptoms of decline (Redondo *et al.*, 2015). An even higher prevalence was found in Bavaria, southern Germany, where symptoms were observed in more than 50% of rivers and in 32% of the stands surveyed (Jung & Blaschke, 2004). Surveys in Hungary and northeastern France observed *P. alni* on 30.9%, 17% and 55% of sampled trees respectively (Koltay, 2007; Thoirain, Husson & Marçais, 2007; Aguayo *et al.*, 2014). Long term monitoring is only available in UK, where incidence increased from 3% in 1994 to 11% in 2003 (Webber, Gibbs & Hendry, 2004). However, as pointed out by Fisher *et al.* (2012), establishing the true magnitude of impacts from *P. alni* on European alder stands requires more coordinated monitoring. The reports in Figure 1 and Table 1 give an incomplete picture of the present situation, since detection of the pathogen in these areas may merely reflect monitoring efforts.

Even though *P. alni* is the most important causal agent in the observed decline of alders, other species of *Phytophthora* may also cause similar symptoms. For instance, the generalist pathogen *P. plurivora* has been recurrently observed infecting alders (Jung & Blaschke, 2004; Jung & Burgess, 2009; Redondo *et al.*, 2015), and other stressors, including flooding, may also induce alder dieback with some symptoms similar to those caused by infection. Thus there is a need to confirm the presence of *P. alni* in suspected cases of infection (Brasier, 2003).

Given the rapid expansion of the pathogen, a key factor for the long-term viability of the alder population in Europe is the development of natural resistance or tolerance to the disease. In a recent study, insights on the existence of heritable resistance were identified by (Chandelier *et al.*, 2015), pointing to the potential of a natural adaptation to the pathogen. Similar results were found in UK, where moderate resistance could be identified in some of 15 provenances of alder studied (Gibbs, 2003). However, whether development of inherent resistance through natural selection will occur at a sufficient pace to minimize environmental impacts remains to be seen.

Interactions with the biotic and abiotic environment

Interactions between *P. alni* and its host are likely to depend on additional biotic and abiotic environmental factors, which can exacerbate or hinder the spread and impact of the pathogen. For example, temperature strongly influences both the pathogen itself, and subsequent impacts of the disease (Schumacher *et al.*, 2006). Cold winter conditions, especially involving long periods of heavy frost, seem to significantly reduce the overwintering survival in *P.* x *alni* (Černý & Strnadová, 2012). Similarly, Redondo *et al.*, (2015) showed that the distribution of *P.* x *alni* in Sweden was restricted to the areas with milder winter conditions, while *P. uniformis* was recovered from the whole surveyed area, including areas with harsh winter conditions. Low temperatures could slow the impact of *P. x alni* on individual alder stands, and its spread through catchment areas. In addition, sporulation efficiency, based on number of sporangia, has been found to be positively correlated with temperature (Chandelier *et al.*, 2006), and summer water temperature in particular has been related to *P. alni* prevalence in France (Thoirain *et al.*, 2007). Nevertheless, very warm and hot summer temperatures have been shown to limit disease incidence (Aguayo *et al.*, 2014). It is also known for some of the *Phytophthora* species involved in alder dieback that sporangia production is correlated with increased light conditions (Plourde & Green, 1982), and it is thus possible that increased levels of light following canopy dieback might favour further spread of the disease.

The effect of nutrients on the disease cycle is poorly understood. Electrical conductivity of the water, which reflects concentrations of ions, including nutrient ions, has been shown to affect zoospore survival in a laboratory study (Kong, Lea-Cox & Hong, 2012). In the field, a relationship between number of diseased trees and TON in streams was observed in one study (Gibbs *et al.*, 1999), but no such relationship was seen in another (Thoirain *et al.*, 2007). However, both studies were correlational, and it is hard to disentangle whether the positive associations between nutrients and the disease are causal.

Interactions between the pathogen and other organisms in the water or riverbanks have not been assessed. In particular, it is possible that pre-existing microbial communities might interact with zoospores, affecting their activity and production, and modulating infection rates, as shown for other *Phytophthora* patho-systems (Yang, Crowley & Menge, 2001). Similarly hyperparasites, microplankton and other organisms feeding on zoospores might also interact with zoospores, though these interactions have not been quantified (Gleason *et al.,* 2009; Gleason *et al.,* 2014).

Additional environmental stressors, such as insect outbreaks or flooding, may interact with the impacts of *P. alni* and accelerate decline in alder stands that may already be under substantial pressure (Jung, Blaschke & Oßwald, 2000; Jung, 2009). For example, *Alnus* species are vulnerable to attack from several insect pests, including the beetles *Agelastica alni, Plagiosterna aenea* and *Cryptorhynchus lapathi* and the moth *Argyresthia goedartella* (McVean, 1953; Cech & Hendry, 2003; Borowski, Piętka & Szczepkowski, 2012), and from other pathogens, such as the fungi *Armillaria* spp. and *Chondrostereum spp.* (Cech & Hendry, 2003). In addition, severe flooding in the summer growth phase of alders may cause mortality due to anoxia. Even though alders are adapted to wet conditions, rapidly increasing water levels may nevertheless cause the oxygen transport to the root zone to collapse (Claessens, 2003). Such damages have been recorded along several European rivers during flooding after large summer rains during the past decade (Cech & Hendry, 2003; Vyhlídková *et al.*, 2005). Experimental investigation of the joint impacts of flooding and *P. alni* have demonstrated that the combination of these factors can have particularly deleterious impacts on young alder plants (Strnadová *et al.*, 2010).

Projected consequences of *P. alni* on stream ecosystems

P. alni is one of several tree pathogens currently causing substantial economic and ecological damage on riparian trees in Europe. Other notable diseases affecting riparian vegetation include Dutch Elm disease (*O. novo-ulmi*), contributing to declines of *Ulmus* spp., and *Hymenoscyphus fraxineus* causing Ash dieback on *Fraxinus* spp. (Brasier & Buck, 2001; Gross *et al.*, 2014; Wallace *et al.*, 2015). However, while these other tree species often occur in riparian vegetation (especially *Fraxinus*), both elm and ash trees lack many of the unique attributes of alder which underpin its particular importance for stream and river environments (Box 1). Any change in species composition of riparian trees can be expected to cause major changes in stream ecosystems, due to the strong potential influences of differences in functional traits among tree species on stream ecosystem structure and function (Kominoski *et al*. 2013). Due to its key role as a highly moisture tolerant riparian plant influencing both the physical structure of stream channels (bank stability, root habitat structures, shading) and the biological functioning of its food webs (as an N-rich detrital energy and nutrient source), dieback of *Alnus* due to *P. alni* is particularly likely to have strong impacts on the structure and function of running waters (Fig. 4).

These impacts are likely to go through distinct stages, depending on the progress of the disease through affected stands. Initially, the delivery of high quality alder litter into running water ecosystems will be reduced, reflecting not only wholesale leaf dieback, but also the reduced size and quality of the affected leaves. This will reduce resource quantity and quality for both microbial decomposers and detritivores in the stream environment. However, the knock-on consequences of this are likely to be even more far-reaching. The decomposition of new leaf litter constitutes only one important linkage in a larger freshwater “litter processing chain” (Heard, 1994) which regulates the transformation of allochthonous energy sources (chiefly leaf litter) in headwater streams and its subsequent export to downstream reaches and through the landscape (Wallace & Webster, 1996; Bundschuh & McKie, in press). The activities of microbes and detritivores result in the generation of fine particulate organic matter (FPOM) from the leaf material, most notably in the form of shredder faecal particles (Graça, 2001). This FPOM is transported downstream and further consumed by detritivores feeding on smaller particle sizes

(Wallace & Webster, 1996), including filter feeders and collectors (Heard, 1994; Bundschuh & McKie, in press). These invertebrates are then important components in the diet of vertebrate predators, including amphibians and fish. Thus, a key question is whether the impairment in inputs of a high-quality litter species into freshwater ecosystems can be compensated for by increases in other resources, including other types of leaf litter, or if the loss of alder will alter nitrogen dynamics and overall productivity at local or larger scales (Goldman, 1961; Piccolo & Wipfli, 2002; Compton *et al.*, 2003; Wallace *et al.*, 2015)

As the infection spreads through a stand, one of two broad alternatives may occur. Either alder will be progressively replaced by another riparian plant species, or it will not be replaced, and the stream will move towards a treeless state (Fig. 4). Generally speaking, the alternative tree species in the case of alder decline are few, and lack some of the characteristic attributes of alder. This situation is especially critical in boreal regions where the pool of candidate replacement riparian species (e.g. *Salix*) is limited by more severe climatic conditions, in contrast with more Southern locations where a more diverse range of alternatives may exist, including alien tree species. An example of the latter is Caucasian wingnut tree, *Pterocarya fraxinifolia*, which in some British streams has become the dominant riparian tree species (Riley *et al.*, 2006).

Replacement of alder frequently entails a change in the dominant riparian vegetation, most often willow (*Salix* sp.). *Salix* litter is neither as nitrogen rich as *Alnus*, and often not as palatable for consumers (Wipfli & Musslewhite, 2004; Going & Dudley, 2008). Increases in the abundance of more refractory litter will slow the overall speed of decomposition (Mineau et al. 2012; Handa *et al.*, 2014). This in turn will potentially decrease the rate of release of finer particles supporting the productivity of the detrital part of the stream food web (Heard & Richardson, 1995; Jonsson & Malmqvist, 2005; Hladyz *et al.*, 2011; Wallace *et al.*, 2015). Alternatively, replacement of alder with other species producing nutrient rich, palatable litter, such as *Fraxinus*, may better mitigate some of the potential food-web effects of alder loss. However, such species may be more environmentally constrained than *Salix*, and hence less likely to succeed in some of the agricultural areas most affected by *P. alni* (Aguiar *et al.*, 2013). Regardless of which species replaces alder, it is likely that nitrogen dynamics at both local (Handa *et al.*, 2014) and catchment scales will be affected (Compton *et al.*, 2003), reflecting the loss of a large, nitrogen fixing plant (Kominoski *et al*. 2013)

Apart from direct impacts associated with altered detrital inputs, a change in the dominant riparian species might also alter the physical characteristics of stream and riparian environments, with knock-on consequences for biota and food webs. For example, *Salix* spp often produce branches and dense fibrous root mats which can help stabilize river banks (Shields, Bowie & Cooper, 1995), but excessive root growth can also create a narrower channel, altering currents and changing the distribution of microhabitats for biota (Burns, 1990). Replacement of alder with less shade-giving species is likely to increase the amount of light reaching the stream bed, potentially stimulating algal productivity with further effects on the remaining food web (McKie

& Cranston, 2001; Burrell *et al.*, 2014). These effects might include substantial shifts in both autotrophic and heterotrophic species communities (Wallace *et al.*, 2015).

Other riparian species may also not be as effective at stabilizing river banks as alder (Claessens, 2003; Claessens *et al.*, 2010; Černý & Strnadová, 2010). Černý and Strnadová (2010) report decreased riverbank stability in Czech riparian habitats impacted by *P. alni*, especially smaller streams. This increases the risk for erosion and bank slippage, and elevated levels of sedimentation which not only can threaten sensitive species, but can also hinder key ecosystem processes such as algal productivity and litter decomposition, as substrates become buried (Davies & Nelson, 1994; Matthaei, Piggott & Townsend, 2010). This problem is likely to be most acute during the dieback stage, as dead alder trees fall, breaking up moist river banks. Agricultural streams, already strongly affected by erosion, may be particularly vulnerable where alder play a key role in stabilizing the banks. In the longer term, consequences for erosion depend on whether the alder is replaced, and by which species.

In cases where alder is not replaced by another tree species, the changes are likely to be even more profound. These changes can be projected from studies comparing forested and open streams (Stone & Wallace, 1998; Swank, Vose & Elliott, 2001; Kiffney, Richardson & Bull, 2003; McKie & Malmqvist, 2009; Schade *et al.*, 2011; Mineau et al. 2012). These and several other studies show that loss of leaf litter input, shade and subsequent increase of radiation from sun have substantial effects on stream ecosystems. At the base of the food web, the increase in insolation typically drives an increase in autochthonous productivity (Brosofske *et al.*, 1997; Kiffney *et al.*, 2003). This has potential to drive an increase in the overall productivity in the system, since algae grow rapidly and are typically characterized by more available carbon and other nutrients, including high quality lipids synthesized by aquatic algae (Fuller, Roelofs & Fry, 1986; Muller-Navarra *et al.*, 2000; Shurin, Gruner & Hillebrand, 2006). While not necessarily differing in overall biodiversity, fully open stream channels often differ markedly from shaded channels in the functional composition of communities (McKie & Cranston, 2001), with more algal grazing species and fewer detritivores (Kiffney *et al.*, 2003; Gjerløv & Richardson, 2004). Increases in insolation are, however, not necessarily positive for overall ecosystem integrity, especially in systems already impacted by nutrient enrichment, where the lack of shade-limitation on algal productivity increases the risk of eutrophication, associated with lowered oxygen levels and increased fish mortality (Mallin *et al.*, 2006; Burrell *et al.*, 2014; Schade *et al.*, 2011)

Increases in solar radiation will also raise temperature and thereby potentially stimulate increases in productivity and ecosystem processes (Beschta, 1997; O'Gorman *et al.*, 2012). However, this may also impact temperature-sensitive aquatic plant and animal species, including cold stenothermic fish species like brown trout (*Salmo trutta*). A large number of European trout populations inhabit streams that are on the margin of having lethal water temperatures during summer, particularly given projected rises in temperature associated with global warming (Jonsson & Jonsson, 2009; Elliott & Elliott, 2010). Notably, higher water temperatures may also increase the range of *P. alni* (Chandelier *et al.*, 2006; Thoirain *et al.*, 2007) which could lead to higher disease levels. However, very high summer temperatures have been shown to have a negative impact on the disease (Aguayo *et al.*, 2014) which may limit the damage in some areas. As a combination of optimal summer temperatures and warmer winters appear to be favorable for the disease we may expect future climate change to subsequently exacerbate the disease development in some areas while others may experience a decrease (Aguayo *et al.*, 2014). This suggests that, at least in northern Europe, any further spread of the pathogen may interact with rising temperatures to accelerate alder decline, a key shading riparian species, and thereby further stress temperature-sensitive species.

The influences of management may strongly affect which outcome occurs – replacement of alder with another riparian species, or wholesale loss of riparian vegetation. Often it may be desirable to replant another tolerant species like *Salix*, to at least avoid the more severe effects of vegetation loss. However, this may be at the longer term cost of hindering the recovery of alder at local and landscape scales, if and when the pathogen diminishes.

***P. alni* and stream ecosystems: research needed**

Our review of the spread of *P. alni* and its impacts on alder, and our projection of the ecosystem effects of the associated decline in alder as a key riparian plant species, is solidly grounded in both currently available epidemiological information, and on both empirical and theoretical insights drawn from stream ecology. Nevertheless substantial knowledge gaps remain, which complicates making solid recommendations for control of the pathogen and management of its impact, or to forecast its current and possible future extent and level of impact. Thus there is clearly a pressing need to improve the empirical understanding of the impacts of *P. alni* at multiple levels of ecological organisation, particularly given the scale of dieback already observed in many regions, and the potential for climate change to facilitate the spread of the species in the future. Future research needs to focus on three broad topics: (i) the pathogen itself, (ii) the interaction between alder and the pathogen, and (iii) on the ecosystem impacts of the specific trajectory of alder decline induced by *P. alni*, at both local and whole-catchment scales. In all cases, there is a particular need for investigations into how key environmental factors, including climate change, nutrients, hydrological parameters and other biota, might constrain or enhance both the spread and potential impacts (at both the individual plant- and whole ecosystem scales) of the pathogen.

In focussing on the pathogen, there is a need for a better characterisation of the different species within the *P. alni* complex, with regards to their environmental tolerances, virulence and rates of evolution and potential adaptation to novel environments. This should be linked to research on the processes facilitating the spread of the pathogen, whether anthropogenic (e.g. associated with the nursery trade or fishing activities) or incidental (dispersal during flood events, or by birds), and should also incorporate the likely effects of future climate change, which may affect the geographic distribution of the different species and the severity of the disease. More research is required on persistence of the pathogen, for example through quantification of zoospores in water filtrates. High-throughput sequencing in combination with *Phytophthora* specific primers has been used to describe *Phytophthora* species communities in river systems (Català, Pérez-Sierra & Abad-Campos, 2015) and could potentially be used to monitor *P. alni*. The potential for other tree species to support *P. alni* at low levels even in the absence of alder should also be addressed. A novel issue arising from the current review is whether the effects of the pathogen on riparian and stream microclimates, arising from losses of shade, or changed nutrient or hydrological cycles as the foundational alders die, enhances or hinders the progress of an infection through the stand, or into new stands.

Taken together, an improved understanding of all the above factors would greatly assist in identification of alder stands most vulnerable not only to invasion but also to the heaviest disease outbreaks, both in the present and under future global change scenarios. The factors regulating the production and dispersal of the zoospores, and eventual new infection rates are especially worthy of research attention, including both abiotic (e.g. nutrients) and biotic (competitors or consumers) factors which might potentially be manipulated to limit their further spread within systems (Gleason *et al.*, 2009). Similar attributes require investigation in the host plant, including the importance of environmental context for susceptibility of the plant to infection, particularly given that stressed individuals may be susceptible to zoospore attack, and the potential for resistance to develop in different species or even populations of alder. Accurate assessments of such vulnerability will in turn facilitate the development of well-targeted strategies for minimizing the spread of the pathogen into the most vulnerable alder stands. For example, current research indicates that the different species within the *P. alni* complex differ in environmental tolerance. This has implications for the potential of various species to colonise and spread in different regions after accidental dispersal events. An understanding of the species posing the greatest potential threat in different regions, based on their environmental preferences and virulence, can then be applied in efforts to monitor and contain the spread of the pathogen. Such efforts might range from instituting monitoring aimed at early detection in systems likely to be most vulnerable to particular *P. alni* species, to the planting of resistant alder strains in impacted areas, if and when such strains are identified.

The focus of research on the impacts of *P. alni* should address not only its effects on populations of alder, but also knock-on impacts on the stream ecosystems linked to those populations. Such research needs to be strongly connected with the different stages of infection, and ultimately should aim at assessing the need and utility of specific management actions at each stage. Thus, there is a need for quantification not only of the length of the “die-back” phase following infection of a new stand (which may last up to 10 years), but also of the impacts of *P. alni* on the quantity and quality of allochthonous alder litter into stream detrital food webs during this phase. Such investigations should further consider the responses of both microbial decomposers and detritivorous consumers in the stream environment, not only to the reduction in resource quality, but also to the presence of the microbial pathogen on the leaves. Responses of consumers can be characterised in terms of feeding and growth rates, faecal particle production, and even patterns of reproductive allocation. Impacts on wider ecosystem functioning can be assessed through quantification of other ecosystem processes (primary production, ecosystem respiration), and even through incorporating the impacts of *P. alni* on carbon and nutrient inputs and processing into biogeochemical models of nutrient flux. Other ecosystem-level impacts of the decline in alder should also be quantified relative to the stage of infection. For example, the vulnerability of banks to slippage and erosion may differ between the dieback- and post-infection stages, and changes in channel morphology and hydrology may similarly vary as the infection proceeds. In cases where impacted streams are regularly sampled as part of routine biomonitoring, it might be possible to exploit existing time-series data to address some of the changes in stream biodiversity and physico-chemical characteristics before and after the infection of the riparian stand. However, an assessment of the true extent of the impacts of *P. alni* at whole catchment and larger scales will require integrated field and laboratory research programs, where biodiversity and ecosystem processes are investigated in replicated infected and uninfected streams in concert with detailed laboratory characterisation of the genetics and physiology of the dominant *P. alni* species. Space-for-time sample designs are likely to be necessary to capture the temporal dimension of the impacts of *P. alni*, since the progress of *P. alni* infection through an individual stand (>10 years) exceeds the length of most individual research programs (<3 years).

Once an infection has passed through an alder stand, implications for in-stream food-webs and habitats largely depend on the type of trees replacing the alder, if any. A key question is whether it will become possible to rehabilitate riparian stands of alder at some point, or whether the pathogen remains persistent in the system in the longer term so that any attempts to re-establish alder runs a high risk of failure. In that sense, it is critical to predict whether natural adaptation is likely to occur at a sufficiently rapid pace so impacts remain limited, or whether resistant planting stock should be obtained by breeding. Indeed, the persistence of the pathogen, not only locally but also at regional scales, might have important implications for post-infection management. Nevertheless, there may be other measures that might assist in eliminating or at least suppressing the pathogen at a regional scale, including delaying any attempts to rehabilitate alder. If it is not possible to rehabilitate alder in the medium-long term, then managers are faced with a choice to either allow riparian vegetation to follow a natural pathway of recovery and succession or foster the establishment of alternative tree species (Fig. 4). There may often be strong reasons not to allow the vegetation to recover naturally, particularly if it entails leaving dead and potentially still infected alder biomass for an extended period, or in cases where succession culminates in an open stream without any riparian vegetation. Otherwise, this choice will likely reflect a balance between favouring a tree species with resource-related characteristics similar to those of alder (e.g. producing higher quality litter, or even a non-native N-fixing species, such as some species of *Acacia*) and species hardy enough to tolerate some of the harsher stream-side environments occupied by alder, and providing at least some of the same benefits of alder, such as shade and bank stabilization (especially *Salix*).

The increased trade and travel due to globalization combined with a warmer climate is likely to increase the pressure from invasive species, with stream and rivers, as “corridor habitats” ramifying landscapes, are particularly vulnerable. The microbial dimension of invasive species has been largely overlooked so far in aquatic research, and an increase in collaborations between microbial pathologists and freshwater ecologists is crucial for advancement of knowledge in this field. The spread of the *P. alni* disease of alders is particularly alarming, due to the key role alder plays in the structure and functioning of these ecosystems. Running waters in a future European landscape lacking alder would not only look quite different in terms of appearance, but might well also function quite differently, due to the impairment of this nitrogen fixing species which underpins stream channel structure and in-stream food webs.

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BOX 1: Importance of alder trees for stream ecosystems.

- Alder trees are adapted to wet conditions, and are a prominent component of riparian vegetation along many freshwater shorelines in temperate and boreal areas of the northern hemisphere. Alder thereby contributes to maintenance of shade conditions and cooler temperatures, important for numerous stream species. The capacity of alders to thrive in wet conditions limits the pool of potential replacement species in many areas (Claessens, 2003; Malanson, 1993).
- Alder is a nitrogen fixing plant, reflecting symbioses with N-fixing bacteria (*Frankia alni*) associated with root nodules.
- As a consequence of N-fixation, alder produces litter that is substantially more nitrogen rich than other riparian species, while at the same time not being overly rich in refractory carbon compounds (Waring, 2007). These properties make it attractive for aquatic detritivores, as shown in different studies (Iversen, 1974; Otto, 1974; Grafius & Anderson, 1979; Irons, Oswood & Bryant, 1988; Friberg & Jacobsen, 1994). Leaf litter degraded by aquatic microbes and detritivores is a prominent component of nutrient and energy budgets in forested streams, and alder, when present, contributes to these pools substantially (Piccolo & Wipfli, 2002; Compton *et al.*, 2003).
- The presence of alder appears to affect N-dynamics at multiple scales. At a local scale, the presence of *Alnus* litter results in accelerated overall leaf decomposition, apparently reflecting the transfer of N to more nutrient poor litter species within the litter layer (Handa *et al.*, 2014). At larger scales, the presence of *Alnus* in a catchment can increase N export (Compton *et al.*, 2003).
- The intermingled root systems of alder trees increase river bank stabilization (Claessens *et al.*, 2010; Piégay, Pautou & Ruffinoni, 2003; Černý & Strnadová, 2010)
- Alder trees are used by a wide variety of terrestrial invertebrates, a portion of which die and fall on to the water surface, where they serve as food for fish and other aquatic predators (Wipfli, 1997).
- Alder roots, especially the characteristic "adventitious" roots which extend beyond the bank, create important habitat for invertebrates and fish (Flory & Milner, 1999; Erős, *et al.*, 2003; Brauns *et al.*, 2007).
- Well-vegetated shorelines are of importance for the recreational and aesthetic values humans derive from streams and rivers, including sport fishing and other outdoor activities (Burns, 1990).
- Alder is a relatively shade intolerant riparian plant, which together with willow (*Salix* spp.), are pioneer species recolonizing riparian habitats after disturbances, and is often prominent along moderately degraded channels (Hibbs, DeBell & Tarrant, 1994; Newton & Cole, 1994; Malanson, 1993).

BOX 2: Phytophthora – the "plant destroyers"

Phytophthora is a genus of Oomycetes (Oomycota) which contains a number of species causing extensive damages to crops and wild plants (Kroon *et al.*, 2012; Hansen, Reeser & Sutton, 2012; Erwin & Ribeiro, 1996), often imposing substantial economic costs (lost productivity, costs of control (Kovacs *et al.*, 2011). The name is appropriately derived from the Greek words *phytón* (plant) and *phthorá* (destruction). The most well-known species, *Phytophthora infestans*, was the active agent behind the Potato blight which caused the Great Irish famine 1845-1849. While often referred to as a fungal-like organisms, Oomycota actually belong to another kingdom, Chromista. *Phytophthora* spp. are morphologically similar to certain fungi but unlike the latter, they are more closely related to plants than animals. *Phytophthora* species can reproduce both sexually and asexually. Most *Phytophthora* species are soil and waterborne although aerial dispersal occurs in some species. In streams and soil, swimming zoospores are an important vector for the spread of infections.

A great majority of *Phytophthora* species are considered alien in the ecosystem where they cause damage. Many studies point to the fact that nursery trade of living plants is the most important pathway for introduction of *Phytophthora* species into new environments (eg Moralejo *et al.*, 2009; Rytkönen *et al.*, 2012; Prospero *et al.*, 2013).

Table 1. *P. alni*, current reported distribution. The true distribution in each region is often unknown.

Region	Local distribution	Reference
Austria	Reported	Cech (1997)
Belgium	Reported	Claessens (2005)
Czech Republic	Widespread in western Czech Republic	Černý *et al.* (2008)
France	Widespread in northern France	Streito *et al.* (2002), Thoirain *et al.* (2007)
Germany	Widespread in southern. Germany	Jung and Blaschke (2004)
Hungary	Reported	Szabó *et al.* (2000), Nagy *et al.* (2003)
Ireland	Reported	Brasier *et al.* (2004)
Italy	Northern Italy	Santini *et al.* (2001)
Lithuania	Reported	Brasier *et al.* (2004)
The Netherlands	Reported	Brasier *et al.* (2004)
Norway	Southern Norway, near Oslo	Strømeng (2012)
Poland	Reported	Oszako (2005); Pintos Varela *et al.*(2010)
Portugal	Northern Portugal	T. Jung, personal communication
Spain	North-western Spain	Pintos Varela *et al.*(2010), Redondo *et al.*, (2015)
Sweden	Southern- and mid- Sweden	Olsson (1999), Redondo *et al.* (2015)
Switzerland	Reported	S. Prospero, personal communication
UK	Southern. England (widespread) and Scotland	Brasier *et al.* (1995), Gibbs *et al.* (1999), Adams *et al.* (2008), Aguayo *et al.* (2013)
USA	Alaska & Oregon	Adams *et al.* (2008), Aguayo *et al.* (2013)

Fig 1. Overview of current known occurrences of *P. alni*. The true distribution in each region is often poorly known. See table 1 for information on local distribution.

Fig 2. An infected and dying alder stand in SW Sweden. Säve River near Gothenburg. Photo Ulf Bjelke.

Fig 3. The stem of an infected alder showing typical symptoms of *P. alni*. Photo Jonás Oliva.

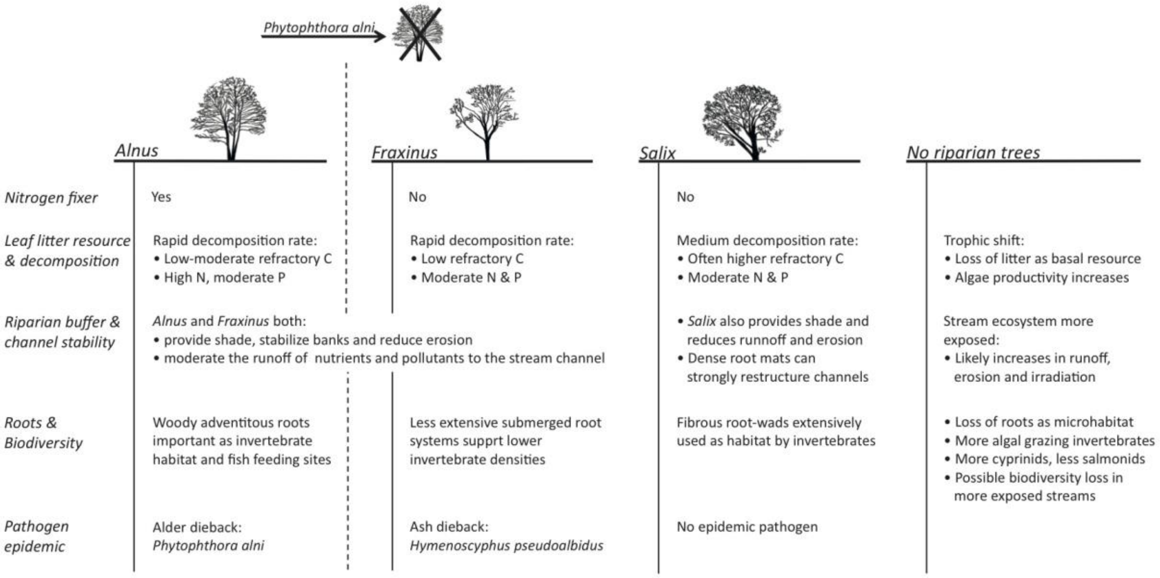
Fig. 4: Key ecological attributes of alder and three potential replacement taxa in Europe: ash (*Fraxinus*) and Willow (*Salix*), together with projected consequences of a complete loss of riparian trees. Key references: (Shields, Bowie & Cooper, 1995; Brauns *et al.*, 2007; Bingham, 2009; Schindler & Gessner, 2009; Handa *et al.*, 2014).


No known occurrence
Occurrence reported
Substantial damages reported

Fig. 1

Fig 2.

Fig. 3



	Alnus	*Fraxinus*	*Salix*	*No riparian trees*
Nitrogen fixer	Yes	No	No	
Leaf litter resource & decomposition	Rapid decomposition rate: • Low-moderate refractory C • High N, moderate P	Rapid decomposition rate: • Low refractory C • Moderate N & P	Medium decomposition rate: • Often higher refractory C • Moderate N & P	Trophic shift: • Loss of litter as basal resource • Algae productivity increases
Riparian buffer & channel stability	*Alnus* and *Fraxinus* both: • provide shade, stabilize banks and reduce erosion • moderate the runoff of nutrients and pollutants to the stream channel		• *Salix* also provides shade and reduces runnoff and erosion • Dense root mats can strongly restructure channels	Stream ecosystem more exposed: • Likely increases in runoff, erosion and irradiation
Roots & Biodiversity	Woody adventitous roots important as invertebrate habitat and fish feeding sites	Less extensive submerged root systems supprt lower invertebrate densities	Fibrous root-wads extensively used as habitat by invertebrates	• Loss of roots as microhabitat • More algal grazing invertebrates • More cyprinids, less salmonids • Possible biodiversity loss in more exposed streams
Pathogen epidemic	Alder dieback: *Phytophthora alni*	Ash dieback: *Hymenoscyphus pseudoalbidus*	No epidemic pathogen	

Fig. 4