



From leaf to continent: The multi-scale distribution of an invasive cryptic pathogen complex on oak

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ABSTRACT

The spatial distribution and niche differentiation of three closely related species (*Erysiphe alphitoides*, *Erysiphe quercicola* and *Erysiphe hypophylla*) causing oak powdery mildew was studied at scales ranging from the European continent, where they are invasive, to a single leaf. While *E. alphitoides* was dominant at all scales, *E. quercicola* and *E. hypophylla* had restricted geographic, stand and leaf distributions. The large-scale distributions were likely explained by climatic factors and species environmental tolerances, with *E. quercicola* being more frequent in warmer climates and *E. hypophylla* in colder climates. The

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extensive sampling and molecular analyses revealed the cryptic invasion of *E. quercicola* in nine countries from which it had not previously been recorded. The presence of the three species was also strongly affected by host factors, such as oak species and developmental stage. Segregation patterns between *Erysiphe* species were observed at the leaf scale, between and within leaf surfaces, suggesting competitive effects.

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1. Introduction

Fungi have been increasingly recognised as an important group among invasive species (Desprez-Loustau et al., 2007; Van der Putten et al., 2007; Mallon et al., 2015; Dickie et al., 2017), with some devastating consequences in the case of plant and animal pathogens (Fisher et al., 2012; Roy et al., 2017). Human-mediated transport has been identified as a major pathway for the introduction of non-native micro-organisms, e.g. forest pathogens (Liebhold et al., 2012). Microbial invasions are thus clear evidence that microbial cosmopolitanism (the absence of dispersal limitations) postulated in the “everything is everywhere” hypothesis is not the general rule (Green and Bohannan, 2006; Martiny et al., 2006).

One acute problem in studying the spatial distribution of microbes, including fungi, which may explain apparent species cosmopolitanism, is the relatively low taxonomic resolution provided by morphological characters (Green and Bohannan, 2006). For example, molecular analyses have shown that many ‘morpho-species’ of fungi hide a complex of genetically divergent species, called cryptic species, with follow-up studies providing evidence for some differentiation in their ecology and biogeography (Taylor et al., 2000). In particular, many plant diseases that were formerly believed to be caused by a single pathogen species were later shown to be due to a complex of multiple cryptic species (Fitt et al., 2006). For example, Eucalyptus leaf spot is associated with more than 60 species of *Mycosphaerella* (Crous and Groenewald, 2005), and grapevine downy mildew is caused by five *Plasmopara* species in North America (Rouxel et al., 2013).

The existence of cryptic species may have important implications in the context of invasions, notably by causing so-called cryptic invasions (Geller et al., 2010). Invasions may be unrecognized due to the morphological similarity between native and introduced species (Geller, 1999). In the recent European ash dieback, it took years to identify the exotic origin of the fungal pathogen (*Hymenoscyphus fraxineus*), closely related to a native non-pathogenic species, impeding the implementation of quarantine measures (Gross et al., 2014). Moreover, some invasions regarded as caused by a single species may hide several invasion events of different species (Mackie et al., 2012). For example, fungal chytridiomycosis has been identified as one of the major drivers of the decline of amphibians worldwide and was initially thought to be caused by the single species *Batrachochytrium dendrobatidis* (Fisher et al., 2009). However, a closely related species that preferentially infects salamanders has been recently detected and described (Martel et al., 2013). Cryptic species, although morphologically similar, often display some level of ecological divergence which could play a role in the invasion process. For example, differences in terms of environmental tolerance may lead to some geographical segregation in introduced areas (Mackie et al., 2012).

In the case of pathogens, as shown in the *Batrachochytrium* complex, adaptation to the plant or animal host is a major driver of ecological divergence and speciation (Le Gac et al., 2007; Giraud et al., 2010). Moreover, the ability to perform host shifts to non co-evolved hosts in the introduced area is a key process of pathogen invasions in wild communities (Slippers et al., 2005; Woolhouse et al., 2005). Differences in levels of host specialization within a species complex may cause different invasion patterns between cryptic species (Saleh et al., 2012).

Here we focus on oak powdery mildew, a foliar disease first recorded in the beginning of the 20th century in Europe, causing seedling mortality and tree decline, especially in the two most common European oaks, *Quercus robur* and *Quercus petraea* (Marçais and Desprez-Loustau, 2014). Recent molecular studies suggest a multiple invasion with three closely related fungal species in the *Erysiphe* genus putatively originating from Asia (Takamatsu et al., 2007; Mougou et al., 2008). The most common species, known as *Erysiphe alphitoides*, was described as a new species in 1912 (under the name of *Microsphaera alphitoides*) and regarded as the causal agent of the new invasion in Europe (Griffon and Maublanc, 1912). The second species, *Erysiphe hypophylla*, tentatively identified from slightly different symptoms and morphology, was assumed to cause an independent invasion, starting a few decades later from northern Europe (Roll-Hansen, 1961). The third species, *Erysiphe quercicola*, was first described in Asia (Limkaisang et al., 2006; Takamatsu et al., 2007) and recently detected in France (Mougou et al., 2008) and later Spain (Desprez-Loustau et al., 2017). Its date of introduction in Europe remains unknown.

The overarching aim of this study is to understand the multi-scale spatial distribution of the cryptic species forming the invasive complex with the ultimate goal of understanding their invasive behaviour. Our working hypothesis is that species show some degree of niche separation, which may translate into differences in their distribution across multiple spatial scales. More specifically, we address the following questions:

- What is the spatial distribution of the three *Erysiphe* species, ranging from a large scale (i.e. the European continent) and local scale (i.e. stand level) to the micro-scale (i.e. leaf level)? At which spatial scales do the different species co-occur?
- Do the fungal species differ in their biogeographical distribution at the continental scale due to differences in their climatic niche and their ability to attack different oak species?
- At the stand scale, is the pathogen complex the same on trees of different developmental stages?
- At the scale of single leaves, where direct and plant-mediated interactions between the pathogen species are expected to occur, do species segregate between and within leaf surfaces?

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