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Review and synthesis

Drivers of emerging fungal diseases of forest trees

Luisa Ghelardini [a], Alessia Lucia Pepori [a], Nicola Luchi [a], Paolo Capretti [a,b], Alberto Santini [a,*]

[a] Institute for Sustainable Plant Protection, National Research Council C.N.R., Via Madonna del Piano, 10 50019 Sesto Fiorentino, Italy
[b] Dipartimento di Scienze delle Produzioni Agroalimentari e dell'Ambiente DiSPAA, Università di Firenze, Piazzale delle Cascine 28, 50144 Firenze, Italy

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ABSTRACT

In order to prevent emerging infective diseases (EIDs), which increasingly threaten trees of agro-forest and urban ecosystems, a thorough understanding of the factors causing them is necessary. In this paper we reviewed the current knowledge about the changes in the interplay between environment (with its components climate and human activity), pathogens and host plants that drive fungal EIDs of forest trees. We described seven groups of drivers that may be involved individually or together, at once or successively, in the emergence of an infective disease, and we illustrated them by examples.

In the past century plant EIDs mostly resulted from the introduction of alien pathogens to new geographic areas as a consequence of international trade (i). However, other factors also played an important role, as for instance climate change (ii), which acts as a strong evolutionary force potentially enhancing the fitness or driving the expansion of the distribution range of pathogens, and/or weakening host plants i.e. predisposing them to infection. Global trade made geographically isolated pathogens spread beyond their natural range and hybridize with related species. Hybridization (iii) between previously isolated fungal pathogens has driven the emergence of new organisms with different and/or wider host range than the parental species. In some cases EIDs were caused by a hypervirulent strain of a known pathogen or by a completely new species, whose origin is still unclear (iv), which might be due to the development of novel traits or the acquisition of virulence from other species through horizontal gene transfer (HGT). The sudden appearance of unforeseen diseases may be driven by cryptic disease agents, i.e. microorganisms indistinguishable from known species except for unapparent traits involved in pathogenesis, by pathogens with an extended latency period, or by endophytes capable of turning into pathogens after environment changes (v). New associations between introduced insect vectors and native tree pathogens (vi), or vice versa, may result into more efficient transmission and extended host- or geographic range of pathogens. The global use of intensively managed forest plantations (vii) of non-native trees or of a small number of clones of the same species over huge areas has increased the attacks by pathogens, which were accidentally introduced and/or adapted to new hosts.

While the idea of totally preventing new EIDs appears unrealistic, it may be possible to reduce their occurrence, and the related damages and costs, by managing the drivers of disease emergence.

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* Corresponding author.
E-mail address: alberto.santini@cnr.it (A. Santini).

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1. Introduction

Emerging infectious diseases (EIDs) are an increasing threat to human health, agriculture and biodiversity conservation (Jones et al., 2008). In human medicine, infections are defined as 'emerging' if they have newly appeared, or their incidence, distribution range or both suddenly increase. Although the sudden appearance of these diseases may seem enigmatic or inexplicable, the drivers of EIDs, i.e. the underlying causal factors of emergence, could be found in virtually all cases that were carefully studied (Morse, 2004). During the 1990s there was considerable debate on whether the emergence of 'new' diseases was due to a *de novo* evolution of pathogenic agents or due to the transfer of existing and previously isolated agents to new host populations (the so-called "microbial traffic"). According to Lederberg et al. (1992) the emergence of many 'new' diseases is due to changes in the environment or in human ecology. Changes in the environment are probably among the factors causing most of the emerging diseases. According to Morse (2004), ecological changes (i) are the most important drivers of EIDs, for instance those due to agricultural or economic development or to climate change, followed by (ii) changes in human demography and behavior; (iii) travel and commerce; (iv) technology and industry; (v) microbial adaptation and change; (vi) the breakdown of public health measures. Morse (2004) also underlined that these factors need not be mutually exclusive. Ultimately, the alteration, of mainly anthropogenic origin, in the interplay between pathogens, host and the environment, i.e. the triangle of factors limiting a disease epidemics or 'disease triangle' (Gäumann, 1950; McNew, 1960), drives the emergence of novel disease patterns and pathogens with new traits (Engering et al., 2013; Scholthof, 2007).

This picture mostly applies to emerging infectious plant diseases (plant EIDs). Plant EIDs are often related to biological invasion, an event that is generally human-mediated and linked to economic growth and climate change, both of which provide manifold opportunities to introduce and spread alien pathogens (Dunn and Hatcher, 2015). In the recent past, the huge, continual increase of global travel and trade, and inadequate quarantine policies and phytosanitary regulations in many countries, have implicated a continuous introduction, in instances intentional or inadvertent, of alien species that may be dangerous and become invasive (Anderson et al., 2015; McNeely, 2006). In the last century, the distribution range of many plant pathogens was in fact artificially expanded this way much beyond their natural limits, with huge disturbances to ecosystems and severe socio-economic impacts (Bebber et al., 2014; Santini et al., 2013). A review of the Pro-Med database revealed that in the past few decades the main driver of the world's plant EIDs was the introduction of new and previously unrecognized pathogens (Anderson et al., 2004), including not only the arrival of totally new organisms, but also the transfer of new virulent strains or the emergence of new aggressive strains of native pathogens. Besides pathogen introduction, some related phenomena can drive the rise of new plant EIDs. Various causes of disease emergence in forest tree species will be reviewed in the following sections (a schematic outline of the subject is reported in Fig. 1). More than one driver may be involved, at once or at subsequent times, in the emergence of an infective disease, as illustrated by the examples below.

In the future, the continuing large-scale perturbations due to human activities including the compounded effects of different anthropogenic stressors, the so-called 'megadisturbance', will probably have large and difficult-to-predict impacts on forest ecosystems, changing species composition and altering biogeochemical cycles and ecosystem dynamics (Cohen et al., 2016; Frank et al., 2015; McDowell and Allen, 2015; Millar and Stephenson, 2015). Under such uncertain conditions, other drivers of forest disease emergence, known or unknown at the present time, might become prevalent or arise in a new or different way. As never before, researchers, professional foresters and other professions from the natural and social sciences are called to collaborate in an interdisciplinary effort to understand how forest ecosystems, including anthropogenic biomes, novel and urban forests, will respond to these disturbances, and to design new sustainable conservation and management actions (Lugo, 2015).

2. Seven pathways driving the emergence of diseases threatening natural and planted forest ecosystems around the world

2.1. Invasions by alien pathogens

Alien invasive organisms may have significant negative effects on populations, communities and ecosystems (Cameron et al., 2016; Vilà et al., 2011) and their management involves a huge economic cost (Hoffmann and Broadhurst, 2016). Invasions by alien pests and pathogens have caused huge damage to forests, nearly destroying some tree species, and produced significant changes in the involved ecosystems (Kenis et al., 2009; Lovett et al., 2016).

Many studies confirmed that the main entrance pathway of tree pests is the trade of live plants. As a rule, tree pathogens are accidentally introduced through commercial trade of wood or wood products and live plants, especially ornamental woody plants (Brasier, 2008; Liebhold et al., 2012; Santini et al., 2013; Xu et al., 2006). Horticulture is a global industry. For instance, in 2014 the European Union (EU) imported about 84,000 tonnes of live plants from 108 countries in five continents in 2014 (Fig. 2), while more than 500,000 tonnes were exported to 153 countries (DESA/UNSD, United Nations Comtrade database, http://comtrade.un.org).

The huge volumes of plants traded and the rapid turnover of commercial varieties and origins preclude phytosanitary inspections as a first-choice strategy for preventing the introduction of plant pathogens via the plant nursery pathway (Bradley et al., 2012; Roy et al., 2014). In fact, despite the intensification of phytosanitary measures worldwide, the number of newly established alien tree pests and the damage they provoke continue to increase (Aukema et al., 2010; Eschen et al., 2015).

The importance of fungi as disease agents is increasing both in animals and plants. Fisher et al. (2012) have reported a 13-fold worldwide increment of the number of plant diseases caused by fungi in 15 years. This trend is confirmed by the exponential increase of the number of invasive fungal pathogens of trees, which became established in Europe in the last 30 years (Santini et al., 2013), whereas it does not apply to the US (Aukema et al., 2010). This discrepancy may be due to historical and political differences between the EU and the US. Until the 19th century, exports of plant material and industrial products as well as human migrations,