Forest Ecology and Management 357 (2015) 248–258

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Pre-existing forests as sources of pathogens? The emergence of *Armillaria ostoyae* in a recently planted pine forest

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ARTICLE INFO

Article history:
Received 30 June 2015
Received in revised form 21 August 2015
Accepted 24 August 2015

Keywords:
Disease emergence
Land-use change
Fungal forest pathogen
Pinus
Root-rot disease

ABSTRACT

Fungi are among the principal causal agents of emerging plant diseases, which are a matter of worldwide concern. Changes in land use, such as the expansion of cultivated areas, are implicated in the emergence of fungal diseases, but have been less often reported for native species plantations. In the maritime pine (*Pinus pinaster*) forest of the Landes de Gascogne (south-western France), pine mortality due to the root rot fungus *Armillaria ostoyae* (*Basidiomycete*) has been increasing over the last 30 years. The first cases of this disease occurred in 1920 only few years after a period of rapid major change to the landscape. During the second half of the 19th century the landscape was transformed from marshes to the largest monospecific maritime pine plantation forest in Europe. We carried out two surveys (0.24 and 1 million hectares) of *Armillaria* root rot disease in the Landes area, to investigate the spatial distribution of pathogen damage and to determine the role of historical factors in the establishment of this pattern. For the two surveys, spatial analyses and generalised linear models revealed a significant effect on the current geographical distribution of *A. ostoyae* disease of the proportion of pre-existing forest in the vicinity of afforested areas and a significant effect of the proximity of the first forests planted in the coastal dunes. These results suggest that *A. ostoyae* was commonly distributed in pre-existing forest areas, and that most of these fragments acted as source for the colonisation of newly planted forests. Better predictions on the risk of establishment of new disease foci in this forest area can be achieved from these results.

1. Introduction

Climate change, anthropogenic parasite introductions and changes in land use, particularly those resulting in a loss of biological diversity, have been strongly implicated in the emergence of fungal diseases in recent decades (Anderson et al., 2004). The emergence of fungal pathogens has long been observed in agrosystems, and has been frequently found to be associated with intensification and expansion of crop distribution ranges worldwide (Stukenbrock and McDonald, 2008). The high density and genetic uniformity of cultivated hosts favour the development of a large local inoculum. This, together with the adaptation of pathogens to such homogeneous environments, may account for these emergences (Ennos, 2001; Stukenbrock and McDonald, 2008). Disease emergence associated with changes in forest landscapes has been reported less frequently than disease emergence in crops, possibly because both large forest plantations are more recent and research in agriculture is much more documented than forest research (Ennos, 2001, 2015; Holdenrieder et al., 2004; Pinon and Frey, 1997). Increasing demand for wood is driving an increase in tree plantation worldwide of about 5 million hectares per year (FAO, 2007, 2013). This increase in surface of planted forests will probably lead to larger numbers of disease outbreaks in these ecosystems in the future. Actually, it has been reported in several studies that plantations of native tree species have favoured the spread of endemic pathogens and the constitution of a large local inoculum, by connecting pre-existing small fragmented host populations. For example, this situation is thought to apply to *Microcyclus ulei*, the endemic agent of South American rubber tree leaf blight, a disease that almost entirely eliminated Brazilian rubber tree (*Hevea brasiliensis*) plantations at the beginning of the 20th

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http://dx.doi.org/10.1016/j.foreco.2015.08.028
0378-1127/

century (Lieberei, 2007). Native tree species plantations may have also contributed to the increase in the frequency of fusiform rust (*Cronartium quercuum*) on pine plantations in the southern USA (Perkins and Matlack, 2002) or *Diplodia pinea* in Europe (Fabre et al., 2011). The decrease in species diversity in planted forests, favouring contact between host individuals, was also identified as a possible cause of the increase in reported disease incidence, as described for several root rot diseases in North American and North European planted coniferous forests (Gerlach et al., 1997; Korhonen et al., 1998; Morrison et al., 1988; Pautasso et al., 2005). However, in each of these previous studies, the spatial effect of pre-existing forests as a source of inoculum for the closest afforested areas has not been tested.

The pine forest of the Landes de Gascogne, in south-west France, is a large indigenous species plantation of about 1 million hectares. This region underwent major landscape and environmental changes due to the plantation of an intensively managed forest for resin and wood production, which replaced the original moors and marshes. Until the end of the 18th century, the Landes forest consisted mostly of small, fragmented woods (25 ha on average) in the central part of the present-day forest, with a few larger forests stands (280 ha on average) located behind the coastal dunes and in the eastern part of the area (Vallauri et al., 2012). During the second half of the 19th century, attempts were made to develop the local economy, which was previously based on an agro-pastoral system, by draining most of the moors with a wide and deep network of ditches and by planting a forest consisting of a single native species, the maritime pine (*Pinus pinaster*). In as little as half a century, beginning in the mid-19th century, forest cover increased from 130,000 to 843,000 hectares, including 780,000 ha of mostly continuous maritime pine plantations (Dupuy, 1994; Thiveaud, 1992; Vallauri et al., 2012). This massive afforestation may have provided for native pathogens, such as the root rot fungus *Armillaria ostoyae*, favorable conditions for outbreaks, firstly by favoring the rise of a large inoculum in a monospecific host population, and secondly by increasing the connectivity between former sparse ancient forest stands.

A. ostoyae (Romagn.) Herink, a *basidiomycete* from the *Agaricaceae* family responsible for *Armillaria* root-rot disease, is thought to be endemic in the Landes de Gascogne. In this area, other *Armillaria* species are present (*A. mellea*, *A. gallica* and *A. tabescens*), but they rarely infect living maritime pines (Guillaumin et al., 1993). Therefore, *Armillaria* disease will refer in this study to maritime pine mortality due to *A. ostoyae*. This disease was first observed on the west coast of France shortly after the major landscape changes described above (Guyot, 1928). *A. ostoyae* is a pathogen of coniferous species, and it rarely infects other plant species (Guillaumin, 1986; Guillaumin et al., 1993). It spreads principally by an underground dispersal mechanism involving differentiated mycelial structures called subterranean rhizomorphs, which grow from infected pieces of wood towards uninfected roots. The disease can spread over only short distances via this mechanism, but small patches of disease, resulting in the infection of only a few trees, can lead to the disease covering several hectares (Lung-Escarmant and Guyon, 2004; Prospero et al., 2008). This species also produces basidiospores, which are dispersed by the wind after the production of fruiting bodies in the autumn, resulting in the infection of fresh wood a few hundred meters away (Legrand et al., 1996). Genetic studies of *A. ostoyae* in Landes de Gascogne have suggested that this spore-based dispersal mechanism plays a major role in the establishment of new disease foci (Dutech et al., 2011; Prospero et al., 2008). Although the intensive silviculture performed in the Landes de Gascognes (i.e. in general thinning at 10, 15, 20 and 30 years old and felling at 55 years old (CRPF, 2008)) could favour the colonisation of fresh stumps, its process has not been directly demonstrated *in situ* for *A. ostoyae* (Rishbeth, 1988), and its importance in the Landes de Gascogne remains to be quantified. In addition to this parasitic behaviour, *A. ostoyae* can also behave as a saprophyte, colonising the dead wood in the soil of many hardwood and softwood species (Guillaumin and Legrand, 2005; Legrand and Guillaumin, 1993). This large host range for saprophytism enables the fungus to persist in a forest stand for long periods, even after the death of all hosts in the immediate vicinity (Smith et al., 1992).

Over the last 30 years, the number of reports of the disease in the east of the Landes area has increased and shows a gradient of density increasing from the western coast to the eastern part of the forest (Aumonier, 2007; Lévy and Lung-Escarmant, 1998). In addition, Prospero et al. (2008) showed that genetic diversity of *A. ostoyae* populations was greater in the west than in the east of the forest massif; a genetic pattern in agreement with a spatial expansion of the population to east. However, these previous inventories may yield an incorrect estimate of the disease distribution. On the one hand, they did not take into account the uneven nature of reports associated with the non-homogeneous distribution of forest areas, the difficulties to access of some parts of the massif (e.g. absence of roads, military areas, etc.), a lower intensity of survey in areas with lower economic values (e.g. north of the massif, border of rivers, natural areas, etc.), and the effect of the host age affecting the ability of *A. ostoyae* to infect the host (Gibson, 1960; Lung-Escarmant and Guyon, 2004; Redfern, 1978). On the other hand, these inventories were based on reports of high mortality (large disease foci of several hectares) that may bias the estimates of geographical distribution of the disease, if the smallest disease foci (one to few pine trees) were differently distributed. Finally, although the role of pre-existing forests as the source of initial inoculum was assumed to explain this spatial distribution of the disease in the massif (e.g. Prospero et al., 2008), this hypothesis have not been tested yet. The recent digitisation of historical maps of the region before the establishment of the large pine plantations (Vallauri et al., 2012) made it possible to perform this spatial analysis for the first time in this forest area.

Two sources of colonisation were tested in the present study. First, we hypothesized that most of the pre-existing forests were the source of colonisation for the new pine planted areas in the vicinity of these pre-existing forests. This colonisation of new forest areas from a close source should lead to a local aggregation of the disease, still observed today, provided the spread of *A. ostoyae* is slow in the massif since the first plantations (i.e. the establishment of new disease foci is a rare event, and dispersal of basidiospores is mainly at few hundred meters) (Dutech et al., 2011, unpublished data). Several studies on *Armillaria* species previously showed that new plantations on pre-existing forests with a previous disease history, showed a greater incidence of the disease in these plantations than those on agricultural land (e.g. Gibson, 1960; Leach, 1937; Swift, 1972). However, at our knowledge, no study has tested the effect of the spatial proximity between pre-existing forests and new planted forests on the distribution of *Armillaria* disease. Because in the Landes de Gascogne, there is no evidence that *A. ostoyae* populations were present in most of these pre-existing forests before plantations, this putative origin must be specifically tested. Second, we tested the effect of spatial distances separating these new planted areas from the western coast on the current spatial distribution of *A. ostoyae*. The pine forests of the coastal dune could have also significantly affected this distribution in the massif because the first large maritime pine plantations, were established in this area, to stabilise the dune and drain water from the marshes (16,000 ha planted in 1840, and 56,000 ha in 1862 over a total area of about 100,000 ha (Goursaud, 1880). Therefore, these first plantations may also have served as sources of inoculum in the first steps of the *A. ostoyae* range expansion, in addition to the pre-existing forests.