

Widespread Phytophthora infestations in European nurseries put forest, semi-natural and horticultural ecosystems at high risk of
Phytophthora diseases

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Summary

An analysis of incidence of Phytophthora spp. in 732 European nurseries producing forest transplants, larger specimen trees, landscape plants and ornamentals, plus 2525 areas in which trees and shrubs were planted, is presented based on work conducted

by 38 research groups in 23 European countries between 1972 and 2013. Forty-nine *Phytophthora* taxa were recorded in 670 nurseries (91.5%); within these nurseries, 1614 of 1992 nursery stands (81.0%) were infested, although most affected plants appeared healthy. In forest and landscape plantings, 56 *Phytophthora* taxa were recovered from 1667 of 2525 tested sites (66.0%). Affected plants frequently showed symptoms such as crown thinning, chlorosis and dieback caused by extensive fine root losses and/or collar rot. Many well-known highly damaging host–*Phytophthora* combinations were frequently detected but 297 and 407 new *Phytophthora*–host associations were also observed in nurseries and plantings, respectively. On average, 1.3 *Phytophthora* species/taxa per infested nursery stand and planting site were isolated. At least 47 of the 68 *Phytophthora* species/taxa detected in nurseries and plantings were exotic species several of which are considered well established in both nurseries and plantings in Europe. Seven known *Phytophthora* species/taxa were found for the first

1 Introduction

Phytophthora is a genus of major importance within the Oomycota, kingdom Straminipila, currently comprising approximately 150 described species and informally designated taxa, most being primary plant pathogens which are responsible for over 66% of all fine root diseases and more than 90% of all collar rots of woody plant species (Tsao 1990; Brasier 2009; Jung et al. 2011; Kroon et al. 2012). *Phytophthora* species can be highly invasive and, after introduction to a new continent, may affect growth, vitality and longevity of trees, sometimes destabilizing whole ecosystems. Due to a lack of co-evolution between introduced *Phytophthora* spp. and endemic plants, hosts in the invaded region are usually more susceptible than host plants in the native range. Some of the most destructive and well-documented epidemics of trees and forests are caused by alien *Phytophthora* species; Jarrah dieback in Western Australia and littleleaf disease of pines in the south-eastern USA, New Zealand and the Dominican Republic by *P. cinnamomi* (Oak and Tainter 1988; Shearer and Tippett 1989; Jung and Dobler 2002); mortality of *Chamaecyparis lawsoniana* in Oregon by *P. lateralis* (Hansen et al. 2000; Jules et al. 2002) and *Austrocedrus chilensis* in Patagonia by *P. austrocedrae* (Greslebin et al. 2007); ink disease of *Castanea* species in Europe and the USA by *P. cinnamomi* and *P. cambivora* (Vettraino et al. 2001, 2005; Jung et al. 2013a); and the extensive mortality of *Quercus* spp. and *Notholithocarpus densiflorus* in California and *Larix kaempferi* in the UK and Ireland by *P. ramorum* (Rizzo et al. 2002; Brasier and Webber 2010; Grunwald et al. 2012).€

In Europe, large-scale surveys for soilborne *Phytophthora* species in over 4000 forests and semi-natural ecosystems have been undertaken since the mid-1990s stimulated by several devastating declines and diebacks of major forest and riparian tree species (Brasier et al. 1993; Jung and Blaschke 1996, 2004; Jung et al. 1996, 2000, 2013a; Gallego et al. 1999; Hansen and Delatour 1999; Vettraino et al. 2001, 2002, 2005; Streito et al. 2002; Balci and Halmschlager 2003a,b; Gibbs et al. 2003; Jung 2009; Orlikowski et al. 2011). In Mediterranean and temperate regions of Europe, 20 *Phytophthora* species and taxa, including the introduced wide host range pathogens *P. cambivora*, *P. cinnamomi* and *P. plurivora*, and the oak-specific *P. quercina*, have regularly been found to be associated with both a chronic decline and a rapid mortality of *Quercus* species characterized by progressive destruction of fine root systems that predispose affected oaks to droughts and secondary pathogens and pests (Brasier et al. 1993; Jung et al. 1996, 2000, 2013a; Robin et al. 1998; Balci and Halmschlager 2003a, b; Vettraino et al. 2002; Jonsson et al. 2005; PÉerez-Sierra et al. 2013). Since the early 1990s, a root and collar rot epidemic caused by the interspecific hybrids *P. 9 alni* (PAA) and *P. 9 multiformis* (PAM) and *P. uniformis* (PAU) has caused high levels of mortality of *Alnus* spp. in riparian and forest stands in most parts of Europe (Streito et al. 2002; Gibbs et al. 2003; Brasier et al. 2004; Jung and Blaschke 2004; Jung et al. 2013a; Husson et al. 2015). Also there has been a recent upsurge in ink disease of *Castanea sativa* in Southern and Eastern Europe and the UK (Vettraino et al. 2001, 2005; Jung et al. 2013a). The most recent of these threats which is causing great concern to foresters, arboriculturists and conservationists across Europe is the widespread decline and dieback of European beech (*Fagus sylvatica*), an important tree species in Western and Central Europe and in mountain areas of Eastern and Southern Europe, forming almost pure stands on many sites. Since the late 1990s, an increasing number of beech stands in Austria, Belgium, Germany, Italy, Poland, Romania, Sweden, the Czech Republic and the UK are showing crown transparency and dieback, small-sized and often yellowish foliage and eventual mortality. *Phytophthora cambivora*, *P. cactorum* and *P. plurivora* were consistently associated with the disease causing extensive fine root losses, root and collar rot, and aerial bleeding cankers on stems (Jung et al. 2005, 2013a; Brown and Brasier 2007; Jung 2009). Another 11 *Phytophthora* species showed scattered distribution in beech stands sometimes causing serious decline and mortality on a local or regional scale such as *P. kernoviae* and *P. ramorum* in the UK and *P. pseudosyringae* in Germany and Italy (Brown and Brasier 2007; Jung 2009; Jung et al. 2013a).

Both soilborne and airborne *Phytophthora* species can survive unsuitable conditions with resting structures in soil, infected roots and organic debris; hence, movement of soil particles and roots, particularly with plants for planting, is generally considered the major pathway for *Phytophthora* species (Shearer and Tippett 1989; Erwin and Ribeiro 1996; Brasier 2008; Jung et al. 2013a). *Phytophthora* infestations of nursery stock are well documented in Australia and the USA (Hardy and Sivasithamparam 1988; MacDonald et al. 1994; Davison et al. 2006; Schwingle et al. 2007; Yakabe et al. 2009; Bienapfl and Balci 2014; Parke et al. 2014), and initial work suggests a similar situation in Europe (Themann et al. 2002; Moralejo et al. 2009; Perez-Sierra and Jung 2013). Most work has focused on ornamental nurseries and the economic losses damping-off and root and collar rots cause to the nurseries and ornamental industry in general. However, recent epidemics and small-scale surveys of alder, birch, beech and fir fields in Finland, Germany and Poland (Lilja et al. 1996; Orlikowski et al. 2004; Jung 2009) have drawn attention to the role of infested nursery stock as major pathway of *Phytophthora* diseases into forests and semi-natural ecosystems within and between continents.

This paper reports on a series of small- and large-scale surveys for *Phytophthora* infestations of (i) forest nurseries, nurseries producing large trees for amenity and landscape plantings, horticultural and ornamental nurseries and (ii) forest, riparian, amenity, landscape and ornamental plantings and horticultural plantations in 23 European countries conducted by 38 research groups between 1972 and 2013, with most surveys conducted after 2000. The implications of the results for forestry, horticulture, conservation and plant biosecurity in Europe and possible solutions are discussed.

2 Materials and methods

2.1 Nurseries and plantings sampled

Anonymity was a precondition for all participating nursery owners and many owners of plantings; therefore, only national codes rather than precise locations and names are stated. Although most nurseries were selected randomly, some analyses were carried out in response to requests from the owners.

Between 1972 and 2013, 304 woody and herbaceous plant species in 1992 nursery stands, 629 fields with plants in the ground (hereafter referred to as nursery fields) and 1363 container stands (including plants in trays and in larger pots) were surveyed for *Phytophthora* infestations. Types of production for the nurseries in the 18 European states are detailed in Table 1. Of the 732 nurseries examined, 261 were wholesale and 424 were retail outlets, and 47 nurseries were publically owned by, for example, state forestry administrations.

Table 2 displays the types of plants grown in the nursery fields and container stands.

To study the pathway from nurseries into natural, semi-natural and horticultural ecosystems, 2525 forest, amenity, landscape, riparian and ornamental plantings and horticultural plantations with 478 woody and herbaceous plant species and taxa in 20 European countries were examined for *Phytophthora*-related disease symptoms and *Phytophthora* infestations (Table 1). Twenty-seven plantings were mixed amenity/ornamental plantings. Most forest and riparian plantings and approximately half of the amenity and landscape plantings were selected randomly. The remaining amenity and landscape plantings and the majority of the ornamental and/or horticultural plantings were examined following reports of damage.

Further analysis of the nursery to forest ecosystems pathway was possible through searches of the database of the French Département de la Santé des Forêts (DSF). These data enabled determination of the relationship between the planting of nursery seedlings and presence of ink disease, induced by *P. cinnamomi*, on oaks. In France, ink disease is currently restricted to the Aquitaine and Midi-Pyrenees regions (Marçais et al. 2004). All reports of *Quercus robur*, *Quercus petraea* and *Quercus pubescens* with information on the establishment type of the stand were selected, and reports of ink disease in planted and naturally regenerated stands, respectively, were compared using logistic regression in R software.

2.2 Sampling strategies

Sampling strategies varied over time and between research groups performing the surveys reported here. Generally, however, in nurseries, between 10 and 40 plants of 1–3 years old per field or container stand were harvested together with adhering soil. If present, seedlings with symptoms such as wilting, dieback, chlorosis and root and collar rot were preferentially sampled.

In nurseries producing advanced stock, plants were between 1 and 20 years old, and either containerized or rootpruned, balled and wrapped in burlap. With 1- to 3-year-old plants, sampling was carried out as described above. For older trees, 3–10 trees per species and field were randomly selected, 2–3 soil samples taken from the root ball of each tree and the soils combined to a bulked sample of approximately 1 l per tree.

In forest, amenity and landscape plantings, 3–10 symptomatic trees per species and planting were selected and soil samples taken as described for advanced stock.

When necrotic root or collar lesions were present, bark samples including the cambium were taken from the lesions and transported to the laboratory for further analyses, following published methods (Jung and Blaschke 2004). Symptomatic shoots and foliage were also sampled in ornamental nurseries or plantings by cutting and wrapping in moist tissue for transport to the laboratory in cool boxes.

2.3 Detection and identification methods

Phytophthora spp. were isolated from samples mainly using baiting methods, with leaves, green apples or hemp seed as baits over flooded soil or washed root systems (Erwin and Ribeiro 1996; Jung et al. 1996; Themann et al. 2002; Jung 2009). An alternative method of placing moistened soil in green apples (cv. Granny Smith) was sometimes used (Erwin and Ribeiro 1996; Jung et al. 1996). Different baits and media used in subsequent isolations in individual countries are listed in Table 1. Necrotic bark samples were washed repeatedly in distilled water over 1–3 days to remove excess polyphenols before either plating parts of the lesions on selective media or placing the bark in distilled water and baiting with oak and beech leaflets (Jung 2009).

Colonies growing from baits and bark pieces were transferred to V8-juice agar (V8A; Erwin and Ribeiro 1996) for initial confirmation as *Phytophthora* species. Identifications were made by comparing colony growth patterns, cardinal temperatures of growth and microscopic morphological characteristics with those of species descriptions in the literature (e.g. Erwin and Ribeiro 1996; Jung et al. 1999, 2002, 2003, 2011; Werres et al. 2001; Brasier et al. 2003a,b; Brasier et al. 2004, 2005; Greslebin et al. 2007; Balci et al. 2008; Hansen et al. 2009; Jung and Burgess 2009; Scott et al. 2009; Hong et al. 2011; Nechwatal et al. 2013; Ginetti et al. 2014; Henricot et al. 2014; Scanu et al. 2014a). Self-sterile isolates were crossed with tester strains of known mating types from CBS (Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands) to stimulate production of oogonia. Sporangia were observed on 15-mm squares cut from the growing edge of a 5- to 7-dayold culture grown on V8A at 20°C in the dark, and flooded for 24–36 h in 90-mm Petri dishes with non-sterile soil extract or pond water (Jung et al. 1996). Once the technologies and databases became available, confirmation of identifications was made using polymerase chain reaction (PCR) to amplify ITS-rDNA, followed by sequencing and comparison against sequences in databases such as GenBank and *Phytophthora*DB (e.g. Cooke et al. 2000; Cullen et al. 2001).

3 Results

3.1 Nursery surveys

3.1.1 Diversity and distribution of *Phytophthora* species and infestation rates in nurseries

In total, 49 *Phytophthora* taxa including 42 *Phytophthora* species and subspecies, four informally designated *Phytophthora* taxa and three previously unknown *Phytophthora* taxa were isolated from 81% of the 1992 tested fields and container stands in 91.5% of 732 nurseries surveyed (Table 2; Fig. 1). In the 101 infested nurseries with at least five tested stands, 3.6 *Phytophthora* taxa per nursery were detected. With 88.3–97.1%, mean infestation levels of the different types of nurseries at the nursery level were comparable. At the level of the individual nursery stand, however, mean infestation levels in the different nursery types ranged from 68.5 to 77.6% in mixed and ornamental nurseries, respectively, and 81.5% in forest nurseries to 90.5% and 92.3% in horticultural and advanced tree nurseries, respectively. The frequency of *Phytophthora* infestation was almost identical in both field and container stands, at 80.1

and 81.4%, respectively. Marketing category had a weak influence on *Phytophthora* infestation level. Infestation in the 261 tested wholesale nurseries (95.8% of nurseries and 88.4% of nursery stands) was higher than that in the 424 retail nurseries (88.4% and 77.2%) and the 47 administration nurseries (95.7% and 78.1%).

Mean infestation levels in nursery stands varied considerably with tree/crop species. Amongst trees grown for forest, riparian, amenity and landscape plantings with over 10 tested nursery stands, infestations of approximately 10–20% occurred in *Picea omorika*, *Picea glauca* and *Juniperus* spp., compared with 100% in both *Quercus ilex* and *Quercus suber*, 96.2% in *Castanea sativa*, 93.8% in *Pinus radiata* and 90.2% in *Chamaecyparis lawsoniana* (Tables S2, S4, S6). For horticultural plant species with over 10 tested nursery stands, the extremes were represented by *Lactuca sativa* and *Vitis vinifera* (38.5% and 58.3%, respectively) and seven *Citrus* species/hybrids and *Olea europea* (all 100%) (Table S7). Amongst ornamental plant species with over five tested nursery stands, several species were all infested, whereas the lowest infestation rates were for *Vinca minor* (42.9%) and *Forsythia 9 intermedia* (50%) (Table S8). Highest diversity in *Phytophthora* species was found in nursery stands of *Alnus glutinosa* and *C. lawsoniana* (each 13 *Phytophthora* taxa), *Q. robur* and *Buxus sempervirens* (each 12 *Phytophthora* taxa), *Taxus baccata* (11), *Viburnum tinus* (10), *Q. ilex* (9) and *Fagus sylvatica* (8).

In the 1614 infested nursery stands, 2076 *Phytophthora* taxon–nursery stand associations were found with 1827 identified to *Phytophthora* species level (Fig. 1). Multiple isolates of a *Phytophthora* taxon from the same nursery stand were considered as one record. The most commonly sampled *Phytophthora* species were *P. plurivora*, *P. cinnamomi*, *P. cactorum*, *P. nicotianae*, *P. ramorum* and *P. citrophthora*, all alien invasive species in Europe (Fig. 1). First records for Europe included *P. chrysanthemi*, *P. foliorum* and *P. quercetorum*, whereas *P. asparagi*, *P. bilorbang*, *P. humicola*, *P. ilicis*, *P. inundata*, *P. uliginosa* and *P. taxon 'Walnut'* are first records in European nurseries.

Nursery surveys confirmed known or assumed host specificities or preferences of several *Phytophthora* taxa including, amongst others, *P. 9 alni* (PAA) and *P. uniformis* (PAU) and *Alnus* spp., *P. foliorum* and *Azalea* sp., *P. ilicis* and *Ilex aquifolium*, and *P. quercetorum* and *P. quercina* and *Quercus* species. In one German nursery, however, *P. quercina* was isolated from the rhizosphere of 2-year-old *F. sylvatica* seedlings growing in a former *Quercus* field. In contrast, for many known wide host range species, between 18 and 81 host associations were recorded (Tables S1–S8).

Thirteen of the 49 *Phytophthora* spp. occurred in all three major climatic regions, although frequency and composition of the populations differed considerably (Fig. 2). Of the 304 surveyed plant species, 21 were present in all three climatic regions, whereas 14 and 12 species were shared between the Atlantic region and the Mediterranean and subcontinental to continental regions, respectively; the latter two regions shared 10 plant species. In 187 nurseries tested in Atlantic regions, 23 *Phytophthora* taxa were detected in 83.5% of the 653 sampled stands (Fig. 2a). In humid and mild climates, *Phytophthora* species with a predominantly aerial lifestyle and frost-sensitive *Phytophthora* species with subtropical to tropical origins accounted for 41% and 36% of the *Phytophthora*–nursery stand associations, respectively. The most common species were *P. ramorum* and *P. cinnamomi* (Fig. 2a). In subcontinental to continental regions, 26 *Phytophthora* taxa were recovered from 576 of the 841 nursery stands surveyed in 228 of the 276 nurseries (Fig. 2b). Aerial and frost-sensitive *Phytophthora* species represented 7.5% and 12.2% of *Phytophthora*–nursery stand associations, respectively. In contrast, species adapted to survive severe winter frost represented 82.1% of *Phytophthora*–nursery stand associations. *Phytophthora plurivora* and *P. cactorum* were the most common species followed by *P. cinnamomi*. Thirty-four *Phytophthora* taxa were isolated from 494 of 498 nursery stands tested in 269 Mediterranean nurseries (Fig. 2c). The proportion of frostsensitive thermophilous species was 46.2%, whereas predominantly aerial *Phytophthora* species represented 11.6% of *Phytophthora*–nursery stand associations. *Phytophthora nicotianae* was the most common species followed by *P. citrophthora*, *P. cinnamomi* and *P. cryptogea*. Thirteen *Phytophthora* taxa were exclusive to Mediterranean nurseries.

3.1.2 *Alnus* stands

Eleven *Phytophthora* species, plus *P. taxon 'PgChlamydo'*, were isolated from 76.6% of the 64 fields and container stands of *Alnus* spp. in 78.2% of the 55 nurseries assessed in seven countries (Fig. 3a; Tables 2, S1). PAA and PAU were detected in 20% and 6.3% of all *Alnus* fields, respectively. Infestation rates were highest in Germany, where eight nurseries hosted three or more *Phytophthora* taxa per *Alnus* field. In a Bavarian nursery, a single field was infested with eight different *Phytophthora* taxa (PAA, PAU, *P. cambivora*, *P. gonapodyides*, *P. megasperma*, *P. plurivora*, *P. syringae* and *P. taxon 'PgChlamydo'*), and five *Phytophthora* species were recovered from the rhizosphere of a single *A. glutinosa* plant. PAA and PAU were only present in *Alnus* fields established with nursery stock bought in from other nurseries and/or when surface water had been used for irrigation (Table S1).

3.1.3 *Castanea sativa* stands

Of 52 nursery stands of *C. sativa* tested in 37 nurseries in seven countries, 96.2% were *Phytophthora*-infested. *Phytophthora cinnamomi* and *P. cambivora* were the most common species (Fig. 3c; Tables 2 and S2).

3.1.4 *Fagus* stands

Nine *Phytophthora* species were isolated from 79.7% of 64 stands of *F. sylvatica* and *F. orientalis* in 82% of 50 nurseries in six countries. *Phytophthora cactorum*, *P. cambivora*, *P. gonapodyides* and *P. plurivora* were recovered from 18.8, 21.9, 12.5 and 50% of the beech fields, respectively (Fig. 3d; Tables 2 and S3). At least one of these four pathogens was present in over 75% of the 64 *Fagus* stands tested (Table S3).

3.1.5 *Quercus* stands

Almost 90% of 121 fields and container stands of 11 oak species surveyed in 87% of the 77 nurseries tested in eight countries were infested with 16 *Phytophthora* species in total (Fig. 3b; Tables 2 and S4). Over all countries, *P. cinnamomi*, *P. cactorum*, *P. plurivora*, *P. cambivora* and *P. quercina* were most frequently isolated (Table 2). However, diversity differed considerably between nurseries in Atlantic and subcontinental to continental, and in Mediterranean regions. In Germany, the Netherlands, Poland, Serbia, the UK and temperate regions of France and Spain, *P. cactorum*, *P. plurivora* and *P. quercina* were most common, whereas in Italy, Portugal and Mediterranean regions of France and Spain, *P. cinnamomi*, *P. cambivora* and *P. cryptogea* prevailed. *Phytophthora quercetorum* was isolated in one Portuguese forest nursery from four *Quercus* spp. in different container stands (Table S4), a first record in Europe.

Overall, 65.3% of the 121 fields and container stands of *Quercus* spp. were infested by at least one Phytophthora species involved in widespread decline and dieback of mature oak stands. In 10 stands, more than one oak pathogen was found.

3.1.6 Fields and container stands of other broadleaved species

Sixty other broadleaved woody species from 39 genera in 24 families widely used for forest, riparian, amenity and landscape plantings were surveyed in 232 fields and container stands of 123 nurseries in 15 countries. Seventeen Phytophthora species and three informally designated Phytophthora taxa were detected in 195 stands (84.1%) of 104 nurseries (84.6%) (Fig. 3e; Tables 2 and S5). The most common species were *P. cactorum*, *P. plurivora* and *P. cinnamomi*. Five Phytophthora spp. were isolated from 18 of 26 nursery fields of nine *Acer* spp. with *P. plurivora* and *P. cactorum* being the most common. In 13 of the 14 *Arbutus unedo* stands tested in five countries, and in the 10 tested stands of *I. aquifolium* in Italy, Poland and Spain, *P. cinnamomi* and a range of other Phytophthora spp. were found. In Finland and Poland, *P. cactorum* was recorded in 14 of 20 forest nursery fields of *Betula pendula* tested. Five of the nine fields of *Fraxinus excelsior* in Germany and Poland were infested by *P. plurivora* and *P. cambivora*. Four and five Phytophthora spp., respectively, were present in six of the seven *Juglans regia* fields and in all seven container stands of *Laurus nobilis* sampled in five countries. Ten of 13 stands of five *Prunus* spp. in six countries were infested by *P. cambivora* and five other Phytophthora species. In 74% of 19 *Tilia* fields in Germany and Poland, *P. cactorum* and *P. plurivora* and another six Phytophthora spp. were found (Table S5).

3.1.7 Fields and container stands of conifer species

A range of 21 Phytophthora taxa was detected in 302 of 482 stands of 45 conifer species tested in 187 forest, advanced tree and ornamental nurseries (Fig. 3f; Tables 2 and S6). Phytophthora *cinnamomi* and *P. plurivora* were most common. Eight of nine *Abies alba* fields in seven forest nurseries were infested with *P. plurivora* and four other Phytophthora spp. (Table S6). Thirteen Phytophthora species were detected in 47 of 51 fields and container stands of *C. lawsoniana* in 44 nurseries with *P. cinnamomi*, *P. plurivora* and *P. cryptogea* being the most common. All seven nursery fields of *Larix decidua* tested in Austria and Poland were infested; *P. cactorum* was most common. Of 21 *Picea abies* forest nursery stands in Germany and Poland, 12 were infested by five Phytophthora species with *P. plurivora*, *P. cambivora* and *P. gonapodyides* being the most frequent. In contrast, only *P. citrophthora* was found in five of 28 ornamental *P. abies* fields in Poland. Twelve Phytophthora species were isolated from 89 of 132 nursery stands of 13 *Pinus* spp. in 15 countries (Table S6). Most frequent were *P. cinnamomi*, *P. cactorum*, *P. cryptogea* and *P. plurivora*. In five Mediterranean countries, 29.4% and 26.5% of the 34 nursery stands of *Pinus brutia*, *Pinus elliottii*, *Pinus halepensis*, *Pinus pinaster* and *Pinus pinea* were infested by *P. cinnamomi* and *P. cryptogea*, respectively. Phytophthora *cinnamomi* was also isolated from nine of 17 container stands of *P. radiata* in 11 Spanish nurseries, while 24 of 37 *Pinus sylvestris* stands in five countries were infested by *P. cactorum*, *P. plurivora* and another four Phytophthora taxa. Phytophthora *cinnamomi* and *P. plurivora* were also present in seven of 10 forest nursery stands of *Pseudotsuga menziesii* in France, Germany and Spain. Eleven Phytophthora species, including *P. cinnamomi* and *P. plurivora*, were recovered from 30 of 50 *T. baccata* nursery stands sampled in 10 countries. In 81 nursery stands of *Thuja occidentalis* and *Thuja plicata* tested in seven countries, the infestation rate was 43.2%, with Phytophthora *plurivora* and *P. cinnamomi* being the most common. Lowest infestation rates were found in 57 stands of *Picea omorica* and *P. glauca* and 40 stands of *Juniperus* spp.

3.1.8 Summary of Phytophthora incidence in fields and container stands of forest nurseries

Data on the occurrence of Phytophthora species from all forest stands of *Alnus*, *Castanea*, *Fagus*, *Quercus*, other broadleaved woody species and conifers are summarized in Fig. 4.

In the 486 fields and container stands of 77 tree and shrub species tested in 165 forest nurseries of 13 countries, 26 Phytophthora taxa were isolated from 396 stands in 155 nurseries. The most common species were *P. cinnamomi*, *P. cactorum*, *P. plurivora* and *P. cambivora*.

3.1.9 Fields and container stands of horticultural species

Thirty-three horticultural crop and fruit tree species in 22 genera were surveyed in 146 nurseries in eight countries. Eighteen Phytophthora taxa were recovered from 29 plant species in 268 of 308 stands (Fig. 3g; Tables 2, S7). Phytophthora *nicotianae*, *P. citrophthora* and *P. palmivora* were most common. Almost all 67 nursery stands of six *Citrus* spp. and *Poncirus trifoliata* 9 *C. sinensis* in Italy and Spain were infested by *P. nicotianae* and *P. citrophthora*. Moreover, *P. palmivora* was isolated from all 29 nursery stands of *Olea europea* in Italy. Phytophthora spp. which can attack forest trees were isolated from 25.5% of horticultural nursery stands (*P. cactorum*, *P. cinnamomi*, *P. citrophthora*, *P. cryptogea*, *P. plurivora*, *P. syringae*, *P. ramorum*).

3.1.10 Fields and container stands of broadleaved ornamental species

Surveys of 142 broadleaved ornamental species from 118 genera were performed in 660 stands of 333 nurseries in 15 countries; 33 Phytophthora taxa were recovered from 132 plant species in 582 stands of 305 nurseries (Fig. 3h; Tables 2 and S8). The most common isolations were of *P. ramorum*, *P. nicotianae*, *P. plurivora*, *P. cinnamomi* and *P. citrophthora*. Phytophthora *ramorum* was particularly common in 177 stands that included *Camellia*, *Pieris*, *Rhododendron* and *Viburnum* species and varieties. The ornamental species tested were too numerous to present full results here; details are given in Table S8. However, 556 of the 660 ornamental stands contained at least one of 19 Phytophthora taxa known to damage a wide range of native European trees and shrubs and exotic plantation trees. In 11.8% and 2.9% of these stands, two and three of these Phytophthora species, respectively, were found, while 1.4% contained four or five Phytophthora spp.

3.2 Health condition and symptoms on nursery plants

Apart from damping-off of a few-month-old seedlings, scattered chlorosis and dieback of older plants due to root and collar rot, and scattered leaf necrosis and shoot dieback of *Rhododendron* species and hybrids, the majority of tested nursery plants in all nurseries in temperate climates appeared visually healthy. The following exceptions are noteworthy:

- After heavy rain, root and collar rot by *P. cactorum*, *P. cambivora* and *P. plurivora* caused scattered or patchy wilting and mortality of 1- to 3-year-old *F. sylvatica* seedlings in seven German forest nurseries (Fig. 5a).

- In seven Finnish forest nurseries, collar rot lesions on *B. pendula* seedlings caused by *P. cactorum* were detected in annual inspections between 1991 and 2004.
- In Poland, root rot, chlorosis, wilting and mortality caused by *P. cactorum* and *P. plurivora* occurred in patches of forest nursery seedlings of *A. alba*, *F. sylvatica*, *B. pendula*, *A. glutinosa* and *Sorbus aucuparia* during hot periods in summer.
- One- to three-year-old plants of *A. glutinosa* appeared vigorous and non-symptomatic. However, in several German nurseries infested by PAA, bark necrosis developed at the collar or on main roots of previously non-symptomatic plants after 1 week of flooding in baiting tests (Fig. 5b).
- In one German ornamental nursery, over 50% of 200 000 *Calluna vulgaris* seedlings succumbed to root infections caused by *P. cinnamomi* and *P. plurivora*.

In Mediterranean climates and in Atlantic regions of north-western Spain, typical above-ground symptoms, root and collar rot and scattered or patchy mortality were observed on a wide range of woody and herbaceous species in the majority of tested nurseries (Figs. 5c–g).

3.3 Surveys in forest, riparian, amenity, landscape, horticultural and ornamental plantings

3.3.1 Diversity and distribution of Phytophthora species and infestation rates in plantings

In total, 46 *Phytophthora* species plus five informally designated and five new *Phytophthora* taxa were isolated from 1667 of 2525 plantings tested in 20 European countries (Fig. 6; Table 3). Infestation levels of forest, riparian, amenity and landscape, horticultural and ornamental plantings were 79.3, 94.0, 56.6, 83.1 and 49.9%, respectively. Numbers of *Phytophthora* species detected varied considerably, depending on the plant species. High diversity occurred in plantings of *T. baccata* (18 taxa), *A. glutinosa* (14), *Rubus idaeus* (13), *Q. robur* (12), *Prunus laurocerasus* (10), *F. sylvatica* (9) and *C. lawsoniana* (9). *Phytophthora* diversity in plantings depended on numbers of plant species tested. Greatest diversity was in a British ornamental and amenity planting where 15 different *Phytophthora* taxa were isolated from 33 different species and varieties of plants. A Croatian ornamental and amenity planting had nine *Phytophthora* spp. from 11 plant species and the two Slovakian landscape plantings each had seven *Phytophthora* taxa from 32 and 15 plant species, respectively.

In the 1667 infested plantings, 2227 different *Phytophthora*–planting associations were found, of which 2016 were identified to species level (Fig. 6; Table 3). Multiple isolates of a *Phytophthora* taxon from the same planting site were considered as a single record.

Invasive pathogens with wide host range, including *P. plurivora* (11.2% of all plantings; 147 plant taxa), *P. cinnamomi* (10.1%; 65 plant taxa), *P. nicotianae* (8.5%; 34 plant taxa), *P. cryptogea* (6.9%; 111 plant taxa) and *P. cactorum* (6.7%; 97 plant taxa), were most common (Fig. 6; Tables 3, S1–S3, S9–S13). PAA was the only host-specific species with a relatively high isolation frequency. Isolations of *P. gregata*, *P. sansomeana*, *P. rosacearum* and *P. taxon 'Ceanothus'* were first records for these four pathogens from ornamental woody plants in Europe (Tables S3, S10–S13). Moreover, *P. multivora*, *P. pini*, *P. polonica*, *P. pseudosyringae*, *P. psychrophila*, *P. quercina*, *P. tentaculata*, *P. tropicalis*, *P. uliginosa* and *P. taxon 'Forestsoil'* were recorded from plantings in Europe for the first time (Tables 3, S1, S3–S4, S9–S12). Isolations of *P. erythroseptica* from seven ornamental host species, *P. porri* from *Sambucus* sp. and *P. rubi* from nine host species, all in the UK, were first records for these pathogens from woody plant species (Tables S10–S13). *Phytophthora* taxon 'gregata-like' from *Abies nordmanniana* in Austria and *P. taxon 'organica'* from *Sambucus nigra* and *B. pendula* in Germany, *P. taxon 'porri-like'* from *Penstemon* sp. in the UK, *P. taxon 'sansomeana-like'* from *Prunus domestica* trees in Germany and *P. taxon 'sojae-like'* from *Albizia julibrissin* trees in Croatia were previously unrecorded taxa.

The planting surveys confirmed known or assumed host specificities or preferences of several *Phytophthora* taxa, including PAA, PAM and PAU and *Alnus* spp., *P. ilicis* and *I. aquifolium*, *P. quercina* and *Quercus* spp., and *P. ramorum* and *Camellia*, *Pieris*, *Rhododendron* and *Viburnum*. However, in one amenity planting in the UK, PAA was present in the rhizosphere of the non-host species *T. baccata*.

Nineteen of the 56 *Phytophthora* taxa were found in all three major climatic regions. Frequencies and composition of the *Phytophthora* populations in plantings differed between the climatic regions (Fig. 7). Of the 304 surveyed plant species, 21 were common to all three climatic regions, while 14 and 12 species were shared between the Atlantic, Mediterranean and subcontinental to continental regions, respectively; plantings in the latter two regions had 10 plant species in common. In the Atlantic climate, 38 *Phytophthora* taxa were detected in 935 of 1798 sampled plantings (Fig. 7 a). *Phytophthora* species with predominantly aerial lifestyles and frost-sensitive species accounted for 11.6% and 23.6% of *Phytophthora*–planting associations, respectively. The most common species were *P. cinnamomi*, *P. plurivora* and *P. cryptogea* (Fig. 8). Nine taxa (*P. austrocedrae*, *P. erythroseptica*, *P. hibernalis*, *P. ilicis*, *P. kernoviae*, *P. porri*, *P. primulae*, *P. pachypleura* and *P. taxon 'porri-like'*) were exclusively isolated from plantings in Atlantic regions. In subcontinental to

continental regions, 31 *Phytophthora* taxa were recovered from 314 of the 319 plantings surveyed (Fig. 7b). Only two predominantly aerial species, *P. ramorum* and *P. pseudosyringae*, were infrequently found while frost-tolerant species occurred in 98.4% of the plantings and accounted for 98.8% of identified *Phytophthora*–planting associations. *Phytophthora plurivora*, *P. cactorum* and PAA were most common (Fig. 7b). Thirty-seven *Phytophthora* taxa occurred in the 408 Mediterranean plantings sampled (Fig. 7c). The proportion of frost-sensitive thermophilous species was 45.9%, whereas predominantly aerial *Phytophthora* species accounted for only 6.4% of *Phytophthora*–planting associations. *Phytophthora nicotianae* was the most common species followed by *P. citrophthora*. Nine *Phytophthora* taxa (*P. acerina*, *P. asparagi*, *P. gregata*, *P. humicola*, *P. medicaginis*, *P. rosacearum*, *P. sojae*, *P. tentaculata* and *P. taxon 'sojae-like'*) were only found in Mediterranean plantings (Fig. 7c).

3.3.2 *Alnus* plantings

Of 265 *Alnus* plantings, 206 were infested by a total of 15 *Phytophthora* taxa (Fig 3a; Tables 3 and S1). In 213 forest plantings, the 48 riparian plantings and the four amenity plantings of *A. glutinosa* and *A. incana* in eight of 11 countries, PAA was the most frequently isolated species. In Bavaria, necrotic collar lesions yielded PAA in 63 of 70 forest and riparian plantings surveyed (Tables 3 and S1). PAM and PAU were isolated from collar rot lesions in 11 plantings in Germany, Spain and the UK, and in eight plantings in Austria, Croatia, Germany, Poland and Spain, respectively (Tables 3 and S1). In five plantings in Bavaria and Austria, *P. plurivora* was the exclusive causal agent of collar rot lesions and in another six plantings *P. plurivora* occurred with PAA.

3.3.3 *Castanea sativa* plantings

In total, 10 *Phytophthora* species were isolated from 50 of the 62 forest plantings and from seven of the 12 amenity and landscape plantings of *C. sativa* in Germany, Greece, Italy, Portugal, Slovakia, Spain and the UK (Fig. 3c; Tables 3 and S2). *Phytophthora cinnamomi* and *P. cambivora* were found in 54.1% and 20.3% of *Castanea* plantings, respectively.

3.3.4 *Fagus sylvatica* plantings

Eleven *Phytophthora* species were isolated from soil samples and collar rot lesions in 32 of the 34 forest and amenity plantings of *F. sylvatica* surveyed in Germany, Slovakia, Spain, Sweden and the UK. *Phytophthora cambivora* and *P. plurivora* were most common followed by *P. cactorum* (Fig. 3d; Tables 3 and S3). From 88.2 and 29.4% of the beech plantings, one and two of these three beech pathogens, respectively, were recovered (Table S3).

3.3.5 *Quercus* plantings

Seventy-three forest and 40 amenity and landscape plantings of 12 *Quercus* taxa in 10 countries were surveyed, and 101 were infested by a total of 15 *Phytophthora* species (Fig. 3b; Tables 3 and S9). *Phytophthora plurivora*, *P. cinnamomi* and *P. quercina* were most common over all plantings surveyed, but frequencies differed between climatic regions. *Phytophthora cinnamomi* was isolated from 18 of 21 Mediterranean oak plantings in Italy, Spain and Portugal, and from 11 of 35 Atlantic oak plantings in Spain and the UK, but was not found in subcontinental to continental plantings (Table S9). In contrast, *P. plurivora* and *P. quercina* were present in 51.7 and 29.3%, respectively, of subcontinental to continental oak plantings in six countries, but rarely occurred in Mediterranean or Atlantic plantings (Table S9). Seventy-two of 113 oak plantings were infested by at least one *Phytophthora* species associated with decline of mature oak stands. In 12 plantings, two of these pathogens were found (Fig. 5b; Table S9).

The Departement de la Sante des For^et (DSF) database contained 497 reports of oak (mainly *Q. robur*) stands with health problems from SW France for which establishment by either planting or seed regeneration was documented. With 14 of 18 stands suffering from *P. cinnamomi*-induced cankers, the majority of reports were from planted stands, while only 14% of reports dealing with a health problem other than *P. cinnamomi* referred to plantings. The odds ratio was 21.5 (likelihood chi-square = 35.1, $p < 0.001$). Mean prevalence of cankered trees in plantings was 11.3% (range 2–22%).

3.3.6 Plantings of other broadleaved species

Twenty-eight *Phytophthora* taxa were recovered from 224 of 365 forest, riparian, amenity and landscape plantings, with 99 other broadleaved tree and shrub species surveyed in 16 countries (Fig. 3e; Tables 3 and S10). *Phytophthora plurivora* and *P. cactorum* were the most common species isolated. Thirty-seven of 47 plantings of 10 *Acer* spp. were infested, with *P. plurivora*, *P. cactorum* and *P. cambivora* the most frequent species present (Table S10). *Phytophthora* spp. were isolated from 15 of 17 plantings of *Aesculus hippocastanum* tested with *P. cactorum* and *P. plurivora* being the most common (Table S10). Seventeen of 18 plantings of *Tilia* spp. were infested, *P. cactorum* and *P. plurivora* being the most frequent. In eight of 14 *A. unedo* plantings in Portugal and the UK, *P. cinnamomi* and six other *Phytophthora* species were found. Also five of the nine plantings of *Juglans regia* and eight of the nine plantings of *Laurus nobilis* in Spain and the UK hosted *Phytophthora* with *P. cinnamomi* being the most common in both. In six countries, 36 of 58 sampled plantings of eight *Prunus* spp. were infested by 12 *Phytophthora* taxa (Table S10).

3.3.7 Conifer plantings

In 192 of 342 plantings of 32 conifer species in 11 countries, 23 *Phytophthora* taxa were detected: *P. cinnamomi* (11 species), *P. plurivora* (17 species) and *P. cryptogea* (10 species) were the most common (Fig. 3f; Tables 3 and S11). Amongst the conifer species or genera with over five surveyed stands, highest infestation was found in plantings of *C. lawsoniana*, *Pinus* spp., *T. occidentalis*, *T. plicata* and *T. baccata* (57–77%).

3.3.8 Summary of *Phytophthora* incidence in forest plantings

Four hundred and eleven afforestations and reforestations including two *Alnus* spp., *C. sativa*, *F. sylvatica*, six *Quercus* spp., 11 other broadleaved tree species and 12 conifer species were surveyed in 13 countries, with 23 *Phytophthora* taxa isolated from 326 plantings. The most common were *P. cinnamomi*, PAA, *P. plurivora*, *P. cambivora* and *P. gonapodyides* (Fig. 4).

3.3.9 Horticultural plantings

Thirty-seven *Phytophthora* taxa were found in 572 of 688 plantings of 59 fruit tree and horticultural crop species surveyed in 11 countries (Fig. 3g; Tables 3 and S12). *Phytophthora nicotianae* and *P. citrophthora* occurred frequently in the 244 Citrus and Poncirus plantings tested (Tables 3 and S12). *Phytophthora nicotianae* was present in all Citrus plantings in Italy but only in three of the 75 plantings in Galicia, north-western Spain. Also *P. citrophthora* was more frequent in Citrus plantations in Italy than in Galicia, where *P. hibernalis* and *P. citricola* were more common (Table S12). Five *Phytophthora* species were detected in 23 of 33 apple orchards tested in seven countries; *P. cactorum* was most common, followed by *P. plurivora*. Surveys of 36 olive tree plantings in Croatia, Italy and Spain revealed a total of nine *Phytophthora* species in all plantings with *P. palmivora* and *P. inundata* being the most frequent. The nine orchards of *J. regia* surveyed in Greece, Italy and Slovakia were infested by *P. cactorum* and *P. cambivora*. In seven countries, 13 *Phytophthora* taxa were isolated from 21 of 36 tested *Prunus* orchards. The most common were *P. cactorum* and *P. taxon* 'PgChlamydo' in *Prunus avium*, *P. cactorum* and *P. plurivora* in *Prunus domestica*, and *P. megasperma* and *P. inundata* in *Prunus persica*. In a German orchard, both *P. sansomeana* and *P. taxon* 'sansomeana-like' were isolated from *P. domestica* (Table S12). In

total, 14 *Phytophthora* taxa were present in 36 of 56 raspberry plantings sampled in four countries, with *P. rubi* and *P. megasperma* being the most common.

3.3.10 Ornamental plantings of broadleaved species

In total, 755 ornamental plantings of 281 broadleaved woody and herbaceous species were sampled in eight countries. Thirty *Phytophthora* taxa were isolated from 377 plantings (Fig. 3h; Tables 3 and S13). Most widespread were *P. plurivora* and *P. cryptogea*. Amongst species sampled in over five plantings, the highest infestation rates were found in *Buxus sempervirens*, *Camellia japonica*, *Lavandula* spp., *Pieris* spp., *Rhododendron* spp., *Rosa* spp., *Rosmarinus officinalis* and *Viburnum* spp. (Table S13). The ornamental species tested were too numerous to present full results here; details are given in Table S13. However, of 755 ornamental plantings tested, 339 had at least one of 21 *Phytophthora* taxa known to damage a wide range of European and exotic tree and shrub species. Approximately 10% of the tested stands had more than one of these aggressive tree pathogens present. In seven countries, 96 plantings of 13 *Rhododendron* species and various *Rhododendron* hybrids were surveyed, with a total of 13 *Phytophthora* taxa isolated from 72 plantings. Most common was *P. ramorum* followed by *P. plurivora* and *P. syringae*.

3.4 Health condition and disease symptoms of plants in various types of plantings

Because of the diversity of plant species and the large number of plantings tested, observed symptoms are presented for only the most commonly sampled plant species.

All 152 forest, riparian and amenity plantings of *Alnus glutinosa*, *A. incana* and *A. cordata* from which PAA, PAU, PAM, *P. cinnamomi* or *P. plurivora* were isolated had necrotic lesions with tarry or orange-brown spots on the outer bark and orange, flame-shaped discoloration of the inner bark, extending from the collar to 1.5 m, and small, chlorotic and sparse foliage, dieback, heavy fructification with unusually small cones and scattered or patchy mortality were found (Fig. 8a–c). Disease incidence was highest in PAA-infested stands. In a detailed survey of 2219 five- to 17-year-old *A. glutinosa* trees in 15 PAA-infested forest plantings in Bavaria, collar rot incidence was 52.5–23.8% in 2003, increasing to 62.3–20.8% in 2004. In the same period, overall mortality increased from 2.8% to 5.3%.

In all 50 *Phytophthora*-infested forest plantings of *C. sativa* in Greece, Italy, Portugal and Spain and in six of the 12 amenity plantings, most of the 5- to 28-year-old trees showed severe root and collar rot symptoms, with small and sparse foliage, dieback and mortality (Fig. 8d).

In 31 of 32 forest and amenity plantings of *Quercus ilex*, *Q. suber* and *Q. faginea* tested in Italy, Portugal and Spain, extensive fine root losses mainly caused by *P. cinnamomi* and severe crown symptoms, including stunted growth, thinning, dieback and wilting and high mortality levels, were observed (Fig. 8e–f). In a 14-year-old, 850-ha afforestation in southwestern Andalusia, 10% of *Q. ilex* trees were dead and almost all living trees were in decline, 50% showing over 40% defoliation. In 2008/2009 in a national park in Extremadura, 260 ha of *Eucalyptus camaldulensis* plantations were harvested and re-forested with 2-year-old *Q. ilex*. In 2011, *P. cinnamomi* had caused severe dieback and mortality in over 50% of randomly selected plants. In Sardinia, *P. cinnamomi* caused over 50% mortality in a 10-year-old 70-ha afforestation of *Q. ilex*, *Q. suber* and *Pinus pinaster* following a wet spring in 2011 (Fig. 8e–f).

In 47 of 49 forest plantings of *Q. petraea*, *Q. robur* and *Q. rubra* in Germany, Poland, Serbia and Spain, and in all 36 amenity and landscape plantings of eight *Quercus* spp. in seven countries, scattered or patchy distributions of typical root and crown symptoms and mortality were found (Figs 8g, 9a).

In five 8- to 15-year-old afforestations on former agricultural land in Germany, 2000 trees of various broadleaved species were examined in 2003 and root and collar rot symptoms (Fig. 9b), with reduced growth, chlorotic foliage and dieback (Fig. 9c) caused by *Phytophthora cambivora* were found in 73.6% of the 1417 *F. sylvatica* trees tested. Similar symptoms were also common in most other forest and amenity plantings of *F. sylvatica* analysed in Germany, Slovakia, Spain, Sweden and the UK.

In 37 infested amenity and landscape plantings in five countries, *A. hippocastanum*, *C. betulus*, *Tilia cordata*, *T. platyphyllos* and *T. 9 europaea* showed extensive loss of fine roots, with thinning crowns, chlorosis and dieback (Fig. 9d). In some *A. hippocastanum* trees, bleeding bark lesions extended from the collar to 3 m stem height (Fig. 9e).

Most plantings of 10 *Acer* spp. in six countries had extensive loss of fine and lateral roots, collar rot, crown dieback and scattered mortality due to *Phytophthora* infections (Fig. 9f). In five afforestations in northern Germany, over 50% of 408 *A. pseudoplatanus* trees showed root and collar rot symptoms and crown decline caused by *P. cambivora*. Four Italian

A. pseudoplatanus afforestations had similar symptoms caused by *P. acerina*.

Fine root losses, crown decline, wilting and scattered mortality occurred in most of the *Phytophthora*-infested forest, amenity and landscape plantings of *C. lawsoniana* (Fig. 9g), *Juniperus* spp., *Sequoiadendron giganteum*, *Taxodium distichum*, *Taxus baccata*, *Thuja occidentalis* and *T. plicata* in six countries. Collar rot of individual trees was infrequent. In several *Phytophthora*-infested afforestations of *Pinus pinaster*, *P. halepensis* fine root loss and symptoms of 'little leaf disease' were common (Fig. 8e).

Typical *Phytophthora*-related symptoms were also widespread in horticultural and ornamental plantings, but the number of affected plant species was too numerous to present data on symptoms or disease incidence of specific host plants.

4 Discussion

The surveys reported in this large-scale analysis of *Phytophthora* infestations in Europe clearly demonstrated that nursery stands across Europe are almost ubiquitously infested by a large array of *Phytophthora* species, confirming results from previous small-scale studies (Themann et al. 2002; Jung and Blaschke 2004; Jung 2009; Moralejo et al. 2009). In total, 49 *Phytophthora* taxa were recovered from 81% of the 1992 nursery stands in 91.5% of the 732 nurseries tested in 18 European countries. Frequencies of *Phytophthora* infestation in forest, advanced tree, horticultural and ornamental nurseries were comparable, ranging from 88.3 to 97.1% at the nursery level and from 78.6 to 92.3% at the level of the nursery stands. Mean infestation levels were almost identical in container stands and in fields with production of plants in soil. This result was surprising as in the latter production system an accumulation of soilborne *Phytophthora* species over years is inevitable if plants are regularly bought in from other nurseries and planted in these fields, whereas container production offers many options to avoid pathogen contamination. However, purchasing container plants from other nurseries without prior testing for potential *Phytophthora* infestations and generally poor nursery practices such as overly

dense plantings and close proximity of various plant species enabling cross-infections, reuse of compost or plastic containers without sterilization, use of unfiltered surface water or recirculation of irrigation water without filtering or sterilization, storing containerized nursery stock on poorly drained surfaces or even on the ground, and collection of dead plants and plant debris near the production area all facilitate introduction, reintroduction and spread of *Phytophthora* spp. in container nurseries (Ferguson and Jeffers 1999; Themann et al. 2002; Perez-Sierra and Jung 2013). Many of the container nurseries tested in the present work regularly purchased container plants from other nurseries. In addition, many of the poor nursery practices listed above were commonly observed. Infestation levels of nurseries were also independent of plant marketing category, a result that was not unexpected considering the fundamental changes in the nursery sector over the last three decades. Economic pressure and changes in consumer demands have stimulated consolidations through mergers and acquisitions creating larger companies, causing increased vertical specialization and complexity of the international plant distribution chain (Dehnen-Schmutz et al. 2010; Drew et al. 2010). Currently, wholesale, retail and administration nurseries are almost exclusively reselling nursery stock bought in from a relatively low number of large producers with national and international distribution, from brokers or from other wholesalers and retailers. Due to intense vertical and horizontal trade, individual plants often flow largely unregulated through several nurseries both within and between countries before being sold to a consumer (Dehnen-Schmutz et al. 2010; Drew et al. 2010). Such a system provides optimal conditions for the rapid spread of soilborne pathogens like *Phytophthora* spp. which can be transported when suppressed by fungicides and fungistatic chemicals on non-symptomatic host plants or as passive hitchhikers on non-host plants (Brasier 2008; Perez-Sierra and Jung 2013). In one Bavarian nursery for example, the oak-specific *P. quercina* was isolated from the rhizosphere of seedlings from the non-host species *F. sylvatica* sampled in a field where *Q. robur* was grown 2 years prior.

The risk of aggressive *Phytophthora* species spreading with visually healthy host plants is convincingly demonstrated by the work reported here and by Migliorini et al. (2015). Generally, the majority of nursery plants tested in intensively managed nurseries often with regular use of fungicides and fungistatic chemicals and professional irrigation regimes, avoiding wet or waterlogged soil conditions and wetting of above-ground plant organs, appeared visually healthy. As the European system of plant biosecurity is based principally on visual inspections for symptoms, it is impossible for both plant inspectors and buyers of plants to detect masked *Phytophthora* infestations (Jung and Blaschke 2004; Brasier 2008; Perez-Sierra and Jung 2013). The weakness of the current system, discussed in detail below, is highlighted by the following striking examples taken from a long list of *Phytophthora*-infested non-symptomatic host plants or non-host plants detected in the European nursery trade during this work. In Greece, *P. multivora* and *P. ramorum*, both exotic wide host range pathogens aggressive on *Rhododendron* spp. in particular, were isolated in 2011 from visually healthy *Rhododendron* plants imported from Belgium and accompanied by EU plant passports (Table S8). In Croatia, a diverse population of 23 described species or designated taxa of *Phytophthora* including *P. multivora*, *P. ramorum*, recently introduced exotic species like *P. parvispora* and *P. niederhauserii*, and several previously unknown *Phytophthora* taxa were detected between 2007 and 2013 on plants imported from nurseries in Italy and the Netherlands which were also accompanied by EU plant passports (Tables S5–S8). The newly described *P. pachypleura* (Henricot et al. 2014) was isolated in an Italian nursery from *A. japonica* plants imported from a French nursery. In Bavaria and Austria, most *Phytophthora*-infested plants found in forest nurseries and nurseries producing large specimen trees originally came from producers in Northern and Western Germany or the Netherlands, before being grown for one or more years in the fields of retail nurseries. Long-distance spread of *Phytophthora* species with infested nursery stock was also demonstrated on other continents, including Australia, despite the strict quarantine regulations and extensive phytosanitary controls of nursery stock (Davison et al. 2006), and the United States, where *P. ramorum* was spread from ornamental nurseries in California and Oregon to nurseries in at least 14 eastern states of the US despite emergency quarantine regulations in place for this specific pathogen (Goss et al. 2009; Grunwald et al. 2012). In this instance, the pathogen was not intercepted during mandatory phytosanitary controls and evidence of spread came from molecular trace-back studies of already established *P. ramorum* populations (Goss et al. 2009). Using a network analysis, Pautasso et al. (2010) demonstrated that spread of *P. ramorum* in the UK also occurred via the nursery trade.

Even though the *Phytophthora* infestations would have been detected during the phytosanitary inspections at the exporting nurseries, transport and sale of most infested nursery plants could not have been prevented as only five *Phytophthora* species, *P. fragariae*, *P. kernoviae*, *P. lateralis*, *P. ramorum* and *P. rubi*, are included on the EPPO A2 quarantine list, despite the fact that many other exotic *Phytophthora* species are causing large-scale epidemic diebacks and mortality of forest trees in Europe (Brasier et al. 1993; Jung et al. 1996, 2000, 2013a; Vettraino et al. 2001, 2002; Streito et al. 2002; Balci and Halmshlager 2003a,b; Gibbs et al. 2003; Jung and Blaschke 2004; Jung 2009).

A key finding of the present study was that the most aggressive *Phytophthora* species to the respective tree or crop species were regularly found in both nursery stands and young plantings (Tables S1–S13). An invasive pathogen may be spread to natural forest stands several times, although it will not necessarily successfully establish. However, the specific life strategy of *Phytophthora* spp., based on highly resistant oospores facilitating long-term survival, chlamydospores for medium- and short-term survival, the multicyclic production of sporangia releasing motile zoospores able to infect healthy unwounded tissues of vigorous hosts, their often high aggressiveness, and the either wide host ranges or very specific adaptations to certain host plants, arguably make *Phytophthora* species the most notorious and successful invasive plant pathogens in existence (Erwin and Ribeiro 1996; Hansen et al. 2012; Jung et al. 2013a,b). Consequently, continuous high-frequency spread of these aggressive pathogens of trees and crops with infested nursery stock will inevitably lead to further large-scale establishment in forests, horticultural systems and the wider environment. This effect was convincingly demonstrated by a trace-back study in 75 river systems in Bavaria where mortality of natural riparian alder forests was almost exclusively found in rivers with the presence of *P. 9 alni*-infested alder plantings in their upper catchment areas (Jung and Blaschke 2004). Using the following line of reasoning, the results of the present nursery and planting surveys provide strong circumstantial evidence of high-frequency spread of *Phytophthoras* via infested nursery stock to the wider environment. The planting surveys demonstrated the presence of 56 *Phytophthora* species and taxa in 66% of over 2500 tested plantings. As all plants in planting sites came from nurseries whereas all nursery plants were seed-grown, the finding of similar mean infestation rates for forest (79.3%), riparian (94%) and horticultural plantings (83.1%) on the one hand and nursery stands in forest (81.5%), advanced tree (92.3%) and

horticultural (90.5%) nurseries on the other hand constitutes clear indirect evidence of the spread of *Phytophthora* spp. from nurseries to plantings. This is particularly the case with afforestations of previous arable fields, meadows and pastures, where previous presence of typical tree pathogens like *P. cambivora*, *P. cinnamomi* and *P. plurivora* and host-specific pathogens such as *P. 9 alni* and *P. quercina* is highly unlikely. Further evidence comes from the comparison of infestation rates between forest plantings and seed-regenerated or mature forests. The analysis of the DSF database showed that *P. cinnamomi* is mainly found within planted oak forests in SW France, while being comparatively rare in seed-regenerated forests of the same region. Moreover, mean infestation rates found in planted young oak (87.7%) and beech (94.1%) stands (80.7%) in this study were considerably higher than mean infestation rates of the 558 and 265 mature declining stands of oaks (62.4%) and beech (81.5%) examined across Europe in the last 20 years (Jung et al. 2013a). Also for *C. sativa*, the general *Phytophthora* infestation rate was clearly higher in 50 young forest plantings in this work (80.7%) than in 35 mature forests (65.7%) examined across Europe (Vettrano et al. 2005). If *P. cinnamomi* is considered alone, the difference between young plantings and mature forests is even higher (76% versus 25.7%). Finally, clear evidence for the importance of the nursery pathway was recently presented for the destructive diseases caused in the UK by the invasive exotic *P. lateralis* and *P. austrocedrae* on *C. lawsoniana* and *Juniperus communis*, respectively (Green et al. 2013, 2015).

Due to the high number and the random selection of forest nursery stands and forest plantations, the results presented here can be extrapolated to approximate the magnitude of *Phytophthora*-infested forest plantings at the European scale. Since the early 1990s, national subsidy programmes and several EU programmes, like EEC Regulation 2080/92, stimulated massive afforestations of agricultural and arable land, increasing the area of planted forests in Europe (excluding the Russian Federation) between 1990 and 2010 by 6 million hectares (Anonymous 2010, 2011a,b). If the mean infestation rate of forest nursery stands and forest plantings is 80%, we can estimate an approximate total area of 4.8 million hectares of new forests potentially infested by *Phytophthora* planted in Europe over the last two decades. Given an average size of European afforestations of 7 hectares (http://ec.europa.eu/agriculture/envir/report/en/forest_en/report.htm), *Phytophthora* species were almost certainly inadvertently spread to approximately 686 000 new sites. In addition, between 1998 and 2007, 1.1 million hectares of harvested or burned mature forests were reforested per year by planting, totalling approximately 22 million hectares between 1990 and 2010, of which ca. 17.6 million hectares possibly were established with *Phytophthora*-infested nursery stock. Given the importance of plantations for European forestry, this informed estimate is of outstanding importance as the devastating impacts of this unprecedented large-scale spread of *Phytophthora* pathogens into the European forests and the implications for forestry and nature conservation are evident. In the EU afforestation programmes, broadleaved species represented 57% of the planted area, followed by conifers with 32%, mixed stands with 7% and fast-growing plantation trees with 4% (Anonymous 2006), and proportions were similar in most national afforestation programmes. During the last twenty years, almost 50% of the afforestations in Europe were made in the Iberian peninsula, mainly by planting mixed or pure stands of *Q. suber* and *Q. ilex* (Barbero 2000). According to our data, 86% of these afforestations probably are infested by *P. cinnamomi*, a pathogen that represents a serious threat to the future of both oak species in the area.

Broadleaved tree species also have a dominant role in new silvicultural reforestation programmes, with the aim of replacing unnatural pure conifer plantations with mixed forests, in order to increase the stability of the ecosystems against predicted climatic change effects. There is a prominent example in Bavaria where 255 000 hectares of spruce monocultures are being transformed to pure or mixed forests of *F. sylvatica*, 50 000 hectares via planting of nursery stock (Ammer et al. 2005; http://baysf.de/de/home/unternehmen_wald/aktuelles/detailansicht/article/168/blatt-fuer-blatt.html). However, 89% of the *Fagus* stands tested in German nurseries in the present study were infested by at least one *Phytophthora* species involved in widespread decline and dieback of beech forests. Against a background of almost ubiquitous infestations of forest nursery stands and forest plantings of *F. sylvatica*, *Quercus* spp., *C. sativa*, *Alnus* spp. and many other forest tree species with aggressive invasive *Phytophthora* species that can cause large-scale dieback and mortality of mature forests of these tree species, the likely success and usefulness of the European afforestation and reforestation programmes must be seriously questioned. Continuous root and collar infections by *Phytophthora* spp. will not only lead to premature decline and mortality of a high proportion of the infested plantings as demonstrated by the present study. Once established in the planting sites, *Phytophthora* species will inevitably spread through zoospore production in soil water and with resting spores in soil particles adhering to animal hooves and paws, hikers' boots and tyres of vehicles, including logging machines and cars, to neighbouring forests and water courses. The impact of large-scale use of infested nursery stock on natural ecosystems was demonstrated previously by the devastating root and collar rot epidemic of *Alnus* spp. in Europe, caused by PAA, PAM and PAU (Streito et al. 2002; Gibbs et al. 2003; Jung and Blaschke 2004; Jung et al. 2013a).

On a global scale, the area of planted forests increased between 1990 and 2010 by 86 million hectares (Anonymous 2010, 2011a). The majority of this increase was in China where 50 million ha were afforested, and in North America where afforestation and reforestation activities comprised a total area of 18 million ha (Anonymous, 2011a). Although a series of surveys since the mid-1990s demonstrated high infestation rates of US ornamental nurseries with at least 31 *Phytophthora* species (MacDonald et al. 1994; Ferguson and Jeffers 1999; Lamour et al. 2003; Testa et al. 2005; Linderman and Davis 2006; Dart et al. 2007; Schwingle et al. 2007; Donahoo and Lamour 2008; Warfield et al. 2008; Goss et al. 2009; Yakabe et al. 2009; Hulvey et al. 2010; Olson and Benson 2011; Bienapfl and Balci 2014; Parke et al. 2014), the situation in forest nurseries is largely unknown. Also in China, Canada, Mexico and other countries with high rates of afforestation and reforestations, such as Australia, Brazil, Chile, India, Indonesia, Myanmar and Vietnam, no data on *Phytophthora* infestations of forest nurseries are available, and large-scale surveys are urgently required to assess the risk posed by the nursery pathway to the world's forests.

For plant biosecurity and disease management, it is of utmost importance to know which of the *Phytophthora* species and taxa detected in nurseries and plantings during this study are indigenous in Europe and which must be considered as alien invasive pathogens. Parameters commonly used as indirect indicators of the alien origin of a pathogen include consistent association with decline and dieback of common indigenous plant species or proven high aggressiveness to these plants in pathogenicity trials, occurrence in undisturbed natural ecosystems of other continents without associated disease, low genetic variability and close phylogenetic relatedness to other non-native species (Ko et al. 1978; Arentz and Simpson 1986; Oudemans and Coffey 1991; Erwin

and Ribeiro 1996; Goodwin 1997; Dobrowolski et al. 2003; Cooke et al. 2005; Ivors et al. 2006; Rea et al. 2010, 2011; Ginetti et al. 2014). Based on cumulative, though indirect evidence, 59 of the 68 *Phytophthora* species detected in the nursery and planting surveys of the present work, 41 of the 49 *Phytophthora* taxa in 69% of nursery stands and 48 of the 56 *Phytophthora* taxa in 59% of the plantings were probably introduced to Europe (Table 4).

The ITS Clade 6 species *P. bilobang*, *P. gonapodyides*, *P. lacustris*, *P. megasperma*, *P. taxon 'PgChlamydo'* and *P. taxon 'Forestsoil'* are infrequently associated with diseases of forest trees and agricultural crops in Europe (Erwin and Ribeiro 1996; Jung et al. 1996, 2000, 2013a; Jung and Blaschke 2004; Jung 2009; Orlikowski et al. 2011; Nechwatal et al. 2013). However, they are common in healthy or undisturbed natural ecosystems in Europe, North America and Asia (Hansen and Delatour 1999; Reeser et al. 2011; Huai et al. 2013). Their origins, therefore, remain cryptic. These six taxa were found in 3.8% of the nursery stands and in 5.1% of the plantings.

Due to scattered but widespread distribution in stands of *F. sylvatica* and *Quercus* spp. in Europe, inconsistent association with native diseased trees in highly favourable disease situations and relatively low aggressiveness in pathogenicity trials, *P. pseudosyringae* and *P. psychrophila* from ITS Clade 3 are most likely native to Europe (Jung et al. 1996, 2002, 2003, 2013a; Jung and Blaschke 2004; Jung 2009; Perez-Sierra et al. 2013). The indigenous nature of *P. pseudosyringae* is also supported by the fact that European isolates have higher genetic variability than isolates from the USA where this pathogen is usually associated with bark cankers of oaks and tanoaks (Linzer et al. 2009). Being very closely related to *P. pseudosyringae* and *P. psychrophila* and occurring as a relatively mild leaf pathogen in natural stands of *I. aquifolium* in remote mountain forests in Sardinia and Corsica (Scanu et al. 2014b), *P. ilicis* is also most likely indigenous in Europe. *Phytophthora ilicis*, *P. pseudosyringae* and *P. psychrophila* were present in less than one per cent of the surveyed nursery stands and plantings.

During a survey of ornamental nurseries in Eastern Spain and the Balears, Moralejo et al. (2009) detected 16 alien *Phytophthora* taxa also found in the present study and two other likely non-native taxa, *P. kelmania* from ITS Clade 9 and *P. 'pseudo-citricola'* from the '*P. citricola* complex'. The number of described species and designated taxa of *Phytophthora* has increased dramatically over the last 20 years (Brasier 2009; Kroon et al. 2012), and 44 of the 64 *Phytophthora* taxa detected in the present study were unknown to science before 1990. Although no *Phytophthora* species has ever been intercepted during port inspections of plants-for-planting from another continent, it is beyond reasonable doubt that the intercontinental nursery trade is the major pathway for movement of *Phytophthora* species between continents as demonstrated for many fungal pathogens and insect pests (Erwin and Ribeiro 1996; Webber and Brasier 2005; Jones and Baker 2007; Brasier 2008; Grunwald et al. 2012; Liebhold et al. 2012; Hantula et al. 2013; Santini et al. 2013; Eschen et al. 2014). Almost 70% of all insect pests and pathogens that established between 1860 and 2006 in the US were introduced with live plants (Liebhold et al. 2012). Similarly, the number of invasive forest pathogens (IFPs) in Europe has increased exponentially since 1800, and for 57% of the 123 established IFPs, the most likely pathway was trade in living plants (Santini et al. 2013). Apart from *Phytophthora* species, several bacterial and fungal pathogens that caused devastating epidemics of trees in Europe were introduced with living plants, including *Erwinia amylovora* causing fireblight of rosaceous trees, *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* the causal agents of several waves of Dutch Elm Disease and, more recently, *Hymenoscyphus fraxineus*, causing ash dieback (Brasier 2008; Queloiz et al. 2011; Santini et al. 2013; Baral et al. 2014). In the USA, annual plant imports increased between 1967 and 2010 by 500% reaching 3.2 billion in 2007 (Liebhold et al. 2012). Similar trends and figures for Europe come from the recently completed EU-funded project ISEFOR (Increasing Sustainability of European Forests) during which import data from main ports of entry in the 10 countries Belgium, Cyprus, Czech Republic, Estonia, Finland, France, Italy, the Netherlands, Poland and Slovakia were analysed in detail. In 2010, in total 4.3 billion living plants were imported from overseas with the Netherlands accounting for almost 99% of all such imports. With 3.6 billion plants, Africa was the most important supplier, followed by Asia with 456 million plants, North and South America with 181 million and 81 million plants, respectively, and Oceania with 2.4 million plants. Between 2007 and 2010, the volume of imported woody plants increased by 44%, and in 2010, the proportion of woody plants reached 20.8% of all imported plants (Ludovic Rigoux, Universite Libre de Bruxelles, Belgium, pers. comm. 11 December. 2012). The volume of imported plants has long surpassed the port inspection capacities by several orders of magnitude. In the USA, only 2% of imported nursery stock is inspected by APHIS (Brasier 2008). Considering the fact that in the EU, no more than 3% of the imported consignments are subject to phytosanitary inspections (unpublished results, EU COST Action FP 1002 'Pathway Evaluation and Pest Risk Management In Transport [PERMIT]'), such enormous numbers of living plants provide ample opportunities for the unintentional introduction of pests and pathogens, in particular *Phytophthora* spp., travelling as passive hitchhikers in roots and adhering soil particles of both host and non-host plants (Brasier 2008; Perez-Sierra and Jung 2013). This problem is of particular concern against the background of an estimated number of between 150 and 500 unknown *Phytophthora* species living unnoticed in a balanced equilibrium with co-evolved host plants in their natural habitats (Brasier 2009).

Fundamental changes in the international plant distribution chain, for example increased complexity; increasingly blurred roles and distinctions of companies trading in and transporting plants; specialization of companies resulting in the flow of individual plants through several nurseries; favourable climate and low costs for producing plants overseas; more efficient and rapid transport systems, packaging and shipping technologies; e-commerce; and changed consumer demands, in particular the demand for novel and exotic plants and 'instant landscapes', are factors responsible for the exponential increase in the international trade in plants-for-planting and have extended the range of plant origin, availability and viability (Brasier 2008; Dehnen-Schmutz et al. 2010; Drew et al. 2010; Liebhold et al. 2012). The dimension of the threat posed by invasive pathogens has spurred research projects like ISEFOR (2011–2014) and FORTHREATS (European network on emerging diseases and invasive species threats to European Forest Ecosystems; 2007–2009), mentioned above, the establishment of several European COST Actions, such as FP 0801 'Established and Emerging *Phytophthora*: Increasing Threats to Woodland and Forest Ecosystems in Europe', FP 1002 (PERMIT), FP1103 'Fraxinus dieback in Europe: elaborating guidelines and strategies for sustainable management (FRAXBACK)' and FP 1401 'A global network of nurseries as early warning system against alien tree pests (Global Warning)', and the IUFRO (International Union of Forest Research Organizations) units 7.02.09 'Phytophthora in Forests and Natural Ecosystems' and 7.03.12 'Alien Invasive Species and International Trade'. All projects and networks have clearly stated that current international plant health protocols based on random visual inspections for symptoms of

listed quarantine organisms (Schrader and Unger 2003) have failed and must be considered as outdated and seriously flawed. This conclusion is confirmed by the compelling evidence presented in this paper. The almost ubiquitous infestations of nurseries and plantings across Europe and the facts that none of the 59 putatively exotic *Phytophthora* taxa detected in the present study had been intercepted at the ports of entry and that the spread of the quarantine organism *P. ramorum* was not halted despite strict quarantine regulations demonstrate failures of plant biosecurity in Europe. Most of the ca. 150 currently known species and designated taxa of *Phytophthora* were unknown to science before they turned up in other continents as invasive aggressive pathogens of native plants or plantation crops (Erwin and Ribeiro 1996; Brasier 2008; Hansen 2008; Hansen et al. 2012; Jung et al. 2013a). Eradication or containment of introduced *Phytophthora* species in the wider environment is impossible because of the highly successful survival strategies of these organisms, the lack of suitable registered biocides and insufficient allocation of human and financial resources to plant biosecurity. Therefore, the prevention of further introductions of unknown, potentially invasive *Phytophthora* spp. and other pathogens must be given highest priority in plant biosecurity. In this context, article VI.2 of the International Plant Protection Convention (IPPC) that prohibits phytosanitary measures against unregulated pests appears to be paradoxical since in the current system regulations can only be implemented following a pest risk assessment which in turn implies that the pathogen has to be known (Schrader and Unger 2003; Brasier 2008). A solution to this dilemma is the adoption of a pathway regulation approach based on pathway risk analyses, and risk-based inspection regimes performed by an adequate number of skilled staff using molecular high-throughput detection tools. These protocols are recommended at the ports of entry and in nurseries to minimize the risks of further introductions and dissemination of both known and, even more importantly, unknown potential pathogens to Europe. Such an approach would follow the lead of the strict quarantine system in Australia which has proven bioeconomic benefits (Keller et al. 2007).

Best management practices for reducing the risk of introduction and dispersal of *Phytophthora* spp. in nurseries were recently presented in the comprehensive review of Parke and Grunwald (2012) and will not be discussed in detail here.

In conclusion, it is abundantly clear that the ubiquitous *Phytophthora* infestations of nursery stock represent a serious threat to tree health and ecosystem stability on a European scale and that the current phytosanitary system will allow further introductions of potentially invasive *Phytophthora* pathogens to Europe and other continents with subsequent dissemination via the nursery trade. Instead of small corrections to an outdated and poorly performing system, a new holistic and integrated systems approach is urgently required, which must encompass (i) a major change in the phytosanitary system from a host-by-host and pest-by-pest approach to a pathway regulation approach with high-frequency inspections of high-risk consignments using molecular high-throughput detection methods (e.g. Scibetta et al. 2012), and (ii) due to failure of self-regulation in the industry an international certification system and a mandatory hygiene code for the production and trading of non-infested nursery stock. The overdue improvements to regulation of the nursery industry must consider the complexities in the nursery trade and address all agents involved. As even partial code compliance can result in complete failure to prevent introduction and spread of invasive *Phytophthora* species, regular controls of compliance and rigorous enforcement of regulations will be necessary. In addition, public information campaigns to develop consumer awareness of the importance of invasive pathogens will be helpful as public attention would be a strong incentive for the nursery industry to build up a positive reputation by distributing only clean stock (Drew et al. 2010).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. *Phytophthora* – infestation of fields and container stands of forest nurseries, and forest, riparian, amenity and landscape plantings of four *Alnus* spp. in Austria, Bulgaria, Croatia, Czech Republic, Germany, Hungary, Poland, Portugal, Spain, Sweden and the United Kingdom.

Table S2. *Phytophthora* – infestation of nursery fields and container stands, and forest, amenity, and landscape plantings of *Castanea sativa* in France, Germany, Greece, Hungary, Italy, Poland, Portugal, Slovakia, Spain and the United Kingdom.

Table S3. *Phytophthora* – infestation of nursery fields and container stands, and forest, amenity and landscape plantings of *Fagus* spp. in Austria, France, Germany, Poland, Serbia, Slovakia, Spain, Sweden and the United Kingdom.

Table S4. *Phytophthora* – infestation of 121 nursery fields and container stands of 11 *Quercus* spp. in France, Germany, Italy, the Netherlands, Poland, Portugal, Serbia and Spain.

Table S5. *Phytophthora* – infestation of 232 nursery fields and container stands of 60 broadleaved tree and shrub species for forest and amenity plantings in Austria, Croatia, Finland, France, Germany, Greece, Hungary, Italy, the Netherlands, Norway, Poland, Portugal, Spain, Switzerland and the United Kingdom.

Table S6. *Phytophthora* – infestation of 482 fields and container stands of 45 conifer species in forest nurseries and advanced tree nurseries in Austria, Croatia, France, Germany, Hungary, Italy, Norway, Poland, Portugal, Spain, Sweden and the United Kingdom.

Table S7. *Phytophthora* – infestation of 308 horticultural nursery fields and container stands of 33 horticultural species in Croatia, Hungary, Italy, Norway, Poland, Spain, Sweden and the United Kingdom.

Table S8. *Phytophthora* – infestation of nursery fields and container stands of 142 ornamental broadleaved tree, shrub and herbaceous taxa in Austria, Croatia, Finland, France, Germany, Greece, Hungary, Italy, the Netherlands, Norway, Poland, Spain, Sweden, Switzerland and the United Kingdom.

Table S9. *Phytophthora* – infestation of 113 forest, amenity and landscape plantings of 12 *Quercus* spp. in Germany, Italy, Luxembourg, Poland, Portugal, Serbia, Slovakia, Spain, Switzerland and the United Kingdom.

Table S10. *Phytophthora* – infestation of 365 forest, amenity, landscape and riparian plantings of 99 broadleaved tree and shrub species in Austria, Croatia, Finland, Germany, Greece, Hungary, Italy, the Netherlands, Poland, Portugal, Serbia, Slovakia, Spain, Sweden, Switzerland and the United Kingdom.

Table S11. *Phytophthora* – infestation of 342 forest, amenity and landscape plantings of 32 conifer species in Austria, Croatia, Germany, Italy, Norway, Poland, Portugal, Slovakia, Spain, Sweden and the United Kingdom.

Table S12. *Phytophthora* – infestation of 688 horticultural plantings of 59 horticultural crop and fruit tree species in Austria, Bulgaria, Croatia, Germany, Greece, Hungary, Italy, Slovakia, Spain, Sweden and the United Kingdom.

Table S13. *Phytophthora* – infestation of 755 ornamental plantings of 281 broadleaved tree, shrub and herbaceous species in Croatia, Germany, Hungary, Italy, Spain, Sweden, Switzerland and the United Kingdom.

Fig. 1. Diversity and frequency of alien, native and cryptic *Phytophthora* taxa in 1992 fields and container stands of 732 forest, advanced tree, horticultural and ornamental nurseries in 18 European countries. Multiple isolates of a *Phytophthora* taxon from the same nursery stand were considered as one record. Abbreviated *Phytophthora* names are explained in footnote 1 of Table 2.

Fig. 2. Diversity and frequency of alien, native and cryptic Phytophthora taxa in fields and container stands of forest, advanced tree, horticultural and ornamental nurseries in different climatic regions of Europe a: 653 fields and container stands of 187 nurseries in Atlantic regions (ES, FR, GB, NL); b: 841 fields and container stands of 276 forest, advanced tree, horticultural and ornamental nurseries in subcontinental to continental regions of Europe (AT, CH, DE, FI, HU, NO, PL, RS, SE, UA); c: 498 fields and container stands of 269 nurseries in Mediterranean regions of Europe (ES, FR, GR, IT, HR, PT, TR). Multiple isolates of a Phytophthora taxon from the same nursery stand were considered as one record. Abbreviated Phytophthora names are explained in footnote 1 of Table 2.

Fig. 3. Diversity and frequency of Phytophthora taxa in a: 64 nursery stands and 265 plantings of a: *Alnus* spp. in 10 European countries (AT, CZ, DE, ES, GB, HR, HU, PL, PT, SE); b: 121 nursery stands of 11 *Quercus* spp. in eight European countries (DE, ES, FR, IT, NL, PL, PT, RS); c: 52 nursery stands and 74 plantings of *Castanea sativa* in 10 European countries (DE, FR, ES, GB, GR, HU, IT, PL, PT, SK); d: 64 nursery stands of *Fagus sylvatica* and *F. orientalis* and 34 plantings of *F. sylvatica* in eight European countries (AT, DE, ES, FR, GB, PL, SE, SK); e: 232 nursery stands of 60 other broadleaved tree and shrub species in 15 European countries (AT, CH, DE, ES, FI, FR, GB, GR, HR, HU, IT, NL, NO, PL, PT); f: 482 nursery stands of 45 conifer taxa in 12 European countries (AT, DE, ES, FR, GB, HR, HU, IT, NO, PL, PT, SE); 308 nursery stands of 33 horticultural tree and crop taxa in eight European countries (ES, GB, HR, HU, IT, NO, PL, SE); g: 669 nursery stands of 142 ornamental plant taxa in 15 European countries (AT, CH, DE, ES, FI, FR, GB, GR, HR, HU, IT, NL, NO, PL, SE). Abbreviated Phytophthora names are explained in footnote 1 of Table 3.

Fig. 4. Diversity and frequency of Phytophthora taxa in 486 forest nursery stands of 74 tree and shrub species in 14 European countries (AT, DE, ES, FI, FR, GB, HR, IT, PL, PT, RS, SE, TR, UA) and in 411 forest plantings of 32 tree and shrub species in 13 European countries (AT, CZ, DE, ES, FI, GR, HU, IT, PL, PT, RS, SE, SK). Abbreviated Phytophthora names are explained in footnote 1 of Table 3.

Fig. 5. Phytophthora symptoms of both field-grown and containerized forest nursery stock; a. Patch dieback and mortality of 2-year-old *Fagus sylvatica* seedlings caused by *Phytophthora cambivora* in Northern Germany; b. Collar rot caused by *P. alni* after 1 week flooding on a visually healthy 2-year-old *Alnus glutinosa* seedling in Eastern Germany; c. Collar rot caused by *P. cinnamomi* on a 2-year-old *Castanea sativa* in Sardinia; d. Patch dieback and mortality caused by *P. cambivora* and *P. cinnamomi* in a *C. sativa* field in Sardinia; e. Patch dieback and mortality caused by *P. cinnamomi* in a *Juglans regia* field in Sardinia f. Wilting and mortality of 2-year-old *Quercus ilex* in Extremadura caused by *P. cambivora*; g. Chlorosis, wilting and mortality of *Pinus halepensis* in Extremadura caused by *P. cryptogea* and *P. taxon* 'PgChlamydo'.

Fig. 6. Diversity and frequency of alien, native and cryptic Phytophthora taxa in 2525 forest, riparian, amenity, landscape and ornamental plantings, and horticultural plantations of 478 broadleaved and conifer tree, shrub and herbaceous taxa (species, cultivars, hybrids) in 20

European countries. Multiple isolates of a Phytophthora taxon from the same nursery stand were considered as one record. Abbreviated Phytophthora names are explained in footnote 1 of Table 3.

Fig. 7. Diversity and frequency of alien, native and cryptic Phytophthora taxa in riparian, amenity, landscape and ornamental plantings, and horticultural plantations in different climatic regions of Europe; a: 1798 plantings in Atlantic regions (ES, FR, GB, NL); b: 408 plantings in Mediterranean regions (ES, FR, GR, IT, HR, PT, TR); c: 319 plantings in subcontinental to continental regions (AT, CH, DE, FI, HU, NO, PL,

RS, SE, UA). Multiple isolates of a Phytophthora taxon from the same nursery stand were considered as one record. Abbreviated Phytophthora names are explained in footnote 1 of Table 3.

Fig. 8. Phytophthora symptoms in forest and landscape plantings; a. Collar rot with tarry spots on the outer bark caused by *Phytophthora x alni* (PAA) on 10-year-old *Alnus glutinosa* in Bavaria; b. Orange-brown, tongue-shaped lesion of inner bark caused by PAA on a 12-year-old *Alnus incana* in Bavaria; c. Chlorosis, dieback and mortality of 8-year-old *A. glutinosa* in Bavaria caused by PAA; d. Dieback and mortality caused by *P. cambivora* and *P. cinnamomi* in a 12-year-old *Castanea sativa* planting in Sardinia; e. Sudden wilting and mortality of *Quercus suber* and thinning, chlorosis and small-sized needles of *Pinus pinaster* caused by *P. cinnamomi* in a 10-year-old afforestation in Sardinia; f. Sudden wilting and mortality of *Quercus ilex* and *Q. suber* caused by *P. cinnamomi* in a 10-year-old afforestation in Sardinia; g. 25-year-old

Quercus palustris in a recently established landscape planting in Slovakia showing thinning, chlorosis and dieback of the crown due to fine root losses caused by *P. cactorum*, *P. cambivora*, *P. plurivora* and *P. quercina*.

Fig. 9. Phytophthora symptoms in forest, amenity and landscape plantings in Germany; a. Small suberized roots of a 10-year-old *Q. robur* in a landscape planting with extensive losses of lateral roots and fine roots and open cankers caused by *P. quercina* and *P. plurivora*; b. Girdling collar rot lesion caused by *P. cambivora* on *F. sylvatica* in a 10-year-old afforestation; c. Chlorosis and slow decline of a 12-year-old *Fagus sylvatica* in an afforestation due to root and collar rot caused by *Phytophthora cambivora*; d. 12-year-old *Tilia platyphyllos* in a landscape planting with advanced chlorosis, thinning and dieback of the crown due to severe fine root losses caused by *P. cactorum* and *P. plurivora*; e. 10-year-old *Aesculus hippocastanum* in an urban park with *P. plurivora* collar rot and orange exudations extending up to 4 m stem height; f. Dead and chlorotic *Acer pseudoplatanus* trees in a 5-km-long roadside planting severely infested by *P. cambivora*, *P.*

plurivora and *P. gonapodyides*; g. 10-year-old landscape hedgerow planting of *Chamaecyparis lawsoniana* with thin chlorotic crowns (right side), wilting (centre) and mortality (left side) due to root rot caused by *P. cryptogea*.