

Impacts of exotic forest pathogens on Mediterranean ecosystems: four case studies

Matteo Garbelotto · Marco Pautasso

Accepted: 12 December 2011
© KNPV 2011

Abstract Mediterranean ecosystems are hotspots of biodiversity. Because of a coincidence of high species richness and human presence, Mediterranean biodiversity is particularly threatened by processes such as habitat degradation, fragmentation and loss, pollution, climate change and introduction of invasive species. Invasive tree pathogens are among the problematic exotic species of California, Chile, the Mediterranean, South Africa and Australia. In this review, we provide an update on a selection of non-native tree pathogens currently posing a threat in Mediterranean ecosystems. The impact of exotic forest pathogens range from large-scale tree and shrub mortality in native ecosystems (*Phytophthora ramorum* on the West Coast of the USA) to disruption of plantations of exotic (e.g., *Seiridium cardinale* on planted Monterey cypress in California, *Fusarium circinatum* on Monterey pine worldwide) and native trees (introduction of the North American *Heterobasidion irregulare* in stone pine woodland in Italy). Genetic analyses are instrumental

in improving our understanding and management of these outbreaks. There is a need for more empirical data on how novel pathosystems are likely to develop under novel climates, as well as interdisciplinary collaborations among forest pathologists, theoretical modellers and climatologists. The magnitude of the observed effects of some exotic tree diseases makes it important to try and minimize the risk of the inadvertent movement of plant pathogens when planning assisted migration activities to enable plant species to cope with rapid climate change.

Keywords Biodiversity · Forest health · Geographical genetics · Global change · Host susceptibility · Landscape epidemiology · Multiple trade-offs · Sudden Oak Death · Transmission rates · Tree fungal pathogens

Emergent diseases and Mediterranean ecosystems

Emergent diseases are diseases on the rise. Indeed, there is evidence for an increase in the number of new reports of plant pathogens in the scientific literature over the last 20 years (Dehnen-Schmutz et al. 2010). Although such increase is less marked for tree pathogens (at least in North America: Aukema et al. 2010) and may in part be a consequence of a parallel rise in the number of observers, there are many plausible non-artefactual explanations for an increasing number of emerging plant diseases. More numerous and stronger long-distance trade links, the already

M. Garbelotto
Department of Environmental Science,
Policy and Management, Ecosystem Sciences Division,
University of California,
Berkeley, CA 94720, USA

M. Pautasso (✉)
Centre d'Ecologie Fonctionnelle et Evolutive (CEFE),
CNRS,
1919 route de Mende,
34293 Montpellier Cedex 5, France
e-mail: marco.pautasso@cefe.cnrs.fr

observed recent climate warming, homogenization of agricultural and forested landscapes, large-scale planting of exotic ornamental species in urbanized areas: all these processes are likely to have contributed to many recent invasions of exotic plant pathogens (Anderson et al. 2004; Brasier 2008; Loo 2009; Tubby and Webber 2010; Stenlid et al. 2011).

Mediterranean ecosystems are particularly affected by exotic forest diseases, given the combination of: (1) richness in plant hosts, (2) mild and wet winters which tend to favour pathogen development, and (3) dense human population/frequent visits by tourists, with plenty of opportunities for pathogen introduction (Mooney and Dunn 1970; Blondel and Aronson 1995; Scarascia-Mugnozza et al. 2000; Garbelotto 2008; Cox and Underwood 2011). These ecosystems also have more to lose from such outbreaks, given the high species richness and presence of endemics (plant species with a narrow distribution) in Australia, California, Chile, the Mediterranean, and South Africa (Cowling et al. 1996; Médail and Quézel 1999; Mooney et al. 2001; Araújo 2003). Also for Mediterranean ecosystems, it is unlikely that a disproportionate presence of plant pathologists in these regions could explain the number of emerging plant pathosystems. More likely, the outbreaks reviewed in this paper were enabled by the combination of the favourability of Mediterranean climate for agriculture, gardening and tourism and the global connectivity deriving from the similar climate in these regions (which allows easy translocation of plants already adapted to very similar environmental conditions; Lavorel et al. 1998; Sanz-Elorza et al. 2009; Arianoutsou et al. 2010).

Emerging diseases can be the consequence of the introduction of:

- (i) new pathogens on native hosts,
- (ii) new hosts attacked by native pathogens,
- (iii) exotic pathogens on exotic hosts, and
- (iv) pathogens on off-site native hosts.

High disease incidence and severity can be reached in any of these combinations, as disease expression is generally favoured by novel host-pathogen combinations (often due to lack of co-evolution, although we may only see successful interactions, possibly also due to a file-drawer problem; Parker and Gilbert 2004; Giraud et al. 2010; Litchman 2010; Wingfield et al. 2010; Philibert et al. 2011). However, there is increasing evidence that higher ecological fitness of an exotic pathogen may cause an emergent disease (Garbelotto

et al. 2010) as predicted by the general theory of invasion biology (Parker and Gilbert 2004; Moloney et al. 2009; Blackburn et al. 2011). Whilst the dispersal of successful pathogens is typically efficient, rapid and largely unstoppable, plant hosts are traditionally fixed to their place of birth and can only slowly track climate shifts with seed (or, for some species, cutting) dispersal. There is a debate in conservation biology about the future necessity to facilitate plant dispersal by actively transferring individual plant populations so as to enable them to cope with rapid climate warming (Hunter 2007; Ricciardi and Simberloff 2009; Richardson et al. 2009; Gray et al. 2011). Such debates do not generally consider that plants can be more at risk to exotic diseases if planted in new locations. On the other hand, plant health is also at risk if the climate shifts outside of the usual physiological limits.

The disease triangle is a classic way to summarize the contributions of host, pathogen and environment in producing disease. Whilst climate change can be easily integrated in the disease triangle, given its environmental nature (Jeger and Pautasso 2008; Garrett et al. 2009; Sturrock et al. 2011), there is also a need to distinguish situations pertaining to native vs. exotic hosts and/or pathogens in such representations. Adapting the classic disease triangle to climate change and novel host-pathogen combinations is important to improve understanding and prediction of emerging plant pathosystems. Prediction is generally made difficult when novel pathogens are generalists, operate in a different climate than in their region of origin and have alternate hosts and various lifestyles. Other things being equal, a combination of natural and human spread makes prediction harder than natural spread alone (even if the latter is combined with vectors). Complexity in the genetics of the pathogen and/or host(s) does not generally help accurate prediction, although the presence of high genetic variability in the host(s) may facilitate the emergence of resistance to the exotic pathogen (which in turn often shows reduced genetic variability due to its exotic nature).

In the following, we provide four Mediterranean case studies for:

- (i) a group of exotic forest pathogens (*Phytophthora* spp., with particular focus on *P. ramorum* in California; Rizzo et al. 2005),
- (ii) a native pathogen on an exotic host (*Seiridium cardinale* on Monterey cypress planted outside

- its distributional range in California; Raddi and Panconesi 1981; Smith 2010),
- (iii) an exotic pathogen-native host combination that has the potential to become an exotic pathogen-exotic host combination in other parts of the world (*Fusarium circinatum* on *Pinus radiata* in California; Wingfield et al. 2008), and
 - (iv) a case of an exotic pathogen (*Heterobasidion irregulare*) interacting with a closely related native pathogen (*H. annosum*) in Italy (Asiegbu et al. 2005; Garbelotto et al. 2010).

P. ramorum is an emerging pathogen with a polycyclic asexual disease cycle favoured by water availability both in woodlands and plant nurseries, both in European countries and the Western USA (no sexual reproduction has been observed outside of labs yet; Parke and Lucas 2008). *S. cardinale* has caused substantial cypress mortality across the Mediterranean, Australia, Africa and California (Graniti 1986). This aggressive pathogen is favoured by warm and wet conditions, but its incidence appears to be related also to the frequency of wounds (caused by frost or other causes). In the Mediterranean, it may also have exploited the symbiotic relationship between a non-aggressive fungus (*Pestalotiopsis furea*) and a seed bug, which can colonize fungus-infected cones and contributes to its dispersal (Battisti et al. 1999). *F. circinatum* is one of the most important pathogens of *Pinus* species. It is active in the South-Eastern USA, Mexico, Chile, Haiti, Korea, South Africa, Spain, and, since 1986, California (Watt et al. 2011). Its common name, pine pitch canker, refers to the resin exuded from infected hosts, which can be affected at any stage of development and on various parts, from shoots to cones, stems and seeds (Dreaden and Smith 2010). *Heterobasidion* spp., a causal agent of root- and butt-rot, is probably the most economically damaging forest pathogen in the boreal hemisphere (La Porta et al. 2008). The disease spreads over long distances through basidiospores landing on freshly-cut stumps, and over short distances via mycelium taking advantage of root grafts of the infected stump with other trees (Korhonen and Stenlid 1998).

Native hosts and exotic pathogens (*Phytophthora* spp.)

Phytophthoras are oomycete pathogenic organisms causing a great variety of symptoms on a wide range

of host plants (Brasier and Hansen 1992; Tyler et al. 2006; Beakes et al. 2011). Our knowledge of these species is still fragmentary, suffice to say that over the last 15 years the number of known *Phytophthora* species has increased by about 40 (Érsek and Ribeiro 2010). Several Phytophthoras pose a substantial threat to native ecosystems, including *P. cinnamomi* (Cahill et al. 2008), *P. lateralis* (Hansen 2008), *P. alni* (Érsek and Nagy 2008), and *P. ramorum* (the causal agent of Sudden Oak Death in the West Coast of the USA (Hüberli and Garbelotto 2012), of Sudden Larch Death in the British Isles (Brasier and Webber 2010) and of twig dieback and leaf blight on various ornamental plants in both North America and Europe (Xu et al. 2009). For many of these species, there is a clear linkage between dispersal through plant trade pathways and subsequent impacts in natural ecosystems (Jules et al. 2002; Jung and Blaschke 2004; Husson et al. 2010; Goss et al. 2011; Moslonka-Lefebvre et al. 2011; Chadfield and Pautasso 2012).

Since it can be reasonably assumed that the likelihood of entry is proportionate to the traded volume of susceptible or potentially infected plant host material (Krcmar 2008; MacLeod et al. 2010; Marini et al. 2011), the increase over the last decades in traded plants (Dehnen-Schmutz et al. 2010; Lemmetty et al. 2011) cannot but have increased the risk of introducing *Phytophthora* species in countries where they were not yet present. Establishment and spread potentials are related to the number of introduction events, but are also limited by the presence of suitable climate and hosts. The risks of entry, establishment and, to a limited degree, spread, can be reduced by detection efforts. Detection is more difficult for those pathogens for which there is little biological and social (in terms of past management efforts) knowledge, in case of asymptomatic infective potential, and for generalist pathogens which affect many plant species, particularly if these are traded in high volumes and across the globe (Webber 2010).

As *Phytophthora* species often fulfill many of these requirements, they are thus likely troublesome pathogens. Symptoms of *Phytophthora* species are often generic and affected plants can be asymptomatic (Denman et al. 2009). Diagnosis is problematic because some Phytophthoras are hard to culture (Hayden et al. 2004), taxonomic expertise is lacking and molecular techniques need to be validated. For *P. ramorum*, there has been much progress in

developing molecular tools for rapid and accurate detection (e.g., Kong et al. 2004; Bilodeau et al. 2009; Tomlinson et al. 2010; Vettrai et al. 2010). However, given that it cannot be assumed that the latest techniques are adopted immediately by all plant phytosanitary control agents, there is still a question of how reliable real-world plant passporting schemes for this and similar pathogens are (EFSA PLH 2011; Tsopelas et al. 2011).

The non-specificity of some diagnostic tools can have in some cases some beneficial side effects, as shown by *P. ramorum* surveys which resulted in the concurrent detection of other foliar *Phytophthora* species (*P. foliorum*, *P. kernoviae*, *P. nemorosa*, *P. pseudosyringae*) (e.g. Donahoo et al. 2006; Wickland et al. 2008; Linzer et al. 2009; Moralejo et al. 2009b; Schlenzig 2011). For some of these species, subsequent study revealed low genetic diversity in their introduced range, as would be expected in case of exotic organisms, following founder effects at the introduction stage (Garbelotto 2008; Linzer et al. 2009; Grünwald and Goss 2011). For *P. lateralis*, the exotic nature in North America (suggested by its low genetic variability and high virulence) was confirmed by the finding of this species in old-growth yellow cedar (*Chamaecyparis obtusa*) forests in Taiwan (Brasier et al. 2010). Along with the other Asiatic species, this species of *Chamaecyparis* is considered more resistant to *P. lateralis* than the American cedar species, which are succumbing to the exotic disease with the exception of wilderness areas untouched by roads (Hansen 2008).

Studies of invasive *Phytophthora* species in Mediterranean ecosystems provide evidence that the overall impacts of exotic tree pathogens can be reasonably described as a function of a limited number of factors:

- the number of introduction events,
- the transmission rate of the pathogen,
- the density of susceptible/sporulating hosts,
- the favourability of climatic conditions,
- the permeability of the landscape (e.g. due to the presence of corridors linking natural habitats),
- the synchronicity between host susceptibility and pathogen life cycle, and
- the spatial variation in susceptibility of hosts.

With the exception of spatial variation in susceptibility of hosts, for all these factors there is a positive association with overall pathogen impacts. Instead, absent or reduced spatial variation in susceptibility of

hosts is likely to favour these pathogens, because the presence of resistant individuals will lead to fragmentation and, potentially, to protection of the patches of susceptible hosts (a concept which is known as herd immunity in animal epidemiology). Some of the factors will tend to interact with each other at various scales (e.g. increased host density may result in higher landscape connectivity). However, an understanding of each of these aspects of a pathosystem and of their variability across a region of interest is required for accurate prediction of potential impacts.

For *P. ramorum* on the West Coast of the USA, the magnitude of the observed impacts is likely to have been at least in part a consequence of the several independent introductions into California woodlands from nurseries (Mascheretti et al. 2009). The density of susceptible and sporulating hosts is generally high across much of coastal California, and is becoming higher due to the main sporulating host, bay laurel (*Umbellularia californica*), not being lethally affected by the pathogen (DiLeo et al. 2009). Bay laurel is instead favoured by the epidemic in tanoak (*Notholithocarpus densiflorus*) woodlands, as tanoak density is strongly reduced by the disease. The removal of a moderately sporulating and lethally affected host from the ecosystem (tanoak), and the increase in density of the host on which *P. ramorum* survives dry summers and abundantly sporulates in rainy winters and springs (bay laurel), will lead to an increased production of inoculum over time (Cobb et al. 2010). This provides an interesting counterfactual instance against the classic SIR (Susceptible-Infected-Removed) epidemiological model where disease progressively dies out by itself as susceptible hosts become infected, then die or become immune and are thus removed from the infectious compartment (Harwood et al. 2009). The presence in the *P. ramorum* woodland life-cycle (Parke and Lucas 2008) of a dead-end host is reminiscent of the life cycle of West-Nile virus and other zoonotic diseases only affecting human beings (or other mammals) as an aside (although *P. ramorum* does not infect people, it can be carried over long distances under their muddy shoes).

Current Californian climate appears to be sufficiently suitable for *P. ramorum*. This implies that the other regions blessed by Mediterranean climate (from Spain to Greece, from Chile to South Africa and Western Australia) are also at risk, particularly in the presence of susceptible and sporulating hosts - there are indeed

many such host species in the Mediterranean (Vettraino et al. 2009) and in Australia (Hüberli et al. 2009; Ireland et al. 2012). The next question is whether and how climate change is likely to affect this suitability. Whilst increased summer drought appears to be a common forecast for the future Mediterranean climate (Resco de Dios et al. 2007; Giannakopoulos et al. 2009; Johnstone and Dawson 2010), there is more uncertainty about how California's precipitations will turn out to be at the middle and end of the century (Miller et al. 2003; Maurer 2007; Battles et al. 2008). This is a key uncertainty to assess how climate change is likely to affect the *P. ramorum* epidemic, given the important role of the synchronicity between host phenology and pathogen activity in spring (Dodd et al. 2008). One aspect in predictive models that has been often overlooked (except for those pathosystems where hosts have major genes for resistance and pathogens are characterized by avirulence genes; reviewed in Parker and Gilbert 2004) is the contribution of intraspecific variation in susceptibility. A recent study (Hüberli et al. 2012) shows that the presence of highly susceptible bay laurel populations allows for dramatic SOD outbreaks even in areas that climatically are less favourable to pathogen sporulation and/or infection. This aspect will need to be considered carefully to refine predictive models (Harwood et al. 2009; Meentemeyer et al. 2011; Václavík et al. 2012).

Even if the long-term development of the landscape in terms of connectivity from the point of view of *P. ramorum* may be just as uncertain as the amount, timing and duration of spring precipitations over the course of the 21st century, it is already clear that the pathogen is able to jump from patch to patch of susceptible vegetation over distances of up to a few kilometers, probably a combination of natural and human dispersal (Mascheretti et al. 2008). Thus, it makes sense to decrease the risk posed by dispersal pathways associated with hiking, plant nurseries and other human activities. In the long-term, identifying resistant oaks is also an important strategy. But are there any *P. ramorum*-resistant oak individuals (Hayden et al. 2011)? Up to complete plot-level mortality of tanoak stems was observed in the Big Sur region (Davis et al. 2010). In Marin County, the vast majority of asymptomatic tanoaks in 2000 have been infected by *P. ramorum* in the subsequent eight years (McPherson et al. 2010). If resistance to *P. ramorum* can be found, a targeted breeding

and planting scenario may lead to a change in the *P. ramorum*-permeability of the landscape which could slow down pathogen dispersal and overall impacts. Similar programs have been advocated and are being attempted for other pathosystems such as *P. cinnamomi* on *Eucalyptus marginata* in Australia (Stukely and Crane 1994), *Cryphonectria parasitica* on *Castanea dentata* in New England (Dalglish and Swihart 2011), and Dutch Elm Disease in Mediterranean ecosystems (Santini et al. 2008). There is a question of where funding for such large-scale activities may be found, given the dwindling resources available for basic epidemiological research on this pathogen due to the widespread budget cuts.

Exotic host, native pathogen (*Seiridium cardinale*)

Seiridium cardinale is a fungal pathogen of cypress species. It was first described in California on the native *Cupressus macrocarpa* in the 1920s and now causes a potentially lethal bark canker disease on a range of cypress species worldwide (Graniti 1998). *S. cardinale* is believed to be native in California, but the question then arises of why it suddenly started to be such a serious problem there. Using an approach similar to human forensics, and assuming that the pathogen will be more genetically diverse in its native range than in its introduced range (due to founder effects; Andrivon 1996; Garbelotto 2008; Stukenbrock and McDonald 2008), it has been possible to shed light on the origin of the pathogen. California populations are indeed much more genetically diverse than European ones, and a minimum spanning network confirms that California populations are very likely to be ancestral to those found in North Africa and Europe (Della Rocca et al. 2011b). It should be noted that higher genetic variability does not necessarily translate in higher variability in adaptation: it is well known that neutral markers are suitable to reconstructing the origin of organisms, but tell us little about adaptation (Holderegger et al. 2006; Pautasso 2009; Sork and Waits 2010).

The incidence of disease caused by *S. cardinale* in California depends on cypress species, location and abundance of planted cypresses:

- Leyland cypress (an artificial ornamental tree) is heavily infected in any location,

- Monterey cypress (*C. macrocarpa*) is occasionally infected, but only in inland locations where it does not grow naturally and is always planted, and
- Italian cypress (*Cupressus sempervirens*) is occasionally infected when planted at high densities, otherwise sporadically (Della Rocca et al. 2011a).

The latter pattern is likely to be a case of density dependence: disease is only able to sustain itself when host density is above a certain threshold (Burdon and Chilvers 1982). In the case of Monterey cypress, the non-adaptation of the species to frost may make it more susceptible to the pathogen, which needs wounds in order to infect the tree (La Porta et al. 2008). Further research is needed to shed light on these issues. A similar situation is found in Trentino, a region in North-Eastern Italy where *C. sempervirens* is at its northern limit for growth (Notaro and De Salvo 2010) and where isolated trees are temporarily escaping from the disease (Zocca et al. 2008).

Exotic host and pathogen (*Fusarium circinatum*)

Pine pitch canker, caused by the fungus *Fusarium circinatum*, is one of the most important pine diseases worldwide. The geographical origin of the pathogen is thought to be Mexico and/or Southern Florida (Gordon 1996). In fact, *Pinus oocarpa*, a Mesoamerican pine species which occurs from Southern Sonora to Northern Nicaragua, is resistant against pitch canker, so that it is thought to have coevolved with the pathogen. Incidentally, this pine species shows above-average levels of genetic diversity relative to other conifers (Dvorak et al. 2009), confirming the rule that high genetic diversity tends to confer resistance to diseases, not just at the level of populations within a species, but also interspecifically (Peakall et al. 2003; Gil et al. 2004; Parker and Gilbert 2004). The pathogen was first reported in California in 1986 and has since spread both in natural ecosystems and pine plantations, causing brown-flagging of twigs, branch dieback and resin-soaked cankers (Correll et al. 1991; Garbelotto et al. 2008).

The main host in California (as well as in other regions) is Monterey pine, *Pinus radiata*, which is a key exotic tree in plantations worldwide, due to its rapid growth (Ganley et al. 2009). Although *Pinus radiata* is native in some parts of California, it is now only present in just a handful of the original

locations. The species has been planted in some other parts of California where it was not originally present, hence the use of this case study for a combination of exotic host and exotic pathogen. *F. circinatum* too is favoured by wounds created by insects, weather, or mechanical damage. The spread of pitch canker in California is thought to be dependent on insects, more as wounding factors than vectors – the pathogen is generally not able to invade intact plant tissue (Gordon et al. 2001). However, insects are not the only relevant factor for disease spread: a spore trapping study over a 12-month period showed high variability in spore densities among sampling points (Garbelotto et al. 2008). Together with the documented association of trapping frequency with temperature (negative) and rainfall (positive), this finding underlines: (i) the importance of replication with multiple trapping points in such studies, and (ii) the variability at the landscape level in pathogen propagules, which in turn can affect the regional pattern of disease severity (Holdenrieder et al. 2004).

Although pitch canker is currently mainly confined to regions with Mediterranean or subtropical climate, climate change may substantially expand the area at risk, particularly in Europe (Watt et al. 2011). In the Basque region of Spain (currently showing sub-oceanic, rather than a typical Mediterranean climate), the pathogen has been recently introduced, and is posing a serious threat to *Pinus radiata* plantations and native pine woodlands. In this region, *F. circinatum* was shown to have low genetic diversity, which suggests the existence of a newly arrived, clonally propagating pathogen population (Iturrirxa et al. 2011).

The combination of exotic host and exotic pathogen is particularly troublesome, as exotic trees may be outside of their ideal growing conditions, and exotic pathogens may have escaped controlling factors operating within their native range. However, there is no simple link between host stress and vulnerability to biotic agents. Likewise, unless recent climate change has made conditions more suitable for the exotic pathogen, it is not just the host, but also the pathogen that may be under stress given the novel situation. In summary, the case study of pine pitch canker in *Pinus radiata* plantations of California and other regions provides a good example of the enhanced susceptibility to introduced diseases of forests lacking species, functional and genetic diversity (Pautasso et al. 2005). This of course

does not rule out that introduced pathogens may be a major agent of disturbance even if forests are diverse and made up of native species, in particular in the presence of climatic changes that may enhance the transmission potential of such pathogens.

Exotic and native pathogen (*Heterobasidion irregulare* vs. *H. annosum*)

Pinus pinea (stone pine) in the Mediterranean is a further example of a genetically impoverished but widespread species (Vendramin et al. 2008). *P. pinea*, whose human dispersal throughout the Mediterranean probably goes as back as the one of *Cupressus sempervirens*, *Castanea sativa* and *Juglans regia*, is not a recent child of globalization, as *P. radiata*, but a charismatic species typical of the coastal Mediterranean landscape. What is not typical in Central Italian stone pine woodlands at the present time, is the tree mortality due to a legacy of the U.S. army World War II liberation campaign, i.e. the introduced North American fungal pathogen *Heterobasidion irregulare* (Gonthier et al. 2004, 2007). The known natural range of *H. irregulare* includes Canada (Quebec and Ontario), most of the USA and Mexico where pine hosts are present, Cuba, and the Dominican Republic (Otrosina and Garbelotto 2010).

The inadvertent introduction of *H. irregulare* at Castelporziano, Italy, probably happened via movement of infected wood (e.g. crates or latrines brought by the American troops). As a result, two phylogenetically distinct fungi, which evolved separately in North America and in Eurasia, are now in contact (Linzer et al. 2008; Otrosina and Garbelotto 2010). This sudden co-occurrence is leading to genetic exchanges between the two taxa, although the European *H. annosum* is only sporadically present in the habitat colonized by the more assertive American species (Gonthier and Garbelotto 2011). *H. irregulare* has been suggested to be ecologically more adapted to the Mediterranean climate than the European native species (D'Amico et al. 2007; Scirè et al. 2011), but pathogenicity on *Pinus sylvestris* and *Pinus pinea* appears not to differ between North American, European and introduced North American *Heterobasidion* isolates (Garbelotto et al. 2010). What really differs is the sporulation potential, much higher for the North American species during dry summers (Garbelotto et

al. 2010). This examples highlights that outbreaks of exotic pathogens can be explained by ecological/biological factors rather than by increased pathogenicity due to lack of co-evolution. Plant pathologists need to follow more closely the general theory of biological invasion in order to explain some emergent diseases, rather than uncritically relying on the concept of lack of resistance due to absence of co-evolution of pathogen and host (Parker and Gilbert 2004).

Synthesis of the four case studies

It is well known that a pathogen will invade if its transmission rate is higher than its mortality rate. In turn, the transmission rate depends on several intrinsic and extrinsic factors:

- the reproductive potential of the pathogen (including the ability to withstand disturbances, competition and/or predation),
- the dispersal ability of the pathogen,
- the density of susceptible/sporulating hosts,
- environmental and climatic factors, and
- the permeability of the landscape.

Although it is easy to conceptually understand each of these factors, it has proven difficult to properly estimate the actual transmission rate of an invasive organism, because of the varying magnitude of the trade-offs among the factors above.

In the case studies mentioned in this paper, different strategies appear to be equally advantageous to increase the invasiveness of causal agents. For example, *P. ramorum* is limited by its dispersal ability (normally 1–10 m) and by the fairly narrow conditions leading to infection (requiring at least several hours of wetness and temperatures between 15 and 22°C), but these limits are counterbalanced by the very high susceptibility of naïve hosts and by an enormous reproductive potential that allows the pathogen to achieve huge inoculum populations in a very short period of time (by repeated infection of foliar hosts within a cycle as short as 48 h). These factors make *P. ramorum* a classic r-strategy pathogen: the ability to concentrate its infection in a short period of time is a clear advantage for establishment in Mediterranean ecosystems, where rainfall is often concentrated in short spells.

On the contrary, the pine pitch canker pathogen appears to be able to sporulate and infect in less

constraining conditions, although two studies from California (Schweigkofler et al. 2004; Garbelotto et al. 2008) indicate clearly that wet and cool conditions increase sporulation levels. In many respects, *F. circinatum* is close to a K-strategy organism, with a much longer infection period. In California, a longer infection period has been counterbalanced by varying susceptibility of hosts. Hosts in their natural environment appear to be rather resistant, and it has been shown that infected trees may display signs of systemic induced resistance (Bonello et al. 2006), thus lowering the overall negative effect of the organism on tree populations. However, it is likely that an epidemic caused by the exotic *F. circinatum* on a planted exotic host (e.g., *P. radiata* in Europe or the Southern hemisphere) may be more problematic than what has been reported in California.

The case of *Seiridium cardinale* is particularly interesting. A recent study based on a genetic analysis of California and Mediterranean populations of the pathogen has shown that *S. cardinale* is likely to be native to California (Della Rocca et al. 2011b). The presence of many resistant tree species in California supports this finding, but it may appear puzzling that the first epidemic caused by *S. cardinale* was actually reported in California. A closer observation makes it clear that the California epidemic was originally reported on *C. macrocarpa* (Monterey cypress) planted in inland areas well outside of its native coastal range. In a recent survey, Garbelotto and Della Rocca (unpublished data) found that *C. macrocarpa* in its native natural range is basically unscathed by the pathogen, while it is infected when it is planted off-site in inland locations. The ornamental artificial hybrid Leyland cypress (obviously not a native plant being the result of ornamental breeding crosses) is completely susceptible to the disease, independent of site conditions. The widespread planting of Leyland cypress, desirable as an ornamental and a windbreak because of its fast growth rate, has greatly enhanced the spread of *S. cardinale* in California, and has led to an almost complete demise of this species from the market. However, Leyland cypress is still used in other parts of the world where *S. cardinale* has just been introduced (Della Rocca et al. 2011a). An immediate stop of sales of this tree species may be required in order to slow down the progression of this pathogen in such areas. An additional species that was shown to be highly susceptible to *S. cardinale* in California is *C. sempervirens* (Italian cypress): again,

this represents an exotic host in California and in the course of the survey mentioned above, a clear density-dependence factor was shown with areas characterized by high density of *C. sempervirens* also characterized by high disease incidence. In summary, it appears that of the various factors determining transmission, cypress canker takes advantage of the increased susceptibility of the host due to off-site plantings. The evidence presented here suggests that assisted migration of tree populations needs to be fine-tuned to avoid these kinds of outbreaks.

Finally, the introduction of the North American *H. irregulare* in Italy, presumably by American troops during World War II, highlights a completely different and often underestimated mechanism of invasiveness. *H. irregulare* has proven to cause substantial mortality of the widespread Mediterranean species *Pinus pinea*. This was surprising because the closely related congener *H. annosum* is already present in the area where *H. irregulare* was introduced. However, comparative studies focusing on pathogenicity and sporulation potential have indicated that the exotic species is not more virulent than the native one, but simply better adapted to sporulate in the dry Mediterranean climate. This ability has allowed the exotic pathogen to establish itself in areas only marginally occupied by its sister taxon. This last case suggests that emergent diseases are not always explained by an increased susceptibility of hosts naïve to exotic introduced organisms, but can also be due to an increased ecological fitness of exotic pathogens. In the case of the North American *H. irregulare*, increased transmission seems to be a consequence of increased sporulation and increased adaptation to dry environments, without any increased pathogenicity. This example shows that our ability to predict the behaviour of invasive plant pathogens will be improved by broadening our analysis to include both host susceptibility and general ecological fitness of introduced pathogens.

More empirical studies are needed to understand how the factors listed above will interact and result in increased (or decreased) transmission ability of potential invasive pathogens. As long as this information is not available, our predictive ability is seriously hampered. Prediction is further complicated by the forecasted rapid climate shifts. It is nonetheless clear that these and other pathogens have the potential of becoming much more damaging under novel climatic

conditions, not just in Mediterranean ecosystems (Fabre et al. 2011; Ganley et al. 2011; Raison and Khanna 2011; Rohr et al. 2011). Declining forest health, in turn, is likely to lead to diminishing ecosystem services, including the provision of water, carbon sequestration and clean air (Adams et al. 2011; Lamsal et al. 2011; Olofsson et al. 2011; Hicke et al. 2012). In the Mediterranean more than elsewhere, these processes are likely to operate through changes in forest fire regimes. There is thus a need to incorporate climate change considerations in the modelling of invasions of exotic tree pathogens, and to encourage interdisciplinary collaborations on the issue (Carnicer et al. 2011; Lemons 2011; Matías et al. 2011; Wilkinson et al. 2011).

Emerging pathosystems vs. assisted migration

The case studies presented in this overview are merely the tip of the iceberg of the emerging plant health issues in Mediterranean ecosystems (Ocasio-Morales et al. 2007; Moralejo et al. 2008, 2009a; Vacher et al. 2008; Scott et al. 2009; Greslebin and Hansen 2010; Lushaj et al. 2010). Tree health is reported to be declining from many regions of the world, including those with Mediterranean climate (Allen et al. 2010; Fischer et al. 2010), and pathogens may play a role in many of these cases. Studies of regional outbreaks of tree pathogens have focused:

- on the genetic structure of pathogen populations (e.g., *Ophiostoma ulmi* and *O. novo-ulmi* in Spain, Solla et al. 2008; *Gremmeniella abietina* in Spain, Botella et al. 2010; *Cryphonectria parasitica* in France and Switzerland, Dutech et al. 2010; Prospero and Rigling 2011; *Phytophthora pinifolia* in Chile, Durán et al. 2010),
- and on spatial patterns of host health decline and on environmental features associated with disease expression or tree mortality (e.g., cork oak (*Quercus suber*) mortality in Portugal, Costa et al. 2010; *Phytophthora cambivora* on chestnut in Italy; Vannini et al. 2010; *Abies pinsapo* decline in relic stands in Spain; Linares et al. 2010).

These approaches can provide insights as to the potential pathways of introduction and dispersal of the pathogens involved, the likely time since introduction and further impacts to be expected, as well as the

management options available to mitigate disease impacts once exotic pathogens have become established.

The case studies reviewed in this contribution combined with the many other arising plant health issues in Mediterranean ecosystems demonstrate that there is an inherent risk in the plant trade pathways across the globe as inadvertent sources of unexpected, unknown and unwanted pathogens. There is also a potential plant health issue in the making when people consciously expand plant host ranges to regions either not climatically matching the requirements of a species, or in conditions of reduced genetic diversity (due to monocultures, plantations, founder effects). Obviously, when the two patterns co-occur (introduction of exotic pathogens and of exotic hosts), then we have to “expect the unexpected” (Webber 2010), or predict unpredictability. The problem is further complicated by the recent realization that artificial expansion of the range of many plant species could well be a necessary mid-term strategy to make it possible for plant species with low dispersal potential to track the predicted rapid climate shifts (McLachlan et al. 2007; Hoegh-Guldberg et al. 2008; Pautasso et al. 2010; Seddon 2010; Loss et al. 2011; McLane and Aitken 2011; Weeks et al. 2011).

The threat posed by emergent forest pathogens may be reduced: (i) by lowering the likelihood of introduction, (ii) by limiting the probability that people will contribute to pathogen dispersal, (iii) by decreasing the vulnerability of ecosystems (e.g., by maintaining high levels of biodiversity at the regional, interspecific and genetic level), and (iv) by mitigating impacts once pathogens are established (e.g., by focusing on inoculum reduction strategies at particularly important sites). We argue here that these considerations need to be taken into account when devising assisted migration programmes, otherwise we risk to end up in replicating throughout the planet the Sudden Oak/Larch Death experience whilst trying to save biodiversity from climate change.

Acknowledgements Many thanks to C. Brasier, M.I. Clara, K. Dehnen-Schmutz, S. Frankel, P. Gonthier, E. Hansen, J. Hayden, O. Holdenrieder, M. Jeger, V. Kertesz, C. Manceau, S. Mascheretti, M. Moslonka-Lefebvre, G. Nicolotti, J. Parke, S. Prospero, T. Rafoss, D. Rizzo, S. Tramontini, A. Vannini, A. Vettraino, S. Vos, X. Xu, J. Webber for insights and discussions, and to T. Matoni and anonymous reviewers for helpful comments on a previous draft. This review is based on a presentation by M. Garbelotto at the Climate Change and Plant Disease Management Conference, University of Evora, Portugal, 10–12 November 2010.

References

- Adams, H. D., Luce, C. H., Breshears, D. D., Allen, C. D., Weiler, M., Hale, V. C., Smith, A. M. S., & Huxman, T. E. (2011). Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. *Ecohydrology*, in press doi:10.1002/eco.233
- Allen, C. D., Macalady, A. K., Chenchouni, H., et al. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660–684. doi:10.1016/j.foreco.2009.09.001.
- Anderson, P. K., Cunningham, A. A., Patel, N. G., Morales, F. J., Epstein, P. R., & Daszak, P. (2004). Emerging infectious diseases of plants: Pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution*, 19, 535–544. doi:10.1016/j.tree.2004.07.021.
- Andrivon, D. (1996). The origin of *Phytophthora infestans* populations present in Europe in the 1840s: A critical review of historical and scientific evidence. *Plant Pathology*, 45, 1027–1035. doi:10.1046/j.1365-3059.1996.d01196.x.
- Araújo, M. B. (2003). The coincidence of people and biodiversity in Europe. *Global Ecology and Biogeography*, 12, 5–12. doi:10.1046/j.1466-822X.2003.00314.x.
- Arianoutsou, M., Bazos, I., Delipetrou, P., & Kokkoris, T. (2010). The alien flora of Greece: taxonomy, life traits and habitat preferences. *Biological Invasions*, 12, 3525–3549. doi:10.1007/s10530-010-9749-0.
- Asiegbu, F. O., Adomas, A., & Stenlid, J. (2005). Conifer root and butt rot caused by *Heterobasidion annosum* (Fr.) Bref. s.l. *Molecular Plant Pathology*, 6, 395–409.
- Aukema, J. E., McCullough, D. G., Von Holle, B., Liebhold, A. M., Britton, K., & Frankel, S. J. (2010). Historical accumulation of nonindigenous forest pests in the continental United States. *BioScience*, 60, 886–897. doi:10.1525/bio.2010.60.11.5.
- Battisti, A., Roques, A., Colombari, F., Frigimelica, G., & Guido, M. (1999). Efficient transmission of an introduced pathogen via an ancient insect-fungus association. *Naturwissenschaften*, 86, 479–483. doi:10.1007/s001140050658.
- Battles, J. J., Robards, T., Das, A., Waring, K., Gillies, J. K., Biging, G., et al. (2008). Climate change impacts on forest growth and tree mortality: A data-driven modeling study in the mixed-conifer forest of the Sierra Nevada, California. *Climatic Change*, 87, 193–231. doi:10.1007/s10584-007-9358-9.
- Beakes, G. W., Glockling, S. L., & Sekimoto, S. (2011). The evolutionary phylogeny of the oomycete “fungi.” *Proto-plasma*, in press doi:10.1007/s00709-011-0269-2
- Bilodeau, G., Pelletier, G., Pelletier, F., Lévesque, C., & Hamelin, R. C. (2009). Multiplex real-time polymerase chain reaction (PCR) for detection of *Phytophthora ramorum*, the causal agent of sudden oak death. *Canadian Journal of Plant Pathology*, 31, 195–210.
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., et al. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, 26, 333–339. doi:10.1016/j.tree.2011.03.023.
- Blondel, J., & Aronson, J. (1995). Biodiversity and ecosystem function in the Mediterranean Basin. Human and non-human determinants. In G. W. Davis & D. M. Richardson (Eds.), *Mediterranean-type ecosystems. The function of biodiversity* (pp. 43–119). Berlin: Springer.
- Bonello, P., Gordon, T. R., Herms, D. A., Wood, D. L., & Erbiling, N. (2006). Nature and ecological implications of pathogen-induced systemic resistance in conifers: A novel hypothesis. *Physiological and Molecular Plant Pathology*, 68, 95–104. doi:10.1016/j.pmpp.2006.12.002.
- Botella, L., Tuomivirta, T. T., Kaitera, J., Carrasco Navarro, V., Diez, J. J., & Hantula, J. (2010). Spanish population of *Gremmeniella abietina* is genetically unique but related to type A in Europe. *Fungal Biology*, 114, 778–789. doi:10.1016/j.funbio.2010.07.003.
- Brasier, C. M. (2008). The biosecurity threat to the UK and global environment from international trade in plants. *Plant Pathology*, 57, 792–808. doi:10.1111/j.1365-3059.2008.01886.x.
- Brasier, C. M., & Hansen, E. M. (1992). Evolutionary biology of *Phytophthora*. Part II: Phylogeny, speciation, and population structure. *Annual Review of Phytopathology*, 30, 173–200. doi:10.1146/annurev.py.30.090192.001133.
- Brasier, C., & Webber, J. (2010). Sudden larch death. *Nature*, 466, 824–825. doi:10.1038/466824a.
- Brasier, C. M., Vettraino, A. M., Chang, T. T., & Vannini, A. (2010). *Phytophthora lateralis* discovered in an old growth *Chamaecyparis* forest in Taiwan. *Plant Pathology*, 59, 595–603. doi:10.1111/j.1365-3059.2010.02278.x.
- Burdon, J. J., & Chilvers, G. A. (1982). Host density as a factor in plant disease ecology. *Annual Review of Phytopathology*, 20, 143–166. doi:10.1146/annurev.py.20.090182.001043.
- Cahill, D. M., Rookes, J. E., Wilson, B. A., Gibson, L., & McDougall, K. L. (2008). *Phytophthora cinnamomi* and Australia's biodiversity: Impacts, predictions and progress towards control. *Australian Journal of Botany*, 56, 279–310. doi:10.1071/BT07159.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., & Peñuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences USA*, 108, 1474–1478. doi:10.1073/pnas.1010070108.
- Chadfield, V., & Pautasso, M. (2012). *Phytophthora ramorum* in England and Wales: which environmental variables predict county disease incidence? *Forest Pathology*, in press doi:10.1111/j.1439-0329.2011.00735.x
- Cobb, R. C., Meentemeyer, R. K., & Rizzo, D. M. (2010). Apparent competition in canopy trees determined by pathogen transmission rather than susceptibility. *Ecology*, 91, 327–333. doi:10.1890/09-0680.1.
- Correll, J. C., Gordon, T. R., McCain, A. H., Fox, J. W., Koehler, C. S., Wood, D. L., et al. (1991). Pitch canker disease in California: Pathogenicity, distribution and canker development on Monterey pine (*Pinus radiata*). *Plant Disease*, 75, 676–682. doi:10.1094/PD-75-0676.
- Costa, A., Pereira, H., & Madeira, M. (2010). Analysis of spatial patterns of oak decline in cork oak woodlands in Mediterranean conditions. *Annals of Forest Science*, 67, 204. doi:10.1051/forest/2009097.

- Cowling, R. M., Rundel, P. W., Lamont, B. B., Arroyo, M. K., & Arianoutsou, M. (1996). Plant diversity in Mediterranean-climate regions. *Trends in Ecology & Evolution*, *11*, 362–366. doi:10.1016/0169-5347(96)10044-6.
- Cox, R. L., & Underwood, E. C. (2011). The importance of conserving biodiversity outside of protected areas in Mediterranean ecosystems. *PLoS One*, *6*, e14508. doi:10.1371/journal.pone.0014508.
- D'Amico, L., Motta, E., Annesi, T., Scirè, M., Luchi, N., Hantula, J., et al. (2007). The North American P group of *Heterobasidion annosum* s.l. is widely distributed in *Pinus pinea* forests of the western coast of central Italy. *Forest Pathology*, *37*, 303–320. doi:10.1111/j.1439-0329.2007.00501.x.
- Dalgleish, H. J., & Swihart, R. K. (2011). American chestnut past and future: Implications of restoration for resource pulses and consumer populations of Eastern U.S. Forests. *Restoration Ecology*, in press doi:10.1111/j.1526-100X.2011.00795.x
- Davis, F. W., Borchert, M., Meentemeyer, R. K., Flint, A., & Rizzo, D. M. (2010). Pre-impact forest composition and ongoing tree mortality associated with sudden oak death in the Big Sur region, California. *Forest Ecology and Management*, *259*, 2342–2354. doi:10.1016/j.foreco.2010.03.007.
- Dehnen-Schmutz, K., Holdenrieder, O., Jeger, M. J., & Pautasso, M. (2010). Structural change in the international horticultural industry: Some implications for plant health. *Scientia Horticulturae*, *125*, 1–15. doi:10.1016/j.scienta.2010.02.017.
- Della Rocca, G., Danti, R., & Garbelotto, M. (2011a). First report of *Seiridium unicorne* causing bark cankers on a Monterey cypress in California. *Plant Disease*, *95*, 619. doi:10.1094/PDIS-01-11-0052.
- Della Rocca, G., Eyre, C., Danti, R., & Garbelotto, M. (2011b). Sequence and SSR analyses of the fungal pathogen *Seiridium cardinale* indicate California is the most likely source of the Cypress canker epidemic for the Mediterranean region. *Phytopathology*, *101*, 1408–1417. doi:10.1094/PHYTO-05-11-0144.
- Denman, S., Kirk, S. A., Moralejo, E., & Webber, J. F. (2009). *Phytophthora ramorum* and *P. kernoviae* on naturally infected asymptomatic foliage. *EPPO Bulletin*, *39*, 105–111. doi:10.1111/j.1365-2338.2009.02243.x.
- DiLeo, M. V., Bostock, R. M., & Rizzo, D. M. (2009). *Phytophthora ramorum* does not cause physiologically significant systemic injury to California bay laurel, its primary reservoir host. *Phytopathology*, *99*, 1307–1311. doi:10.1094/PHYTO-99-11-1307.
- Dodd, R. S., Hüberli, D., Mayer, W., Harnik, T. Y., Afzal-Rafii, Z., & Garbelotto, M. (2008). Evidence for the role of synchronicity between host phenology and pathogen activity in the distribution of sudden oak death canker disease. *New Phytologist*, *165*, 203–214. doi:10.1111/j.1469-8137.2008.02450.x.
- Donahoo, R., Blomquist, C. L., Thomas, S. L., Moulton, J. K., Cooke, D. E. L., & Lamour, K. H. (2006). *Phytophthora foliorum* sp. nov., a new species causing leaf blight of azalea. *Mycological Research*, *110*, 1309–1322. doi:10.1016/j.mycres.2006.07.017.
- Dreaden, T., & Smith, J. (2010). Pitch canker disease of pines. FOR236, School of Forest Resources and Conservation, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida. Accessed August 2011 at <http://edis.ifas.ufl.edu/fr298>
- Durán, A., Gryzenhout, M., Drenth, A., Slippers, B., Ahumada, R., Wingfield, B. D., et al. (2010). AFLP analysis reveals a clonal population of *Phytophthora pinifolia* in Chile. *Fungal Biology*, *114*, 746–752. doi:10.1016/j.funbio.2010.06.008.
- Dutech, C., Fabreguettes, O., Capdevielle, X., & Robin, C. (2010). Multiple introductions of divergent genetic lineages in an invasive fungal pathogen, *Cryphonectria parasitica*, in France. *Heredity*, *105*, 220–228. doi:10.1038/hdy.2009.164.
- Dvorak, W. S., Potter, K. M., Hipkins, V. D., & Hodge, G. R. (2009). Genetic diversity and gene exchange in *Pinus oocarpa*, a mesoamerican pine with resistance to the pitch canker fungus (*Fusarium circinatum*). *International Journal of Plant Science*, *170*, 609–626. doi:10.1086/597780.
- EFSA Panel on Plant Health (PLH). (2011). Scientific opinion on the pest risk analysis on *Phytophthora ramorum* prepared by the FP6 project RAPRA. *EFSA Journal*, *9*(2186). doi:10.2903/j.efsa.2011.2186.
- Érsek, T., & Nagy, Z. A. (2008). Species hybrids in the genus *Phytophthora* with emphasis on the alder pathogen *Phytophthora alni*: a review. *European Journal of Plant Pathology*, *122*, 31–39. doi:10.1007/s10658-008-9296-z.
- Érsek, T., & Ribeiro, O. K. (2010). An annotated list of new *Phytophthora* species described post 1996. *Acta Phytopathologica et Entomologica Hungarica*, *45*, 251–266. doi:10.1556/APhyt.45.2010.2.2.
- Fabre, B., Piou, D., Desprez-Loustau, M.-L., & Marçais, B. (2011). Can the emergence of pine Diplodia shoot blight in France be explained by changes in pathogen pressure linked to climate change? *Global Change Biology*, *17*, 3218–3227. doi:10.1111/j.1365-2486.2011.02428.x.
- Fischer, J., Zenger, A., Gibbons, P., Stott, J., & Law, B. S. (2010). Tree decline and the future of Australian farmland biodiversity. *Proceedings of the National Academy of Sciences USA*, *107*, 19597–19602. doi:10.1073/pnas.1008476107.
- Ganley, R. J., Watt, M. S., Manning, L., & Iturriza, E. (2009). A global climatic risk assessment of pitch canker disease. *Canadian Journal of Forest Research*, *39*, 2246–2256. doi:10.1139/X09-131.
- Ganley, R. J., Watt, M. S., Kriticos, D. J., Hopkins, A. J. M., & Manning, L. J. (2011). Increased risk of pitch canker to Australasia under climate change. *Australasian Plant Pathology*, *40*, 228–237. doi:10.1007/s13313-011-0033-2.
- Garbelotto, M. (2008). Molecular analysis to study invasions by forest pathogens: Examples from Mediterranean ecosystems. *Phytopathologia Mediterranea*, *47*, 183–203.
- Garbelotto, M., Smith, T., & Schweigkofler, W. (2008). Variation of spore dispersal of *Fusarium circinatum*, the causal agent of pine pitch canker, over a 12-month period at two locations in Northern California. *Phytopathology*, *98*, 137–143. doi:10.1094/PHYTO-98-1-0137.
- Garbelotto, M., Linzer, L., Nicolotti, G., & Gonthier, P. (2010). Comparing the influences of ecological and evolutionary factors on the successful invasion of a fungal forest pathogen. *Biological Invasions*, *12*, 943–957. doi:10.1007/s10530-009-9514-4.
- Garrett, K. A., Nita, M., De Wolf, E. D., Gomez, L., & Sparks, A. H. (2009). Plant pathogens as indicators of climate

- change. In T. Letcher (Ed.), *Climate change: Observed impacts on planet earth* (pp. 425–437). Dordrecht: Elsevier.
- Giannakopoulos, C., Le Sager, P., Bindi, M., Moriondo, M., Kostopoulou, E., & Goodess, C. M. (2009). Climatic changes and associated impacts in the Mediterranean resulting from a 2°C global warming. *Global and Planetary Change*, *68*, 209–224. doi:10.1016/j.gloplacha.2009.06.001.
- Gil, L., Fuentes-Utrilla, P., Soto, A., Cervera, M. T., & Collada, C. (2004). English elm is a 2,000-year-old Roman clone. *Nature*, *431*, 1053. doi:10.1038/4311053a.
- Giraud, T., Gladieux, P., & Gavrillets, S. (2010). Linking the emergence of fungal plant diseases with ecological speciation. *Trends in Ecology & Evolution*, *25*, 387–395. doi:10.1016/j.tree.2010.03.006.
- Gonthier, P., & Garbelotto, M. (2011). Amplified fragment length polymorphism and sequence analyses reveal massive gene introgression from the European fungal pathogen *Heterobasidion annosum* into its introduced congener *H. irregulare*. *Molecular Ecology*, *20*, 2756–2770. doi:10.1111/j.1365-294X.2011.05121.x.
- Gonthier, P., Wamer, R., Nicolotti, G., Mazzaglia, A., & Garbelotto, M. M. (2004). Pathogen introduction as a collateral effect of military activity. *Mycological Research*, *108*, 468–470. doi:10.1017/S0953756204240369.
- Gonthier, P., Nicolotti, G., Linzer, R., Guglielmo, F., & Garbelotto, M. (2007). Invasion of European pine stands by a North American forest pathogen and its hybridization with a native interfertile taxon. *Molecular Ecology*, *16*, 1389–1400. doi:10.1111/j.1365-294X.2007.03250.x.
- Gordon, T. R. (1996). Pitch canker disease of pines. *Phytopathology*, *96*, 657–659. doi:10.1094/phyto-96/0657.
- Gordon, T. R., Storer, A. J., & Wood, D. L. (2001). The pitch canker epidemic in California. *Plant Disease*, *85*, 1128–1139. doi:10.1094/PDIS.2001.85.11.1128.
- Goss, E. M., Larsen, M., Vercauteren, A., Werres, S., Heungens, K., & Grünwald, N. J. (2011). *Phytophthora ramorum* in Canada: Evidence for migration within North America and from Europe. *Phytopathology*, *101*, 166–171. doi:10.1094/PHYTO-05-10-0133.
- Graniti, A. (1986). *Seiridium cardinale* and other cypress cankers. *EPPO Bulletin*, *16*, 479–486. doi:10.1111/j.1365-2338.1986.tb00309.x.
- Graniti, A. (1998). Cypress canker: A pandemic in progress. *Annual Review of Phytopathology*, *36*, 91–114. doi:10.1146/annurev.phyto.36.1.91.
- Gray, L., Gylander, T., Mbogga, M., Chen, P. Y., & Hamann, A. (2011). Assisted migration to address climate change: Recommendations for aspen reforestation in western Canada. *Ecological Applications*, *21*, 1591–1603. doi:10.1890/10-1054.1.
- Greslebin, A. G., & Hansen, E. M. (2010). Pathogenicity of *Phytophthora austrocedrae* on *Austrocedrus chilensis* and its relation with mal del ciprés in Patagonia. *Plant Pathology*, *59*, 604–612. doi:10.1111/j.1365-3059.2010.02258.x.
- Grünwald, N. J., & Goss, E. (2011). Evolution and population genetics of exotic and re-emerging pathogens: Novel tools and approaches. *Annual Review of Phytopathology*, *49*, 249–267. doi:10.1146/annurev-phyto-072910-095246.
- Hansen, E. M. (2008). Alien forest pathogens: *Phytophthora* species are changing world forests. *Boreal Environment Research*, *13*, 33–41.
- Harwood, T. D., Xu, X. M., Pautasso, M., Jeger, M. J., & Shaw, M. (2009). Epidemiological risk assessment using linked network and grid based modelling: *Phytophthora ramorum* and *Phytophthora kernoviae* in the UK. *Ecological Modelling*, *220*, 3353–3361. doi:10.1016/j.ecolmodel.2009.08.014.
- Hayden, K. J., Rizzo, D., Tse, J., & Garbelotto, M. (2004). Detection and quantification of *Phytophthora ramorum* from California forests using a real-time polymerase chain reaction assay. *Phytopathology*, *94*, 1075–1083. doi:10.1094/PHYTO.2004.94.10.1075.
- Hayden, K. J., Nettel, A., Dodd, R. S., & Garbelotto, M. (2011). Will all the trees fall? Variable resistance to an introduced forest disease in a highly susceptible host. *Forest Ecology and Management*, *261*, 1781–1791. doi:10.1016/j.foreco.2011.01.042.
- Hicke, J. A., Allen, C. D., Desai, A. R., Dietze, M. C., Hall, R. J., Hogg, E. H., et al. (2012). Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology*, in press doi:10.1111/j.1365-2486.2011.02543.x.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D. B., Parmesan, C., Possingham, H. P., et al. (2008). Assisted colonization and rapid climate change. *Science*, *321*, 345–346. doi:10.1126/science.1157897.
- Holdenrieder, O., Pautasso, M., Weisberg, P. J., & Lonsdale, D. (2004). Tree diseases and landscape processes: The challenge of landscape pathology. *Trends in Ecology & Evolution*, *19*, 446–452. doi:10.1016/j.tree.2004.06.003.
- Holderegger, R., Kamm, U., & Gugerli, F. (2006). Adaptive vs. neutral genetic diversity: Implications for landscape genetics. *Landscape Ecology*, *21*, 797–807. doi:10.1007/s10980-005-5245-9.
- Hüberli, D., & Garbelotto, M. (2012). *Phytophthora ramorum* is a generalist plant pathogen with differences in virulence between isolates from infectious and dead-end hosts. *Forest Pathology*, in press doi:10.1111/j.1439-0329.2011.00715.x.
- Hüberli, D., Ireland, K., Smith, I., Dell, B., Ormsby, M., Rizzo, D., et al. (2009). Australasia is at high risk of a *Phytophthora ramorum* epidemic. In: *Phytophthoras in Forests and Natural Ecosystems*. Proceedings of the Fourth Meeting of IUFRO Working Party S07.02.09, PSW-GTR-221, pp. 184–187.
- Hüberli, D., Hayden, K. J., Calver, M., & Garbelotto, M. (2012). Intraspecific variation in host susceptibility and climatic factors mediate epidemics of sudden oak death in western US forests. *Plant Pathology*, in press. doi:10.1111/j.1365-3059.2011.02535.x.
- Hunter, M. L. (2007). Climate change and moving species: Furthering the debate on assisted colonization. *Conservation Biology*, *21*, 1356–1358. doi:10.1111/j.1523-1739.2007.00780.x.
- Husson, C., Halkett, F., & Marçais, B. (2010). A statistical model to detect asymptomatic infectious individuals with an application in the *Phytophthora alni*-induced alder decline. *Phytopathology*, *100*, 1262–1269. doi:10.1094/PHYTO-05-10-0140.
- Ireland, K. B., Hüberli, D., Dell, B., Smith, I. W., Rizzo, D. M., & Hardy, G. E. St. J. (2012). Potential susceptibility of Australian native plant species to branch dieback and bole

- canker diseases caused by *Phytophthora ramorum*. *Plant Pathology*, in press doi:10.1111/j.1365-3059.2011.02513.x
- Iturrutxa, E., Ganley, R. J., Wright, J., Heppe, E., Steenkamp, E. T., Gordon, T. R., et al. (2011). A genetically homogenous population of *Fusarium circinatum* causes pitch canker of *Pinus radiata* in the Basque Country, Spain. *Fungal Biology*, 115, 288–295. doi:10.1016/j.funbio.2010.12.014.
- Jeger, M. J., & Pautasso, M. (2008). Plant disease and global change – the importance of long-term data sets. *New Phytologist*, 177, 8–11. doi:10.1111/j.1469-8137.2007.02312.x.
- Johnstone, J. A., & Dawson, T. E. (2010). Climatic context and ecological implications of summer fog decline in the coast redwood region. *Proceedings of the National Academy of Sciences USA*, 107, 4533–4538. doi:10.1073/pnas.0915062107.
- Jules, E. S., Kauffman, M. J., Ritts, D. R., & Carrol, A. L. (2002). Spread of an invasive pathogen over a variable landscape: A non native root rot on Port Orford Cedar. *Ecology*, 83, 3167–3181. doi:10.1890/0012-9658(2002)083[3167:SOAIPO]2.0.CO;2.
- Jung, T., & Blaschke, M. (2004). *Phytophthora* root and collar rot of alders in Bavaria: Distribution, modes of spread, and possible management strategies. *Plant Pathology*, 53, 197–208. doi:10.1111/j.0032-0862.2004.00957.x.
- Kong, P., Hong, C. X., Tooley, P. W., Ivors, K., Garbelotto, M., & Richardson, P. A. (2004). Rapid identification of *Phytophthora ramorum* using PCR-SSCP analysis of ribosomal DNA ITS-1. *Letters in Applied Microbiology*, 38, 433–439. doi:10.1111/j.1472-765x.2004.01510.x.
- Korhonen, K., & Stenlid, J. (1998). Biology of *Heterobasidion annosum*. In S. Woodward, J. Stenlid, R. Karjalainen, & A. Hüttermann (Eds.), *Heterobasidion annosum: Biology, ecology, impact and control* (pp. 43–70). Wallingford: CAB International.
- Krcmar, E. (2008). An examination of the threats and risks to forests arising from invasive alien species. Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.
- La Porta, N., Capretti, P., Thomsen, I. M., Kasanen, R., Hietala, A. M., & Von Weissenberg, K. (2008). Forest pathogens with higher damage potential due to climate change in Europe. *Canadian Journal of Plant Pathology*, 30, 177–195.
- Lamsal, S., Cobb, R. C., Cushman, J. H., Meng, Q., Rizzo, D. M., & Meentemeyer, R. K. (2011). Spatial estimation of the density and carbon content of host populations for *Phytophthora ramorum* in California and Oregon. *Forest Ecology and Management*, 262, 989–998. doi:10.1016/j.foreco.2011.05.033.
- Lavorel, S., Canadell, J., Rambal, S., & Terradas, J. (1998). Mediterranean terrestrial ecosystems: Research priorities on global change effects. *Global Ecology and Biogeography Letters*, 7(3), 157–166.
- Lemmetty, A., Laamanen, J., Soukainen, M., & Tegel, J. (2011). Emerging virus and viroid pathogen species identified for the first time in horticultural plants in Finland in 1997–2010. *Agricultural and Food Science*, 20, 29–41. doi:10.2137/145960611795163060.
- Lemons, J. (2011). The urgent need for Universities to comprehensively address global climate change across disciplines and programs. *Environmental Management*, 48, 379–391. doi:10.1007/s00267-011-9699-z.
- Linares, J. C., Camarero, J. J., & Carreira, J. A. (2010). Competition modulates the adaptation capacity of forests to climatic stress: Insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *Journal of Ecology*, 98, 592–603. doi:10.1111/j.1365-2745.2010.01645.x.
- Linzer, R. E., Otrrosina, W. J., Gonthier, P., Bruhn, J., Laflamme, G., Bussi eres, G., et al. (2008). Inferences on the phylogeography of the fungal pathogen *Heterobasidion annosum*, including evidence of interspecific horizontal genetic transfer and of human-mediated, long-range dispersal. *Molecular Phylogenetics and Evolution*, 46, 844–862. doi:10.1016/j.ympev.2007.12.010.
- Linzer, R. E., Rizzo, D. M., Cacciola, S. O., & Garbelotto, M. (2009). AFLPs detect low genetic diversity for *Phytophthora nemorosa* and *P. pseudosyringae* in the US and Europe. *Mycological Research*, 113, 298–307. doi:10.1016/j.mycres.2008.11.004.
- Litchman, E. (2010). Invisible invaders: Non-pathogenic invasive microbes in aquatic and terrestrial ecosystems. *Ecology Letters*, 13, 1560–1572. doi:10.1111/j.1461-0248.2010.01544.x.
- Loo, J. A. (2009). Ecological impacts of non-indigenous invasive fungi as forest pathogens. *Biological Invasions*, 11, 81–96. doi:10.1007/s10530-008-9321-3.
- Loss, S. R., Terwilliger, L. A., & Peterson, A. C. (2011). Assisted colonization: Integrating conservation strategies in the face of climate change. *Biological Conservation*, 144, 92–100. doi:10.1016/j.biocon.2010.11.016.
- Lushaj, B. M., Woodward, S., Ke a, N., & Intini, M. (2010). Distribution, ecology and host range of *Armillaria* species in Albania. *Forest Pathology*, 40, 485–499. doi:10.1111/j.1439-0329.2009.00624.x.
- MacLeod, A., Pautasso, M., Jeger, M. J., & Haines-Young, R. (2010). Evolution of the international regulation of plant pests and challenges for future plant health. *Food Security*, 2, 49–70. doi:10.1007/s12571-010-0054-7.
- Marini, L., Haack, R. A., Rabaglia, R. J., Toffolo, E. P., Battisti, A., & Faccoli, M. (2011). Exploring associations between international trade and environmental factors with establishment patterns of exotic Scolytinae. *Biological Invasions*, 13, 2275–2288. doi:10.1007/s10530-011-0039-2.
- Mascheretti, S., Croucher, P., Vettrano, A., Prospero, S., & Garbelotto, M. (2008). Reconstruction of the sudden oak death epidemic in California through microsatellite analysis of the pathogen *Phytophthora ramorum*. *Molecular Ecology*, 17, 2755–2768. doi:10.1111/j.1365-294X.2008.03773.x.
- Mascheretti, S., Croucher, P. J. P., Kozanitas, M., Baker, L., & Garbelotto, M. (2009). Genetic epidemiology of the Sudden Oak Death pathogen *Phytophthora ramorum* in California. *Molecular Ecology*, 18, 4577–4590. doi:10.1111/j.1365-294X.2009.04379.x.
- Mat as, L., Zamora, R., & Castro, J. (2011). Repercussions of simulated climate change on the diversity of woody-recruit bank in a Mediterranean-type ecosystem. *Ecosystems*, 14, 672–682. doi:10.1007/s10021-011-9437-7.
- Maurer, E. P. (2007). Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. *Climatic Change*, 82, 309–325. doi:10.1007/s10584-006-9180-9.

- McLachlan, J. S., Hellmann, J. J., & Schwartz, M. W. (2007). A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, *21*, 297–302. doi:10.1111/j.1523-1739.2007.00676.x.
- McLane, S., & Aitken, S. (2011). Whitebark pine (*Pinus albicaulis*) assisted migration potential: testing establishment north of the species range. *Ecological Applications*, in press doi:10.1890/11-0329.1
- McPherson, B. A., Mori, S. R., Wood, D. L., Kelly, M., Storer, A. J., Svihra, P., et al. (2010). Responses of oaks and tanoaks to the sudden oak death pathogen after 8 y of monitoring in two coastal California forests. *Forest Ecology and Management*, *259*, 2248–2255. doi:10.1016/j.foreco.2010.02.020.
- Médail, F., & Quézel, P. (1999). Biodiversity hotspots in the Mediterranean basin: setting global conservation priorities. *Conservation Biology*, *13*, 1510–1513. doi:10.1046/j.1523-1739.1999.98467.x.
- Meentemeyer, R. K., Cunniffe, N. J., Cook, A. R., Filipe, J. A. N., Hunter, R. D., Rizzo, D. M., et al. (2011). Epidemiological modeling of invasion in heterogeneous landscapes: Spread of sudden oak death in California (1990–2030). *Ecosphere*, *2*, 17. doi:10.1890/ES10-00192.1.
- Miller, N. L., Bashford, K. E., & Strem, E. (2003). Potential impacts of climate change on California hydrology. *JAWRA Journal of the American Water Resources Association*, *39*, 771–784. doi:10.1111/j.1752-1688.2003.tb04404.x.
- Moloney, K. A., Holzapfel, C., Tielbörger, K., Jeltsch, F., & Schurr, F. M. (2009). Rethinking the common garden in invasion research. *Perspectives in Plant Ecology, Evolution and Systematics*, *11*, 311–320. doi:10.1016/j.ppees.2009.05.002.
- Mooney, H. A., & Dunn, E. L. (1970). Convergent evolution of Mediterranean-climate evergreen sclerophyll shrubs. *Evolution*, *24*(2), 292–303.
- Mooney, H. A., Arroyo, M. T. K., Bond, W. J., Canadell, J., Hobbs, R. J., Lavorel, S., et al. (2001). Mediterranean-climate ecosystems. In: global biodiversity in a changing environment. *Ecological Studies*, *152*, 157–199. doi:10.1007/978-1-4613-0157-8_9.
- Moralejo, E., Belbahri, L., Calmin, G., García-Muñoz, J. A., Lefort, F., & Descals, E. (2008). Strawberry tree blight in Spain, a new disease caused by various *Phytophthora* species. *Journal of Phytopathology*, *156*, 577–587. doi:10.1111/j.1439-0434.2008.01397.x.
- Moralejo, E., García-Muñoz, J. A., & Descals, E. (2009a). Susceptibility of Iberian trees to *Phytophthora ramorum* and *P. cinnamomi*. *Plant Pathology*, *58*, 271–283. doi:10.1111/j.1365-3059.2008.01956.x.
- Moralejo, E., Perez-Sierra, A. M., Alvarez, L. A., Belbahri, L., Lefort, F., & Descals, E. (2009b). Multiple alien *Phytophthora* taxa discovered on diseased ornamental plants in Spain. *Plant Pathology*, *58*, 100–110. doi:10.1111/j.1365-3059.2008.01930.x.
- Moslonka-Lefebvre, M., Finley, A., Dorigatti, I., Dehnen-Schmutz, K., Harwood, T., Jeger, M. J., et al. (2011). Networks in plant epidemiology: From genes to landscapes, countries and continents. *Phytopathology*, *101*, 392–403. doi:10.1094/PHYTO-07-10-0192.
- Notaro, S., & De Salvo, M. (2010). Estimating the economic benefits of the landscape function of ornamental trees in a sub-Mediterranean area. *Urban Forestry & Urban Greening*, *9*, 71–81. doi:10.1016/j.ufug.2009.09.001.
- Ocasio-Morales, R. G., Tsopeles, P., & Harrington, T. C. (2007). Origin of *Ceratocystis platani* on native *Platanus orientalis* in Greece and its impact on natural forests. *Plant Disease*, *91*, 901–904. doi:10.1094/PDIS-91-7-0901.
- Olofsson, J., Ericson, L., Torp, M., Stark, S., & Baxter, R. (2011). Carbon balance of Arctic tundra under increased snow cover mediated by a plant pathogen. *Nature Climate Change*, *1*, 220–223. doi:10.1038/nclimate1142.
- Otrosina, W. J., & Garbelotto, M. (2010). *Heterobasidion occidentale* sp. nov. and *Heterobasidion irregulare* nom. nov.: A disposition of North American *Heterobasidion* biological species. *Fungal Biology*, *114*, 16–25. doi:10.1016/j.mycres.2009.09.001.
- Parke, J. L., & Lucas, S. (2008). Sudden oak death and ramorum blight. The Plant Health Instructor, accessed March 2011, available online at: <http://www.apsnet.org/edcenter/intropp/lessons/fungi/Oomycetes/Pages/SuddenOakDeath.aspx>
- Parker, I. M., & Gilbert, G. S. (2004). The evolutionary ecology of novel plant-pathogen interactions. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 675–700. doi:10.1146/annurev.ecolsys.34.011802.132339.
- Pautasso, M. (2009). Geographical genetics and the conservation of forest trees. *Perspectives in Plant Ecology, Systematics and Evolution*, *11*, 157–189. doi:10.1016/j.ppees.2009.01.003.
- Pautasso, M., Holdenrieder, O., & Stenlid, J. (2005). Susceptibility to fungal pathogens of forests differing in tree diversity. In M. Scherer-Lorenzen, Ch Koerner, & D. Schulze (Eds.), *Forest diversity and function* (pp. 263–289). Berlin: Springer. doi:10.1007/3-540-26599-6_13.
- Pautasso, M., Dehnen-Schmutz, K., Holdenrieder, O., Pietravalle, S., Salama, N., Jeger, M. J., et al. (2010). Plant health and global change – some implications for landscape management. *Biological Reviews*, *85*, 729–755. doi:10.1111/j.1469-185X.2010.00123.x.
- Peakall, R., Ebert, D., Scott, L. J., Meagher, P. F., & Offord, C. A. (2003). Comparative genetic study confirms exceptionally low genetic variation in the ancient and endangered relictual conifer, *Wollemia nobilis* (Araucariaceae). *Molecular Ecology*, *12*, 2331–2343. doi:10.1046/j.1365-294X.2003.01926.x.
- Philibert, A., Desprez-Loustau, M.-L., Fabre, B., Frey, P., Halkett, F., Husson, C., et al. (2011). Predicting invasion success of forest pathogenic fungi from species traits. *Journal of Applied Ecology*, *48*, 1381–1390. doi:10.1111/j.1365-2664.2011.02039.x.
- Prospero, S., & Rigling, D. (2011). Invasion genetics of the chestnut blight fungus *Cryphonectria parasitica* in Switzerland. *Phytopathology*, in press doi:10.1094/PHYTO-02-11-0055
- Raddi, P., & Panconesi, A. (1981). Cypress canker disease in Italy: biology, control possibilities and genetic improvement for resistance. *European Journal of Forest Pathology*, *11*, 340–347. doi:10.1111/j.1439-0329.1981.tb00104.x.
- Raison, R. J., & Khanna, P. K. (2011). Possible impacts of climate change on forest soil health. In B. P. Singh et al. (Eds.), *Soil health and climate change* (pp. 257–285). Berlin: Springer. doi:10.1007/978-3-642-20256-8_12.

- Resco de Dios, V., Fischer, C., & Colinas, C. (2007). Climate change effects on Mediterranean forests and preventive measures. *New Forests*, *33*, 29–40. doi:10.1007/s11056-006-9011-x.
- Ricciardi, A., & Simberloff, D. (2009). Assisted colonization is not a viable conservation strategy. *Trends in Ecology & Evolution*, *24*, 248–253. doi:10.1016/j.tree.2008.12.006.
- Richardson, D. M., Hellmann, J. J., McLachlan, J. S., Sax, D. F., Schwartz, M. W., Gonzalez, P., et al. (2009). Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Sciences USA*, *106*, 9721–9724. doi:10.1073/pnas.0902327106.
- Rizzo, D. M., Garbelotto, M., & Hansen, E. M. (2005). *Phytophthora ramorum*: Integrative research and management of an emerging pathogen in California and Oregon forests. *Annual Review of Phytopathology*, *43*, 309–335. doi:10.1146/annurev.phyto.42.040803.140418.
- Rohr, J. R., Dobson, A. P., Johnson, P. T. J., Kilpatrick, A. M., Paull, S. H., Raffel, T. R., et al. (2011). Frontiers in climate change–disease research. *Trends in Ecology & Evolution*, *26*, 270–277. doi:10.1016/j.tree.2011.03.002.
- Santini, A., La Porta, N., Ghelardini, L., & Mitterpergher, L. (2008). Breeding against Dutch elm disease adapted to the Mediterranean climate. *Euphytica*, *163*, 45–56. doi:10.1007/s10681-007-9573-5.
- Sanz-Elorza, M., Mateo, R. G., & González Bernardo, F. (2009). The historical role of agriculture and gardening in the introduction of alien plants in the western Mediterranean. *Plant Ecology*, *202*, 247–256. doi:10.1007/s11258-008-9474-2.
- Scarascia-Mugnozza, G., Oswald, H., Piussi, P., & Radoglou, K. (2000). Forests of the Mediterranean region: Gaps in knowledge and research needs. *Forest Ecology and Management*, *132*, 97–109. doi:10.1016/S0378-1127(00)00383-2.
- Schlenzig, A. (2011). A duplex PCR method for the simultaneous identification of *Phytophthora ramorum* and *P. kernoviae*. *EPPO Bulletin*, *41*(1), 27–29. doi:10.1111/j.1365-2338.2010.02431.x.
- Schweigkofler, W., O'Donnell, K., & Garbelotto, M. (2004). Detection and quantification of airborne conidia of *Fusarium circinatum*, the causal agent of pine pitch canker, from two California sites using a real-time PCR approach combined with a simple spore trapping method. *Applied and Environmental Microbiology*, *70*, 3512–3520. doi:10.1128/AEM.70.6.3512-3520.2004.
- Scirè, M., Motta, E., & D'Amico, L. (2011). Behaviour of *Heterobasidion annosum* and *H. irregulare* isolates from central Italy in inoculated *Pinus pinea* seedlings. *Mycological Progress*, *10*, 85–91.
- Scott, P. M., Burgess, T. I., Barber, P. A., Shearer, B. L., Stukely, M. J. C., Hardy, G. E. St J. et al. (2009). *Phytophthora multivora* sp. nov., a new species recovered from declining *Eucalyptus*, *Banksia*, *Agonis* and other plant species in Western Australia. *Persoonia*, *22*, 1–13.
- Seddon, P. J. (2010). From reintroduction to assisted colonization: Moving along the conservation translocation spectrum. *Restoration Ecology*, *18*, 796–802. doi:10.1111/j.1526-100X.2010.00724.x.
- Smith, J. A. (2010). *Seiridium* canker of Leyland cypress. FOR279, School of Forest Resources and Conservation, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida. Accessed August 2011 at <http://edis.ifas.ufl.edu/fr341>
- Solla, A., Dacasa, M. C., Nasmith, C., Hubbes, M., & Gil, L. (2008). Analysis of Spanish populations of *Ophiostoma ulmi* and *O. novo-ulmi* using phenotypic characteristics and RAPD markers. *Plant Pathology*, *57*, 33–44. doi:10.1111/j.1365-3059.2007.01692.x.
- Sork, V. L., & Waits, L. (2010). Contributions of landscape genetics – approaches, insights, and future potential. *Molecular Ecology*, *19*, 3489–3495. doi:10.1111/j.1365-294X.2010.04786.x.
- Stenlid, J., Oliva, J., Boberg, J. B., & Hopkins, A. J. M. (2011). Emerging diseases in European forest ecosystems and responses in society. *Forests*, *2*, 486–504. doi:10.3390/f2020486.
- Stukely, M. J. C., & Crane, C. E. (1994). Genetically based resistance of *Eucalyptus marginata* to *Phytophthora cinnamomi*. *Phytopathology*, *84*, 650–656. doi:10.1094/Phyto-84-650.
- Stukenbrock, E. H., & McDonald, B. A. (2008). The origins of plant pathogens in agro-ecosystems. *Annual Review of Phytopathology*, *46*, 75–100. doi:10.1146/annurev.phyto.010708.154114.
- Sturrock, R. N., Frankel, S. J., Brown, A. V., Hennon, P. E., Kliejunas, J. T., Lewis, K. E., et al. (2011). Climate change and forest diseases. *Plant Pathology*, *60*, 133–149. doi:10.1111/j.1365-3059.2010.02406.x.
- Tomlinson, J. A., Dickinson, M., Hobden, E., Robinson, S., Giltrap, P. M., & Boonham, N. (2010). A five-minute DNA extraction method for expedited detection of *Phytophthora ramorum* following prescreening using *Phytophthora* spp. lateral flow devices. *Journal of Microbiological Methods*, *81*, 116–120. doi:10.1016/j.mimet.2010.02.006.
- Tsopelas, P., Paplomatas, E., Tjamos, S., Soulioti, N., & Kalomoiras, E. (2011). First report of *Phytophthora ramorum* on *Rhododendron* in Greece. *Plant Disease*, *95*, 223. doi:10.1094/PDIS-08-10-0607.
- Tubby, K. V., & Webber, J. F. (2010). Pests and diseases threatening urban trees under a changing climate. *Forestry*, *83*, 451–459. doi:10.1093/forestry/cpq027.
- Tyler, B. M., et al. (2006). *Phytophthora* genome sequences uncover the evolutionary origins and mechanisms of pathogenesis. *Science*, *313*, 1261–1266. doi:10.1126/science.1128796.
- Vacher, C., Vile, D., Helion, E., Piou, D., & Desprez-Loustau, M.-L. (2008). Distribution of parasitic fungal species richness: influence of climate versus host species diversity. *Diversity and Distributions*, *14*, 786–798. doi:10.1111/j.1472-4642.2008.00479.x.
- Václavík, T., Kupfer, J. A., & Meentemeyer, R. K. (2012). Accounting for multi-scale spatial autocorrelation improves performance of invasive species distribution modelling (iSDM). *Journal of Biogeography*, in press doi: 10.1111/j.1365-2699.2011.02589.x
- Vannini, A., Natili, G., Anselmi, N., Montagni, A., & Vettriano, A. M. (2010). Distribution and gradient analysis of Ink disease in chestnut forests. *Forest Pathology*, *40*, 73–86. doi:10.1111/j.1439-0329.2009.00609.x.
- Vendramin, G. G., Fady, B., González-Martínez, S. C., Hu, F. S., Scotti, I., Sebastiani, F., et al. (2008). Genetically depauperate but widespread: the case of an emblematic Mediterranean

- pine. *Evolution*, 62, 680–688. doi:10.1111/j.1558-5646.2007.00294.x.
- Vettraiño, A. M., Ceccarelli, B., & Vannini, A. (2009). Susceptibility of some Italian ornamental and forestry species to *Phytophthora ramorum*. In: *Phytophthoras in Forests and Natural Ecosystems. Proceedings of the Fourth Meeting of IUFRO Working Party S07.02.09, PSW-GTR-221*, pp. 137–139.
- Vettraiño, A. M., Sukno, S., Vannini, A., & Garbelotto, M. (2010). Diagnostic sensitivity and specificity of different methods used by two laboratories for the detection of *Phytophthora ramorum* on multiple natural hosts. *Plant Pathology*, 59(2), 289–300. doi:10.1111/j.1365-3059.2009.02209.x.
- Watt, M. S., Ganley, R. J., Kriticos, D. J., & Manning, L. K. (2011). *Dothistroma* needle blight and pitch canker: The current and future potential distribution of two important diseases of Pinus species. *Canadian Journal of Forest Research*, 41, 412–424. doi:10.1139/X10-204.
- Webber, J. (2010). Pest risk analysis and invasion pathways for plant pathogens. *New Zealand Journal of Forestry Science*, 40, S45–S56.
- Weeks, A. R., Sgro, C. M., Young, A. G., Frankham, R., Mitchell, N. J., Miller, K. A., et al. (2011). Assessing the benefits and risks of translocations in changing environments: A genetic perspective. *Evolutionary Applications*, 4, 709–725. doi:10.1111/j.1752-4571.2011.00192.x.
- Wickland, A. C., Jensen, C. E., & Rizzo, D. M. (2008). Geographic distribution, disease symptoms and pathogenicity of *Phytophthora nemorosa* and *P. pseudosyringae* in California, USA. *Forest Pathology*, 38, 288–298. doi:10.1111/j.1439-0329.2008.00552.x.
- Wilkinson, K., Grant, W. P., Green, L. E., Hunter, S., Jeger, M. J., Lowe, P., et al. (2011). Infectious diseases of animals and plants: An interdisciplinary approach. *Philosophical Transactions of the Royal Society London B*, 366, 1933–1942. doi:10.1098/rstb.2010.0415.
- Wingfield, M. J., Hammerbacher, A., Ganley, R. J., Steenkamp, E. T., Gordon, T. R., Wingfield, B. D., et al. (2008). Pitch canker caused by *Fusarium circinatum* – a growing threat to pine plantations and forests worldwide. *Australasian Plant Pathology*, 37, 319–334. doi:10.1071/AP08036.
- Wingfield, M. J., Slippers, B., Roux, J., & Wingfield, B. D. (2010). Fifty years of tree pest and pathogen invasions, increasingly threatening world forests. In D. M. Richardson & D. M. Richardson (Eds.), *Fifty years of invasion ecology: The legacy of charles elton* (pp. 89–99). Oxford: Wiley-Blackwell. doi:10.1002/9781444329988.ch8.
- Xu, X. M., Harwood, T. D., Pautasso, M., & Jeger, M. J. (2009). Spatio-temporal analysis of an invasive plant pathogen (*Phytophthora ramorum*) in England and Wales. *Ecography*, 32, 504–516. doi:10.1111/j.1600-0587.2008.05597.x.
- Zocca, A., Zanini, C., Aimi, A., Frigimelica, G., La Porta, N., & Battisti, A. (2008). Spread of plant pathogens and insect vectors at the northern range margin of cypress in Italy. *Acta Oecologica*, 33, 307–313. doi:10.1016/j.actao.2008.01.004.