Symposium contribution / Contribution à un symposium

Forest pathogens: friend or foe to biodiversity?[1]

R.S. Winder and S.F. Shamoun

Abstract: Biological diversity in forest ecosystems results from evolutionary processes driven by ecological imperatives linked to pathogens, symbionts, fire, climate, and competition or impacts from other agents of disturbance. To understand the behavior of microorganisms and microbial pathogens, it is necessary to have a comprehensive appreciation for the diversity of their functional attributes in their natural habitats. Where niches are complex, evolution is guided by more than simple host–pathogen relationships. Moreover, the negative attributes of a pathosystem are not always obvious at different scales or in different contexts. Deleterious impacts on one species (e.g., mortality, parasitism) may benefit another species through reduced competition or enhanced nutrient cycling. Species with pathogenic behavior also display mutualistic and symbiotic benefits (e.g., mycorrhizal fungi and endophytic antagonists found in grasses) or useful attributes as biological control agents. Preserving the diversity of natural areas while controlling forest pests is both a challenge and an opportunity. The challenge is to understand pest niches more thoroughly, while the opportunity is to have a wiser use of both timber and nontimber forest resources.

Key words: ecology, community, evolution, ecosystem, biological control.

Résumé : La diversité biologique des écosystèmes forestiers résulte de processus évolutifs soumis à des impératifs écologiques liés aux organismes pathogènes, aux symbiotes, au feu, au climat et à la compétition ou aux effets d'autres agents de perturbation. Pour mieux comprendre le comportement des microorganismes et des microbes pathogènes, il est nécessaire d'avoir un portrait global de la diversité de leurs caractéristiques fonctionnelles dans leurs habitats naturels. Là où les niches sont complexes, l'évolution dépend de facteurs qui vont au-delà des simples relations entre hôte et agent pathogène. De plus, les caractéristiques négatives d'un pathosystème ne sont pas toujours évidentes à toutes les échelles ou dans tous les contextes. Des effets délétères pour une espèce (p. ex., la mortalité, le parasitisme) peuvent être bénéfiques pour une autre espèce par le biais d'une compétition moins grande ou d'un cycle nutritif amélioré. Des espèces au comportement pathogénique présentent aussi des avantages mutualistes et symbiotiques (p. ex., champignons mycorhiziens et endophytes antagonistes trouvés dans les graminées) ou des caractéristiques utiles en tant qu'agents de lutte biologique. La préservation de la diversité des zones naturelles lors de la lutte contre les parasites des forêts est à la fois un défi et une opportunité. Le défi consiste à mieux comprendre les niches des parasites alors que l'opportunité est une meilleure utilisation de la matière ligneuse et des ressources non ligneuses de la forêt.

Mots clés : écologie, communauté, évolution, écosystème, lutte biologique.

Introduction

"Plant pathogens play Jekyll and Hyde roles in the structure, dynamics and evolution of natural plant communities" (Gilbert 2002)

Pathogens are entities that can incite disease. Tree and forest vegetation pathogens often exist in equilibrium with natural forest communities, so their critical ecological roles are not easily discernible. Forest pathogens are major agents of forest diversity and are important elements in shaping forest structure, composition, succession, and landscape patterns. They likewise are regulated by the forest ecosystem (Castello et al. 1995; van der Kamp 1991). As destructive agents in areas dedicated for timber production, forest pathogens can cause mortality, reduce fitness of individual forest plants, or affect composition of plant communities. Troubles abound, but a short list of examples from Canadian forests might include such things as root-rot pathogens (e.g., *Armillaria* spp. and *Phellinus* spp.), rusts (e.g.,

R.S. Winder and S.F. Shamoun.[2] Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Road, Victoria, BC V8Z 1M5, Canada.

[2]Corresponding author (email: sshamoun@pfc.cfs.nrcan.gc.ca)

Cronartium ribicola J.C. Fisch., causal agent of white pine blister rust), and mistletoes (e.g., *Arceuthobium* spp., the "dwarf mistletoe" that infects numerous conifer species) (Manion 1981). But pathogens can also be considered beneficial, as they help to maintain plant species diversity, facilitate succession processes, and enhance the genetic diversity and structure of host populations. Moreover, forest pathogens are often held in check by other organisms. For example, the wood-rotting fungus *Phlebiopsis gigantea* (Fr.) Jul., registered in the United Kingdom as PG Suspension™ and in Finland as RotStop™, has been used as a biological control agent to reduce the spread of the causal agent of annosus root and butt rot, *Heterobasidion annosum* (Fr.) Bref. (Rishbeth 1963; Pratt 1999; Roy et al. 2003). Biological control of the root pathogen *Armillaria ostoyae* (Romagn.) Herink using *Hypholoma fasciculare* (Huds. ex Fr.) has also been investigated in Canada (Chapman and Xiao 2000). Another documented example of suppression involves the action of nitrogen-fixing *Frankia* spp., in which the mutualistic bacteria encourage vigorous growth of red alder, *Alnus rubra* Bong., as a "natural biological control of laminated root-rot disease". The pathogen involved, *Phellinus weirii* (Mur.) Gilb., requires the presence of susceptible roots in order to spread. Because red alder is not susceptible to the rot, sufficiently vigorous root growth presents a physical obstruction to spread of the pathogen (Thies and Sturrock 1995). Regarding suppression, it is also possible to make use of the biocontrol potential inherent in phytopathogens for management of forest weeds (Wall et al. 1992). *Chondrostereum purpureum* (Pers.: Fr.) Pouzar is a wood-inhabiting fungus that invades the cambium and sapwood of mostly hardwood trees and shrubs. It is currently marketed as a wood decay promoter and biological control agent for woody weeds under the trade name BioChon™ in Europe, Myco-Tech ™ in eastern Canada, and Chontrol™ in western Canada (Evans et al. 2001). Another example is the white-rot fungus *Cylindrobasidium leave* (Pers.:Fr.) Chamuris, a phytopathogen registered as Stumpout™ for control of resprouting wattle stumps and introduced tree species in South Africa (Ginns and Lefebvre 1993; Lennox et al. 2000).

Elucidation of natural disease roles and understanding the impacts of detrimental and beneficial diseases on forest biodiversity requires integrating knowledge of dynamics, evolutionary process, and spatial structure of both host and pathogen populations and an appreciation for how destructive actions at one scale can be the foundation for positive outcomes at another.

Defining terms

For a discussion of pathosystems in natural settings and their relationship to complex ecosystems, it is necessary to explain what is meant by "plant disease" and "biodiversity".

Plant disease

Most definitions of plant disease state or imply that plant disease is "any malfunctioning of host cells and tissues that results from continuous irritation by a pathogenic agent or environmental factor and leads to development of symptoms" (Agrios 1988). However, to accommodate the "beneficial plant diseases", we agree with the definition stated by

C.L. Wilson: "dynamic interaction of a pathogen and host in cells of the host and pathogen".

Using this definition, plant diseases can be further classified, on the basis of their economic impact, into pathological plant diseases that result in the suffering of plants and (or) man and beneficial plant diseases that result in benefits to the plant and (or) man (Wilson 1977).

Biodiversity

At a global level, the simplest definition for biodiversity is probably "the full variety of life on Earth" (Takacs 1996). This kind of sweeping definition is, of course, open to revision and debate as various concepts of biodiversity are considered (Faith 2003). In local contexts, there is a connotation of biodiversity that is often taken to be "the diversity of species living in an area or region" or the "diversity of niches in an area or region", for example, "biodiversity in Canada" or "biodiversity of the boreal forest". We will use these concepts interchangeably.

Biodiversity and forestry

Biodiversity is a major concern in forestry because threats to biodiversity could negatively impact sustainable timber harvests. Natural or anthropogenic disturbances often have direct impacts on ecosystem species, and these may have indirect impacts on other species at various trophic levels in the overall forest ecosystem. To cite just one extreme example, strip mining creates soil conditions intolerable for most ectomycorrhizal fungi, necessitating bioremediation with *Pisolithus tinctorius* (Pers.) Cok. & Couch to improve conifer growth and survival (Marx et al. 1982). But to see things only through the lens of commercial forestry operations would be to take a very narrow view of potential impacts on humans and society, because there are also higher concerns. When speaking about current climate change threats to global ecosystems, James Lovelock, author of the Gaia hypothesis, said,

> "The natural ecosystems of the Earth are not just there for us to take as farmland; they are there to sustain the climate and the chemistry of the planet." (Kirby 2004)

From this viewpoint, the health of diverse forest ecosystems is not just a commercial concern; it is a vital necessity.

Biodiversity and pathogens

Biodiversity emerges as the result of the many interactive factors that create niches for speciation. In forests and other natural areas, drivers of biodiversity can include climate (especially along altitudinal, longitudinal, and precipitation gradients) (Gaston 2000), fire (a positive or negative influence depending on ecosystem adaptations) (Nasi et al. 2002), predation (e.g., insects such as bark beetles) (Heath and Alfaro 1990), competition for various resources (e.g., correlation between diversity and the intensity of nutrient utilization) (Loreau 1998), opportunities for long-term symbioses (e.g., the large number of mycorrhizal fungal species) (van der Heijden et al. 1999), and finally parasitism and disease (Castello et al. 1995; Reynolds et al. 2003). Just as diseases control the geographic distribution of agricultural crops, they also affect the distribution of forest spe-

cies. In fact, soil pathogens are considered an important part of the negative microbial feedback that helps to determine species richness over large environmental gradients (Reynolds et al. 2003).

Regarding pathogens and biodiversity, the influences are two-way. One standard way of visualizing this is the "disease pyramid". This model views the outcome of a pathosystem as an interaction between the pathogen, the host, and the environment, with human influences adding a fourth dimension (Agrios 1988). In forest ecosystems, human influences are certainly pronounced, but other creatures may have dominant influences in a particular area. In British Columbia, Canada, outbreaks of *Dendroctonus ponderosae* Hopkins (mountain pine beetle) are a dominant factor in certain stands. Their influence on the occurrence and spread of blue-stain fungi (Nevill and Safranyik 1996) is probably more important than other human influences. Keeping this and other examples in mind, the fourth dimension of a disease pyramid for forestry should probably comprise all of the living environmental agents (biodiversity). This would be an axis distinct from the dimension corresponding to abiotic environmental influences.

Pathosystem outcomes could also be expected to change over long periods of time, as pathogens, hosts, and the diverse creatures affecting them coevolve. It may not be usual to view disease outcomes in this way, but in a natural setting without major impacts from human plant breeding, evolution describes the level of pathosystem development and involvement with the other living components of the ecosystem. A revised disease pyramid showing biodiversity and evolution as factors is shown in Fig. 1.

Pathosystems, biodiversity, and evolution

In forest ecosystems, we have noticed several persistent themes at the intersection of pathosystems, biodiversity, and evolution. They are (1) the nonconformity of organisms regarding strict definitions (i.e., When is a pathogen a pathogen?), (2) the surprising resilience of ecosystem components contrasting with the "brittleness" of the systems that incorporate them, and (3) the complexity of the evolutionary milieu.

When is a pathogen a pathogen?

Forest species such as trees and grasses can harbor mutualistic endophytes that are antagonistic to pathogens and insects. However, environmental stresses can trigger pathogenic behavior in these organisms. This point has been used to propose the use of these endophytes as environmentally safe biological control agents of competing forest vegetation in reforestation areas (Dorworth and Callan 1995). This conversion from one mode to the other was reported in detail for attempts to control marsh reedgrass (*Calamagrostis canadensis* Michx. Beauv.), a grass that suppresses tree seedlings in reforestation areas of northern Canada. In greenhouse and growth chamber trials with the general pathogen *Fusarium avenaceum* (Corda: Fr.) Sacc., different temperature and lighting conditions caused some isolates to change their behavior, with damage to marsh reedgrass shifting toward either the endophytic or pathogenic end of the spectrum (Winder 1999). This picture was

Fig. 1. A disease pyramid showing axes relevant to forest pathosystems (modified from Agrios 1988). The pyramid is a portrayal of the range of disease outcomes within six dimensions or parameters. At the base of the pyramid, two axes indicate that variability within pathogens and hosts will shift their interaction in favor of one or the other. This interaction is also influenced by variable abiotic or physical parameters, shown at the base as an environmental axis. Variable interaction of all these factors with biodiversity is indicated at the apex, because antagonistic or symbiotic organisms often play prominent roles in disease outcomes. On the vertical axis inside the pyramid, the variable impacts of timing and disease progress interact with all the preceding factors. Evolution is portrayed as a dimension linked to the time axis and the other factors, wherein the nature of a pathogenic interaction changes over many generations.
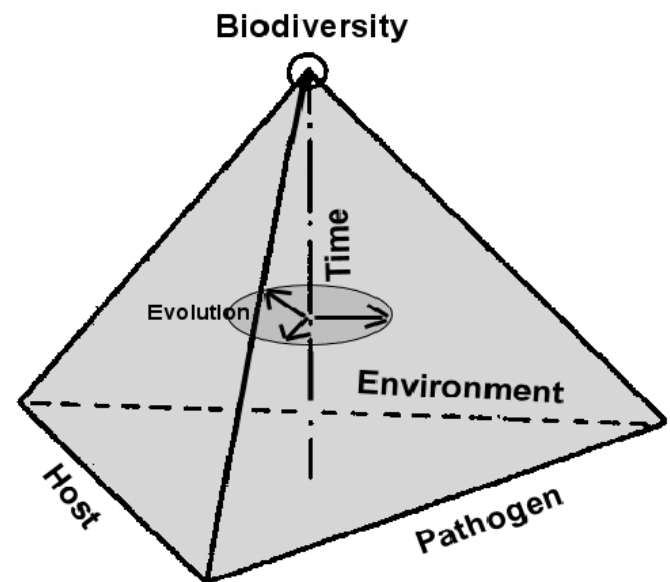
further complicated by results showing that under certain conditions, particularly when allelopathic straw extracts were present, *F. avenaceum* simultaneously caused some nonlethal damage to the grass, while blocking attack by a more lethal pathogen closely resembling *Colletotrichum graminicola* (Ces.) Wils. (Winder 1996). So, organisms can be both pathogenic and mutualistic, and these properties are not necessarily an either–or proposition.

Resilient species: the *Cryphonectria* – American chestnut pathosystem

> "It is not beyond the grasp of science to restore the American chestnut to economic importance. It could be accomplished within the next 50 years." (Griffin 2004)

> "Efforts to restore the American chestnut focus on natural blight resistance found in a few surviving trees of the species in the natural range, strains of the blight fungus with reduced virulence (hypovirulence), and introduction of Asian chestnut blight resistance into American chestnut through breeding programs." (Griffin 2000)

The American chestnut (*Castanea dentata* (Marsh.) Borkh.) was once an integral and dominant part of the hardwood flora of eastern North America. The tree was known for its straight bole, highly durable wood, and sweet nuts

(Smith 2000). It was devastated throughout its range by *Cryphonectria parasitica* (Murr.) Barr, a fungus introduced from Asia and discovered in New York City in the early 1900s. Local spread by wind- and rain-disseminated spores occurred as a result of wound infections, while longer distance dispersal probably occurred via birds or through the movement of infected wood. But the American chestnut has survived, principally as shoots produced from living root systems that continue to sprout or in the few trees isolated at extremes of its range. The pathogen also endures when shoots become infected at 1–12 years of age, perpetuating the cycle of blight (Griffin 2000).

Humans may be able to influence the resilience of the pathogen, however. With the discovery of hypoviruses (i.e., dsRNA genetic elements) in hypovirulent strains of *Cryphonectria parasitica*, there is renewed hope that biological control of chestnut blight may be possible. The concept of biological control of *Cryphonectria parasitica* with hypovirulent strains of *Cryphonectria parasitica* is appealing from biological, environmental, and economic perspectives (Milgroom and Cortesi 2004). There are major challenges to using this approach. Laboratory and field tests have revealed the presence of many genetically different strains of *Cryphonectria parasitica*. When the strains are incompatible, their hyphal filaments often fail to fuse so that hypovirus transmission is prevented. By understanding the genes that regulate compatibility, researchers selecting strains for hypovirus introductions will be able to choose strains that can more successfully interact with large numbers of compatibility types (MacDonald and Fulbright 1991). Nuclear integration can also provide an important advantage for the hypovirus, as it allows transmission to occur during sexual reproduction. The barriers of incompatibility do not exist during sexual reproduction (Milgroom and Cortesi 2004). Therefore, when normal strains mate with those carrying hypoviruses, about one-half of the wind-borne sexual spores that are produced carry the hypovirus (Choi and Nuss 1992).

Humans may also be able to engineer the host in favor of its survival. A number of chestnut breeding programs are developing blight-resistant American chestnut trees using the backcross method. This breeding strategy can transfer blight resistance from Chinese chestnut to American chestnut, while retaining the desirable growth, form, and adaptability of American chestnut (Burnham et al. 1986). The future outlook for this pathosystem is therefore evolving. The resilience and persistence of chestnut as understory saplings, along with breeding program efforts, may soon restore the chestnut monarchy in eastern North America's hardwood forests.

Brittle systems: the Dwarf mistletoe – conifer pathosystem

"The role of dwarf mistletoes in natural conifer ecosystems has often clashed with human interests and harvesting practices, but with understanding of the ecology, epidemiology, population dynamics of the mistletoes and the silvics of their hosts, wiser management practices may follow." (Shamoun et al. 2003)

Dwarf mistletoes of the genus *Arceuthobium* (Viscaceae) are plants that are obligate parasites of conifers within the families Pinaceae and Cupressaceae. Among the forest pathogens causing mortality in natural conifer species ecosystems, dwarf mistletoes and root diseases are perhaps the most significant. Dwarf mistletoes rely upon the host for support, mineral nutrients, a portion of their required carbon compounds, water, and possibly other growth factors. Thirty-four New World species and eight Old World species of dwarf mistletoe are currently recognized. In North America, the greatest species diversity is located in northwestern Mexico and the western United States, where 28 of the 34 New World species are present. Ranges of five species of dwarf mistletoe — *Arceuthobium americanum* Nutt. ex Engelm. in Gray, *Arceuthobium laricis* (Piper) St. John, *Arceuthobium douglasii* Engelm., *Arceuthobium tsugense* (Rosendahl) G.N. Jones, and *Arceuthobium pusillum* Peck. — extend into Canada (Hawksworth and Wiens 1996).

Dwarf mistletoes cause annual economic losses amounting to an estimated 11.3×10^6 m^3 of lumber in the western United States and 3.8×10^6 m^3 of lumber in western Canada. The economic impact of this loss is difficult to calculate, but totals of several billion dollars annually have been estimated (Hawksworth and Wiens 1996). Infection of young trees by dwarf mistletoe results in high mortality, while infection of older trees results in decreased needle length, length of needle-bearing branches, needle surface area, and total number of needles. As severity of dwarf mistletoe infection increases, growth in diameter and height decreases, resulting in reduced production. In some host–parasite combinations, mortality is increased by dwarf mistletoe infection (Hawksworth and Wiens 1996). Climate, topography, and other site factors may influence the distribution and intensity of dwarf mistletoe, but it is the dynamics of the forest that most affect the dynamics of mistletoe populations (Parmeter 1978). The history of fire and harvesting practices are critical factors. Severely infested stands may have substantial accumulation of fuel for fires, and it is believed that pockets of heavy infestation can become foci of major forest fires, which tend to sanitize stands. In a manner similar to fire, large clearcuts with no residual host trees can eliminate the dwarf mistletoe from managed stands. This can be an extremely effective control strategy.

Unfortunately, when selective timber harvesting is used to preserve ecosystem components, the fragile nature of mistletoe-infested stands is exposed. Preserved stands act as reservoirs of infection for the surrounding cut areas, ensuring the persistence of pathogen pressure on trees from a young age. Ironically, forest health is then endangered by management methods aiming to preserve overall diversity. The resiliency of a forest ecosystem might not be equal to that of its individual parts if, as in this example, pathogens and human disturbance patterns interact to exacerbate stresses. Under these circumstances, a counterbalancing control strategy is needed to reduce the threat.

Development of an effective biocontrol program for management of dwarf mistletoe, particularly in variable-retention silviculture systems, requires technology for mass production of the biocontrol agent, an efficient delivery sys-

tem, and a sound strategy for deployment. Optimal strategies focus on reducing mistletoe spread from residual trees bordering or within regeneration areas through timely treatment with biocontrol agents that kill or deflower the parasite. The selection of specific treatment areas and regimes is based on an understanding of the epidemiology of the control agent, the population dynamics of the mistletoe, and the silvics of the host species. The areas requiring treatment can be identified during preharvest prescription or during surveys preceding silvicultural treatments. Threshold mistletoe ratings for treatment, in relation to stand attributes such as mean diameter at breast height, age, and density can also be identified, and a spatial-statistical computer model can simulate various deployment strategies (Shamoun and De Wald 2002). It should be possible to protect new plantations from early mistletoe infestation where the constraints of regeneration have required the retention of a significant number of infected residual trees (Shamoun et al. 2003). In the areas where timber production is not the primary management objective, dwarf mistletoe has positive effects and is considered an important agent of biodiversity. Several insects have been observed to feed on dwarf mistletoe shoots, including larvae of *Mitoura spinetorum* (Lycaenidae), the thickest hairstreak butterfly, *Dasypyga alternosqualmella* (Pyralidae), *Filatima natalis* (Gelechidae), *Neoborella tumida* (Miridae), and *Pityophthorus arceuthobii* (Scolytidae). Several mites, spiders, and bird species have been observed to use dwarf mistletoes fruits as a food source and witches brooms as nesting sites (Hawksworth and Wiens 1996).

Complexity in the evolutionary milieu

Multifaceted roles

Organisms with mixed attributes present problems in comprehending the evolution of their true ecosystem roles and functions, beyond nomenclature and disease etiology. A famous example is the Périgord black truffle (*Tuber melanosporum* Vittad.), a mycorrhizal symbiont that attacks surrounding vegetation to form a brûlé (barren spot) around the host tree (Plattner and Hall 1995). From the perspective of the host, *Tuber melanosporum* is a beneficial symbiont. From the perspective of the surrounding grasses and other plants, the fungus is definitely a pathogen. So, it is important to realize that from an evolutionary viewpoint, pathosystem niches are not always distinguished by a single function.

Understanding the role of forest pathosystems is also sometimes a matter of appreciating the scale of impacts. Root diseases caused by fungi such as *Armillaria* spp. and *Phelinus* spp. can certainly be devastating to trees on a local scale. The forest communities created by the action of these pathogens are often regarded as "root disease climaxes" (van der Kamp 1991). But across a landscape, these pathogens are responsible for opening gaps in the forest, which creates opportunities for other tree species to become established (Castello et al. 1995). Forests could be very homogeneous without pathogen activity. In this case, the nature of a niche is complex; local biodiversity may suffer, while landscape-level biodiversity is enhanced.

Synergy in large substrates

The structure of the forest environment is more complex than that of an agricultural ecosystem, with much of it consisting of massive trees, woody debris, or various stages between the two. For example, cut stumps can usefully be regarded as an intermediate substrate between the living standing tree and felled timber, partly because of their possession of an intact root system and partly because at least initially they may contain living tissues that remain functional for varying periods of time (Rayner and Boddy 1986). In Canada and the Netherlands, it has been demonstrated that application of *Chondrostereum purpureum* mycelium to the cut surfaces of hardwood stumps reduces the number and viability of resprouts (de Jong et al. 1990; Wall 1990); this is a useful property where the biological suppression of less valuable tree species is desired (Shamoun 2000). But these biological control studies have also raised another interesting point: stumps and trees killed by pathogens support a diverse succession of microbial species. *Chondrostereum purpureum* generally produces basidiocarps about 18 months after infection of red alder stumps. In one experiment, the production of *Chondrostereum purpureum* basidiocarps occurred on 66% of the stumps treated with *Chondrostereum purpureum*, about 19% of stumps treated with chemical herbicides, and 43% of stumps in formulation and slash controls. Basidiocarps of *Trametes versicolor* (L.) C.G. Loyd, *Schizophyllum commune* (L.) Fr., and other basidiomycetes were also observed on many of the stumps in these treatments. In a follow-up assessment, basidiocarps of *Chondrostereum purpureum* were observed on 23% of the stumps treated with the fungus. On the other treatments, occurrence of *Chondrostereum purpureum* was less than 2%. No living sprouts were found on any stump bearing *Chondrostereum purpureum* basidiocarps. Evidence of secondary colonization and advanced decay was apparent. Basidiocarps of *Trametes versicolor*, *S. commune*, other basidiomycetes, and ascocarps of some ascomycetes were recorded on many of the stumps (Shamoun 2000).

Generally, mycoherbicides will persist locally at an elevated level then return to endemic levels as the targeted weed population is depressed (Charudattan 1988). In the case of *Chondrostereum purpureum*, the fungus is thought to persist as a saprophyte and then return to endemic levels as its substrate (fresh wood) is depleted. As a primary invader of wounds, *Chondrostereum purpureum* causes sapwood stain, decay, and eventually host death (Rayner and Boddy 1986). Upon weakening of the host, *Chondrostereum purpureum* is replaced by other more aggressive saprobic fungi such as *Trametes versicolor* and *S. commune* (Shamoun 2000). These fungi may interact in a dynamic fashion to accomplish the death of the host. It is interesting that the rapid succession ensures *Chondrostereum purpureum* will not persist at high levels following the inundation of an area for biocontrol treatment.

Diverse niches and symbiotic legacies

Pathosystem niches are not always distinguished by one particular type of host. A well-known example would be circulative plant viruses that also propagate within their in-

sect vectors (Gray and Banerjee 1999). A more specific example from our own forestry experience involves the recent identification of bacteria associated with dead larvae of *Dendroctonus ponderosae* in the wilderness of interior British Columbia (Winder and Macey 2004). Bacteria identified from larval corpses using fatty acid methyl ester analysis included species commonly associated with insects, but they also included potentially phytopathogenic species such as *Pseudomonas syringae* van Hall, *Pseudomonas fluorescens* Migula, and *Erwinia chrysanthemi* Burkholder et al., as well as *Rahnella aquatilis* Izard et al., an enteric bacteria that is also often found in the rhizosphere in Canada (Berge et al. 1991). With such a diverse array of niches, these bacteria are clearly affected by more than just one type of host interaction. What is not clear is the degree to which each niche has contributed to evolution of pathogenic or other traits.

To summarize this issue of complexity in forest pathosystems, there may be no simply described niche or "crucible" for the evolution of some pathogens. To understand the behavior of these organisms, we should have a comprehensive grasp of all of the points where selective pressure and niche characteristics have influenced the development of the species.

Conclusions

Are pathogens friends or foes of biodiversity? We conclude that generalities will not easily answer this question. It depends on perspective and the particular details of a pathosystem. If the objective is to grow the maximum amount of timber, then a plant pathogen can present the various direct and indirect threats that we have discussed. But if the objective is to control forest pests (e.g., insects and competing vegetation), maximize diversity within a forest to encourage other commercial values (e.g., nontimber forest products), or preserve other social values (e.g., vital ecosystem services), then pathogens can be an important factor in niche creation and the maintenance of diversity. As disease management techniques advance, it will be important to balance these disparate objectives for the greatest common good of society and the ecosystem.

The complexity of the pathogen situation in forestry also has implications for the study of other plant diseases. Where crop pathogens are also found in natural settings, it may be necessary to comprehend their behavior in those settings to fully understand plant–pathogen interactions. Advances in molecular biology have come a long way towards elucidating some of the details of pathosystem function, but there is still a complex *terra incognita* in the functional maps of pest and host genomes. Understanding the in situ behavior of plant pathogens could go a long way toward resolving some of that complexity.

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