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# Conservation and management of forest fungi in the Pacific Northwestern United States: an integrated ecosystem approach

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## Introduction

The vast forests of the Pacific Northwest region of the United States, an area outlined by the states of Oregon, Washington, and Idaho, are well known for their rich diversity of macrofungi. The forests are dominated by trees in the Pinaceae with about 20 species in the genera *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga*. All form ectomycorrhizas with fungi in the Basidiomycota, Ascomycota, and a few Zygomycota. Other ectomycorrhizal genera include *Alnus*, *Arbutus*, *Arctostaphylos*, *Castinopsis*, *Corylus*, *Lithocarpus*, *Populus*, *Quercus*, and *Salix*, often occurring as understorey or early-successional trees. Ectomycorrhizal fungi number in the thousands; as many as 2000 species associate with widespread dominant trees such as Douglas-fir (*Pseudotsuga menziesii*) (Trappe, 1977). The Pacific Northwest region also contains various ecozones on diverse soil types that range from extremely wet coastal forests to xeric interior forests, found at elevations from sea level to timber line at 2000 to 3000 metres. The combination of diverse ectomycorrhizal host trees inhabiting steep environmental and physical gradients has yielded perhaps the richest forest mycota of any temperate forest zone. When the large number of ectomycorrhizal species is added to the diverse array of saprotrophic and pathogenic fungi, the overall diversity of macrofungi becomes truly staggering.

Issues relating to conservation and management of forest fungi in the

Pacific Northwest must be placed in the context of public land resources and Federal laws regulating forest management. The Pacific Northwest has the greatest amount of Federal forest in the United States, about 9.8 million hectares in Oregon and Washington alone. The lands are managed by the US Department of Agriculture (USDA), Forest Service, and the US Department of the Interior (USDI), Bureau of Land Management and National Parks Service. Each agency has different overall management goals. For example, National Parks do not allow commercial extraction of any forest products. National Park lands are primarily for recreational purposes and also serve as primary biological reserves. Other Federal forest lands vary between roadless wilderness areas with virtually no resource extraction to areas where forests are managed to meet multiple-resource objectives, including timber harvest, recreational access, and conservation of rare species. Several Federal laws and statutes, including the Endangered Species Act, the National Environmental Protection Act, and the National Forest Management Act, provide strict rules governing the planning and implementation of forest management and monitoring activities. These laws also provide for public input in planning and management. Over the last four decades, legal challenges to the development and implementation of forest plans have greatly shaped the current directions for managing public forests. These directions and decisions have direct relevance to the conservation and management of forest fungi.

During the late 1980s and early 1990s a series of lawsuits sharply curtailed the harvest of old-growth forests in the Pacific Northwest. At the centre of the controversy was the old-growth dependent northern spotted owl (*Strix occidentalis*), a rare species protected by the Endangered Species Act. Because the economy of many Pacific Northwest communities relied strongly on timber harvest from Federal forests, this action created political controversy. In 1992, President Clinton held a regional forest conference as a first step toward balancing the economic needs of the region with the protection of endangered species and old-growth forest habitat on Federal land. This eventually led to a scientific assessment of the problem (FEMAT,1993) and development of the Northwest Forest Plan (USDA & USDI, 1994*a*). The plan strives to provide for a sustainable level of timber harvest and persistence of old-growth forest dependent species based on a region-wide allocation of land uses, including reserve and nonreserve areas. As part of the overall scientific assessment process, many rare species requiring old-growth forest habitat were analysed for protection under the land reserves and forest management guidelines. In the final analysis, 234 old-growth dependent, rare, fungal species were listed for additional protection under the Survey and Manage guidelines of the Record of Decision (USDA & USDI, 1994*b*). The Record of Decision is the final legally binding document that defines how the Northwest Forest Plan is to be implemented. The Survey and Manage guidelines detail the course of mitigations required by management to protect the species. Although not a part of the listing process for the Endangered Species Act, this action still represents the first Federal listing of fungal species for protection in the United States and highlights the need for a research programme addressing poorly understood conservation issues for forest fungi.

The Northwest Forest Plan initiated a significant paradigm shift in forest management from an emphasis on timber extraction to ecosystem management. Ecosystem management is a holistic approach to decision making that integrates biological, ecological, geophysical, silvicultural, and socio-economic information into land management decisions to preserve biological diversity and maintain ecosystem functioning while meeting human needs for the sustainable production of forest products and amenities (Bormann et al., 1994; Jensen & Everett, 1994). Planning is typically conducted at broad scales such as watersheds or regional landscapes. Fungi play significant ecosystem roles in nutrient cycling, food webs, forest diseases, and mutualisms, and therefore significantly influence seedling survival, tree growth, and overall forest health. Ecosystem approaches to forest management provide an avenue for integrating our understanding of the biological and functional diversity of forest fungi into recent forest management objectives. It is our contention, and indeed the theme of this chapter, that an ecosystem-based approach provides the most effective means for conserving this vast array of essentially cryptic species.

As the numbers and diversity of fruit bodies of forest fungi were declining in Europe (Arnolds, 1991) and Japan (Hosford *et al*., 1997), the last two decades in the Pacific Northwest witnessed a dramatic increase in the harvest of wild, edible mushrooms with export to Europe, Japan, and elsewhere. In 1992, nearly 2 million kg of edible mushrooms was harvested in the Pacific Northwest, bringing over US$40 million to the economy (Schlosser & Blatner, 1995). Forest managers and the public questioned whether such harvest levels were sustainable or could negatively impact persistence of harvested species (Molina *et al*., 1993). The reproductive biology of these species, their habitat requirements, and effects of mushroom harvest and forest management practices on their continued productivity are poorly understood. Although commercial species are not rare, the conservation of them also lends itself to ecosystem management approaches and has prompted new lines of research.

The overall mission of the Forest Mycology Team of the USDA Forest Service, Pacific Northwest (PNW) Research Station, Corvallis, Oregon, is to provide basic information on the biological and functional diversity of forest fungi and to develop and apply this information in an ecosystem context to both conserve the fungal resource and sustain the health and productivity of forest ecosystems. The research is divided into three problem areas:

1. *Ecology, biology, and functional diversity of forest fungi* This area considers issues related to fungal taxonomy, systematics and phylogeny, understanding and documenting fungal communities in space and time, examining effects of natural and anthropogenic disturbances on the ecology of forest fungi, and exploring important ecosystem functions of forest fungi, particularly their roles in ecosystem resiliency and health.
2. *Conservation biology of forest fungi* This area develops fundamental approaches to determining population dynamics, develops habitat-based models to predict species presence and future potential habitat for rare fungi, develops methods to survey for rare species, and explores management options to conserve old-growth associated fungal species under the guidelines of the Northwest Forest Plan.
3. *Sustainable productivity of commercially harvested edible forest fungi* This area addresses challenges associated with measuring productivity of ephemeral fruit bodies, determines the effects of mushroom harvest and forest management practices on future production, and develops protocols to monitor sustainable productivity of the resource.

This approach addresses fungal resource issues at different scales (species, populations, communities, and landscapes) so that the results are relevant to ecosystem planning. The beneficial mutualistic mycorrhizal fungi are given primary attention because of their importance to forest trees. The remainder of this chapter outlines many issues in these areas, our research approaches and directions, and application of this research to the conservation and management of forest fungi. We begin by discussing basic research components, including ecosystem function, community ecology, and population biology. We conclude by focusing on the development of tools and concepts to apply this knowledge, including applications in inventory and monitoring. Although this research programme is unique to the Pacific Northwest region and the Federal policies on public lands, we believe it provides a relevant framework to approach fungal conservation issues at various scales and for different objectives in other parts of the world.

## Ecosystem functions, fungal communities and populations

### *Ecosystem functions*

Conserving and managing forest fungi requires an understanding of how fungi function in maintaining healthy ecosystems. Educating land managers about how management practices affect the reproduction, growth, and overall function of fungi through workshops and literature is vital to the success of integrating fungal concerns into forest management plans. In our discourse with managers, we emphasise and discuss four critical ecosystem functions as follows.

1. *Nutrient cycling, retention, and soil structure* Almost all fungi participate in nutrient cycling. This is best known for saprotrophs (decomposers), particularly those that degrade wood (cellulose and lignin). Two other roles are equallyimportant, however, in this ecosys tem function. First, fungal mycelia are large sinks for organic carbon and nutrients in the soil. In ectomycorrhizal-dominated forests, a significant portion of the carbon fixed by host trees can go to the mycorrhizal structures and fungal mycelium to support this symbiotic association (Smith & Read, 1997). Some fungal mycelia and ectomycorrhizal root tips turn over rapidly to return nutrients to the soil, whereas other fungal structures such as rhizomorphs retain nutrients in relatively long-lived structures or shunt it to other parts of the mycelium as some sections die. What is important is that fungi are major sinks for maintaining nutrients on site, thereby preventing nutrient leaching and loss from soils. Secondly, fungi exude polysaccharides similar to root exudates,and these ‘organic glues’ (Perry *et al.*, 1989) are important in creating and stabilising soil microaggregates and soil micropores. These soil structures contribute to soil aeration and water movement. Because most terrestrial organisms are strongly aerobic, this fungal contribution to soil microaggregation is critical for overall maintenance of soil health and productivity.

2. *Food webs* Although it is common knowledge that animals from molluscs to mammals (including humans) eat mushrooms, the magnitude of this food source and its ecological importance is underappreciated. The greatest biomass of fungi resides in hidden mycelia that explore soil and organic substrates, and it is here that the importance of fungi in food webs and soil fertility is revealed. Literally tens of thousands of microarthropod species live in forest soils, and about 80% of those are fungivores (Moldenke, 1999). Microarthropods provide the biological machinery to shred the vast quantity of organic matter in forest soils and prepare it for the final mineralisation processes carried out by microbes. Given the large amount of fungal hyphae in forest soils noted above, the magnitude of this soil food web process becomes readily apparent.

   Fruit bodies of fungi (mushrooms and truffles) are also vital food sources for many wildlife, especially forest mammals. Most small mammals depend on hypogeous fruit bodies (truffles) for a significant part of their diets (Maser, Trappe & Nussbaum; 1978). The Pacific Northwest is biologically rich with hypogeous fungi; several species produce fruit bodies year-round (Colgan *et al.*, 1999). This knowledge of food web connections directly relates to the preservation of birds of prey, such as the endangered northern spotted owl, that eat small mammals which themselves subsist almost entirely on hypogeous fruit bodies. Thus, from an ecosystem standpoint, in order for managers to protect these megafauna, they must understand the direct connection to a basic food web component, the fungi.

3. *Fungal plant pathogens* Typically we perceive disease-causing fungi as agents of destruction and gauge their impact by the volume of timber destroyed. Although this is an important consideration, ecosystem management goes beyond timber management by recognising diseases as important processes that create forest structure vital to other species and processes. In addition to providing organic matter for nutrient cycling, for example, standing dead snags or heart rot in live trees create needed habitat for primary cavity nesting birds and secondary cavity users. Forest gaps created in root rot pockets allow for development of understorey plants, contributing to both species richness and increasing browse for large mammals such as deer and elk. Schowalter *et al.* (1997) provide a framework for

integrating the ecological roles of pathogens in managed forests.

4. *Mycorrhizal mutualisms* The benefits of mycorrhizas to plants are well documented and include efficient nutrient uptake, especially phosphorus; enhanced resistance to drought stress; and direct or indirect protection against some pathogens. From an ecosystem standpoint, mycorrhizal benefits extend much further in space and time. In addition to participation in nutrient cycling and food web processes, mycorrhizal fungi provide linkages among plants that affect plant community development and resiliency. Our research has emphasised an understanding of the mycorrhizal specificity between potential plant hosts and fungal association, with direct relevance to the ability of plants to be connected by commonly shared mycorrhizal fungi (Molina, Massicotte & Trappe, 1992). Indeed, many fungi can form mycorrhizas with diverse plant species, including across plant families. Brownlee *et al.* (1983) and Finlay & Read (1986) showed that carbon (photosynthates) can move from a donor to a recipient plant when connected by a common fungus. Simard et al. (1997) later showed under field conditions that a net flow of carbon can move from a donor plant to a shaded recipient plant via mycorrhizal fungus linkages. Thus, understorey plants may receive partial nourishment from overstorey plants via a shared mycorrhizal fungus network.

   Interplant linkages are equally important for other ecological reasons. During early plant succession, pioneering plants maintain or build the mycorrhizal fungal community by supporting it with photosynthates. Late-seral plants can develop mycorrhizas with many of the same fungi supported by early-seral plants and thus benefit from the ongoing active mycorrhizal processes. We believe that the positive feedback interactions of these plant-fungal associations in space and time contribute to ecosystem resiliency after disturbance (Perry *et al.*, 1989; Molina *et al.*, 1992).

### *Fungal communities*

Little is known about the impacts of forest management activities on fungal communities in the Pacific Northwest. To manage effectively for the diversity of forest fungi, it is necessary to identify the fungal species within forests, describe their community structure in space and time, and understand the impacts of both human-induced and natural disturbances on successional dynamics of forest fungi. This approach places fungi into the same context as that of understanding the dynamics of plant communities, a context relevant to forest managers. Data from fungal community studies provide the basis for addressing critical research topics including (1) conservation biology of rare fungal species; (2) fungi as important indicators of forest community dynamics; (3) sustainability of edible, commercially harvested fungi; and (4) development of habitat models for fungi. In this section, we describe some of the primary considerations in setting objectives for the study of fungal communities and then describe our current approaches to determining fungal conununities in forests of the Pacific Northwest. Examples of a few studies are given.

### *Description of fungal communities*

The first step in setting study objectives is defining what the phrase fungal community means. In its simplest definition, a community is a group of organisms sharing a particular place. Community structure is characterised by the numbers of species present, their relative abundance, arid the interactions among species within the community. Characteristics of communities emerge from historical and regional processes. Thus, it is important to define clearly the time and space boundaries of the study. For example, the problem of determining changes in fungal species on a recently dead tree or log differs from problems associated with examining the succession of forest floor fungi over several hundred years of forest development.

If specific functional groups or processes are selected for study, then a guild concept can help to focus the community definition. A guild is a group of species that uses various resources or shares a common function, such as fungi that form ectomycorrhizas or that decompose wood. Studies of fungi, plant host, and environmental relations often target a particular guild. Because ectomycorrhizal fungi have been the focus of most fungal community studies in the Pacific Northwest, they receive primary attention in this section.

Several factors influence mycorrhizal community structure, including plant species and habitat conditions, such as tree composition, tree age, disturbance, and soil nutrients (Molina *et al.*, 1992; Vogt *et al.*, 1992; Gehring *et al.*,1998). The objectives for a community study might examine one causative factor or a combination of factors for effects on community development. The selection of factors strongly influences the study design and sampling intensity. For example, if one is interested in the effects of coarse woody debris (CWD) on ectomycorrhizal community structure, then a simple design of sampling fungi at different distances from large wood in similar forest stands might suffice. However, if one is also interested in the importance of CWD at different stages of forest development, or in forests of different tree densities, then a complex design with different forest treatments is needed, which increases sampling units, time, and expense.

As for most biotic communities, disturbance phenomena often trigger the successional dynamics of fungal communities. For example, changes in plant species composition from forest succession or large-scale disturbances significantly affect ectomycorrhizal species composition and total fruit body production (Dighton & Mason, 1985; Termorshuizen, 1991; Vogt *et al*., 1992; Amaranthus *et al*., 1994; North, Trappe & Franklin, 1997; Waters *et al*., 1997; Baar, Horton & Kretzer, 1999; Colgan *et al*., 1999). Fire and timber harvest are the two main disturbance events in Pacific Northwest forests. Several regional studies have shown a reduction in fruit body production or levels of ectomycorrhiza formation after forest thinning or fire (Harvey, Larsen & Jurgensen, 1980; Parke, Linderman & Trappe, 1984; Pilz & Perry, 1984; Waters, McKelvey & Zabel, 1994; Colgan *et al*., 1999). Severity and length of time since disturbance, however, are key factors in evaluating the effects of fire or tree death on the ectomycorrhizal community (Visser, 1995; Miller, McClean & Stanton, 1998; Horton, Cazares & Bruns, 1998; Jonsson, Dahlberg & Nilsson, 1999; Stendall, Horton & Bruns, 1999; Baar *et al*., 1999) and should be considered in examining fire disturbance effects on fungal community dynamics.

### *Ectomycorrhizal community analysis*

Once the scope and objectives of the study are clearly defined, the appropriate options for sampling the fungal community are considered. Approaches to ectomycorrhizal community analysis include collection of fruit bodies, morphological typing of mycorrhizas, and molecular identification of fungal symbionts. Each approach differentially estimates species dominance. For example, fruit body studies address food resource questions about mammal mycophagy based on fruit body biomass. Identification of mycorrhizal symbionts on root tips best addresses the fungal ommunity transporting nutrients to the host or fungal symbionts available for microarthropod mycophagy. Selection of an approach depends on the objectives of the study. Each approach has strengths and weaknesses in regard to sampling intensity, skills needed, and accuracy in assessing species occurrence, especially at broad spatial scales. These approaches are not mutually exclusive, and most researchers are using a combined approach.

Fruit body surveys poorly reflect the composition of subterranean ectomycorrhizal communities, thereby making interpretations difficult at the community level (Danielson, 1984; Gardes & Bruns, 1996; Dahlberg, Jonsson & Nylund, 1997; Karen *et al.*, 1997; Gehring *et al.*, 1998; Jonsson *et al.*, 1999). Inherent problems with fruit body surveys include the sporadic production of fruit bodies, infrequent surveys, and the omission of easy-to-overlook fruit bodies such as resupinate forms found on the underside of woody debris.

Identification of ectomycorrhizal root tips to broad morphological types (Zak, 1973) became a popular alternative to fruit body collection for defining ectomycorrhizal communities. This method, refined by Agerer (1987-1998), Ingleby, Mason & Fleming (1990), and Goodman et al. (1996), has been applied to glasshouse soil bioassays, as well as field studies. Morphological typing of mycorrhizas is time consuming and taxonomic resolution is low.

More recently, the application of molecular techniques, in particular PCR-RFLP (polymerase chain reaction-restriction fragment length polymorphism) analysis and DNA sequencing, to mycorrhizal community research has improved our ability to identify morphological types to family, genus, or species level (Gardes *et al.*, 1991; White *et al.*, 1990; Gardes & Bruns, 1993; Bruns *et al.*, 1998). Although not a panacea, PCR-based methods significantly improved the study of ectomycorrhizal communities and have enhanced our ability to investigate fundamental aspects of ectomycorrhizal communities in several forest types (Gardes & Bruns, 1996; Dahlberg *et al.*, 1997; Gehring *et al.*, 1998; Horton & Bruns, 1998; Taylor & Bruns, 1999). They allow comparison of the observed diversity of fruit bodies with that of root tips and allow us to study known species that do not grow in culture. Additionally, molecular techniques are useful for taxonomic placement of fungal symbionts to the family level in forests where species fruit infrequently or not at all. Similar to challenges with morphotyping, studying the mycorrhizal community with molecular techniques is time consuming and may require restricting sample size. Restricted sampling might inadequately reflect the wide variances typically seen in ectomycorrhizal root tip community studies.

### *Current fungal community studies in the Pacific Northwest*

Given the size of the region, the diversity of forest types, and the longterm nature of fungal community studies, we have focused on key forest habitats or forest management issues that affect not only fungi but the overall ecosystem management as well. This approach provides the best opportunity to interpret mycological findings and integrate results into forest management plans. It is also cost effective because large-scale forest manipulations are often prohibitively expensive for stand-alone mycological studies.

Because conservation of old-growth forests is a major concern in the Pacific Northwest (only about 10% of the original old-growth forest remains), we have compared the ectomycorrhizal fruit body diversity (both mushroom and truffle) in old-growth (> 400 years old) to younger stands (30-60 years old) of Douglas-fir. We have found a similar number of species in old-growth compared to younger stands. However, the species composition differs, and the number of unique species is greater in old-growth versus younger stands (J. Smith and others, unpublished data). These results provide evidence that some fungal species require old-growth forest habitat and that protecting the remaining old-growth forests is important for maintaining fungal species diversity.

Many forest management experiments in the Pacific Northwest focus on accelerating development of old-growth structure by using various silvicultural approaches such as thinning, green-tree retention, and prescribed burning to return forest tree composition to that found before European settlement and wide-scale fire suppression. We currently have several integrated studies under way in large-scale forest management experiments that examine the effects of these management treatments on fungal diversity and function. One, done in conjunction with the Ecosystem Study in the state of Washington (Carey, Thysell & Brodie, 1999), is designed to manipulate forest stands 60 to 80 years old to hasten their return to old-growth structure and provide habitat for the northern spotted owl (Strix occidentalis); the owl is currently absent from these experimental study sites. The experiment examines silvicultural effects on the diversity of important food web functions. The focus of this study is on the truffle community because this is the primary food base for small mammals, which in turn are the main prey of the northern spotted owl. Our results (Colgan, 1997; Colgan *et al.*, 1999) describe the community structure of dominant truffle species in the treated stands and in small-mammal diets. A key finding was that truffle species dominance shifts under different forest thinning regimes. Within these managed stands, several truffle species fruit year-round, thereby providing an essential food base during winter months. These species can thus be considered keystone species in the ecosystem food web. This type of fungal diversity study allows managers to understand the role of maintaining fungal communities and how specific silvicultural treatments affect their diversity, abundance, and function.

Many forests in the Pacific Northwest and throughout the Western United States are experiencing decline, primarily because of fire suppression and silvicultural management. Decades of fire suppression and selective tree harvest have yielded dense forests of shade-tolerant tree species prone to water stress and catastrophic insect disease outbreaks (Agee, 1993). Forest managers are experimenting with prescribed fire and thinning to improve overall forest health. These experiments also lend themselves to investigating effects on the fungal community. J. Smith and others (unpublished data) are examining the effects of burning and thinning on the fungal community in ponderosa pine (*Pinus ponderosa*) forests. By using primarily PCR-RFLP techniques to document changes in ecto-mycorrhizal fungal community structure they found that fire communities are dominated by few ectomycorrhizal species. Such species may be important to ecosystem resiliency after fire disturbance.

In addition to the studies mentioned above, Pilz & Molina (1996) describe many of the current efforts in the Pacific Northwest aimed at documenting the biological diversity, function, and community dynamics of forest fungi. Additional studies are also under way to examine management treatments such as variable thinning, presence of large woody debris, and soil compaction on fungal diversity and shifts in species dominance. By understanding the effects of various management practices on fungal communities, forest managers can integrate fungal diversity and function into forest management planning.

### *Population biology*

An effort to conserve species, especially rare species, must include some understanding of the population structure and dynamics of the species in question. Our understanding of the population biology of fungi, however, lags far behind that of other taxa for many reasons described below. To deal with the issue of rare fungal species within the Northwest Forest Plan, we thought it important to begin a research programme that explores ways to examine the population structures representative of forest fungal species. Such exploratory research requires large sample sizes not easily obtained from populations of rare taxa so the initial research projects described below are focused on species that are common but represent different life history strategies found in ectomycorrhizal fungi. As techniques become refined, we will address similar questions with rare species.

Two long-term goals of our population genetic research on ectomycorrhizal fungi are to gain some understanding of how past and current land management practices in the Pacific Northwest have altered the dynamics of fungal populations and to use this information to predict how future land management scenarios may affect persistence of fungal populations. Achieving these goals requires an understanding of the spatial and temporal scales at which evolutionarily significant processes occur within and among fungal populations, which processes are most important at spatial scales relevant to management, and how spatial heterogeneity in landscape structure affects these processes (Wiens, 1989, 1997).

### *Problems inherent to the study of fungal populations at forest landscape scales*

Meaningful analysis and interpretation of genetic spatial patterns requires that the extent of any selected study area be large enough to encompass multiple units (discrete populations) affected by gene flow and that individual samples (grain) be dispersed such that variance of process effects within each unit can be quantified (Wiens, 1989). Several ecological characteristics of fungi impede our ability to select scales appropriate for quantifying the relative importance of genetic drift, natural selection, and gene flow within and among populations. Selecting an appropriate extent and grain for population genetic studies requires an understanding of how individuals are distributed across the landscape and how much area discrete populations can cover. This presents an obstacle with fungi because the mass of thread-like mycelium (thallus) that gives rise to fruit bodies is frequently hidden from view. Attempts to characterise the size and distribution of discrete thalli have identified individuals encompassing hectares (Smith, Bruhn & Anderson, 1992), square metres (Baar, Ozinga & Kuyper, 1994), and square centimetres (Gryta *et al.*, 1997). Dahlberg & Stenlid (1990) have also shown that ecological factors such as forest age can influence the size of individuals and alter the mechanism (sexual or vegetative) by which new thalli are established. The range and variance of individual size and distribution unique to each fungal species will dictate the scale at which population boundaries should be encountered, and set the minimum size limit for study area extent.

When sampling fungi in the field, it is impossible to discern what proportion of the fruit bodies collected represent genetically identical individuals, and genetically distinct mycelium masses may produce many fruit bodies simultaneously. Discrete thalli can be established either by sexual reproduction (genets), selfing, or clonal vegetative propagation (ramets) (Todd & Rayner, 1980); evolutionary interpretations hinge on correct estimates of the contribution of each reproductive type to the genetic diversity observed within populations (Avise, 1994). Estimating proportional contributions of individual genets and ramets to the total genetic diversity in a population may not be intuitive. Depending on the mating system of the species, a maximum of 25% or 50% of the monokaryotic spores produced by an individual fruit body can potentially grow and fuse to form genetically novel dikaryotic genets so closely related to the parent mycelium that the two may fuse (Smith et al., 1992). This type of fine-scale genetic structuring coupled with variance in genet size can bias allele frequency and gene flow estimates such that potential dispersal distances are underestimated. Results that are misleading owing to lack of knowledge of fungal reproductive behaviour can lead to poor development of management options.

### *The conceptual foundation of our research approach*

Determining the appropriate scale at which to ask management-oriented questions about fungal population dynamics requires the design of a nonarbitrary, objective method to determine the scales at which important evolutionary processes produce particular genetic spatial patterns. Observations from a mismatch of spatial scales (scale of measurements differs from scale at which the process of interest is acting) can result in erroneous identification of pattern-processes relations because the types or relative influences of processes may change as new spatial domains are entered (Wiens, 1989). For example, at fine scales, biotic factors such as inter- and intraspecific competition, forest stand age, species composition of understorey shrubs, and type and severity of disturbance history may be strongly correlated with patterns of genetic variability. At broad geographic scales, abiotic factors such as climate, rainfall patterns, exposure, and elevation may strongly influence patterns of genetic variability. Fine-sale processes may exert control over the total amount of genetic variability on which large-scale processes can act, and thus may be more relevant to management issues.

Delimitation of fungal population boundaries and identification of dispersal barriers require the development of sampling techniques that facilitate accurate gene flow estimates at forest stand, watershed, and regional spatial scales. These sampling techniques must also account for heterogeneity in landscape cover, disturbance type, and disturbance intensity at each scale. The ultimate goal of such a multiscale sampling regime is to ensure that the scale of measurements and the response of fungal populations to some variable of interest (for example disturbance) fall within the same spatial domain. Variability across fungal species in individual size and distribution, mating system, and dispersal capability makes it impossible to apply a single sampling protocol to all species. Long-term advancement in understanding evolutionary processes critical to maintaining genetic variability in fungal populations requires basic research on how genetic variability in species with different life histories is partitioned at different spatial scales. This fundamental research will lay a general foundation for predicting how land management strategies may affect rare species depending on their life histories. Multiscale genetic studies will also help define scales potentially appropriate for future research on demographics or habitat requirements.

### Current research examples

Building a strong knowledge base requires that basic genetic research be done on model species that will yield large sample sizes and exhibit reliable fruit body production from year to year. One example is the distribution of genetic variation across different spatial scales in three model genera: *Cantharellus*, *Rhizopogon*, and *Suillus*. Research on such common species will provide initial studies with the statistical power sufficient to correctly identify evolutionarily important pattern-process relations (Dizon, Taylor & O'Corry-Crowe, 1995). Golden chanterelles (*Cantharellus formosus*) are an economically important, epigeous fungus that forms mycorrhizal associations with various host species over a broad geographic range (Molina *et al.*, 1993). *Rhizopogon vinicolor* is an ectomycorrhizal species in the Boletales that forms hypogeous, truffle-like fruit bodies but is closely related to epigeous boletes in the genus *Suillus*, including *S. lakei* (Bruns et al., 1989). Both *R. vinicolor* and *S. lakei* are common and distributed throughout the range of Douglas-fir. All three fungal species fruit predictably and abundantly and provide ideal model species with which to initiate base-line genetic studies because they represent diverse life histories in respect to spore dispersal. The epigeous fruit bodies of *Cantharellus formosus* can remain on the landscape continuously producing basidiospores for over a month (Largent & Sime,1995), whereas *Suillus lakei* mushrooms are more ephemeral. Assuming that wind is the primary mechanism of spore dispersal for these two species, the potential for long-distance wind dispersal over time is most likely lower in S. lakei than in *C. formosus*. In contrast, *R. vinicolor* is primarily dispersed by small-mammal mycophagy

(Maser, Maser. & Trappe, 1985) and might be more spore dispersal limited than the two wind-dispersed species. Research on these three species is being undertaken currently by independent scientists in study areas that overlap so that results will be comparable across the life-history types.

Characterisation of genetic patterns at different spatial scales requires multiple, independent, hypervariable markers that measure variation within the nuclear genome of the organism of interest (Bossart & Prowell, 1998). Comparative studies of population-level markers have shown that the use of short, tandemly repeated DNA sequences (microsatellite repeats) is an effective method for detecting variability where other genetic markers fail (Hughes & Queller, 1993). These valuable molecular markers do not exist for any ectomycorrhizal basidiomycete fungus but are under development for these three focal species.

At landscape scales, patterns of genetic isolation and indirect estimates of gene flow among populations are calculated by using estimates of variance in allele frequencies within and among sampling units (Wright, 1951; Slatkin & Barton, 1989). Precision of these statistics requires that sampling units do not encompass multiple random breeding units (genetic neighbourhoods) (Magnussen, 1993; Ruckelshaus, 1998). Wright (1969) showed analytically that as more neighbourhoods are included within sampling units, the genetic variance among sampling units relative to the total variance declines, and the power to detect spatial genetic structuring is lost. Progressing to landscape-scale studies requires that we understand the scale at which random mating occurs in these species. Spatial autocorrelation analysis of genotype locations within forest stands allows estimation of the diameter of areas where random mating occurs (that is, genetic neighbourhoods) via description of isolation by distance patterns over the space that a species occupies (Sokal & Oden, 1991; Epperson, 1993). The information necessary for spatial autocorrelation studies includes mapped locations of fruit bodies collected over a broad range of distances, the distance between every pair of sample points, and the genotypes of each fruit body at multiple, independent loci. Test statistics are calculated for the null hypothesis that the genotypes are randomly located across the study area. Spatial autocorrelation studies are currently under way for *C. formosus, S. lakei,* and *R. vinicolor* in overlapping study areas.

Results of this research will aid in the design of a sampling method that will capture informative variability in genetic patterns and processes at spatial scales relevant to management. Future research efforts will apply the sampling techniques, currently in development, to the study of how heterogeneity in landscape features (for example forest stand age, patterns created by different disturbance regimes) affects rates of gene flow between populations of fungi. Using this line of research to develop a better understanding of how fungi disperse across landscapes will facilitate identification of geographic areas important to the conservation of genetic diversity.

## Applications in inventory and monitoring

### *Identifying and prioritising rare species*

Protecting rare species is often a prominent component in conservation programmes, regardless of the scale of the conservation effort. Resources for study of species biology are scarce, and society places a high value on maintaining rare species. Understanding the causes and consequences of species rarity is important because it is a basis for setting conservation priorities. Thus, it is important that mycologists identify fungal species that are most rare or at risk as one basis for allocating resources to studying particular species.

As noted in our introduction, the Survey and Manage guidelines of the Northwest Forest Plan provide protection of rare, old-growth forest dependent fungi. The species list was compiled by three expert regional mycologists, Joseph Ammirati, William Denison, and James Trappe, and was based on their extensive experience and personal records from over 30 years of collecting macrofungi throughout the region. The list includes gilled, cup, polypore, and truffle fungi (Table 3.1). Within the Survey and Manage programme, each listed species represents a set of hypotheses. Each species is thought to be (1) rare, (2) associated with old-growth forests or legacy components of old-growth forests such as coarse woody debris and (3) not adequately protected by the reserve land allocations and management actions to protect needed habitat. The Survey and Manage programme of work addresses these three hypotheses so that appropriate protection measures can be taken to assure species persistence.

The Survey and Manage conservation programme provides protection only for rare, old-growth forest associated species; we will address some of the unique considerations in conducting extensive surveys for those species in the next section. Two other conservation approaches also have been useful for identifying and prioritising rare fungal species in the Pacific Northwest, Natural Heritage programmes and Rarity, Endangerment, and Distribution lists (RED lists - hence, Red Data lists). These programmes are operated at state levels and cover all species, geographic

Table 3.1. *Fungal genera and number of species listed under the Survey and Manage guidelines of the Northwest Forest Plan*

| Genus | Number of species | Genus | Number of species |
|---|---|---|---|
| *Acanthophysium* | 1 | *Hebeloma* | 1 |
| *Albatrellus* | 4 | *Helvella* | 4 |
| *Alpova* | 2 | *Hydnotrya* | 2 |
| *Arcangeliella* | 3 | *Hydnum* | 2 |
| *Asterophora* | 2 | *Hydropus* | 1 |
| *Baeospora* | 1 | *Hygrophorus* | 3 |
| *Balsamia* | 1 | *Hypomyces* | 1 |
| *Boletus* | 2 | *Leucogaster* | 2 |
| *Bondarzewia* | 1 | *Macowanites* | 3 |
| *Bridgeoporus* | 1 | *Marasmius* | 1 |
| *Bryoglossum* | 1 | *Martellia* | 4 |
| *Cantharellus* | 3 | *Mycena* | 5 |
| *Catathelasma* | 1 | *Mythicomyces* | 1 |
| *Chalciporus* | 1 | *Neolentinus* | 2 |
| *Chamonixia* | 1 | *Neournula* | 1 |
| *Choiromyces* | 2 | *Nivatogastrium* | 1 |
| *Chromosera* | 1 | *Octavianina* | 3 |
| *Chroogomphus* | 1 | *Omphalina* | 1 |
| *Chrysomphalina* | 1 | *Otidea* | 3 |
| *Clavariadelphus* | 6 | *Phaeocollybia* | 13 |
| *Clavicorona* | 1 | *Phellodon* | 1 |
| *Clavulina* | 2 | *Pholiota* | 1 |
| *Clitocybe* | 2 | *Pithya* | 1 |
| *Collybia* | 2 | *Plectania* | 2 |
| *Cordyceps* | 2 | *Podostroma* | 1 |
| *Cortinarius* | 13 | *Polyozellus* | 1 |
| *Craterellus* | 1 | *Pseudaleuria* | 1 |
| *Cudonia* | 1 | *Ramaria* | 28 |
| *Cyphellostereum* | 1 | *Rhizopogon* | 12 |
| *Dermocybe* | 1 | *Rhodocybe* | 1 |
| *Destuntzia* | 2 | *Rickenella* | 1 |
| *Dichostereum* | 1 | *Russula* | 1 |
| *Elaphomyces* | 2 | *Sarcodon* | 2 |
| *Endogone* | 2 | *Sarcosoma* | 2 |
| *Entoloma* | 1 | *Sarcosphaera* | 1 |
| *Fayodia* | 1 | *Sedecula* | 1 |
| *Fevansia* | 1 | *Sowerbyella* | 1 |
| *Galerina* | 5 | *Sparassis* | 1 |
| *Gastroboletus* | 5 | *Spathularia* | 1 |
| *Gastrosuillus* | 2 | *Stagnicola* | 1 |
| *Gautieria* | 2 | *Thaxterogaster* | 2 |
| *Gelatinodiscus* | 1 | *Tremiscus* | 1 |
| *Glomus* | 1 | *Tricholoma* | 1 |
| *Gomphus* | 4 | *Tricholomopsis* | 1 |
| *Gymnomyces* | 2 | *Tuber* | 2 |
| *Gymnopilus* | 1 | *Tylopilus* | 1 |
| *Gyromitra* | 5 | | |

locations, and habitat types within the state (see, for example, Washington Natural Heritage Program, 1997). Both approaches use similar criteria to evaluate species and ranking systems that assign risk status. Species evaluation criteria include pattern of occurrence in space and time, vulnerability of habitat, direct and indirect threats to species decline, degree of protection under current management guidelines, and taxonomic uniqueness. Rankings are based on number of occurrences (rarity), number of individuals, population and habitat trends, and type and degree of threats. Status categories under the natural heritage programme include: endangered, threatened, sensitive, and possibly extinct or extirpated in the state. Two other categories, review and watch, are assigned to species of uncertain status for which additional information is needed before it is assigned to one of the four previous categories.

Red Data lists serve several purposes for fungi (see Arnolds, 1989). They alert mycologists and conservation biologists to issues surrounding rare fungal species and provide information to managers and policy makers responsible for the management and protection of the species. Some of the listed species are useful as candidates for long-term monitoring of status and trends of fungal populations. Scientists can also compare lists from different geographical areas to estimate national and international status of individual species.

Nearly 25 years ago the first reports concerning a decrease in fungal species diversity and the abundance of fungal fruit bodies across a wide geographic area originated from Europe (Schlumpf, 1976; Bas, 1978). This awareness led to creation of Red Data lists in 11 different European countries in the next 15 years (Arnolds & De Vries, 1993). Attention to this phenomenon outside northern Europe was lacking until recently.

In conjunction with the species information generated by the Northwest Forest Plan process, another regional assessment on the ecosystems of eastern Oregon and Washington, and the western parts of Idaho (called the interior Columbia River basin assessment; see USDA & USDI, 1996) led to the inception of the first Red Data lists of macrofungi for any large geographic area outside of northern Europe (Castellano 1997*a*, 1997*b*). The Red Data list for Oregon contains 118 species of macrofungi. It is smaller than the Survey and Manage list for Northwest Forest Plan lands because it evaluates species across the entire state and across all habitat, not just late-successional forest habitat. Some species that are rare on protected Federal land are sometimes more common in younger stands or on other land ownership. The interior Columbia River basin assessment yielded a Red Data list of macrofungi for Idaho (Castellano, 1998) containing nearly 200 fungal species of special concern. Simultaneously, J. Ammirati developed a working list of 57 rare macrofungi for Washington (Washington Natural Heritage Program, 1997). These three listing efforts are considered preliminary. Additional systematic and strategic sampling of habitats is critical to uncover previously undiscovered occupied sites for many of these species. Significant efforts are under way by the USDA Forest Service and USDI Bureau of Land Management to collect these fungi in these regions.

As more fungal surveys occur, these lists will likely change. It is important that mycologists update Red Data lists and other lists, such as those for Natural Heritage programmes, and disseminate the information so that the mycological community and the public can stay abreast of ongoing efforts in cataloguing rare species, prioritising them into risk categories, and monitoring our success in providing for their conservation. As lists are developed for different parts of the world, we can better understand distribution patterns of rarity and key habitats needed for their protection. We also can begin to understand some of the natural and anthropogenic factors that lead to fungal species rarity.

## ***Methodological considerations in fungal inventories***

The Survey and Manage guidelines of the Northwest Forest Plan centre around the adaptive management principle of first providing for species at known sites by appropriate management of habitat (manage) and simultaneously searching for new locations (survey) to learn more about the rarity, range, distribution, and habitat requirements. Gathering range and habitat information for over 200 rare fungal species in a region the size of the Northwest Forest Plan is unprecedented in scope for any fungal inventory programme. Originally, the surveys were to be conducted for at least 10 years to collect enough new information to develop science-based management plans for maintaining species persistence. Given the above survey objectives, several considerations needed to be addressed for effectively implementing regional-scale surveys. This section highlights several fundamental areas that we considered in conducting broad-scale fungal surveys and inventories.

### *Taxonomic expertise*

Taxonomic knowledge is the cornerstone of biology and is essential in efforts to conserve biodiversity. Fungal taxonomy is problematic because our understanding of species is limited; Hawksworth (1991) estimated that less than 5% of the mycota has been described in the scientific literature. Even in well-known and economically important fungal groups, new species are continually described and some species concepts are in flux (e.g. Redhead, Norvell & Danell, 1997; Hughes *et al*., 1999; Sime & Petersen, 1999).

Taxonomists are scarce because of a shift in academic programmes toward molecular systematics and ecology. The depleted ranks of classical fungal taxonomists can be augmented, however, by a cadre of experienced parataxonomists, people with less formal schooling in mycology, who are trained and gain significant experience in fungal identification. Over the past three years, we have trained many Federal agency biologists and botanists in the proper identification and handling of fungal specimens. Such training is essential to conduct the regional surveys. Training also increases the awareness of field staff and managers about the natural history of fungi.

Even when accurate identifications are performed, observations of species occurrences are anecdotes unless a voucher specimen is deposited in a publicly accessible herbarium (Ammirati, 1979). Properly documented voucher collections allow experts to confirm the identification of potentially rare species. We have entered into formal partnerships with regional university herbaria to access the many fungal specimens collected from regional surveys.

### *Survey approaches*

Biological surveys need clearly defined goals. This is also the case when surveying for both rare and potentially rare species. Clearly stated goals and prioritisation of those goals allow one to define which data to collect, where and when to survey, and which species to collect. One can prioritise by species, ranking from most to least important, or by geography, ranking different habitats or regions, for example, by where the most species are expected to occur, or by where there are the least historic data. In practice, with planning and organisation,. multiple goals may be pursued simultaneously. For example, one can visit sites of the rarest species, and while in the vicinity, survey high-priority habitats.

*Prioritising species for survey* Ranking species according to rarity is probably the most frequent approach to conservation prioritisation. We use most of the ranking criteria developed by the natural heritage programmes mentioned previously. These criteria evaluate the rarity and distribution of species, with the highest priority assigned to potentially extinct species, followed by critically imperilled species (typically known from five or fewer locations). The criteria are applied at both the global and local (state) scale, so a species can be extinct in the state, but globally secure. The rank also is evaluated as to the certainty with which it can be applied, and the certainty of taxonomic status.

Once species are prioritised, the task of locating begins. Either historic sites or potential habitat can be targeted; both approaches can be challenging. The rarest species are likely to be known only from historical records that may lack the precision necessary to find the site. Similarly, habitat for rare species is usually poorly defined. Two important goals for visiting historic sites include documenting whether the species still occurs there, and gathering habitat data. An additional bonus comes, not uncommonly, when other rare species are found at such historic sites.

*Prioritising regions for survey* One approach to regional prioritisation is determining appropriate habitat. In many cases, however, species habitat preferences are not known. Herbarium labels are notoriously vague about habitat, with such descriptors as ‘in woods’, ‘under pine’, or ‘in conifer forests’. Nevertheless, for some species there are relatively narrow host or habitat requirements that can guide one to areas of interest. For example, *Gelatinodiscus flavidus* is a rare ascomycete that fruits only on the foliage of *Chamaecyparis nootkatensis*, a conifer with a fairly restricted distribution. Another example is the number of species on the Survey and Manage list that fruit in montane forests, usually including *Abies*, near melting snowbanks. Where specific habitats can be identified, prioritising surveys in those habitats can often extend the documented range of a species.

A second approach that we have used with good success is visiting data-poor areas. The existing regional database of known site locations is analysed to identify a data-poor area, that is an area with few known sites of targeted rare species. After gathering herbarium data for about 135 putatively rare species of fungi, it became apparent that much of the data resulted from a few mycologists visiting a restricted set of collecting areas (Castellano & O’Dell, 1997; Castellano *et al.*, 1999). The data were obviously biased, raising the question of how to use it to best advantage. We have used GAP analysis following the procedures of Kiester *et al.* (1996) to analyse regional distribution of rare fungi site locations and select priority areas for survey. This approach has the advantage that when observations of a species of interest are made in data-poor areas, they are likely to extend the known range or habitat amplitude for the species. Many new observations of Survey and Manage fungi have resulted from applying this strategy (Castellano et al., 1999).

### *Survey techniques*

After selecting where and for which species to survey, one must design an effective survey method. Again, survey methods must have clear objectives. For example, finding occurrences of rare species requires a different approach than testing a hypothesis about their habitat preferences. We have used two primary methods, controlled intuitive and systematic or random sampling methods.

*Controlled intuitive survey* Controlled intuitive survey is the simpler of the two methods. Once the site has been determined, surveyors travel to the site and survey the area, focusing on habitats or microsites where they think the target species is likely to occur. This approach relies on knowledge, experience, observation, and intuition, and may be the most reliable method for locating rare species.

*Systematic or random sampling methods* If information on relative abundance of species, or quantitative comparisons of different sites or habitats are needed, then methods that employ systematic random site and plot selection must be used that standardise survey intensity and meet statistical sampling assumptions. Plots that define a survey area are one way of standardising survey effort. Because fungi tend to occur in clustered patterns on the landscape, long narrow plots are often used; they are more efficient at sampling such distributions than circular plots (T. O'Dell, unpublished data). For truly rare species, however, random and systematic approaches may prove less useful than controlled intuitive surveys because of the low probability of encountering the species of interest. Adaptive sampling methods have been recommended for organisms that are patchily distributed and rare, as is the case for some fungi (Thompson, 1992). In this approach, sampling intensity is increased when the target species is encountered. For example, if a rare fungus is found, more plots or time could be added to the sample in the immediate or nearby vicinity. In this way, more useful information on its population size and habitat association can be gathered.

### *Limitations and inferences*

Uncertainty surrounds the field sampling of fungi. No matter how much sampling is done, species will be undetected owing to seasonal and annual variation in fruiting, limitations to the amount of area scrutinised, and inconspicuousness of fruit bodies. Most macrofungi produce fleshy, ephemeral fruit bodies. Unless sampling occurs during the exact time it is fruiting, a species might go undetected. In the Pacific Northwest, fleshy fungi can be collected every month of the year in one habitat or another, but we tend to sample during limited times to make the most of available survey resources. Some species, therefore, are overlooked simply because they fruit at times when most other species do not, and when we are unlikely to be sampling. During peak fruiting seasons, sampling every two weeks may fail to detect a significant fraction of species compared with weekly sampling (Richardson, 1970). Unless an intensive study is being conducted, however, repeated visits to a site may be impractical. Annual variation in species occurrence can be tremendous, with as little as 5% of species observed at sites in one year recurring the next year (O'Dell, Ammirati & Schreiner, 1999). Many repeated visits to a site are required to determine the presence or absence of a species at that site.

Although we have noted several difficulties in conducting broad-scale, systematic surveys for rare fungi, it is important that mycologists are not discouraged from pursuing the need for fungal inventories. We stress again the importance of defining clear objectives for the surveys, designing the appropriate methods to collect the needed information, and scheduling enough time to conduct the surveys to satisfy the original objectives.

## Modelling habitat as a tool in conserving fungal resources

Unlike conservation of rare plants and animals, which may entail reintroducing species into an area of suitable habitat as part of species recovery and conservation, the primary means of conserving rare fungal species requires protecting habitat and providing future habitat through land management planning. Currently, we understand poorly the specific habitat needs of most fungal species so it is difficult to develop land management options that provide for persistence of habitat and therefore the species. Even as we begin to collect habitat data from our regional surveys, it remains difficult to discern the key environmental and biotic habitat variables to which the fungi in question are responding. Because of this lack of knowledge, we have begun a fungal habitat modelling research project that will allow us to build suitable habitat indices, construct hypotheses around key variables, and then test the model for accuracy in predicting suitable fungal habitat. Because habitat modelling has rarely been attempted for fungi, in this section we first define habitat modelling and, its uses, and then describe unique considerations for modelling fungal habitat and our research approaches.

### *Habitat modelling: definition and uses*

A habitat model is an abstract representation of the physical and temporal space in which an organism lives, including the way it interacts with the surrounding biotic and abiotic environment (Patton, 1997). Habitat modelling can potentially be a powerful tool in the study of fungi and in fungal conservation biology for several reasons. Habitat modelling provides insight into the behaviour of a system and an understanding of the complex interaction between an organism and the environment. As a method for integrating data from diverse research areas, modelling also provides a formal organising framework for generating hypotheses, conducting data analysis, and assisting in determining research directions by helping to define problems and refine questions. Habitat modelling in particular can be used to develop ideas about the distribution and occurrence of forest fungi, thus contributing to the development of conservation strategies.

Land managers need to make decisions, regardless of whether they have sufficient data and understanding of ecosystems. By understanding habitat, we will be able to map geographic areas where particular fungal species are likely to occur. Once occurrence and species habitat relations have been established, simulation of habitat availability under different management scenarios and under various disturbances will allow projections of potentially occupied habitat over time. Although the Northwest Forest Plan mandates surveys for more than 200 species of fungi, limited resources are available for conducting those surveys. Models will help prioritise data-collection efforts by predicting areas where species exist or where more intensive sampling may be desirable (Kiester *et al.*, 1996). The GAP analysis mentioned as a rare species search prioritisation method illustrates a type of modelling that is helping to design regional survey strategies for forest fungi. Using models as ecosystem management tools helps managers to calculate risks of decisions and actions, and provides a method of accountability and support to land management decisions. This will be particularly helpful in developing sustainable harvest strategies for commercially valuable fungi and in predicting the impact of human intervention on fungal survival and productivity.

### *Habitat modelling: challenges and concerns*

What are the habitat needs of a given fungal species? We assume that fungal species are tightly linked biologically to their habitats; that these habitats can be detected, measured, and quantified; and that we are able to detect the fungus itself. Some are habitat specialists, restricted to one or a few host species or a unique vegetation type; others are habitat generalists, associated with various host plants or vegetation types. Our work investigates habitat requirements and modelling for fungal species that exhibit contrasting adaptation strategies: for example, aerial spore dispersal for epigeous species versus small-mammal dispersal for hypogeous species.

Guidelines for habitat model development (US Fish & Wildlife Service, 1981) have been used to generate models for mammals, fish, and birds. Habitat evaluation procedures provide quantification of habitat based on suitability and total area of available habitat. Variables are selected according to three criteria: (1) the variable is important to survival and reproduction of the species, (2) there exists a basic understanding of the habitat-species relation for the variable, and (3) quantifiable data are available and the variable is practical to measure. Few studies of fungi, however, have directly assessed any of these criteria.

We know little about fungal ecology in general, and until recently, we did not have the tools that allowed us to define the individual, let alone populations (see section on ‘Population biology’). Many fungal species disperse passively by wind; however, we do not know the probabilities associated with spores landing in suitable habitat and developing into a fungal individual. For many fungal species, nutritional mode is uncertain, thereby making it difficult to use ‘food source’ as a habitat variable. Taxonomic problems and database biases encumber the study of mycology, as mentioned in the previous section on survey difficulties. The issue of scale also arises when examining mycological data and attempting to define habitat variables. Mycologists often focus on the minutiae and are unaware of larger scale phenomenon that may affect fungal distribution.

### *Current modelling approaches*

We are compiling information and formulating a concept of habitat for several species. For forest fungi, we define habitat as all factors (biotic and abiotic) affecting the probability that a fungus can inhabit, survive, and reproduce in a given place and at a given time. A review of the published literature reveals potential habitat factors that fall into four broad categories: vegetation, climate, topography, and soils.

Vegetation may be the primary factor contributing to ectomycorrhizal fungal habitat, because of host specificity. Molina & Trappe (1982) recognise three groups of ectomycorrhizal fungi based on the relations to host species, ranging from highly host specific to host generalists. Decomposer fungi also show various levels of host-substrate specificity (Swift, 1982). We can use, therefore, the presence or absence of particular host species as an initial indicator for potential habitat. In addition to host specificity, forest stand age and structure, and disturbances such as timber harvest and fire contribute significantly to fungal habitat (see section on 'Fungal communities').

Soil organic matter, including humus and coarse woody debris (CWD), is a substrate for ectomycorrhizal fungi (Harvey, Larsen & Jurgensen, 1976) and decomposer fungi. The CWD may be particularly important as a moisture-retaining substrate, thereby allowing root tips to support active ectomycorrhizas in times of seasonal dryness, on dry sites, or after fire (Harvey, Jurgensen & Larsen, 1978; Amaranthus, Parrish & Perry, 1989, Harmon & Sexton, 1995). Although no data exist for determining quantities of CWD necessary to support viability of forest fungi in the Pacific Northwest, availability of CWD seems to be a factor in establishing some fungi as well as seedlings (Kropp, 1982; Luoma, Eberhart & Amaranthus, 1996). The presence of CWD, therefore, may be associated with habitat for certain fungal species.

Topographic and soil factors important to fungal habitat include elevation, slope, aspect, soil properties, and local microtopography. To date, no studies have presented significant correlations with any of these factors, although mycologists often use such factors intuitively to find forest fungi.

Climate is a complex factor in-fungal distribution and therefore habitat. Seasonal and ecological distribution of fungi as well as fungal productivity are partly determined by temperature and moisture (Norvell, 1995; O'Dell, Ammirati & Schreiner, 1999). Wilkins & Harris (1946) contend that moisture may be the most important single environmental factor controlling fungal reproduction. We know little, however, about the effects of climate on long-term survival of fungi or on timing of mushroom formation. Many scientific researchers, commercial mushroom harvesters and recreational forest users have much experiential knowledge as to when and where particular mushroom species are found. Knowledge- and rules-based modelling methods and expert systems capture such information; both quantitative and qualitative information can be synthesised (Starfield & Bleloch, 1991). In addition, the availability of digital maps and geographic information systems provide opportunities for linking our modelling rules with spatial databases and simulation models for other biological systems. Dreisbach, Smith & Molina (in press) provide more details on our current modelling approaches.

## Sustaining the commercial harvest of edible forest mushrooms

As noted in the introduction, conservation of fungi entails more than protecting rare species. Conservation includes sustaining populations of all fungal species, both rare and common. As described by Arnolds (1991), common fungi can become rare because of habitat loss or large-scale anthropogenic disturbances such as air pollution. The commercial harvest of common, edible mushroom species illustrates a human disturbance that might diminish fungal resources. This section describes our research programme aimed at understanding this resource so that we can continue to enjoy economic gain and culinary delights while sustaining the survival and reproduction of these valuable fungi. We outline edible mushroom harvesting issues and concerns, discuss results from various recent research projects, describe forest management implications of the findings, and consider future directions in edible mushroom research and monitoring.

### *Scope of issues*

Edible mushrooms have been widely collected from the forests of the Pacific Northwest since the 1860s when European settlers began hunting for mushrooms similar to species they had collected in their homelands. Some Native American tribes harvested mushrooms for various uses, but we lack evidence of widespread consumption (Kuhnlein & Turner, 1991). Regionally, amateur mushroom clubs and organised mushroom events date to the 1950s (Brown *et al.*, 1985), and now there are about 34 mycological societies based in the region (Wood, 2000). Academic mycological activities date back to the 1920s for the region. During the 1980s and early 1990s, commercial mushroom harvesting expanded dramatically. The increased public demand for wild edible mushroom-harvesting opportunities has affected all forest landowners in the Pacific Northwest, especially Federal forests.

Federal lands encompass a large portion of suitable mushroom habitat in the Pacific Northwest, and are managed for multiple use, including commercial forest products. Since the 1950s timber has been the major forest product, but environmental concerns and adoption of the ecosystem management philosophy defined in the introduction have led to dramatic

Table 3.2. Important nationally and internationally marketed wild mushrooms harvested from the forests of the Pacific Northwest

| Local common names | Latin name | Use |
|---|---|---|
| American or white matsutake, pine or tanoak mushroom | Tricholoma magnivelare (Peck) Redhead | Food |
| Morels | Various Morchella species | Food |
| Pacific golden chanterelle | Cantharellus formosus Corner (previously called C. cibarius, Redhead et al. 1997) | Food |
| White chanterelle | Cantharellus subalbidus Smith & Morse | Food |
| Hedgehogs | Hydnum repandum L. ex Fr.<br>Hydnuin umbilicatum Peck | Food |
| King bolete | Boletus edulis Bu11.:Fr. | Food |
| Oregon white truffe | Tuber gibbosum Harkn. | Flavouring |
| Oregon black trufe | Leucangium carthusianum (Tul. & C. Tul.) | Flavouring |

reductions in timber harvesting from Federal lands during the 1990s. In response to reduced Federal timber harvests, many forest workers broadened the range of commercial products that they harvested from forests. Other social and ethnic groups joined them for various reasons (Arora, 1999; Love, Jones & Leigel, 1998; Sullivan, 1998). The mushroom industry has benefited from and been encouraged by the development of international markets and increased use of wild mushrooms by gourmet chefs (Schneider, 1999). The harvest of nontimber forest products in general has become a widely recognised industry in the Pacific Northwest and globally (Ciesla, 1998; Lund, Pajari & Korhonen, 1998). In 1992, nearly 11000 people, employed full- or part-time, contributed over US$41.1 million to the economies of Oregon, Washington, and Idaho by harvesting and selling nearly 1.82 million kg (4 million pounds) of wild edible mushrooms (Schlosser & Blatner, 1995). Likely, the harvest has grown since then. Schlosser & Blatner (1995) state that over 25 species of mushrooms and truffles are commercially harvested in the Pacific Northwest. Table 3.2 lists the most economically important species. With the exception of some morels, all of the fungi in Table 3.2 are ectomycorrhizal.

### *Biological anti management concerns*

The magnitude of the commercial mushroom harvest in the Pacific Northwest has raised controversy about conservation of the mushroom resource, particularly regarding harvest effects on species viability and ecosystem function. As part of a comprehensive research programme for managing commercial mushroom harvests, we have conducted several public workshops to gather information on the primary concerns of resource managers, the mushroom industry, and the general public. Those concerns fall into four categories; we present them as a series of questions so readers can envision the scale and complexity of required mycological research.

> *Production and distribution*
>
> How many fruit bodies are being produced? How are they distributed across the landscape or within a given area? How does production differ during a season and from year to year? What is the actual or potential commercial productivity of a given area? What proportion of forest habitat is available and accessible for harvesting? What factors determine productivity and how might they be managed?
>
> *Mushroom harvesting*
>
> How can the sustainability of mushroom harvesting be. assured? What proportion of the crop can be harvested without unacceptable impacts on the fungus itself or other resources? What techniques will mitigate those impacts; does mushroom harvesting increase or decrease subsequent production? Is spore dispersal reduced by removal of immature mushrooms, and, if so, does it impair reproductive success and degrade genetic variability? Is fungal mycelium and subsequent mushroom production affected by search and harvest techniques such as raking, moving woody debris, or digging? Do numerous harvesters trampling the forest floor harm mushroom production? How important are commercially valuable species as food for wildlife, and is human competition for the resource significant?
>
> *Forest land management*
>
> How do various timber harvesting methods (clear cutting, thinning, host species selection) affect subsequent mushroom production? What is the impact of soil compaction or disturbance from logging activities? What are the relations between fire and subsequent mushroom production, especially for morels? How does the intensity and timing of fire influence edible mushroom production? What impacts do grazing, fertilisation, or pesticide application have on mushroom

production? Can mushroom production be improved through habitat manipulation (for example: planting tree seedlings inoculated with specific fungi, thinning understorey brush for sunlight and rainfall penetration, prescribed burning, or irrigation)? Can production be increased across the landscape by managing forests to attain tree age class, structure, and composition optimal for mushroom production?

*Biology and ecology*

What are the important reproductive events in the life cycle of a particular fungus species? How are new colonies or populations established and maintained? What causes them to diminish or perish? How important is spore dispersal to reproductive success, population maintenance, genetic diversity, or adaptability to unique microhabitats? How much genetic diversity exists within and among populations? Are there endemic, narrowly adapted, or unusual populations of otherwise common species? What are the growth rates of fungal colonies in soil and degree of mycorrhizal development by specific fungi on root systems? To what degree do other mycorrhizal or saprotrophic fungi compete with marketable fungi for colonisation sites on host roots or space in the forest soil?

Various measures have been adopted on Federal forest lands to ameliorate impacts until more is known about the long-term consequences of intensive commercial mushroom harvesting. Maintaining appropriate forest habitat is the most important and practical means of sustaining healthy populations of fungi. Essential habitat characters include appropriate host tree species for ectomycorrhizal fungi, coarse woody debris for wood inhabiting fungi and noncompacted soils for both saprotrophic and ectomycorrhizal fungi that fruit on the forest floor. Interim conservation measures that can be used until needed research and monitoring is conducted include no-harvest areas, fallow harvest rotations, limited harvest seasons or times, limited harvest permit numbers, limited harvest quantities, and incentives for leaving nonvaluable older specimens to disperse their spores. The approaches used in any given situation depend on land tenure, land management goals, mushroom values, availability of law enforcement, and especially, support for regulations among harvesters themselves.

Answering the questions above requires scientific investigations at various ecological scales. (soil microniches to regional landscapes) and by using various investigative methods. Some of our approaches are noted below.

### *Research findings and management implications*

In the Pacific Northwest, edible mushroom research is currently concentrated on the three most valuable and widely collected edible forest mushrooms: the American matsutake, morels, and chanterelles. The other species in Table 3.2 also deserve attention. The Forest Service and Bureau of Land Management sponsor many research projects in conjunction with the Pacific Northwest Research Station, but significant research is also being conducted by state universities and mycological societies. Collaboration among public land management agencies, private and corporate forest owners, research institutions, nongovernment organisations, researchers, managers, harvesters, and other stakeholders has greatly broadened the scope and enhanced the quality of past and present research projects. A summary of these research projects can be found in Pilz, Molina & Amaranthus (in press).

Many of the research projects being conducted in the Pacific Northwest are still active or not yet published. Our discussion, therefore, provides a cursory overview of emerging information as it applies to forest management and, where possible, citations for further information.

One of the first and most frequently asked questions about harvest sustainability was whether the greatly increased levels of harvesting would reduce subsequent levels of fruiting. Two approaches have been used to address this issue: experiments to examine harvesting impacts and monitoring projects to detect trends in productivity. Research conducted by the Oregon Mycological Society (Norvell, 1995) concurs with that found by Egli, Ayer & Chatelain (1990) in Switzerland, that picking mushrooms per se does not diminish subsequent fruiting over the period of a decade or more. Search methods, however, can have some impact. Recent studies (D. Pilz and others, unpublished data) of raking forest litter to find young matsutake suggest that raking into the mycelial layer can interfere with fruiting for several years, but that recovery is hastened by replacing the duff. These studies, however, do not address the long-term and broad-scale impacts of intensive commercial harvesting, forest management activities, or regional threats to forest health. Assessing these factors will require long-term monitoring and silvicultural research.

Several research projects in the Pacific Northwest have obtained baseline data on edible mushroom productivity: specifically, the seasonal (summed within a fruiting season) productivity per unit area (by using systematic sampling designs) of given forest stands or habitat types. These productivity values, derived from biologically diverse mixed-conifer stands, tend to be lower than edible mushroom productivity estimates reported elsewhere in the literature (Ohenoja & Koistinen, 1984; Ohenoja, 1988; Slee, 1991; Kalamees & Silver, 1993). Values range from less than 1 kg to as high as 20 kg per hectare per year for chanterelles and American matsutake (Pilz, Molina & Liegel, 1998; Pilz *et al.*, 1999). Typical values for commercially harvested stands range from 3 kg to 10 kg per hectare per year (Pilz & Molina, in press). A common goal of productivity studies conducted by the PNW Research Station is the development of statistically valid, practical and cost-effective monitoring protocols for edible mushrooms (Arnolds, 1992; Pilz & Molina, in press; Vogt *et al.*, 1992).

Sustaining harvests of edible mushrooms that are ectomycorrhizal depends on understanding the relations between the silvicultural characteristics of a stand and mushroom productivity. Tree species, age, growth rates, and density can all potentially influence the quantity of carbohydrates available to ectomycorrhizal fungi for growth and fruiting. Understanding these relations could lead to predictive models that would allow silviculturalists to ascertain the consequences of their stand prescriptions for mushroom productivity. The influence of thinning young stands on edible mushroom productivity is of particular interest in the Pacific Northwest because many forest tree plantations will be commercially thinned in the coming decades, especially on Federal lands where mushroom harvesting is allowed. Preliminary evidence indicates that heavy thinning (many trees removed) can substantially reduce mushroom productivity immediately after the harvest, but that lighter thinning (fewer trees removed) has a lesser impact on productivity (D. Pilz & R. Molina, unpublished data). The rate at which mushroom productivity rebounds as the remaining trees reoccupy a site has yet to be determined. Mushroom productivity might rebound to higher levels as the remaining trees grow more vigorously, but the complicating influence of soil compaction from ground-based thinning equipment will need to be factored into the interpretation of results.

Several genetic studies of edible mushrooms are showing greater species diversity than previously documented by alpha taxonomy. For instance, the west coast Pacific golden chanterelle, previously considered the same as the European *Cantharellus cibarius* Fr. has been shown actually to consist of three or more species, none exactly the same as *C. cibarius* (Redhead *et al.*, 1997; Dunham et cal., 1998). Similarly, morel studies in eastern Oregon have revealed five species of morels fruiting on a burned site, some not yet described (D. Pilz and others, unpublished data). Several mushroom species are harvested as ‘king boletes’ in the Pacific Northwest (*Boletus aereus* Fr., *B. barrowsii* Smith, and *B. edulis*), and *Boletus edulis* itself might actually comprise a species complex here. This level of species diversity is not surprising given the diversity of climates, habitats, soils, and ectomycorrhizal host tree species found in the region. The diversity does, however, present additional challenges to forest managers because unique ecological adaptations likely exist for each species, and they could respond differently to forest management choices. These are just a few examples of the management implications of recent edible mushroom research. Additional research and long-term monitoring are needed, however, to ensure the sustainability of widespread, intensive commercial mushroom harvesting and healthy populations of edible forest fungi.

### *Research and monitoring for sustainability*

Most of the abundant and commercially harvested forest mushrooms, with the exception of some morels, are ectomycorrhizal species. The plentiful carbohydrate nutrition they derive from forest trees probably contributes to their abundant fruit body production. Their mycelial colonies are long-lived, and harvesting does not seem to impair fruiting in the short term. Indeed, humans world-wide have harvested edible forest mushrooms since ancient times (Arora, 1999; and see Chapter 8). So, a perfectly reasonable question is, ‘Why bother monitoring their productivity in the first place?’

Managers of Federal lands in the United States are required to monitor the commercial harvest of natural resources to determine sustainable harvest levels and avoid degrading the environment. In addition to this legal mandate, some of the factors that have contributed to declines of edible mushrooms in Europe (Arnolds, 1991) and Japan (Hosford et al., 1997) are also beginning to impact forests in the Pacific Northwest. These factors include pollution from growing urban areas, thinning ozone, climate change, introduced pathogens, and intensive timber management. Lastly, in any system that has functional thresholds, changes in quantity can translate into changes in kind when the thresholds are exceeded. Commercially harvesting edible forest mushrooms for international markets arguably entails greater and more widespread harvesting pressure than existed historically, and changes such as reduced (or enhanced) spore dispersal or trampling could have unforeseen long-term consequences.

The effort and resources applied to monitoring should be commensurate with resource value, socially acceptable levels of risk, current understanding of how resilient a renewable resource is to harvesting, and perceived threats to the resource. Pilz & Molina (1998, 2000) have proposed a regional programme that combines short-term silvicultural research with long-term but modest monitoring activities. The proposed programme has three components. The research component is intended to develop predictive models relating silvicultural activities to mushroom productivity. Ideally, a widely applicable model can be developed from data on several mushroom species and a range of sites and forest types.

The two monitoring components entail commercially harvested sites and sites where neither mushroom nor timber harvesting are allowed. On the commercially harvested sites, landowners would give co-operating harvesters exclusive access to discrete areas in exchange for information on what is harvested each year. On the natural sites, landowners could co-operate with mycological societies to estimate productivity without harvesting the sampled mushrooms. With various landowners, sites, and co-operators scattered around the region, long-term monitoring of potential trends in fruiting could be accomplished with a minimum of investment by any one participating agency or organisation. The use of standardised sampling methods, prearranged analyses, and a web site for posting annual results would provide all participants with timely results and regular encouragement to remain involved. The flexible co-operative organisation of the monitoring programme would allow co-operators to join or leave the programme as their interest and budgets dictate, although the best information will come from sites that are monitored for many years.

Regardless of further developments in research and monitoring in the Pacific Northwest, commercial harvesting of edible forest mushrooms likely will continue. The resource promises to be renewable and sustainable as long as we maintain healthy forests, understand the impacts of our actions, and remain alert to possible trends.

## Concluding remarks

As noted throughout this chapter, our knowledge is sparse regarding the ecology and natural history of forest macrofungi. There are especially large gaps in our understanding of habitat requirements needed by species for maintaining healthy populations within changing landscapes. Thus, the challenge of conserving this biologically rich array of species remains considerable. Fungal conservation issues in the Pacific Northwest as outined are unprecedented in scale and scope, and so our research programme includes a broad suite of ecological topics that provide a broad knowledge base to apply mycological principles to forest management plans. We use an ecosystem approach to plan and conduct our research at different scales because it provides opportunities to work closely with other forestry and ecological disciplines so that results can be woven into integrated solutions for broad-scale forest management. Fungi are critical ecosystem components, and their immense biological and functional diversity perform essential processes that lead to ecosystem resiliency and health. Our ability to demonstrate and communicate this primary fungal characteristic to other biological scientists, land managers, and the public is key to promoting fungal conservation issues.

We offer the following set of summary statements for mycologists to consider when planning and conducting conservation efforts for fungi.

- Set clear objectives for the study or inventory project. Knowing how the information will be used, and by whom, will guide the assemblage and proper communication of the findings.
- Select the appropriate methodology to meet the objectives. Data should be collected at the same scale at which the organism or process of interest is operating.
- Address mycological concerns within the context of local and regional land and natural resource management issues. This allows for fungi to be considered as part of the land management planning process.
- Explore opportunities to work with research and management colleagues across science disciplines. When possible, conduct mycological investigations within integrated studies that include other taxa and shared objectives such as overall maintenance of biodiversity.
- Emphasise the characterisation of habitat for mycological studies. Protecting fungal habitat at various scales of space and time will provide the most likely solution to the long-term conservation of fungi.
- Develop monitoring projects to inventory fungi periodically at long-term study sites to detect trends in populations. Enlist the help of local mycological societies in data collection.
- Develop quantitative models to help managers make decisions.
- Publish literature and conduct workshops to educate land managers and the public continuously about the importance of

fungi in maintaining healthy ecosystems. They are critical allies and partners in helping to set the conservation agenda for fungi.

## References

Agee, J. K. (1993). *Fire Ecology of Pacific Northwest Forests.* Island Press: Washington, DC.

Agerer, R. (ed.) (1987-1998). *Colour Atlas of Ectomycorrhizas.* 1st -11th delivery. Einhorn-Verlag: Schwabisch Gmund, Germany.

Amaranthus, M. P., Parrish, D. S. & Perry, D. A. (1989). Decaying logs as moisture reservoirs after drought and wildfire. In *Stewardship of Soil, Air and Water Resources,* Proceedings of Watershed 89 (ed. E. Alexander), pp. 191-194. USDA Forest Service. R10-MB-77. USDA Forest Service, Alaska Region: Juneau, Alaska.

Amaranthus, M., Trappe, J. M., Bednar, L. & Arthur, D. (1994). Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. *Canadian Journal* of *Forest Research* **24**, 2157-2165.

Ammirati, J. (1979). Chemical studies of mushrooms: the need for voucher specimens. *Mycologia* **7**1, 437-441.

Arnolds, E. (1989). A preliminary RED data list of macrofungi in The Netherlands. *Persoonia* **14**, 77-125.

Arnolds, E. (1991). Decline of ectomycorrhizal fungi in Europe. *Agriculture, Ecosystems and Environment* **35**, 209-244.

Arnolds, E. (1992). Mapping and monitoring of macromycetes in relation to nature conservation. *McIlvainea* **10**, 4-27.

Arnolds, E. & De Vries, B. (1993). Conservation of fungi in Europe. In *Fungi in Europe: Investigation, Recording and Conservation* (ed. D. N. Pegler, L. Boddy, B. Ing & P. M. Kirk), pp. 211-230. Royal Botanic Gardens: Kew, UK.

Arora, D. (1999). The way of the wild mushroom. *California Wildlife* **52**, 8-19.

Avise, J. C. (1994). *Molecular Markers, Natural History, and Evolution.* Chapman and Hall: New York.

Baar, J., Horton, T. R., Kretzer, A. M. & Bruns, T. D. (1999). Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. *New Phytologist* **143**, 409-418.

Baar, J., Ozinga, W. A. & Kuyper, T. H. W. (1994). Spatial distribution of *Laccaria bicolor* genets reflected by sporocarps after removal of litter and humus layers in a *Pinus sylvestris* forest. *Mycological Research* **98**, 726-728.

Bas, C. (1978). Veranderingen in de Nederlandse paddestolenflora. *Coolia* **21**, 98-104.

Bormann, B. T., Cunningham, P. G., Brookes, M. H., Manning, V. M. & Collopy, M. W. (1994). *Adaptive Ecosystem Management in the Pacific Northwest.* General Technical Report PNW-GTR-341. US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, Oregon.

Bossart, J. L. & Prowell, D. P. (1998). Genetic estimates of population structure and gene flow: Limitations, lessons, and new directions. *Trends in Ecology and Evolution* **13**, 202-206.

*Brown, D., Goetz, C., Rogers, M. & Westfall, D. (1985). Mushrooming in the Pacific Northwest. NAMA XXV.* [25th Anniversary Issue], pp. 29-35. The North American Mycological Association: Charleston; West Virginia.

Brownlee, C. J., Duddridge, A., Malibari, A. & Read, D. J. (1983). The structure and function of mycelial systems of ectomycorrhizal roots with special reference to their role in forming inter-plant connections and providing pathways for assimilate and water transport. *Plant and Soil* **71**, 433-143.

Bruns, T. D., Fogel, R., White, T. J. & Palmer, J. D. (1989). Accelerated evolution of a false-truffle from a mushroom ancestor. *Nature* **339**, 140-142.

Bruns, T. D., Szaro, T. M., Gardes, M., Cullings, K. W., Pan, J. J., Taylor, D. L., Horton, T. R., Kretzer, A., Garbelotto, M. & Li, Y. (1998). A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. *Molecular Ecology* **7**, 257-272.

Carey, A. B., Thysell, D. R. & Brodie, A. W. (1999). *The Forest Ecosystem Study: Background, Rational, Implementation, Baseline Conditions, and Silvicultural Assessment.* USDA Forest Service General Technical Report, PNW-GTR-457: Portland, Oregon.

Castellano, M. A. (1997*a*). Recent developments concerned with monitoring and inventory of fungal diversity in northwestern United States. In *Mycology in Sustainable Development: Expanding Concepts, Vanishing Borders* (ed. M. Palm & I. Chapela), pp. 93-98. Parkway Publishing Inc.: Boone, North Carolina. ‘

Castellano, M. A. (1997*b*). Towards a RED list for Oregon fungi. In *Conservation and Management of Native Plants and Fungi* (ed. T. N. Kaye, A. Liston, R. M. Love, D. L. Luoma, R. J. Meinke & M. V. Wilson), pp. 222-226. Native Plant Society of Oregon: Corvallis, Oregon.

Castellano, M. A. (1998). Toward a RED list for Idaho’s macrofungi. In *Highlighting Idaho’s Rare Fungi and Lichens,* Management Technical Bulletin 98-1 (ed. R. Rosentreter & A. DeBolt). Idaho Bureau of Land Management: Idaho.

Castellano, M. A. & O’Dell, T. (1997). *Management Recommendations for Survey and Manage Fungi.* USDA Forest Service, Regional Ecosystem Office: Portland, Oregon.

Castellano, M. A., Smith, J. E., O’Dell, T. E., Cazares, E. & Nugent, S. (1999). *Handbook to Strategy 1 Fungal Species in the Northwest Forest Plan.* USDA Forest Service General Technical Report PNW-GTR-476. US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, Oregon.

Ciesla, W. M. (1998). *Non-wood Forest Products from Conifers. Non-wood Forest Products 12.* FAO, United Nations: Rome.

Colgan, W. (1997). *Diversity, Productivity, and Mycophagy of Hypogeous Mycorrhizal Fungi in a Variable Thinned Douglas-fir Forest. Ph.* D. Thesis, Oregon State University.

Colgan, W., Carey, A. B., Trappe, J. M., Molina, R. & Thysell, D. (1999). Diversity and productivity of hypogeous fungal sporocarps in a variably thinned Douglas-fir forest. *Canadian Journal of Forest Research* **29**, 1259-1268.

Dahlberg, A., Jonsson, L. & Nylund, J.-E. (1997). Species diversity and distribution of biomass above and below ground among ectomycorrhizal fungi in an old Norway spruce forest in South Sweden. *Canadian Journal of Botany* **75**, 1323-1335.

Dahlberg, A. & Stenlid, A. J. (1990). Population structure and dynamics in *Suillus bovinus* as indicated by spatial distribution of fungal clones. *New Phytologist* **115**, 487-493.

Danielson, R. M. (1984). Ectomycorrhiza association in jack pine stands in northeastern Alberta. *Canadian Journal of Botany* **62**, 932-939.

Dighton, J. & Mason, P. A. (1985). Mycorrhizal dynamics during forest tree development. In *Developmental Biology of Higher Fungi* (ed. D. Moore, L. A. Casselton, D. A. Wood & J. C. Frankland), pp. 117-139. Cambridge University Press: Cambridge, UK.

Dizon, A. E., Taylor, B. L. & O'Corry-Crowe, G. M. (1995). Why statistical power is necessary to link analyses of molecular variation to decisions about population structure. In *Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation* (ed. J. L. Nielsen & D. A. Powers). American Fisheries Society: Bethesda, Maryland.

Dreisbach, T. A., Smith, J. E. & Molina, R. (in press). Challenges of modeling fungal habitat: when and where do you find chanterelles? In *Predicting Species Occurrence: Issues of Scale and Accuracy* (ed. J. M. Scott, P. J. Heglund, M. Morrision, M. Raphael, J. Haufler & B. Wall). Island Press: Covello, California.

Dunham, S., O'Dell, T., Molina, R. & Pilz, D. (1998). Fine scale genetic structure of chanterelle *(Cantharellus formosus)* patches in forest stands with different disturbance intensities. [Abstract] In *Programme and Abstracts, Second International Conference on Mycorrhiza,* July 5-10, 1998 (ed. U. Ahonen-Jonnarth, E. Danell, P. Fransson *et al.).* Swedish University of Agricultural Sciences: Uppsala, Sweden.

Egli, S., Ayer, F. & Chatelain, F. (1990). Der Einfluss des Pilzsammelns auf die Pilzfiora. *Mycologia Helvetica* **3**, 417-428.

Epperson, B. K. (1993). Recent advances in correlation studies of spatial patterns of genetic variation. *Evolutionary Biology* **27**, 95-155.

FEMAT (Forest Ecosystem Management Assessment Team) (1993). *Forest Ecosystem Management: An Ecological, Economic and Social Assessment* [irregular pagination]. US Department of Agriculture, US Department of the Interior (and others): Portland, Oregon.

Finlay, R. D. & Read, D. J. (1986). The structure and function of the vegetative mycelium of ectomycorrhizal plants. I. Translocation of 14C-labelled carbon between plants interconnected by a common mycelium. *New Phytologist* **103**, 143-156.

Gardes, M. & Bruns, T. D. (1993). ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**, 113-118.

Gardes, M. & Bruns, T. D. (1996). Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. *Canadian Journal of Botany* **74**, 1572-1583.

Gardes, M., White, T. J., Fortin, J. A., Bruns, T. D. & Taylor, J. W. (1991). Identification of indigenous and introduced symbiotic fungi in ectomycorrhizae by amplification of nuclear and mitochondrial ribosomal DNA. *Canadian Journal of Botany* **69**, 180-190.

Gehring, C. A., Theimer, T. C., Whitham ,T. G. & Keim, P. (1998). Ectomycorrhizal fungal community structure of pinyon pines growing in two environmental extremes. *Ecology* **79**, 1562-1572.

Goodman, D. M., Durall, D. M., Trofymow, J. A. & Berch, S. M. (1996). A

*Manual of Concise Descriptions of North American Ectomycorrhizae.* Mycologue Publications: Victoria, B.C., Canada.

Gryta, H., Debaud, J.-C., Effosse, A., Gay, G. & Marmeisse, R. (1997). Fine-scale structure of populations of the ectomycorrhizal fungus *Hebeloma cylindrosporum* in coastal sand dune forest ecosystems. *Molecular Ecology* **6**, 353-364.

Harmon, M. E. & Sexton, J. (1995). Water balance of conifer logs in early stages of decomposition. *Plant and Soil* **172**, 141-152.

Harvey, A. E., Jurgensen, M. F. & Larsen, M. J. (1978). Seasonal distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. *Forest Science* **24**, 203-208.

Harvey, A. E., Larsen, M. J. & Jurgensen, M. F. (1976). Distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. *Forest Science* **22**, 393-398.

Harvey, A. E., Larsen, M. J. & Jurgensen, M. F. (1980). Partial cut harvesting and ectomycorrhizae: early effects in Douglas-fir and larch of western Montana. *Canadian Journal of Forest Research* **10**, 436-440.

Hawksworth, D. L. (1991). The fungal dimension of biodiversity: its magnitude and significance. *Mycological Research* **95**, 441-456.

Horton, T. & Bruns, T. D. (1998). Multiple-host fungi are the most frequent and abundant ectomycorrhizal types in a mixed stand of Douglas fir *(Pseudotsuga menziesii)* and bishop pine *(Pinus muricata)*. *New Phytologist* **139**, 331-339.

Horton, T., Cazares, E. & Bruns, T. D. (1998). Ectomycorrhizal, vesicular-arbuscular and dark septate fungal colonization of bishop pine *(Pinus muricata)* seedlings in the first 5 months after growth after wildfire. *Mycorrhiza* **8**, 11-18.

Hosford, D., Pilz, D., Molina, R. & Amaranthus, M. (1997). *Ecology and Management of the Commercially Harvested American Matsutake Mushroom.* General Technical Report. PNW-GTR-412. US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, Oregon.

Hughes, C. R. & Queller, D. C. (1993). Detection of highly polymorphic microsatellite loci in a species with little allozyme polymorphism. *Molecular Ecology* **2**, 131-137.

Hughes, K. W., McGhee, L. L., Methven, A. S., Johnson, J. E. & Petersen, R. H. (1999). Patterns of geographic speciation in the genus *Flammulina* based on sequences of the ribosomal ITS1-5.8S-ITS2 area. *Mycologia* **91**, 978-986.

Ingleby, K., Mason, P. A., Last, F. T. & Fleming, L. V. (1990). *Identification of Ectomycorrhizas.* Publication number 5, Institute of Terrestrial Ecology Research: London.

Jensen, M. E. & Everett, R. (1994). An overview of ecosystem management principles. In *Volume II.- Ecosystem Management: Principles and Applications,* General Technical Report PNW-GTR-318 (ed. M. E. Jensen & P. S. Bourgeron), pp. 6-15. US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, Oregon.

Jonsson, L., Dahlberg, A., Nilsson, M.-C., Zackrisson, O. & Karen, O. (1999). Ectomycorrhizal fungal communities in late-successional Swedish boreal forests, and their composition following wildfire. *Molecular Ecology* **8**, 205-215.

Kalamees, K. & Silver, S. (1993). Productivity of edible fungi in pine forests of the *Mytrillus* and *Vaccinium uliginosum* site types in North-West Estonia. *Aquilo Serie Botanica* **31**, 123-126.

Karen, O., Hogberg, N., Dahlberg, A., Jonsson, L. & Nylund, J.-E. (1997). Inter and intraspecific variation in the ITS region of rDNA of ectomycorrhizal fungi in Fennoscandia as detected by endonuclease analysis. *New Phytologist* **136**, 313-325.

Kiester, A. R., Scott, J. M., Csuti, B., Noss, R. F., Butterfield, B., Sahr, K. & White, D. (1996). Conservation prioritization using GAP data. *Conservation Biology* **10**, 1332-1342.

Kropp, B. R. (1982). Rotten wood as mycorrhizal inoculum for containerized western hemlock. *Canadian Journal of Forest Research* **12**, 428-431.

Kuhnlein, H. V. & Turner, N. J. (1991). Traditional plant foods of Canadian indigenous peoples: nutrition, botany, and use. In *Food and Nutrition in History and Anthropology, Volume 8* (ed. S. H. Katz). Gordon and Breach: New York.

Largent, D. L. & Sime, A. D. (1995). A preliminary report on the phenology, sporulation, and lifespan of *Cantharellus cibarius* and *Boletus edulis* basidiomes in Patrick Point State Park. In *Symposium Proceedings, 43rd Annual Meeting of the California Forest Pest Council,* Nov. *16-17, 1994* (ed. D. H. Adams, J. E. Rios & A. J. Stoere). Rancho Cordova, California.

Love, T., Jones, E. & Liegel, L. (1998). Valuing the temperate rainforest: wild mushrooming on the Olympic Peninsula Biosphere Reserve. In *The Biological, Socioeconomic, and Managerial Aspects of Chanterelle Mushroom Harvesting: the Olympic Peninsula, Washington State,* USA, Ambio Special Report 9 (ed. L. H. Liegel), pp. 16-25. Royal Swedish Academy of Sciences: Stockholm, Sweden.

Lund, G., Pajari, B. & Korhonen, M. (eds) (1998). *Sustainable Development of Non-wood Goods and Benefits From Boreal and Cold Temperate Forests. Proceedings of the International Workshop. 18 22 January 1998, Proceedings No. 23.* European Forest Institute: Joensuu, Finland.

Luoma, D. L., Eberhart, J. L. & Amaranthus, M. P. (1996). Response of ectomycorrhizal fungi to forest management treatments - sporocarp production. In *Mycorrhizas in Integrated Systems: From Genes to Plant Development* (ed. C. Azcon-Aguilar & J. M. Barea), pp. 553-556. Office for Official Publications of the European Communities, European Commission: Luxembourg.

Magnussen, S. (1993). Bias in genetic variance estimates due to spatial autocorrelation. *Theoretical Applied Genetics* **86**, 349-355.

Maser, C., Trappe, J. M. & Nussbaum, R. A. (1978). Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* **59**, 799-809.

Maser, Z., Maser, C. & Trappe, J. (1985). Food habits of the northern flying squirrel *(Glaucomys sabrinus)* in Oregon. *Canadian Journal of Zoology* **63**, 1084-1088.

Miller, S. L., McClean, T. M., Stanton, N. L. & Williams, S. E. (1998). Mycorrhization, physiognomy, and first-year survivability of conifer seedlings following natural fire in Grand Teton National Park. *Canadian Journal of Forest Research* **28**, 115-122.

Moldenke, A. R. (1999). Soil-dwelling arthropods: their diversity and functional roles. In *Proceedings: Pacific Northwest Forest and Rangeland Soil Organism Symposium,* Corvallis, Oregon, March *17-19, 1998* (ed. R. T. Meurisse, W.

G. Ypsilantis & C. Seybold), pp. 33-44. General Technical Report PNW-GTR-461. US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, Oregon.

*Molina, R. & Trappe, J. M.* (1982). Patterns of ectomycorrhizal host specificity and potential among Pacific Northwest conifers and fungi. *Forest Science* **28**, 423-4.58.

Molina, R., Massicotte, H. B. & Trappe, J. M. (1992). Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In *Mycorrhizal Functioning: An Integrative Plant-Fungal Process* (ed. M. F. Allen), pp. 357-423. Chapman and Hall: New York.

Molina, R., O'Dell, T., Luoma, D., Amaranthus, M., Castellano, M. & Russell, K. (1993). *Biology, Ecology, and Social Aspects of Wild Edible Mushrooms in the Forests of the Pacific Northwest: A Preface to Managing Commercial Harvest.* General Technical Report PNW-GTR-309. US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, Oregon.

North, M., Trappe, J. & Franklin, J. (1997). Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. *Ecology* **78,** 1543-1554.

Norvell, L. (1995). Loving the chanterelle to death? The ten-year Oregon chanterelle project. *McIlvainea* **12**, 6-23.

O'Dell, T. E., Ammirati, J. F. & Schreiner, E. G. (1999). Species richness and abundance of ectomycorrhizal basidiomycete sporocarps on a moisture gradient in the *Tsuga heterophylla* zone. *Canadian Journal of Botany* **77**, 1699-1711.

Ohenoja, E. (1988). Effect of forest management procedures on fungal fruit body production in Finland. *Acta Botanica Fennica* 136, 81-84.

Ohenoja, E. & Koistinen, R. (1984). Fruit body production of larger fungi in Finland. 2. Edible fungi in northern Finland, 1976-1978. *Annales Botanici Fennici* **21**, 357-366.

Parke, J. L., Linderman, R. G. & Trappe, J. M. (1984). Inoculum potential of ectomycorrhizal fungi in forest soils of southwest Oregon and northern California. *Forest Science* **30**, 300-304.

Patton, D. R. (1997). *Wildlife Habitat Relationships in Forested Ecosystems.* Timber Press: Portland, Oregon.

Perry, D. A., Amaranthus, M. P., Borchers, J. G., Borchers, S. L. & Brainerd, R. E. (1989). Bootstrapping in ecosystems. *BioScience* **39**, 230-237.

Pilz, D. & Molina, R. (eds) (1996). *Managing Forest Ecosystems to Conserve Fungus Diversity and Sustain Wild Mushroom Harvest.* General Technical Report PNW-GTR-371. US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, Oregon.

Pilz, D. & Molina, R. (1998). A proposal for regional monitoring of edible forest mushrooms. *Mushroom, The Journal* of *Wild Mushrooming* **3**, 19-23.

Pilz, D. & Molina, R. (in press). Sustaining productivity of commercially harvested edible forest mushrooms. *Forest Ecology and Management.*

Pilz, D. P. & Perry, D. A. (1984). Impact of clearcutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. *Canadian Journal* of *Forest Research* **14**, 94-100.

Pilz, D., Molina, R. & Amaranthus, M. P. (in press). Productivity and sustainable harvest of edible forest mushrooms: current biological research and new directions in Federal monitoring. In *Nontimber Forest Products in* *the United States: An Overview of Research and Policy Issues* (ed. M. R. Emery & R. J. McClain). Special Issue of *Journal of Sustainable Forestry.*

Pilz, D., Molina, R. & Liegel, L. (1998). Biological productivity of chanterelle mushrooms in and near the Olympic Peninsula Biosphere Reserve. In *The Biological, Socioeconomic, and Managerial Aspects of Chanterelle Mushroom Harvesting: The Olympic Peninsula, Washington State, USA* (ed. L. H. Liegel), pp. 8-13. Ambio Special Report 9. Royal Swedish Academy of Sciences: Stockholm, Sweden.

Pilz, D., Smith, J., Amaranthus, M. P., Alexander, S., Molina, R. & Luoma, D. (1999). Mushrooms and timber: managing commercial harvesting in the Oregon Cascades. *Journal of Forestry* **97**, *4-11.*

Redhead, S. A. Norvell, L. L. & Danell, E. (1997). *Cantharellus formosus* and the Pacific Golden Chanterelle harvest in western North America. *Mycotaxon* **65**, 285-322.

Richardson, M. J. (1970). Studies on *Russula emetica* and other agarics in a Scots pine plantation. *Transactions* of *the British Mycological Society* **55**, 217-229.

Ruckelshaus, M. H. (1998). Spatial scale of genetic structure and an indirect estimate of gene flow in eelgrass, *Zostera marina. Evolution* **52**, 330-343.

Schlosser, W. E. & Blatner, K. A. (1995). The wild edible mushroom industry of Washington, Oregon and Idaho. *Journal of Forestry* **93**, 31-36.

Schlumpf, E. (1976). Sollen unsere Pilze aussterben? *Schweizerische Zeitschrift Pilzkunde* **54**, 101-105.

Schneider, E. (1999). Favored fungi: part one. *Food Arts,* October, 158-167.

Schowalter, T., Hansen, E., Molina, R. & Zhang, Y. (1997). Integrating the ecological roles of phytophagous insects, plant pathogens, and mycorrhizae in managed forests. In *Creating A Forestry for the 21st Century; the Science of Ecosystem Management* (ed. K. A. Kohm & J. F. Franklin), pp. 171-189. Island Press: Washington, DC.

Simard, S. W., Perry, D. A., Jones, M. D., Myrold, D., Durral, D. M. & Molina, R. (1997). Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* **388**, 579-582.

Sime, A. D. & Petersen, R. H. (1999). Intercontinental interrelationships among disjunct populations of *Melanotus* (Strophariaceae, Agaricales). *Mycotaxon* **71**, 481-492.

Slatkin, M. & Barton, N. H. (1989). A comparison of three indirect methods for estimating average levels of gene flow. *Evolution* **4**, 1349-1368.

Slee, R. W. (1991). The potential of small woodlands in Britain for edible mushroom production. *Scottish Forestry* **45**, 3-12.

Smith, M. L., Bruhn, J. N. & Anderson, J. B. (1992). The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. *Nature* **356**, 428-431.

Smith, S. E. & Read, D. J. (1997). *Mycorrhizal Symbiosis.* Academic Press: London.

Sokal, R. R. & Oden, N. L. (1991). Spatial autocorrelation analysis as an inferential tool in population genetics. *American Naturalist* **138**, 518-521.

Starfield A. M. & Bleloch, A. L. (1991). *Building Models for Conservation and Wildlife Management.* Burgess International Group: Edina, Minnesota.

Stendall, E. R., Horton, T. R. & Bruns, T. D. (1999). Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. *Mycological Research* **103**, 1353-1359.

Sullivan, R. (1998). The mushroom wars. *Men's Journal* (Sept.), 75-79 &

*170-175.*

*Swift, M. J.* (1982). *Basidiomycetes as components of forest ecosystems. In Decomposer Basidiomycetes: Their Biology and* Ecology (ed. J. C. Frankland, J. N. Hedger & M. J. Swift), pp. 307-338. Cambridge University Press: Cambridge, UK.

Taylor, D. L. & Bruns, T. D. (1999). Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: minimal overlap between the mature forest and resistant propagule communities. *Molecular Ecology* **8**, 1837-1850.

Termorshuizen, A. J. (1991). Succession of mycorrhizal fungi in stands of *Pinus sylvestris* in The Netherlands. *Journal of Vegetation Science* **2**, 555-564.

Thompson, S. K. (1992). *Sampling.* Wiley Interscience: New York.

Todd, N. K. & Rayner, A. D. M. (1980). Fungal individualism. *Science Progress (Oxford)* **66**, 331-354.

Trappe, J. M. (1977). Selection of fungi for ectomycorrhizal inoculation in nurseries. *Annual Review of Phytopathology* **15**, 203-222.

US Department of Agriculture, Forest Service; US Department of the Interior, Bureau of Land Management (1994*a*). *Final Supplemental Environmental Impact Statement on Management of Habitat for Late-successional and Old-growth Forest Related Species Within the Range of the Spotted Owl. Vol.* 1, US Department of Agriculture, Forest Service, US Department of the Interior, Bureau of Land Management: Washington, DC.

US Department of Agriculture, Forest Service; US Department of the Interior, Bureau of Land Management (1994*b*). *Record of Decision for Amendments to Forest Service and Bureau of Land Management Planning Documents Within the Range of the Northern Spotted Owl.* [Place of publication unknown].

US Department of Agriculture, Forest Service; US Department of the Interior, Bureau of Land Management (1996). *Integrated Scientific Assessment for Ecosystem Management in the Interior Columbia Basin and Portions of the Klamath and Great Basins*. General Technical Report PNW-GTR-392. US Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, Oregon.

US Fish & Wildlife Service (1981). *Standards for the Development of Habitat Suitability Index Models.* 103-ESM. US Department of the Interior: Washington DC.

Visser, S. (1995). Ectomycorrhizal fungal succession in jack pine stands following wildfire. *New Phytologist* **129**, 389-401.

Vogt, K. A., Bloomfield, J., Ammirati, J. F. & Ammirati, S. R. (1992). Sporocarp production by Basidiomycetes, with emphasis on forest ecosystems. In *the Fungal Community: its Organization and Role in the Ecosystem,* Second edition (ed. G. C. Carroll & D. T. Wicklow), pp. 563-581. Marcel Dekker, Inc.: New York.

Washington Natural Heritage Program (1997). *Endangered, Threatened and Sensitive Vascular Plants of Washington - with Working Lists of Rare Non-vascular Plants.* Department of Natural Resources: Olympia, Washington.

Waters, J. R., McKelvey, K. S., Luoma, D. L. & Zabel, C. J. (1997). Trufe production in old-growth and mature fir stands in northeastern California. *Forest Ecology and Management* **96**, 155-166.

Waters, J. R., McKelvey, K. S., Zabel, C. J. & Oliver, W. W. (1994). The effects of thinning and broadcast burning on sporocarp production of hypogeous fungi. *Canadian Journal of Forest Research* **24**, 1516-1522.

White, T. J., Bruns, T., Lee, S. & Taylor, J. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR Protocols: A Guide to Methods and Applications* (ed. M. A. Innis, D. H. Gelfand, J. J. Sninsky & T. J. White), pp. 315-322. Academic Press: San Diego, California.

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology* **3**, 385-397.

Wiens, J. A. (1997). Metapopulation dynamics and landscape ecology. In *Metupopulation Biology: Ecology, Genetics, and Evolution* (ed. 1. A. Hanski & M. E. Gilpin). Academic Press: London.

Wilkins, W. H. & Harris, G. C. M. (1946). The ecology of the larger fungi. V. An investigation into the influence of rainfall and temperature on the seasonal production of fungi in a beechwood and a pinewood. *Annals of Applied Biology* 33, 179-188.

Wood, M. (2000). North American mycological societies. MykoWeb. http://www.mykoweb.com/index.html.

Wright, S. (1951). The genetical structure of populations. *Annual Eugenetics* **15**, 323-354.

Wright, S. (1969). *Evolution and Genetics of Populations. Vol. 2. The Theory of Gene Frequencies.* University of Chicago Press: Chicago, Illinois.

Zak, B. (1973). Classification of ectomycorrhizae. In *Ectomycorrhizae: Their Ecology and Physiology* (ed. G. C. Marks & T. T. Kozlowski), pp. 43-78. Academic Press: New York.

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