IS STUMPING A WISE SOLUTION FOR THE LONG-TERM: THE PROBLEM OF PHENOTYPE-ENVIRONMENT MISMATCH

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"*Without a better mechanistic understanding of how plants and animals work, we can never be assured of an accurate warning of what lies ahead for life on earth.*" (p 197 Denny and Helmuth, 2009)

INTRODUCTION

Expression of root disease in conifers is often associated with forest practices such as planting, thinning, and harvesting. For example, *Armillaria solidipes,* a resident microbe, is "triggered" by these practices or application of fertilizer. On the other hand, the connection to forest practices is not so clear when spores of *Heterobasidion spp*, are delivered to stump surfaces and initiate new infection centers. Natural situations such as ecophysiological maladaptation (McDonald 1991) and insect outbreaks can also trigger expression from resident pest populations. Generally speaking, most current problems concerning root disease pathogens stem from application of management practices and future problems will surely be exacerbated by global climate change. Development of effective management strategies is hampered by poor understanding of landscape level processes ranging from adaptation and evolution to community interactions such as intraspecific and interspecific competition, parasitism, commensalism, and mutualism. These interactions can cause negative or positive impacts on ecosystem function, such as productivity and expression of disease, depending on the particular mix of players at a specific time and place. A potential avenue to understanding and therefore effectively managing these complex living systems is taking shape in a new discipline – eco-evolutionary dynamics (Fussmann et. al. 2007, Kinnison and Hairston 2007, Hendry et.al. 2011, Morris 2011).

A NEW KID ON THE BLOCK

This new discipline has great potential to assist managers of wild resources (Hendry et. al. 2011). Human activity ranging from global climate change to plant and fish breeding can unwittingly create phenotype-environment mismatches, a central tenet of eco-evolutionary dynamics (see Hendry et al. 2010, 2011). Common forest management activities, such as harvesting, fire management, nursery practice, road building, native and non-native pest management, and management of invasive species, can create these mismatches. Development of options to manage these problems has been slow because theories describing how ecology and evolution operate were historically inadequate.

Eco-evolutionary dynamics involves five pivotal concepts. First, the stage was set for creation of new approaches when sequencing of the human genome failed to provide expected gene-based answers and biologists became aware of the ubiquitous nature of phenotypic plasticity (see Fusco and Minelli 2010). Second, a gene-centric theoretical construct, known as the modern syntheses, has provided an inadequate philosophical basis for the study of evolution and genetics for about 70 years. Recently geneticists and ecologists realized that models focused on inheritance via DNA alone yielded incomplete explanations (Day and Bonduriansky 2011). An extended modern synthesis was formulated that includes provisions for: (1) genomes composed of DNA sequences that produce structural and regulatory genes, and transcription factors (genetic inheritance), (2) epigenomes, composed of various chromatin markers, histone modifications, and noncoding microRNA elements, that obtain and forward biotic and abiotic information (nongenetic

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inheritance), and (3) "interpretive machinery", composed of eco-evolutionary feedback loops, that interprets the DNA code to "manage" gene regulation, developmental plasticity, and rapid evolution (see Danchin et. al. 2011, Day and Bonduriansky 2011, Hauser et. al. 2011, Turcotte et. al. 2011).

Since the concepts of nongenetic inheritance and "interpretive machinery" are so important to the following discussion, let us examine how the genetic philosophy of a cell matured from a genetic "black box" (modern syntheses) to a "niche-sensor/actuator" (extended modern syntheses). The niche, in this case, is the realized and/or evolutionary niche (see Holt 2009, Soberon and Nakamura 2009). From about 1930 to 1985 most biologists viewed genetic machinery as a storehouse and dispensary. However, it was believed that cells could "sense" environmental signals and acclimate to those signals in the current generation. From about 1985 to 1990, evidence began to emerge that connected signals to chromatin marks. During the next 10 years, the concept of chromatin remodeling tied the marks to specific cellular behavior or acclimation. Availability of complete genomes (2000 to 2002) quickly led to the ideas that chromatin interacted with gene regulatory networks and that these networks interacted, in turn, with DNA. By 2007 environmental signals were understood to interact with transcription factors as well as ncRNA. In the last 3 years, it has become clear that DNA, gene-regulatory-networks, chromatin, and environmental signals all interact to foster nongenetic inheritance (see Day and Bonduriansky 2011).

The third major element of eco-evolutionary dynamics is "ecological speciation". Cellular mechanisms appear to initiate pre- and post- zygotic suppression of ecologically undesirable gene flow (Hendry et.al. 2007, Wolf et. al. 2010, Nosil and Schluter, 2011). This concept also arose out of the extended synthesis and it supports the expectation of fine-grained, topography driven, and locally adapted intraspecific subpopulations (microrefugia, see Dobrowski 2010). The fourth point, ecological immunology, has revolutionized our understanding of host-microbe interaction (gene regulation networks, evolutionary feedback loops, and rapid evolution) in both plants and animals (see Sadd and Schmid-Hempel 2008, McDonald 2011, Graham et.al. 2011). Reduced fitness resulting from population outcrossing (outbreeding depression) seems to be particularly common regards pests (Allendorf et.al. 2010, Leimu and Fischer 2010). The fifth and final point relates to community interactions. As draft genomes, metagenomes, and metatranscriptomes accumulate, awareness has surfaced that genome x genome interactions are an important characteristic of ecological communities (Yahara et. al. 2010, Mitra et. al. 2011). In total, these five new concepts spawned the pivotal idea that both evolutionary and ecological processes function on similar scales of time and space. The natural integration was eco-evolutionary dynamics.

MECHANISTIC NICHE MODELING

Too complete the picture, new methodologies designed to connect functional traits (Friesen et.al. 2011) to the landscape are taking shape. This is where community ecology and eco-evolutionary dynamics meld. The most popular approach is correlative climate envelope models but little real understanding is gained by their application (Kearney et. al. 2010). On the other hand, mechanistic niche modeling, which arose from animal investigations and is based on biophysical principles, has been applied to landscape analysis of animal populations (Kearney and Porter 2009) and is being generalized through focus on the niche concept (Berg and Ellers 2010, McGill et.al. 2006, Jackson et.al 2009, Webb et.al. 2010, Chown et.al. 2010, Angilletta and Sears 2011). All of the trait-based techniques start by quantifying the organism/environment interface with either continuous or discontinuous reaction norms (species, population, or genotype performance over an environmental gradient). Reaction norms provide a powerful avenue for linking genetic, evolutionary and population factors to environmental factors across all of life (see McDonald et. al. 2005, Aubin-north and Renn 2009, Nicotra et. al. 2010, Alto and Turner 2010, Hendry et. al. 2011,). Even spore germination over a temperature gradient is a continuous reaction norm (McDonald 1996). It is also significant that an analytical methodology is developing to compare and contrast continuous reaction norms (Izem and Kingsolver 2005, Alto and

Turner 2010). As these new approaches develop, so will our understanding of the ecological impact of nearly all forest management activities. As a result, fundamentally different management options will insure truly sustainable forest ecosystems. So, does existing evidence indicate whether or not eco-evolutionary dynamics applies to the question at hand? Is stumping to control root rot a wise solution?

ECO-EVOLUTIONARY DYNAMICS IN FOREST ECOSYSTEMS?

Given that many, if not most, root rot problems in the Pacific Northwest are associated with planting, thinning, natural disturbances and natural phenotype-environment mismatches (see McDonald 1991), one would suppose that the study of eco-evolutionary dynamics would help, providing eco-evo components exist in conifer ecosystems. Evidence shows that open pollinated seed obtained from natural woods-run western white pine exposed to natural blister rust epidemics increased in rust resistance over a short time. Rust incidence decreased at a rate of 0.025/year in field and nursery tests (McDonald et. al. 2004, McDonald unpublished data). Resistance accumulated (proportion of rust free seedlings in artificial inoculations) at almost the same rate as it did in the breeding program.

Nongenetic inheritance (transgenerational epigenetic inheritance) is common in plants (Hauser et. al. 2011) and is known in conifers (Yakovlev et. al. 2010). In yellow monkeyflower, artificial leaf damage initiated increased production of leaf hairs that lasted for 2 generations (Scoville et. al. 2011). Clones of native grasses exhibited rapid trait shifts to tolerate an invader, cheat grass (Gergen et. al. 2011). Two inbred replicate lines of knotweed parents were used to demonstrate nongenetic inheritance of traits influencing drought tolerance (Sultan et. al. 2009). Poplar clones grown in differing levels of drought stress exhibited divergent ecologic function and transcriptomes when grown in well watered and droughty common gardens (Raj et. al. 2011). This study indicates that plants can accumulate variable epigenomes that track the environment in place. Do these results mean that seed banks, such as those formed by Ribes and white pines, track local environments and produce locally preadapted seeds optimized for microrefugia through a combination of epigenetic tracking and nongenetic inheritance? If true, one would expect a link between serious artificial regeneration problems and current nursery and tree breeding practices.

Theory predicts that ecosystems growing in heterogeneous topography should exhibit cryptic subpopulations or microrefugia (Dobrowsky 2011). Collections of western white pine needle tissue at 15 locations in the early 2000s were used to conduct an AFLP molecular marker test (Kim et. al. 2011) of the validity of subpopulations delineated earlier by isozymes. Depending on the type of analysis, early results were confirmed or not. One analysis indicated 12 of the collections represented individual microrefugia and 3 collections were contained within 1 macrorefugium. I conclude available evidence supports the possibility that eco-evolutionary dynamics is an important component of forest ecosystems.

NATURAL PHENOTYPE-ENVIRONMENT MISMATCHES

In 1983, a westwide investigation of the landscape pathology of Armillaria root disease was initiated (McDonald 1991). The behavior of the genus *Armillaria* was related to interactions among hosts and ecological situations by collecting *Armillaria* isolates and host and site data from randomly located plots. Plant community, management history, elevation, slope, aspect, and soil data were used to describe abiotic and biotic character of each .1 acre plot. Using this template, over 800 randomly located plots were installed throughout the conifer forests of the western United States (McDonald unpublished data). The principal goal of this effort was to uncover a connection between *Armillaria* behavior and the forested environment. Plant community classification was used to provide an ecological context in the absence of effective ways to deal with actual abiotic elements such as soil, elevation, slope, aspect, temperature, and moisture or biotic factors such as host species, competition, management activities, and fire (McDonald et. al. 1991, 2000).

Two important initial findings from this effort were that *A. solidipes* distribution and disease expression are related to moisture and temperature gradients. *Armillaria spp*. rarely occurred on either warm and dry or cold and dry sites and both *A. solidipes* and a nonpathogenic and unnamed *Armillaria spp*., North American Biological Species X, commonly co-occurred on cool and mesic to warm and wet sites. On these sites natural stands exhibited little expression of disease whereas planted or thinned stands and natural stands near roads often showed disease (McDonald et.al. 1987). In an effort to further understand *Armillaria* behavior at the landscape level, 631 habitat-types were reduced to 31 subseries or potential vegetation types (McDonald 1998, McDonald et. al. 2000) by utilizing conifer species to indicate soil temperature (continuous soil temperature reaction norm) and understory shrubs and herbs to indicate soil moisture (soil moisture continuous reaction norm). Each subseries can be viewed as a realized niche since each has an abiotic definition (moisture and temperature vectors) and a biotic definition (community assemblage). Next, stand habitat-type data, digital elevation models, satellite imagery, and digital terrain models were coupled to a multivariate technique, most-similar-neighbor, and used to map subseries on the landscape (McDonald et. al. 2003).

Two exceptions to the general rule stated above were expression of *A. solidipes* caused root rot on natural climax Douglas-fir in the Douglas-fir/Dry Herb subseries and on natural climax subalpine fir in the ColdFir/Dry and Moist Herb subseries. The situation with the DF/DH subseries, that is disease expression on ridges and other dry "islands" in a sea of "wet" subseries, led to the ecophysiological maladaptation hypothesis (McDonald 1991). Disease expression on natural climax subalpine fir is clear but the reason is not. It could be that subalpine fir is adapting to a sea of (dry) and disease is being expressed in islands of "wet". Either way would be a natural phenotype-environment mismatch. The finished map provides a view of realized niches in a given landscape as well as *Armillaria* ecological behavior by realized niche. Thus, new mapping techniques mentioned above (Berg and Ellers 2010, McGill et.al. 2006, Jackson et.al 2009, Webb et.al. 2010, Chown et.al. 2010, Angilletta and Sears 2011) offer a powerful new avenue to understand disease on the landscape by assuming that subseries corresponds to realized niches. Of course, this assumption could be tested experimentally.

ANTHROPOMORPHIC PHENOTYPE-ENVIRONMENT MISMATCHES

Can forest practice initiate phenotype-environment mismatches? The idea of locally adapted populations (ecotypes) has been an integral part of forestry practice for many years as evidenced by establishment of elaborate seed zoning programs. However, since significant problems associated with artificial regeneration, thinning, tree breeding and ecological restoration continue to accumulate, some aspect of our basic understanding of forest ecosystems must be missing. The seed zone effort may be failing due to undetected subpopulations because actions of the niche-sensor/actuator were unknown. Common garden experiments show some broad effects but new experimental designs that include comparisons of hybrid to home or transplant to home are required to uncover hypothesized fine-grained niche boundaries.

One place to look for clues about how ecosystems are actually working is management of wild salmon and some plants (see Laikre et.al. 2010, Hutchings 2011, Sgro et.al. 2010) where a similar suite of problems is evident. Important points are: (1) one generation in captivity dramatically reduces survivability of released fry (Christie et.al. 2011), (2) translocation of wild fry from a home river to a foreign river system reduces survivability and other important traits (Hutchings 2011), and (3) comparison of intraspecific local x local against local x away crosses often show outbreeding depression in growth and life history traits (Hutchings 2011). In herbaceous plants (Hufford and Mazer 2003) and fir (Goto et.al. 2011), similar results were observed. In addition, negative effects of translocation and population crossing within species are enhanced when competition and pests are added to the interaction experiments (Leimu and Fischer 2010, Cremieux et.al. 2010). This is not surprising since biotic factors such as pests, competitors, endophyes,

and mycorrhizea are the environmental vectors that define the realized niche (Soberon and Nakamura 2009, Friesen et.al. 2011). These also happen to be the kinds of traits that are often associated with nongenetic inheritance and tend to be most evident early in the life cycle of individuals (Edmands 2007).

ARTIFICIAL REGENERATION

Differing environments like light, density, nutrients, temperature, moisture, microbe populations, pest exposure, endophytes, and competition can push a genotype in various directions (Friesen et.al. 2011). Since many developmental tracks are not reversible, one possible source of phenotype-environment mismatch is the practice of growing seedlings in nurseries in niches far different than those experienced upon planting. This mismatch even includes the shape and size of the seedling's planting space. Also important are increased potential for negative founder effects due to low population breadth of translocated introductions (even an endemic species) and large reduction in screened population by way of the establishment process, e.g. 400 planted and 200 survived compared to 4000 naturals to 200 (Hufford and Mazer 2003). Given the potential for strong interaction between local parents and local environment, the negative consequences of population translocation could be large. A further caveat is that adults and seedlings may have different realized niches where the seedling niche is more restricted (Jackson et.al. 2009).

THINNING

An active niche-sensor/actuator functioning in forest stands could produce some interesting problems. We know that developmental plasticity plays a significant role in plants (Bouvet et.al. 2002, Stinchcombe et.al. 2010) and that specific sets of interactions can develop in genotypes replicated at different locations (Smith et.al. 2011); so it is reasonable to postulate that stands developing at a certain place and time should in some part be expressing their own unique suite of ecosystem interactions that includes the space they occupy. In heterogeneous topography of the Pacific Northwest (where large stand replacing fire is the norm) the functioning realized niche of an even-aged stand could vary in size from about 100m2 to 500000m2 (2Km2). A commercial thinning operation could compact soil, damage trees, and change densities, light, water, wind gradients and trigger new possibilities.

The operation could increase inoculum loads. For example, many western white pine support epiphytic *A. solidipes* yet express little disease. We carried out a seed-tree cut in a 3 hectare 60 year-old western white pine stand over snow in January 1986 to reduce ground disturbance and by May of 1986 numerous stumps showed active new infections of *A. solidipes*. These were existing epiphytic infections, caused by a single genet, that were activated by cutting. During the next 5 years as the stand regenerated to WWP and Grand fir the activated clone killed numerous grand fir and a few WWP and DF naturally regenerating seedlings (see McDonald et.al. unpublished ms, Ross-Davis et. al. These proceedings). The stand currently supports a high density WWP stand and the aggressive *A. solidipes* genet is still actively killing grand fir seedlings but not WWP. Some questions are; what would have happened under a partial cut or a complete stumping and did the cutting trigger a niche-sensor/actuator in the pathogen?

TREE BREEDING

Tree breeding efforts conducted to date have the potential to cause significant damage to coevolved realized niche interaction structures. Seeds are most often produced at orchards located in abiotic and biotic environments far different than those where seedlings will be planted. This interrupts the parent to offspring continuity of the niche-sensor/actuator. One can hypothesize the interruption would be important in a species like WWP where a rotating (3 to 4 years) seed bank is an important source of new natural seedlings. This assumes transgenerational passage of needed information about the local environment through nongenetic inheritance as discussed above. Potential negative outcomes resulting from ongoing tree breeding are caused by failure to test for outbreeding depression and inadequate delineation of a local population structure. Outbreeding is best detected by reciprocal home x away hybrids and home1 x home2 reciprical hybrids grown under natural conditions at both

homes. Another important option would be assessment of population structure with new high-throughput sequencing techniques such as RAD-tags (Emmerson et.al. 2010) to obtain 4,000 to 30,000 markers instead of the customary 100 to 200. Salmon populations separated by as little as G_{st}=0.02 have exhibited significant outbreeding depression (Edmands 2007). A recent study of population structure of western white pine showed pairwise F_{st} values greater than 0.02 for 12 of 15 subpopulations (Kim et.al. 2011).

HIGH-RESOLUTION MAPPING OF *ARMILLARIA* GENETS

Now, I review some evidence provided by the conifer-Armillaria couplet relating to the question at hand. Two unpublished studies of conifer plantations established for ongoing genetic investigations of western white pine and ponderosa pine at Priest River Experimental Forest in northern Idaho may shed some light on how eco-evolutionary dynamics applies northern Rocky Mountain forest ecosystems.

IDA CREEK

A small 2 acre western white pine plantation was established in 1972 from 120 open pollinated WWP families. These woods-run materials were collected to study natural variation in western white pine in support of the Inland Empire blister rust resistance program (described in McDonald et. al. 2004). The plantation was thinned in 1987, at 16 years of age, by removing alternate rows of the 1.2 m^2 spaced plantation. Over 2000 trees were inspected. Stumps of the removed trees were extracted and root systems of remaining trees were inspected for signs and symptoms of *Armillaria spp.* (Figure 1). The 1325 *Armillaria* isolates were subjected to somatic paring to define genets and species. Somatic pairing classifications have been verified by sequencing the IGS2 region of the genome (data on file USFS Moscow Forestry Sciences Laboratory). The 1325 isolates reduced to 7 genets belonging to *A. solidipes* and NABS X (Figure2).

Ecological behavior of genets was ascertained from collection records to provide one detailed geographic snapshot of *Armillaria* populations.

Next, a map of genet and species occurrence was constructed from location data supplied by the 1.2 meter planting grid (Figure 3). In general, low incidence of pathogenic *A. solidipes* and high incidence of saprophytic *Armillaria* NABS X were found. Two genets of *Armillaria* NABS X, a potential biological control agent, occupied most trees and 5 genets of *A. solidipes*, varied from nonpathogenic to significantly pathogenic.

Trees and *Armillaria* isolates

Proportion of trees (2072 total)

	Living	Dead
Clean	.42	.02
Infected	.07	.03
Epiphytic R	.44	.02

Proportion of isolates (1325 total)

	Rhizos	Fans	Rotten wood
Living trees	.77	.10	.01
Dead trees	.06	.04	.02

Figure 1: Ida Creek tree inspections and *Armillaria* isolate collections.

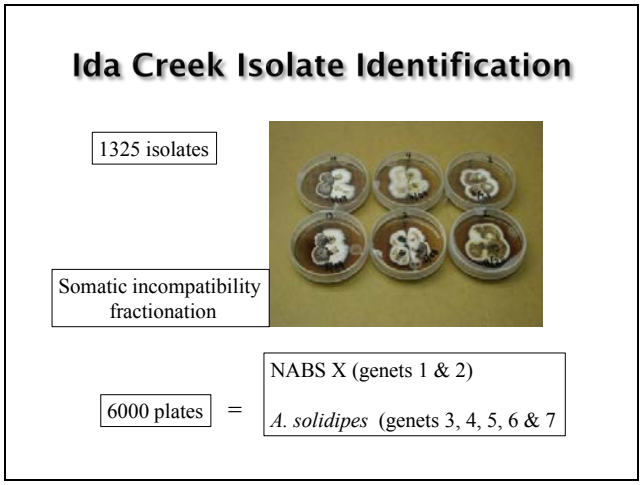

Figure 2: Ida Creek isolate fractionation and identification procedure and results.

Overall ecological behavior and geographical relationships are summarized in Figure 4. Interesting highlights are: (1) neither of the NABS X genets and 4 of the *A. solidipes* genets produced no fruiting bodies during the 10 year observation period, (2) genet 7 produced 4 caps, genet 8 occurred as a single cap (3) NABS X genets freely overlapped *A. solidipes* but not each other, and (4) *A. solidipes*

genets 5 and 7 were geographically split and none of the genets overlapped. Genet variation, in terms of host interaction, was notable (Figure 4) although some genets were underrepresented. Genet 2 dominated with 958 trees with 97% of the occurrences as epiphytic connections on healthy trees and 3% were associated with some resin flow but no fans or rot. *A. solidipes* genet 7 showed disease (no death) on 88% of 129 occurrences and 12% as an epiphyte on healthy trees.

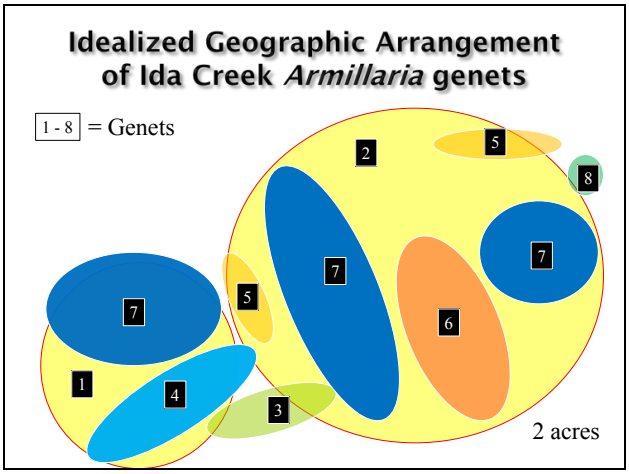

Figure 3: *Armillaria spp* and genets in a 2 acre plantation on the Priest River Experimental Forest in North Idaho.

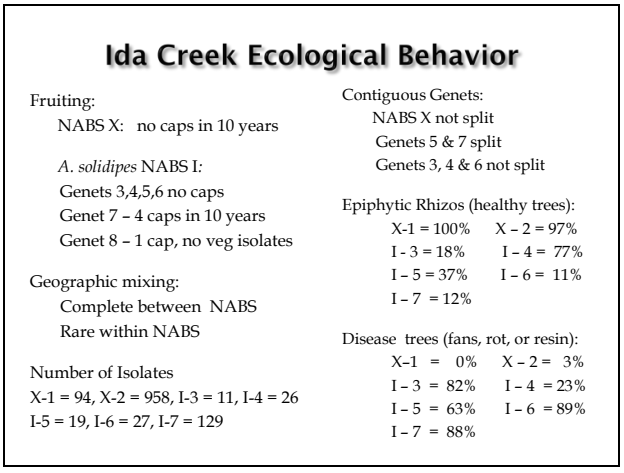

Figure 4: Range of *Armillaria spp* ecological behavior found on the Ida Creek plantation.

PONDEROSA PINE PROVENANCE TEST

A range-wide ponderosa pine provenance planting at Priest River Experimental Forest was established in 1983 on a portion of the site of a 75 year-old planting of exotic conifer species. Nearly all trees in this demonstration plantation were heavily infected with *A. solidipies*. The stand was cut and stumps were removed by excavator and deep roto-tilling. After provenance data collection, trees were extracted at about 8 years of age in the summer of 1990 with the aid of a farm tractor hydraulic lift (McDonald unpublished data). The extracted PP supported numerous infections caused by *A. solidipes* as determined by somatic pairing and IGS2 sequencing. An older range-wide ponderosa pine planting established in 1911, was located about 500 meters NW of the new test. This planting was severely impacted by *A. solidipies* in 1990 (McDonald unpublished data). Eleven percent of the 8 year-old seedlings supported active infections (2% dead, 5% rot and fans, and 4% tiny fans only). Association of infections with seed source has not yet been established. However, about one half of the infected trees supported very small lesions characterized by tiny fans that could not be isolated by our current techniques. Genet and species associations of these fans were not determined. Most lesions, 70%, were not associated with rhizomorphs and therefore could have been initiated from spores. Another interesting finding was that both NABS X and I were isolated from the planting. The main lesson for stumping was that spores could be a significant source of new infections after stumping.

IS CATASTROPHIC NICHE DESTRUCTION A WISE SOLUTION?

Since wholesale removal of large stumps to reduce inoculum loads amounts to catastrophic destruction of a realized niche, one should face the question of eco-evolutionary impact (Weese et.al. 2011). Microbe populations are likely to be significantly affected and their composition will probably significantly influence functional traits of post stumping plant populations (see Friesen et.al. 2011). As discussed above, the perils of artificial regeneration have the potential to be magnified by stumping. The Ida Creek results illustrate potential for interaction complexities just for *Armillaria* species and genets, let alone the remainder of the biosphere. The ponderosa pine example shows potential for significant problems arising from spore reintroductions into a highly disturbed realized niche, even if the disturbed site is regenerated naturally.

Some circumstantial evidence indicates that *Armillaria* NABS X may play a suppressive role regarding *A. solidepes* and that this role may depend on extensive epiphytic rhizomorph networks belonging to a single genet that connects most living woody biomass over 100 to 1000s of square meters (McDonald unpublished data). Further, these networks may be sensitive to disturbance, even stand replacing fire. In the final analysis, the only path to sustainable forest ecosystems may be management systems that emulate natural disturbance regimes (Long 2009), including respect for local realized niches. Otherwise cost of subsidizing ecosystem function may be very high.

Literature discussed and preliminary results presented indicate that an eco-evolutionary dynamic is an important aspect of forested ecosystems. Overlooking or misinterpreting these processes will likely be costly. Significant elucidation of eco-evolutionary dynamics can be uncovered through application of appropriate experimental designs and new genomic tools such as genotyping by sequencing, transcriptome analysis, methylome analysis, metagenomics, genome-wide association studies, and draft sequencing of important interacting species.

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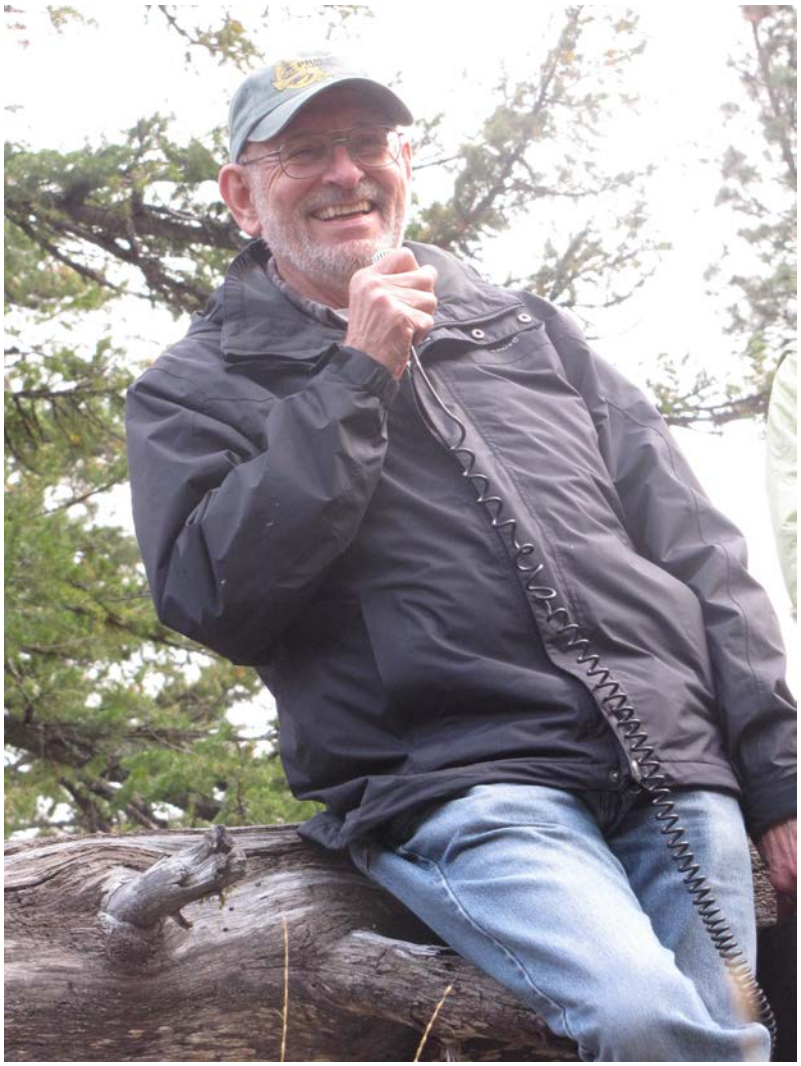

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