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7 Meta-networks of fungi, fauna and flora as agents of complex adaptive systems

Suzanne Simard, Kathy Martin, Alan Vyse and Bruce Larson

Introduction

The interactions and interconnectedness of the parts and processes in forest ecosystems underlie their nature as complex adaptive systems. The parts – the organisms, species, guilds – interact in networks across different genetic, trophic, spatial and temporal scales and the relationships and feedbacks across these various scales create structure, cohesion and emergent properties (Levin, 2005; Whitham et al., 2006). System memory, or the past structures and events (e.g. genes in seed-banks or old trees; snags or coarse woody debris left from a previous disturbance; perennial fungal genes; migratory bird occupation) and environmental variability (e.g. climate driven disturbances) are also important features of complex adaptive systems because they create and maintain diversity and system dynamics (Anand et al., 2010). As we shall see in this chapter, organisms as different as fungi, trees and woodpeckers, and processes as disparate as disturbance, dispersal, facilitation/competition and nutrient cycling, are related through cross-scale meta-networks (comprised of many individual networks) in the development of healthy functioning interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) forests (Bray, 2003).

Meta-networks (Urban, 2005; Simard, 2009) *sensu* meta-community (Filotas et al., 2010) can be considered agents of self-organization because they provide avenues for cross-scale interactions and feedbacks, from which emerge structure and function in complex adaptive systems (Bascompte et al., 2003; Parrot, 2010). When we isolate, manipulate or remove one of the key parts, networks or functions, we find that the effect ripples through the system to affect the other parts, networks and functions, often with unintended consequences. Disrupting network links by reducing the diversity of mycorrhizal fungi, for example, can reduce tree seedling survivorship or growth (Simard et al., 1997a; Teste et al., 2009), ultimately affecting recruitment of old-growth trees that provide habitat for cavity nesting birds and mammals and thus dispersed seed for future generations of trees. Suppression of fire, high-grade logging, or removal of snags or coarse woody debris may also ultimately increase disturbance severity and reduce trees or tree-supported resource persistence that are prime sources of cavities (Drewer et al., 2008). Conserving complex adaptive forest ecosystems, therefore, appears

dependent on maintaining the diversity of its parts and the multiplicity of its interactions (McCann, 2000).

This chapter describes a meta-network involving mycorrhizal fungi, pathogenic fungi, trees, plants and cavity nesting vertebrates that serves as an agent for the self-organization of interior temperate Douglas-fir forest ecosystems. We start by defining networks and meta-networks. We then briefly describe the dominant attributes of interior Douglas-fir forests and the disturbance regimes that shape the heterogeneous spatial pattern and forest dynamics. We next define mycorrhizal networks, which we describe as the foundational network, and how they facilitate regeneration after disturbance and across environmental stress gradients. We follow this with the main contribution of this paper, which is a description of the cross-scale interactions among several component networks of a meta-network – including mycorrhizal and pathogenic fungal networks, vegetation patterns (including spatial pattern, old trees, broadleaved trees and downed wood) and cavity nest webs (bird and mammal) – and the role this meta-network plays in the emergence of complex adaptive forest ecosystems. The effects of land-use and climate change on forest ecosystems and how these effects are expected to interact with the self-organizing networks, disturbance regimes and exotic invaders are then discussed. We end the chapter with a framework for managing interior Douglas-fir forests as complex adaptive systems to cope with climate change and other stressors. This includes changes to forest practices that will conserve key traits for improved adaptability.

Networks and meta-networks

Networks are recognized as ubiquitous in nature and, along with theories of self-organization, emergence and non-linear dynamics, provide a useful lens for observing and understanding forests as complex adaptive systems (Bray, 2003; Parrott, 2010). Using network theory, the topology of the ecosystem, where individuals, species, guilds or functional groups are viewed as nodes and the links are viewed as ecological relationships, can help us understand interactions, feedbacks and emergent properties (Urban, 2005; Barabási, 2009). Network theory has successfully been used, for example, to study the flow of energy or matter through natural ecosystem components (such as feeding relationships between predators and prey in foodwebs), local interactions between disturbances, dispersal and recovery in patch dynamics and the movement of animals, disturbances or water through landscapes (Urban, 2005; Anand et al., 2010). Network analysis has been useful not only in understanding and predicting ecosystem behaviour, but it also has been successfully applied in life sciences (e.g. vascular and nervous systems), social systems, transportation systems and communications (e.g. the internet) (Webb and Bodin, 2008).

Meta-networks are comprised of several nested interacting network components and this concept is useful for understanding cross-scale interactions in natural systems (Figure 7.1). In a meta-network, the component network nodes and links are determined by the parts and scales of interest and these network components

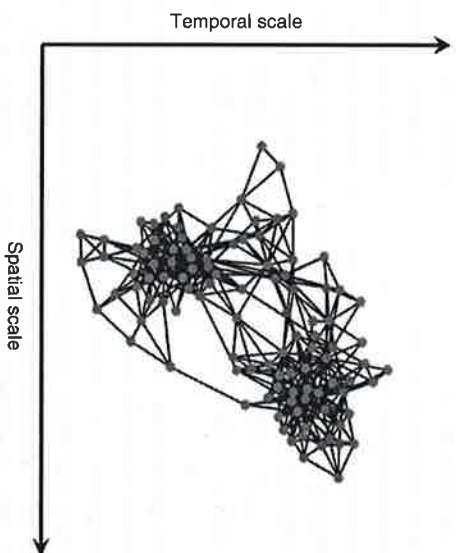


Figure 7.1 Model of a meta-network comprised of several network components that occur at different spatial and temporal scales. Each compartment network has a scale-free topology (see Figure 7.2) and is linked to other networks through structures (nodes) and functions (links or relationships). In this example, the network at the smallest temporal and spatial scale may be a mycorrhizal network linking trees through mycorrhizal fungi and cycling nutrients; the network at the next scale may be a plant community network linking tree clusters interwoven with meadows and dispersing seeds; the next scale may be a nest web linking aspen or old Douglas-fir trees and providing cavities for primary, secondary and tertiary cavity nesters that disperse seeds and spores. (Adapted from http://www.casos.cs.cmu.edu/computational_tools/datasets/external/polbooks/polbooks.html).

are integrated into larger networks at coarser functional scales without substantial loss of information (Urban, 2005; Simard, 2009). In forests, for example, meta-networks might involve small-scale networks of mycorrhizal fungal species with specific niches in nutrient and water acquisition, which are nested within larger-scale networks of trees linked through mycorrhizal fungi for community level cycling of water or nutrients, which in turn are nested within even larger-scale networks of interconnected forests, grasslands and riparian areas interacting through dispersal and energy fluxes, which are further nested within contiguous watersheds interacting through migrations and disturbance, and so on. Organization in meta-networks can result from interactions through any of the nodes (e.g. fungi, trees or watersheds) or links (e.g. nutrient uptake, cycling or fluxes) and these interactions inform the whole.

Meta-networks show high degrees of clustering, where small clusters are nested within larger-scale clusters. Although networks in a meta-network cluster within networks at higher spatial and temporal scales, they do not classify well as direct hierarchies, where organization is restricted from the top-down or from the bottom-up and the links or interactions occur only between a node's

immediate superior or its subordinate. In meta-networks, by contrast, interactions can occur between disparate scales (e.g. between processes at the watershed scale and those at the mycorrhizal fungus scale), even though interactions are most common between adjacent scales. In meta-networks, change is normal and adaptation is constantly occurring as a result of the cross-scale interactions, whereas in direct hierarchies, change is restricted by interactions between adjacent scales. Thus, analysis of networks and meta-networks can help us integrate all the key structures and functions in a system where any node, component, link or network influences the larger meta-network, and where the whole is greater than the sum of its parts (Urban, 2005).

A fundamental property of networks is that the parts (e.g. species) are subject to selective pressures through localized interactions with other parts and processes. These interactions can lead to local adaptation, but can also influence the optimal functioning and evolution of the network or meta-network (Webb and Bodin, 2008). Thus, understanding the dynamic interactions and selection pressures in networks is fundamental to understanding the dynamics of complex adaptive systems.

Recent research shows that networks in healthy natural systems are usually resilient to disturbance because of their spatial and temporal structure. This is because networks in most natural systems have a non-random scale-free (or power-law) structure. In scale-free networks, there are a few 'hubs' that have many connections and many other nodes that have few links (Barabasi, 2009; Parrott, 2010) (Figure 7.2). Examples of hubs may be dominant trees or keystone species, other

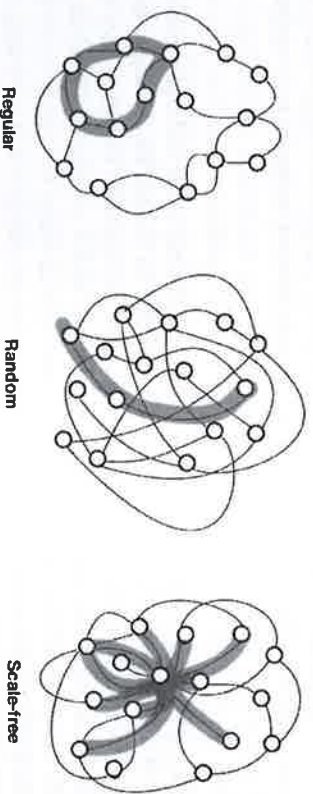


Figure 7.2 Regular, random and scale-free network models. Diversity of networks: the same set of nodes can be linked in many different ways. (a) A regular network, where nearest neighbours are connected, tends to have local groups of highly interconnected nodes. Regular networks are vulnerable to random removal of nodes. (b)

A random network is easily traversed because the number of steps between any two nodes is relatively small. (c) Scale-free networks, distinguished by the presence of a few highly connected (hub) nodes, have local interconnected groups and are easily traversed. Scale-free networks are resistant to random attack but vulnerable to targeted removal of hubs. The thick grey lines highlight sets of connections illustrating the distinctive feature of each network type: local connections (regular) (a), long-range connections (random) (b) and a combination of the two (scale-free) (c). Reproduced, with permission, from Bray (2003).

nodes may be individual subordinate trees or animals, and links may be fungal or root connections or predator–prey relationships. In regular and random networks, by contrast, all nodes tend to have a similar distribution of links. Scale-free networks generally have small-world properties, which means that the path-length between two randomly selected nodes is shorter than that expected in random or regular networks, resulting in functional efficiency of energy or matter transfer (Watts, 1999). Scale-free networks with small-world properties are more resistant against random disturbances because the likelihood of losing a hub at random is small. However, these systems are highly vulnerable to collapse where there is targeted removal of hubs (Albert et al., 2000). In forests, this can happen through disturbances (such as selective bark beetle attack, pathogen infection or logging of specific or large trees), loss of ecosystem architects (such as woodpeckers) or hunting of keystone animal species (such as grizzly bears). Hence, systems that can resist disturbance tend to have a diversity of parts (nodes and links) and an overlap in functionality of those parts, and this allows the efficient replacement of lost parts with other parts of similar functions (Ehrlich and Walker, 1998). Systems that are resistant to disturbance also have flow control and modularity (e.g. patchiness, cliquishness), which reduces the impact of disturbance in the first place by creating barriers to spread (Webb and Bodin, 2008).

Analysis of networks in complex adaptive systems such as forests can be useful for forest management if the long-term objectives are to maintain forests that can provide desired ecosystem goods and services. For example, identification of hubs (e.g. keystone species), connective or overlapping components (e.g. foundational species) or critical rates, inflections or processes (e.g. thresholds) can become important criteria for management decisions. A focus on these critical features of network analysis is strongly supported by dominant theories in ecology and conservation biology. Examples of such theories include: (i) the mass-ratio hypothesis predicting disruption of ecosystem function with the loss of dominant or foundational species (Grime, 1998), (ii) the diversity–productivity (or stability) relationship predicting reduced productivity (or stability) with decreasing diversity (Hooper et al., 2005), (iii) the resource-ratio hypothesis predicting species dominance and system structure based on the ability to compete for limited resources (Tilman, 1985) and (iv) the stress-gradient hypothesis predicting that systems under stress maintain structure increasingly through facilitation rather than competition (Lortie and Callaway, 1996). Thus, network analysis can be used to investigate these theories and relationships to better understand and manage key players or components of complex adaptive systems (Holling, 1973; Albert et al., 2000).

Interior Douglas-fir forests

The role of networks (or webs) in forest dynamics has been studied for a number of species across a range of climatic and site conditions in the interior Douglas-fir forests of British Columbia, Canada (Martin et al., 2004; Vyse et al., 2006; Beller et al., 2010). Interior Douglas-fir occurs on the leeward side of the Pacific Coast Mountains and ranges from Mexico (19°N, 3260 m elevation) to north-central

British Columbia (55°N, 760 m), where low winter temperatures and high snowfall limit seedling establishment (Hermann and Lavender, 1991). Coastal Douglas-fir, *Pseudotsuga menziesii* var. *menziesii* (Millb.) Franco, occurs on the westward side of the Pacific Coast Mountains and is distributed from west-central British Columbia, Canada, to central California, USA. At more southerly latitudes and lower elevations in British Columbia, interior Douglas-fir establishment is limited by summer drought and it is sometimes mixed with ponderosa pine (*Pinus ponderosa* Dougl. ex C. Lawson). At higher elevations or more northerly latitudes, interior Douglas-fir occurs in mixture with lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), hybrid spruce (*Picea glauca* [Mill.] B.S.P. ex X *engelmannii* Parry ex Engelm.) and trembling aspen (*Populus tremuloides* Michx.) (Meidinger and Pojar, 1991). In the more easterly moist, warm climatic region, the interior Douglas-fir forests are more productive and seedling establishment is limited by competition for light. Here, interior Douglas-fir occurs in rich mixtures with up to a dozen other tree species, including western redcedar (*Thuja pliccata* D.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western larch (*Larix occidentalis* Nutt.), paper birch (*Betula papyrifera* Marsh.) and trembling aspen. In the dry forests, interior Douglas-fir is shade tolerant, but it becomes increasingly shade intolerant in wetter climatic regions to the east. Regardless of this variation in forest composition, productivity and shade tolerance dynamics, interior Douglas-fir is a dominant tree species.

The variation in interior Douglas-fir stand composition is determined by a range of biogeoclimatic, genetic and disturbance factors (Meidinger and Pojar, 1991). Despite the relatively simple assemblage of tree species, these forests support a rich assemblage of ectomycorrhizal fungi (EMF) (within-stand richness of approximately 100 EMF species) (Twieg et al., 2007; B. Pickett, unpublished) and approximately 2000 EMF associated with coastal and interior Douglas-fir (Molina et al., 1992) and a rich diversity of vertebrates (e.g. 221 bird species) (Dreyer et al., 2008; K. Martin, unpublished). This richness probably arises from the diverse micro-environments provided by the intricate interplay of topography, climate, disturbances, soils, water bodies and plant communities and by the high genetic diversity within and among interior Douglas-fir populations (Guggler et al., 2010). The richness of both the mycorrhizal fungal and bird communities increases where broadleaved trees occur in mixture with conifers.

Throughout its range, the interior Douglas-fir forest experiences a mixed-severity disturbance regime with low, medium and high severity fires, resulting in a heterogeneous landscape with high spatio-temporal β diversity (Klennner et al., 2008; Perry et al., 2011). This results from top-down climatic and weather influences and bottom-up topographical and historical vegetation patterns (Perry et al., 2011). Low severity fires that leave open multi-aged stands with a grassy herbaceous understorey (Wong, 1999; Klennner et al., 2008; Perry et al., 2011) are more frequent in the drier western parts of the interior Douglas-fir forest. Fires in moister easterly forests tend to be less frequent, more severe and stand replacing, leading to dense, even-aged stands (Simard and Vyse, 2006; Klennner et al., 2008). Low to high severity fires can occur in close proximity in any of these forest types, leaving

a wide range of post-fire conditions, from areas where trees are mildly scorched and the forest floor litter remains intact, to patches where all trees and the forest floor are consumed (Wong, 1999). Studies show that forests with mixed severity fire regimes follow a scale-free patch size distribution, with many small patches and a few large ones (Perry et al., 2011).

The variability created by fire is compounded by a wide range of cyclical insect attacks, infections by pathogens, harvesting practices and windthrow. Defoliators such as western spruce budworm (*Choristoneura occidentalis* Freeman) occur throughout the interior Douglas-fir forests of British Columbia, and Douglas-fir tussock moth (*Orygia pseudotsuga* McDunnough) occurs at lower elevations where forests are sparse and intermixed with grassland; both insects can stress or kill Douglas-fir and create a range of gap sizes. The stress on trees caused by western spruce budworm likely facilitates further infestation by bark beetles and pathogens. Bark beetles in the interior Douglas-fir forests include *Dendroctonus ponderosae* Hopkins, *D. pseudotsugae* Hopkins and *D. brevicornis* LeConte, which kill larger stems as individuals or in extensive groups. Pathogens such as Armillaria root disease and laminated root rot (caused by *Armillaria ostoyae* Romagn. Herink and *Phellinus weirii* [Murrill] R. L. Gilbertson, respectively) infect a small group of susceptible conifer species, including interior Douglas-fir, creating forest gaps of varying sizes, shapes and compositions (van der Kamp, 1991). The two pathogens persist in the roots of old trees and stumps for decades, surviving even fire and clearcutting and their mycelia infect the roots of new trees as they come into contact with the inoculum (van der Kamp, 1991).

Harvesting, an important disturbance agent (Klennner et al., 2008), is overlain on the natural heterogeneity of the forests; it varies widely in method with ecological and socio-economic circumstances, and ranges from high-grading, to fallers selection, to clearcutting. Harvesting coupled with fire suppression has increased understorey densities and reduced older age classes and may have increased the probability of more severe fires and insect outbreaks. The current western spruce budworm outbreak, for example, may have been intensified by extensive high-grading and fire suppression through promotion of dense multi-storied stands and, in turn, the stress resulting from budworm attack may have intensified infestations by other insects and pathogens (Hadley and Veblen, 1992). All of these disturbances are intimately linked to environmental variables such as local climate and soils, and the feedbacks between environment and disturbance types amplify over time. The result is a highly heterogeneous ecosystem that includes a patchy network of tree patches and gaps of varying densities, sizes, shapes and age structures, even within a single hectare or across thousands of hectares, creating a scale-free gap-size distribution (Wong, 1999; Klennner et al., 2008; Perry et al., 2011). These are embedded within a larger network of forests, grasslands, meadows and wetlands of varying ages and compositions. The resulting persistent (memory) network pattern at stand and landscape scales shapes ecosystem properties and processes such as disturbance, dispersal, diversity and succession patterns (Anand et al., 2010).

Mycorrhizas, mycorrhizal networks and response to disturbance

Our analysis of meta-networks is based on the view that the mycorrhizal networks are central to the organization of the other interacting networks because of their critical obligate role in the establishment and growth of trees, which themselves are the foundation of all forests. All forest trees form mycorrhizas involving thousands of fungal species (Molina et al., 1992). A mycorrhiza – literally fungus-root – forms when fungal propagules infect seedling roots, forming a symbiotic and commonly mutualistic relationship. The fungus obtains carbon from the seedling in exchange for nutrients and water that it takes up through its mycelium from the soil (Smith and Read, 2008). Ectomycorrhizas form between roots of tree species in the Pinaceae, Fagaceae and Betulaceae families and fungi in the Basidiomycota and Ascomycota. An ectomycorrhiza consists of a shortened root tip surrounded by a fungal mantle, with hyphae penetrating into the root and the surrounding one or two layers of roots cells (the Hartig net) and extra-natal hyphae emanating from the mantle into the soil. Many species of EMF have a wide range of hosts (i.e. form mycorrhizas with many species of trees or plants) whereas others have a narrow range (associate with only one species or genus of trees or plants). Similarly, many host plants have broad receptivity to a high number of mycorrhizal fungi, whereas some have narrow receptivity (Molina et al., 1992).



Figure 7.3 Mycorrhizal network in a soil profile. The upper portion of the profile is forest floor, where the network predominates and the lower part is mineral soil. The white hyphae are ectomycorrhizal fungi connecting the roots of interior Douglas-fir trees. Photo by Kevin J. Beiler.

Mycorrhizal networks form when the hyphae of a single mycorrhizal fungal individual, or genet, links together two or more plants of the same or different species (Figure 7.3). Host-generalist fungi can link trees of the same or different species, but host-specific fungi obviously can only link together individual trees of the same species. Most tree species in temperate forests of North America are host-generalists that form mycorrhizal networks with other tree and plant species (Figure 7.4). Interior Douglas-fir, in particular, forms ectomycorrhizas with many host-generalist fungi, with the potential to network with plants of many species (Hagerman et al., 2001; Twieg et al., 2007). However, over half of its root system is typically dominated by two host-specific fungi, *Rhizopogon winicolor* and *R. vesiculosus*, which are usually considered a single complex (Basidiomycota, *Villosi*-group sensu Kretzer et al., 2003), with high potential to form mycorrhizal networks exclusive to Douglas-fir (Molina et al., 1992; Kretzer et al., 2003; Twieg et al., 2007). Mycorrhizal networks of established trees can serve as inoculum to colonize nearby seedlings and can create direct belowground pathways that enable plants to exchange resources (Simard et al., 1997b; Selosse et al., 2006). The *Rhizopogon* fungi, in particular, have been considered strong networking species because they form fungal strands (rhizomorphs) important in inter-tree carbon transfer and translocation of nutrients and water from soils to host trees, resulting in increased seedling survival, growth and resistance towards drought and root pathogens (Cairney and Chambers, 1999). Rhizomorphs also define *Rhizopogon* species as ‘exploration-type’ fungi because of their ability to rapidly exploit new environments (Agerer, 2001).

Mycorrhizal networks associated with living or dying trees, along with spores and sclerotia, are important colonization vectors for new trees establishing after a disturbance (Selosse et al., 2006). Even where mycorrhizal networks are disrupted by soil disturbance (e.g. by soil animals or site preparation equipment), mycelial fragments retain inoculum potential and the network can reform quickly. In interior Douglas-fir forests, the role of mycorrhizal networks in seedling colonization diminishes with increased disturbance severity because of the loss of residual trees and plants (Teste et al., 2010). Where all hosts are removed, the amount and diversity of EMF inoculum (as networks or spores) decreases rapidly (Dahlberg, 2002). Following severe fire that removes residual plants and forest floor, ruderal fungi that are dispersed via spores (via mammals, air, or from deeper soils) colonize naturally, regenerating seedlings in interior Douglas-fir forests (Hagerman et al., 2001; Barker et al., 2010). Once colonization occurs (up to five months), the host-generalist fungi grow and anastomose quickly, forming simple mycorrhizal networks that can dominate the EMF community of regenerating interior Douglas-fir seedlings for several years (Smith and Read, 2008; Barker et al., 2010). Following low severity fire or harvesting, by contrast, the mycorrhizal networks of residual plants are the primary vectors of seedling colonization (Dahlberg, 2002). Their species richness and structural diversity increases rapidly as the growing seedlings increase their potential to host a greater diversity of late-seral, carbon-demanding, exploration-type EMF in interior Douglas-fir forests (Twieg et al., 2007; Teste et al., 2009; Barker et al., 2010). Within a few years, the EMF community of interior Douglas-fir is dominated by the *Rhizopogon winicolor*–*R. vesiculosus* complex and



Figure 7.4

Meta-network concept, showing details of mycorrhizal networks and links to other network components typical of interior Douglas-fir forests. The left side of the illustration shows an arbuscular mycorrhizal network connecting Douglas maple and western redcedar belowground, providing a direct pathway for resource transfer and mycorrhizal colonization. Between the Douglas maple and western cedar is a non-mycorrhizal hawksweed forb, which is not linked into the arbuscular mycorrhizal network. The trembling aspen snag, with a shelf fungus and cavity and the decayed western redcedar stump, are linked into the network during early senescence, but these network links likely disconnect within a few years of tree death. The intra- and interspecific arbuscular network linking the maple and cedar is broken in areas, interrupted by grazing soil fauna, such as worms in this case, or other soil invertebrates, voles, mice or squirrels. The centre of the illustration shows the role of small mammals as beneficiaries of and dispersal mechanisms for mycorrhizal fungi – here, a squirrel excavates, consumes and disseminates spores from *Rhizopogon* truffles associated with interior Douglas-fir. The squirrel midden at the base of the senescing black cottonwood in the middle of the illustration is comprised of Douglas-fir seeds and cones and thus is an excellent source of and environment for seedling germinants, whose roots are quickly colonized by the mycorrhizal spores and other fungal inoculum. The senescing cottonwood is an important component of the meta-network – it provides structure for perching and roosting and an insect food source for many bird species in the nest web. The right side of the illustration shows an inter-specific ectomycorrhizal network connecting interior Douglas-fir and paper birch. There is also an intra-specific *Rhizopogon* network linking an older interior Douglas-fir to a younger one. Components of this network are the interconnecting fungal hyphae, truffles (belowground fruiting bodies) and mushrooms (aboveground fruiting bodies). The root graft between the two interior Douglas-fir trees on the right is another belowground pathway for potential resource transfer between individuals. Recently dead or senescing trembling aspen are strongly preferred by woodpeckers for excavation of their tree cavities, such as the Northern Flicker in the snag on the far right side of the illustration. These cavities last for at least 12 years and are used by 30 secondary cavity nesting species, such as squirrels shown here, all aboveground components of the meta-network. Illustration by April A. Anderson.

other exploration-type mycorrhizas (e.g. *Suillus* and *Amantia* species [Basidiomycota]) (Dahlberg, 2002; Barker et al., 2010). Twieg et al. (2007) found that the richness of the EMF species in mixed stands of Douglas-fir and paper birch stabilized 26 years after low-to-moderate severity fire or clearcut disturbance, around the time of canopy closure (Simard and Vysc, 2006). In century-old interior Douglas-fir forests, the *Rhizopogon* complex is joined by up to 63 other host-specific and generalist fungi in a complicated mycorrhizal network (Twieg et al., 2007).

Native trees (e.g. *Thuja* spp.), shrubs (e.g. *Salix* spp., *Acer* spp.), forbs (e.g. *Aster* spp.) and grasses (e.g. *Calamagrostis rubescens* Buckl.) that form arbuscular mycorrhizal fungi (AMF), or exotic invaders that form AMF or are non-mycorrhizal (e.g. *Bromus tectorum* L. or *Centaurea* spp.), are excluded from the mycorrhizal networks of interior Douglas-fir forests (Hagerman et al., 2001; Hagerman and Durall, 2004). Not only are many of these plants competitive with establishing EMF trees, the AMF can inhibit EMF colonization of conifers through biochemical signalling (Haskins and Gehring, 2004). Where regeneration of EMF hosts is delayed or displaced by AMF plant invaders following disturbance, reintroduction of native trees can be difficult due to loss of native inoculum or due to establishment of networks dominated by exotic species (Simard, 2009). Conversely, conserving native mycorrhizal networks by retaining residual plants or by re-establishing native species may be important barriers to exotic invasions in disturbed forests.

Role of mycorrhizal networks in forest development

Mycorrhizal networks do not appear to affect seed germination, but they are important to the establishment of seedlings through their capacity to acquire soil nutrients or water and deter pathogen infection (Molina and Trappe, 1982). Most studies examining mycorrhizal networks in forests have focused on their role in growth and survival of planted or naturally regenerated seedlings (Booth, 2004). Several experiments, for example, show substantially greater establishment, growth and survival of germinants or planted seedlings when linked into the mycorrhizal networks of larger EMF trees or shrubs (Simard et al., 1997a; Horton and Bruns, 1998; Teste et al., 2009; Simard and Bingham, 2012). Few studies, by contrast, have examined the role of networks in the stand dynamics of older forests, or how they interact with other biological networks in meta-networks.

The importance of mycorrhizal networks in gap-phase regeneration of older stands is illustrated in an examination of the *Rhizopogon vinicolor*-*R. vesiculosus* complex in mature (150-year-old) interior Douglas-fir forests in the dry climatic region of the interior British Columbia (Belier et al., 2010; Belier et al., 2012). Multi-locus microsatellite DNA markers were used to examine network topology in six individual interior Douglas-fir stands (30 m x 30 m plots). Belier and colleagues found that almost all Douglas-fir trees in the multi-aged forests were interconnected by the *Rhizopogon* network by no more than three degrees of separation (i.e. by no more than two intermediate linked trees). Moreover, the younger trees had regenerated within the extensive *Rhizopogon* network of old (100–150-year-old trees; 30 m tall) interior Douglas-fir trees (Belier et al., 2010; Figure 7.5a). That

most of the young trees were linked to large, old hub trees indicated the network had scale-free properties (Figure 7.5b). This scale-free topology suggests that the hub trees were important in the resilience and self-organization of the forests. In keeping with this, seedling establishment success in the same forest type increased by 26 per cent where seedlings had full access to the mycorrhizal network of older Douglas-fir trees compared with where they did not (Teste et al., 2009). Access to the network not only improved seedling survival and physiology, but seedlings

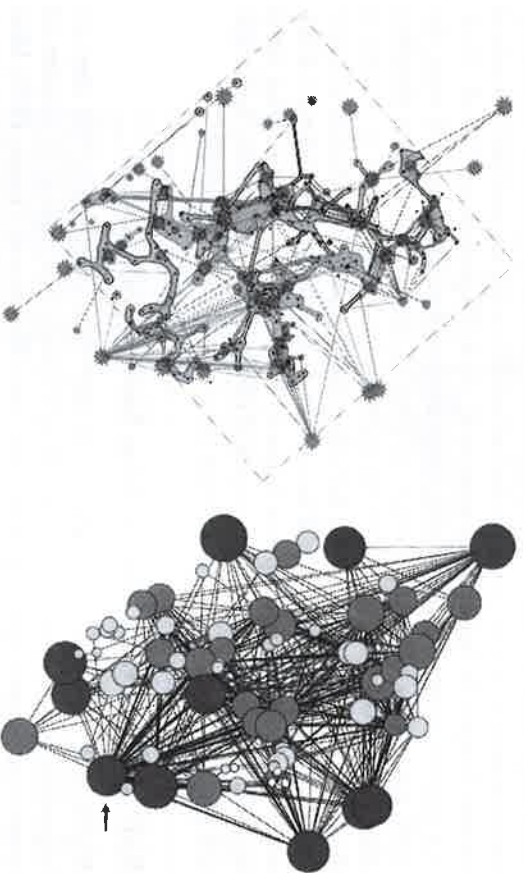


Figure 7.5 Mycorrhizal network topology in interior Douglas-fir forest (two versions of the same network). (a) The top-down spatial topology of Rhizopogon spp. genes and Douglas-fir trees in a 30 × 30 m plot. The plot (square outline) contains 67 trees of various ages (star shapes; sized relative to each tree's diameter). Small black dots mark Rhizopogon ectomycorrhiza sample locations. Samples representative of each fungal gene are outlined in different shades of grey. Rhizopogon vesiculosus genes ($n = 14$) are shaded with a darker grey than Rhizopogon vinicolor genes ($n = 13$). Lines illustrate the linkages between tree roots encountered in Rhizopogon ectomycorrhizas and corresponding source trees aboveground ('root lengths'). An arrow points to the most highly connected tree, which was linked to 47 other trees through eight *R. vesiculosus* genes and three *R. vinicolor* genes inside the plot. (b) Spatially explicit network model showing linkages between interior Douglas-fir trees via shared colonization by *R. vesiculosus* and *R. vinicolor* genes. Circles represent tree nodes, sized according to the tree's diameter and coloured with different shades of grey that increase in darkness with increasing age class. Lines represent the Euclidean distances between trees that are linked. Line width increases with the number of links between tree pairs (i.e. repeated links through multiple fungal genes). An arrow points to the most highly connected tree as in (b). Reproduced, with permission, from Beiler et al. (2010).

were colonized by a more diverse fungal community comprised of multiple long-distance exploration types (Twieg et al., 2007; Teste et al., 2009). The seedlings also received carbon, nitrogen and water transferred from the older trees through this mycorrhizal network (Teste et al., 2009). The scale-free and small world properties of the network suggest the forest was resistant against random removal or death of individual trees, which would have little effect on the connectivity of the network or regeneration capacity (Bray, 2003; Beiler et al., 2010). By contrast, targeted removal of the hub trees, such as through high-grade logging or bark beetles selectively attacking large trees, could have negative effects on new regeneration.

The mixed Douglas-fir with paper birch stands in the moist, warm interior Cedar-Hemlock forests are more productive and regenerate more readily after disturbance than pure interior Douglas-fir stands of the dry forests (Simard et al., 2005), but mycorrhizal networks also play a role in re-establishing ecosystem structures and functions. In these century-old tree species mixtures, establishment success of regenerating Douglas-fir has been greater where seedlings were linked into the species-rich mycorrhizal network of older trees or root systems that survived previous disturbances (Simard et al., 1997a). The mycorrhizal root systems of paper birch that often survive fire, pathogen infections or clearcutting are particularly important by providing a diverse and rapid source of fungal inoculum for colonizing regenerating interior Douglas-fir seedlings (Twieg et al., 2007). Thus, legacy birch roots, stumps and trees have served as critical system memory banks, where they house and disperse mycorrhizal fungal gene pools and scavenge resources for new generations of trees. In clearcuts, Douglas-fir seedlings have benefited not only from mycorrhizal fungal colonization but also from carbon transferred from paper birch through networks, particularly where Douglas-fir is shaded (Simard et al., 1997b). Net carbon transfer has been shown to follow a source-sink photosynthate or nutrient gradient, from carbon- and nutrient-rich paper birch source seedlings to increasingly light-stressed Douglas-fir sink seedlings. Transfer was also dynamic where direction of net carbon transfer reversed twice over the growing season: (1) from rapidly growing Douglas-fir to bud-bursting birch in spring; (2) then reversing, from nutrient and photosynthate-enriched paper birch to stressed understorey Douglas-fir in summer; and (3) reversing yet again, from still-photosynthesizing Douglas-fir to senescent paper birch in the fall (Phillip et al., 2011). The dynamic interplay between paper birch, Douglas-fir and interconnecting fungi, with carbon and nutrients moving in the direction of greater need over the growing season, represents an adaptive self-organizing system.

Traditional models of forest dynamics predict that regeneration patterns are controlled mainly by competitive interactions with neighbours (Simard and Sachs, 2004), but our studies in mixed forests show that facilitation by networks increases regeneration performance and affects interspecific interactions, encouraging a more diverse tree community (Simard et al., 1997). We have found that these mixed forests are not only more species-rich but are also more resistant to insect attack and disease than pure Douglas-fir forests (DeLong et al., 2002; Simard et al., 2005). Mycorrhizal networks may be involved in this resilience. This is suggested in a recent study demonstrating that defence signals can be transferred from

diseased to neighbouring healthy plants through mycorrhizal networks, resulting in up-regulation of defence genes, increased production of defence enzymes and increased disease resistance in connected healthy plants (Song et al., 2010).

As saplings grow, the benefits of resource transfer through networks likely diminish. Indeed, trees should change from net sinks to net sources as they age. The carbon and nutrient drain from large trees to establishing seedlings in the understory has been shown as negligible (Simard et al., 1997b). However, maintaining fungal networks by large trees is necessary for continued uptake of soil resources and provides insurance for regeneration of new seedlings, a stable carbon source for the fungal community and direct pathways for feedbacks that stabilize the forest community. This is particularly important in the mixed disturbance regime of interior Douglas-fir forests, where mycorrhizal networks can even out resource availability in the unpredictable and variable environment (Perry, 1995).

A meta-network: interaction of mycorrhizal networks with tree networks and nest webs

A mycorrhizal network is a foundational network that interacts with other biological networks in interior Douglas-fir forests, together comprising a meta-network. The meta-network includes networks of seed and spore-dispersing mammals, mycorrhizal and pathogenic fungi, forest plant communities, cavity nesting birds and landscapes (Figure 7.6). In this section, we will show that these networks are coupled through dispersal of propagules and acquisition of resources. In networks, such as the cavity nesting community, the supply of resources (e.g. nest sites) is considered a limitation to populations (Aitken and Martin, 2008). Additionally,

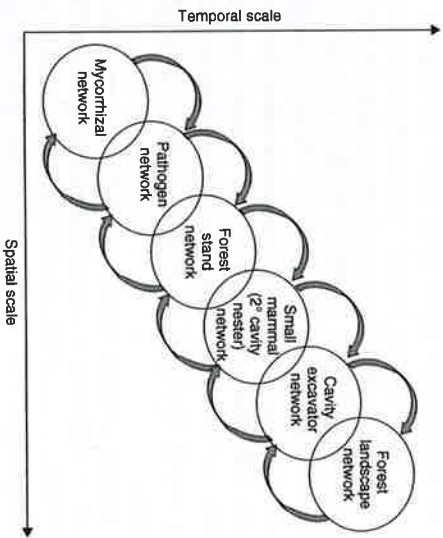


Figure 7.6 Example of a meta-network comprised of sub-networks of mycorrhizal fungi, pathogenic fungi, forest stand and plant communities, seed and spore-dispersing small mammals, cavity nesting birds and small mammals, and forest landscapes. Only interactions between adjacent scales are shown, but interactions also occur between disparate scales.

many networks are involved more in positive (mutualistic) than negative (competitive) species interactions (Bascompte et al., 2003).

In the cavity nesting community, small mammals (e.g. yellow-pine chipmunks [*Tamias amoenus*], northern flying squirrels [*Glaucomys sabrinus*], red squirrels [*Tamiasciurus hudsonicus*] and red-backed voles [*Clethrionomys glareolus*]) live in the stem cavities and canopies of old Douglas-fir trees (Figure 7.4). In the autumn, the red squirrels and northern flying squirrels forage for seed by cutting green cones from the trees and storing them in the ground. They also store cones in middens under logs, at the base of old trees and underground, where they peel the scales to get to the seeds. Because the squirrels fail to find or eat all of the seeds they store, many seeds are left behind. While some of this seed may germinate after being redistributed out of the midden by foraging rodents such as deer mice (*Peromyscus maniculatus*), most germinants originate from seed that falls from cones that open on the tree and escape rodent foraging. The red squirrels and flying squirrels, along with the deer mice, chipmunks and red-backed voles, also forage in the forest floor for *Rhizopogon* truffles, an important part of their diet (Maser et al., 2008). The small mammals consume and disperse the truffles through their feces, spreading spores that colonize the new Douglas-fir germinants. The new germinants also link into the *Rhizopogon* (and other EMF) network of nearby trees, particularly old hub trees that have extensive EMF networks. The vast EMF network of the old trees benefits seedling nutrition by tapping into a much larger pool of soil nutrients and water than the seedling could access on its own and, in exchange, the fungi benefit from sourcing a new generation of fixed carbon. In the very dry forests, seedling establishment success is higher just outside the crown of the old trees (which is where most of the seed falls), the mycorrhizal network is most developed and some shade is provided by the tree crown (Simard, 2009; Teste et al., 2009) (Figure 7.4). In wetter interior Douglas-fir forests, seedling establishment is favoured in full light and on mineral seedbeds, but small mammal dispersal and network facilitation are still important processes (Vyse et al., 2006; Simard and Vyse, 2006). Thus, the small mammal, EMF and tree community networks interact through seed/spore dispersal and resource acquisition to facilitate the establishment of new trees.

The new interior Douglas-fir seedlings commonly establish in clusters centred on the network of the older hub trees. These Douglas-fir tree clusters are interwoven with tree-fall, root disease or insect attack gaps, trembling aspen groves and meadows dominated by AMF grasses and herbs. This network pattern is expressed at a higher spatial scale as a forest plant community network (Figure 7.6). In the meadows, tree establishment is limited by low resource availability (due to soil type and soil resource competition from the herbaceous plant community and neighbouring trees) and the low dispersal of compatible EMF inoculum (Haskins and Gehring, 2004). Gaps also develop and grow due to infection by the common root pathogens, *Armillaria* root disease and laminated root rot. The pathogens spread from tree to tree through the root systems, developing a network of gaps that follows the root network pattern. Trembling aspen and paper birch are more resistant to these pathogens than the conifers and, once the broadleaved species disperse and regenerate into the gaps, they gain dominance within the gaps.

The diseased conifers and aging broadleaved trees eventually become ideal resources for tree cavity nesting birds and mammals because of the frequency with which primary cavity nesters (e.g. woodpeckers, nuthatches) excavate nesting cavities in unhealthy and dead trees (Figure 7.4). Most primary cavity excavators use their tree cavity only once for nesting, but these cavities last on average for 12 to 15 years and therefore are used by a wide diversity of secondary cavity nesting vertebrates (birds and mammals that require a cavity for breeding or roosting but are unable to excavate) (Martin and Eadie, 1999). The resultant 'nest web' is organized in a separate hierarchical network, forming a complex wildlife community that is strongly structured through the bottom-up resource flow of suitable trees for excavation, excavators and naturally occurring holes and available nesting cavities (Figure 7.7; Martin et al., 2004). The birds and mammals in this nest web interact with the plant community network by living in the cavities or canopies of the broadleaved trees or senescing coniferous trees (both of which are

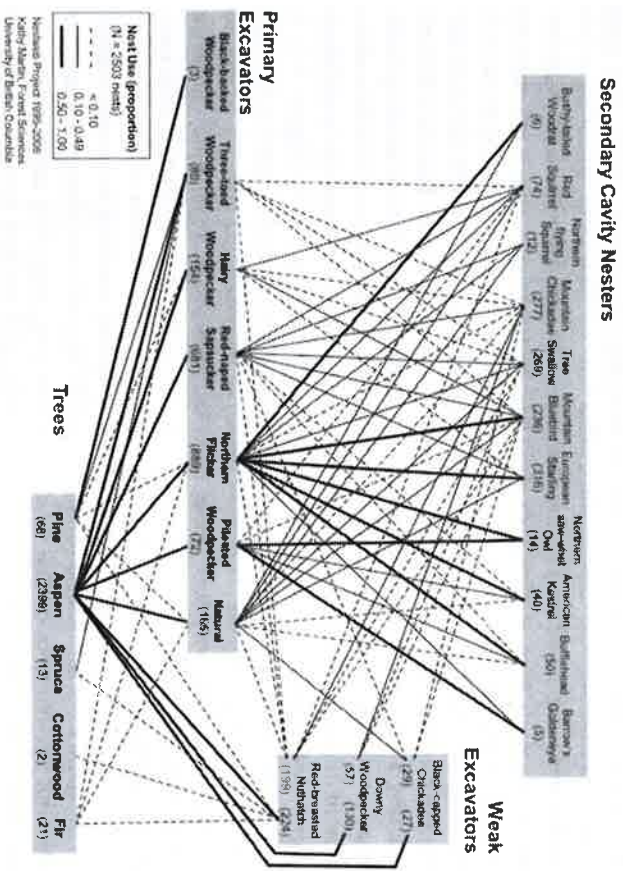


Figure 7.7 A nest web diagramming resource flow (cavity or tree) through the cavity nesting vertebrate community in interior British Columbia. Resource use in the nest web is organized by nidic levels and shows links between species using nests (e.g. secondary cavity nesters and excavators) and the excavator or tree species below that provided the resource. For example, Bufflehead ($n = 50$ nests) primarily used flicker cavities, but regularly (10–49 per cent of cases) occupied cavities excavated by Pileated Woodpeckers and occasionally (<10 per cent) used sapsucker cavities and also used decay-formed cavities. Numbers under each species indicate the number of occupied nests for which there was information on the excavator or tree species used. Nidic links for species with fewer than 15 occupied nests are considered preliminary relationships. Updated with additional data from Figure 5 in Martin et al., 2004.

mycorrhizal hub trees) and these homes become central hubs for seed and truffle foraging and dispersal by small mammals and birds. Thus, the seeds and spores that these vertebrates once dispersed through the forest eventually support a nesting resource for future generations of cavity nesters.

The network of cavity nesters in the dry interior Douglas-fir forests is centred on multi-annual resource supply and demand, which is constructed around limiting resources (Martin et al., 2004; Aitken and Martin, 2008). Cavities are one of the main resource limitations for cavity nesters and these are found primarily in the larger (DBH > 30 cm) trembling aspen trees or old interior Douglas-fir trees that are either alive with early decay, dying or dead (Figure 7.8; Martin et al., 2004). Since they excavate the cavities, woodpeckers and, in particular, northern flickers and pileated woodpeckers, can be considered the 'hubs' of the nest web and the rest of the cavity nesters are other nodes with fewer connections to other nests (Figure 7.7); the nest web thus has scale-free structure (Barabasi, 2009). Even though aspen trees usually comprise a small portion of the stand (<15 per cent), they are used for over 95 per cent of nesting attempts by 32 species of cavity nesting birds and mammals (Figure 7.8). Aspen trees can thus be considered another forest hub that is interacting with the nest web hub (woodpeckers). The remaining 4–5 per cent of cavities are found in older, decaying or dead Douglas-fir, lodgepole pine and hybrid spruce trees. The median persistence of aspen cavities is 12–14 years, but their quality changes through time (entrances get larger, cavity gets deeper) and they become less secure (Edworthy et al., 2012). The secondary cavity nesting birds and mammals that use the cavities also change with cavity age,

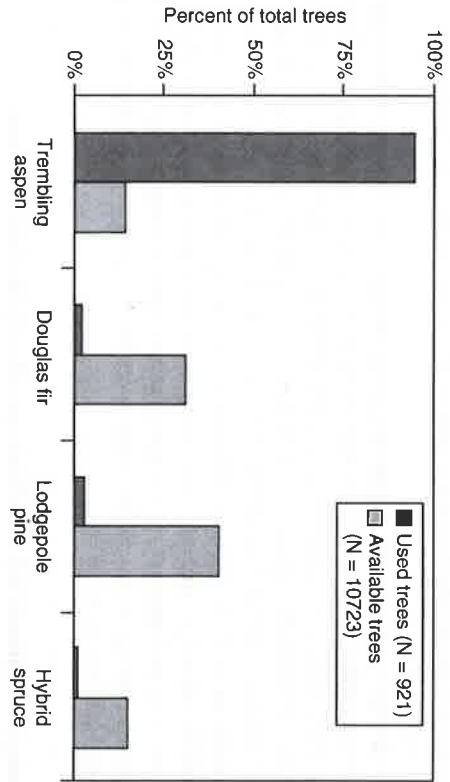


Figure 7.8 Selection of tree species used by cavity nesting birds in relation to availability of trees (>12.5 cm DBH) in interior Douglas-fir forest stands in interior British Columbia. Each used or available tree was included only once, although used trees may have been used more than once during the study and some trees supported multiple used cavities. 'Available trees' includes the most complete and most recent pre-harvest vegetation data set. Updated with additional years of data (1995–2003) from Figure 1a, Martin et al., 2004.

with dominant species such as starlings (*Sturnus vulgaris*) and mountain chickadees (*Parus gambeli*) using the cavities first, then mammals, including red and northern flying squirrels, which tend to use the cavities when they are older and thus larger (Martin, unpublished data). Other bird species, such as tree swallows (*Iridoprocne bicolor*) and mountain bluebirds (*Sialia currucoides*), use older cavities with entrances that are larger than required for their body size because they are subordinate and can only access those cavities remaining after other species have chosen their cavities (Martin et al., 2004; Edworthy et al., 2011). When high-use cavities have been removed experimentally from some stands, starling densities have been found to decline, but mountain bluebird nesting densities have increased, because of their release from competition by starlings (Aitken and Martin, 2008). The nest web is thus an evolving network where each nesting species is a node that changes in population size, depending on the availability and size of cavities and interactions with the other nesting species.

The same types of tree cavity nesting vertebrate networks occur globally, but there is a much lower dependency on excavated cavities outside of North America (Cockle et al., 2011). On other continents, secondary cavity nesting birds are more dependent on cavity formation solely from decay processes that can take one to several centuries, with many holes unsuitable for nesting or roosting (Gibbons and Lindenmayer, 2002). In North American forest ecosystems, woodpeckers provide the primary source of cavities and excavate primarily in unhealthy and recently dead tree stems (Martin et al., 2004). The result is that, in North American forests, excavators can initiate a flow of high quality holes (most useable in contrast to the decay-formed cavities) in more robust trees, probably enabling intricate networks of cavity nesting vertebrates in less mature forest stands than in South America or other continents.

A self-organized complex adaptive system emerges from the interactions among nested networks (small mammals, mycorrhizal fungi, trees and grasses, pathogenic fungi and cavity nesting vertebrates) comprising this meta-network. The system is adaptive because the species involved in the networks are adapting and evolving to the constant change brought by shifts in local interactions within and between networks, as well as shifts in disturbance regimes and climate. The immense variability caused by climate and disturbance is integral to the system dynamics and stability and appears to reinforce co-operation among networks. This tight disturbance–fungi–tree–wildlife interdependency is played out in forests around the world (Maser et al., 2008).

Changes in network facilitation along environmental stress gradients

Predicting climate change effects on forest ecosystems, and how meta-networks and management practices may interact with these changes, can be achieved using space for time experiments. Such an experimental approach has been used to show that mycorrhizal networks facilitate new regeneration more so in dry than moist Douglas-fir forests (Bingham and Simard, 2012), as predicted by the stress-

gradient hypothesis (Lorrie and Callaway, 1996). We tested the stress-gradient hypothesis along environmental gradients caused by disturbance and climate in the interior Douglas-fir forests. We found that naturally regenerated Douglas-fir seedlings received more transferred carbon through mycorrhizal networks from their neighbours where soils were severely disturbed than where they were undisturbed, but only where the seedlings were initially well colonized by EMF (Teste et al., 2010). Here, disturbance created a sufficient source-sink gradient between seedlings for carbon transfer to occur, but receiving seedlings also had to be healthy and colonized well enough to generate adequate sink strength. We also found that network facilitation of seedling establishment increased with climatic aridity, where facilitation was lowest in the moist climate of the interior Cedar-Hemlock forests and highest in the very dry climate of the interior Douglas-fir forests (Bingham and Simard, 2012). Germination and survival of seedlings linked into the network of older Douglas-fir trees was substantially greater in the very dry compared to the wet climate, and this was associated with transfer of water to the new germinants. In the dry climate especially, the mycorrhizal network appeared to extend the niche breadth of interior Douglas-fir seedlings. The results from these two studies agree with theoretical models showing that positive or mutualistic interactions dominate in poor habitat qualities with low above-ground species diversity (and dispersal), but that the importance of mutualisms decreases at the expense of competition in higher habitat qualities with high species diversity (Filotas et al., 2010). The results are also congruent with our earlier work in interior Douglas-fir forests showing that the intensity and severity of competition between trees increases from the very dry climate, where the uneven-aged forests have low productivity, low tree species diversity and high Douglas-fir shade tolerance, to the moist climate, where the tree species-rich forests have high productivity, high diversity and low Douglas-fir shade tolerance (Simard et al., 2005; Heineman et al., 2010). Even in the more favourable climate and site conditions, however, our research with mycorrhizal networks shows that the positive interactions still exist; their effects may simply be masked by the relatively greater effects of competitive interactions.

A decade of drought combined with western spruce budworm and then Douglas-fir bark beetle attack has resulted in extensive dieback of older hub trees in interior Douglas-fir forests in the early twenty-first century (MacLachlan et al., 2007) and reduced seedfall (Huggard et al., 2005). In Bingham and Simard (2012), mortality of hub trees was considerably higher where they were retained in isolation following clearcutting, rather than in groups; in the latter case, neighbours probably protected one another against the increased environmental stress (e.g. root damage, higher moisture stress, windthrow) caused by clearcutting. With hub tree death, the decline in mycorrhizal networks interacted with other stresses, such as reduced seedfall, to reach a threshold at which regeneration was no longer facilitated. Likewise, Teste et al. (2010) found that extremely severe soil conditions caused by forest floor removal and compaction reduced EMF colonization by networks and eliminated facilitative effects on seedling survival. The network facilitative pattern we observed along environmental severity gradients agrees with the

hump-shaped distribution of positive interactions observed in other plant communities (Butterfield, 2009), where competition dominates species interactions in low severity/high productivity environments, facilitation dominates in high severity/low productivity environments, but facilitation effectiveness by very tolerant species declines under extreme environmental stress. Whether facilitators increase or decrease the adaptability of forests therefore depends on the severity of the environmental conditions and the stress tolerance of the trees present (in this case, Douglas-fir hub trees).

Vulnerability of interior Douglas-fir forests to climate change

Climate models predict a dramatic shift in tree species ranges in the interior Douglas-fir forests over the next century (Hamann and Wang, 2006; Wang et al., 2012), typically with mortality of species at their trailing edges and northward and upward migration at their leading edges. Wang et al. (2012) predict a substantial expansion of Douglas-fir climate habitat in British Columbia in the twenty-first century as climate becomes more suitable at higher elevations and more northerly latitudes, while Rehfeldt et al. (2006) project an increase in Douglas-fir habitat over the western USA, then a slight decline by 2090. These predictions do not account for mortality caused by insects, diseases, fire or drought, however, and should be treated cautiously given the extensive mortality currently occurring in interior Douglas-fir forests (Maclauchlan et al., 2007), which may well be rooted partly in changes in climate underway. Moreover, the sensitivity of trees is generally expected to be much greater at their range margins and in ecotones as climate and disturbance regimes change (Woods et al., 2006), and this has been specifically observed with interior Douglas-fir at its northern margins (Griesbauer and Green, 2010).

In spite of predicted range expansion to the north, the dry interior Douglas-fir forests bordered by grasslands in the lower elevation and eastern part of their distribution may change into grasslands as temperatures rise, regional precipitation declines and severe fires remove system memory such as mature trees and advance regeneration (Hamann and Wang, 2006). In dynamics systems theory, climate change behaves here like a strange attractor, pulling ecotone forests into a new stability domain, or 'basin of attraction', that better resembles grasslands (Scheffer et al., 2002). Even today, the severity and extent of disturbance from wildfire and insect outbreaks in the interior Douglas-fir zone appear to be exceeding recent historic limits and causing extensive mortality near the forest-grassland ecotone (Maclauchlan et al., 2007). Some of this mortality is occurring in trees that have encroached into the grasslands during a moister Pacific Decadal Oscillation over the past few decades, and this oscillating tree buffer with climate variability may mitigate sudden shifts. At some threshold scale, however, climate-driven disturbance should trigger a domain shift to grassland. This would affect weather conditions and, through release of CO₂, also affect climate, and these in turn will affect disturbance propagation, resulting in a positive feedback (Kurz et al., 2008).

Management practices that fail to conserve key attributes and processes, including meta-networks and biotic diversity, may amplify the effects of climate shifts and hasten or magnify reorganization. Examples where the absence or loss of native mycorrhizal networks has led to forest collapse or plantation failure occur where forest floor has been removed, exotic grass species have been introduced, or tree species have been introduced to new environments (Simard, 2009; Collier and Bidartondo, 2009). In British Columbia, the historic management paradigm in interior Douglas-fir forests has generally involved harvest of the largest (hub) trees for their high value and slow growth rates, removal of broadleaved trees because of their competitive effects on conifers, introduction of domestic grasses as livestock forage or for erosion control, and planting of seedlings or retention of understory trees to grow into future stands (Vyse et al., 2006). This has resulted in extensive areas of relatively young stands of uniform structure and almost no remaining old growth. Although these practices have not led to system collapse in the past, they will almost certainly disrupt the scale-free meta-network created by fire, insects, fungi and regeneration patterns where they interact with climate change to cross regeneration thresholds. Dynamics systems theory predicts that removal of hubs will make the system more vulnerable to climatic stress and, if regeneration thresholds are exceeded, this may cause the interior Douglas-fir ecosystem to suddenly shift (Bray, 2003). It is possible that current declines in natural regeneration potential, which appear related to interactions between a long history of high-grade logging, spruce budworm attack and climate in the core interior Douglas-fir forests, are the early predictors of sudden shifts in forest structure and function. The rapidity of this change could be reduced with better management approaches that conserve the meta-network, more intact forest and the three- or four-century-old hub trees that are survivors from previous climates, thus allowing forests to adapt, slow down the rate of forest decline and diminish positive feedbacks to climate change and biodiversity losses.

Using our understanding of meta-networks to frame future forest management

To mitigate lags in forest re-assembly and minimize the potential for large carbon pulses to the atmosphere or losses of biodiversity, humans can play an important role in maintaining healthy forests by managing them as complex adaptive systems. This can be done by focusing management practices on protecting key response traits and legacies that are critical in the self-organization of the system and the avoidance of threshold changes (e.g. retaining hub trees for regeneration and cavity legacy potential). This will require maintenance or enhancement of a diversity of genotypes, structures and networks across different genetic, trophic, midic, spatial and temporal scales (Levin, 2005).

The meta-network of patterns and processes in native forests provide an intuitive strategy for their protection, reforestation or restoration. The successful establishment of forest ecosystem networks across a range of disturbance severities in the past suggests that these ecosystems have historically been resilient to the

natural mixed severity disturbance regime (Perry et al., 2011). Provided disturbances are within the range of natural variability, history suggests that the maintenance of key attributes, legacies and system memory should facilitate recovery in time, even in small, severely disturbed patches (Klenner et al., 2008). However, these pieces and processes are under pressure from climate change and large-scale disturbances that are now occurring in the interior Douglas-fir forests (e.g. widespread mountain pine beetle and western spruce budworm infestations, extensive logging disturbance) (Vyse et al., 2006; MacLachlan et al., 2007; Kurz et al., 2008). Great care is therefore needed during tree diebacks or large-scale salvage programmes of vastly disturbed areas to ensure legacies (such as residual trees, plants, snags and coarse woody debris) are retained in an effective distribution through openings and that sites are reforested rapidly enough to retain system memory of the previous forest. For example, in the first four years post-harvest, the annual loss of legacy cavity nesting trees in interior British Columbia increased from 13 per cent annual loss in unharvested sites to 19.5 per cent loss for nesting trees in variable retention patches and 22 per cent loss for isolated nesting trees in clearcuts, given equivalent levels of tree decay (Edworthy et al., 2012). Thus, variable retention harvesting that includes a variety of opening sizes and ages and retains multi-aged patches of conifers and broadleaved trees across the landscape, now and in the future, can help protect legacies and approach natural disturbance effects on the biotic community. Even with this management approach, the range of variability is expected to shift as climate changes, probably entailing recovery to new ecosystem states. This will require flexible and novel management techniques such as assisted migration or manipulation of tree size distributions. The number and size of reserves of unharvested areas in the interior Douglas-fir forests could also be substantially increased. The success of such approaches will depend on our ability to slow the rate of change by conserving key response traits and ecosystem legacies across the landscape.

A critical management target is conservation of genetic legacies for the system memory and adaptive capacity they provide. For example, the range of genetic alleles in older trees can represent successful regeneration in previous climates. Because trees are long lived, rapid changes in the climate can put a premium on these alleles. This means we should be particularly concerned about conservation of trees that are old (i.e. hub trees with large mycorrhizal networks, cavities and deep furrowed, rough bark to provide foraging substrates) and those at the southern or moisture-limited extremes of the spatial range (Aitken et al., 2008). Protecting old hub trees at the trailing edge of a migrating population will be particularly challenging.

Likewise, we need to be concerned about the areas into which a population will migrate. At the leading edges, barriers in tree migration will be dispersal of seeds and spores, competition with existing plants and the colonization of non-local tree genotypes with weakly compatible mycorrhizal fungal symbionts. Conserving a genetically diverse and highly adaptable community of trees, mycorrhizal fungi and biotic dispersal agents at the leading edge of tree species ranges may reduce the risk of deleterious matchings and facilitate regeneration of genetically diverse forests with high adaptive capacity (Whitham et al., 2006).

For protecting forest ecosystem goods and services, it is obvious that harvesting practices need to be transformed so that they retain the oldest or largest trees in the landscape. These trees should be conserved in patches where neighbours protect them against abiotic and biotic stresses and serve as future recruits when the central hub tree dies. Likewise, broadleaved trees should be maintained for their nest webs, mycorrhizal networks, other above- and below-ground diversity, nutrient, carbon and water cycling attributes, disturbance resistance and resilience and the facilitative and protective effects they provide to forests (Martin et al., 2004; Simard and Vyse, 2006; Perry et al., 2011). This contrasts sharply with past practices that have sought to depress the amount of trembling aspen in dry forests and paper birch in moister forests to encourage conifer dominance; today, more severe disturbances may be required to renew the mismanaged broadleaf resources (Vyse and Simard, 2009). Conserving these key trees will not only conserve genetically diverse populations and ecosystems with high adaptive capacity (Whitham et al., 2006), they will also serve as facilitators of regeneration and provide future nesting and rooting sites for forest wildlife communities (Martin et al., 2004; Drever et al., 2008). Equally important is retention of forest floor materials on site for their EMF inoculum and other ecosystem services, even if they are disturbed and redistributed within sites (Graham et al., 1994).

Natural regeneration, especially advanced regeneration, should be incorporated into the regeneration plan after any harvest. This will help conserve the genetic memory of the stand and capitalize on their superior establishment success and survivability. This will require changes in logging and fire protection practices that currently remove advance regeneration and seed trees. Planting patterns should also follow natural spatial and temporal patterns in resource availability or environmental stresses, where clusters of trees are planted in areas or at times where they have the highest probability of survival. Planting should focus on maintaining species diversity, judiciously assisting migration of new genotypes suited to the changing climate and conserving key species at higher risk of being lost, such as ponderosa pine in dry interior Douglas-fir forests and western white pine (*Pinus monticola* Dougl. Ex D. Don) in the moist forests. Where soils are degraded, native soil fungal inoculum should also be restored. In contrast to current practice, seeding with exotic grasses should be avoided as much as possible since most species are AMF or non-mycorrhizal increasers and native plants generally regenerate quickly, even on severely disturbed sites (Huggard et al., 2005; Hamilton and Haussler, 2008). Finally, a large number of trees in each forest should be allowed to grow to an old age so they can serve as legacies (e.g. network hubs, sources of transferred resources, or sources of defence signal transfers) for increasing the adaptive capacity of regenerating seedlings or self-organization potential of disturbed forests.

It is increasingly recognized that healthy plants can transfer nutrients and defence signals to other healthy plants directly through mycorrhizal networks (Simard and Durrall, 2004; Selosse et al., 2006; Song et al., 2010). Even larger amounts appear to be transferred from stressed or dying trees to healthy roots (Simard et al., 2002; Song et al., 2010). Where the dying native forest is protected

(i.e. not salvage logged) until the new generation of trees is established, new seedlings may be poised to capture released nutrients and defence signals via transfer of compounds through the mycorrhizal network of the dying trees before they are acquired by soil microbes. If germinants of native plants can avoid competition with soil microbes by acquiring carbon and nutrients directly from dying trees through a mycorrhizal network, or if they can increase constitutive production of defence enzymes, they may establish more rapidly and with greater vigour, thus increasing competitiveness with non-networking exotic invasive plants and reducing CO₂ feedback to the atmosphere. Mycorrhizal networks connecting new generations with old in forests under climate stress may thus be particularly important in conserving existing forests, facilitating native plant establishment and migration, providing barriers to weed invasion and mitigating large CO₂ losses.

Even with good management and assisted migrations, mature and juvenile tree mortality is expected to increase with climate change (IPCC, 2007). Mortality can be managed in a manner that eases the transition from one forest type to another. For example, retention of a portion of the dying or dead trees (versus broad-scale salvage harvesting) after a disturbance can help conserve the legacies of the original forest and allow the inheritance of system memory by the new forests before the old trees are completely dead. A well-known functional legacy is unsalvaged structure – it provides partial shade that may protect germinants until their roots and mycorrhizal networks are developed enough to tap deeper and more extensive soil resources, and it can be a source of defence signals and resource transfers for increased vigour and resilience of the new generation of trees.

Recommendations for forest management approaches in our changing climate

In this section, we provide recommendations for forest management practices in British Columbia with the objective of maintaining forest stability under a changing climate. This objective incorporates conservation of biological diversity, maintenance of carbon storage capacity and maintenance of other basic functions, structures and services of healthy ecosystems. We have organized our recommendations into three sections: landscape-level planning, stand-level practices and forest governance. Not all of these recommendations are based directly on the findings of our chapter, particularly those for forest governance, but we include them to provide context for recommendations that flow directly from our work.

Landscape-level planning

Landscape- and regional-level planning should aim to maintain complex adaptive patterns and processes that facilitate appropriate fluxes and dispersal of energy, resources, species and disturbances. This will require in-depth knowledge of patterns and processes and should entail managing a multi-faceted pattern of reserves and disturbances. Planning should consider:

- (1) All cutting practices in the province should adopt highly diverse variable retention harvesting that result in a planned variety of opening sizes, configurations, stand compositions and stand ages across the landscape.
- (2) The harvest of old-growth forest should be reduced to conserve genetic and species diversity and to maintain carbon storage; this reduction should be tailored to meet regional variations in past disturbance patterns (including cutting) and expected climatic changes. Over the next 100 years, the interior forests are expected to experience more dramatic changes than the coast.
- (3) Cutting that does occur should be focused on younger stands that have regenerated after disturbances in the last 120 years because of their lower capacity for carbon storage and biodiversity. However, the age at which cut stands are then grown should be increased to conserve genetic alleles from previous climate and to facilitate deep carbon storage.
- (4) Forest reserves should be increased in number and size, particularly in areas with high topographic variability, genetic diversity and productivity. This should include protection of unique habitat features, such as biodiversity hotspots, riparian areas or wetlands and the conservation of genetically diverse biotic communities for their high adaptive capacity. Maintenance of connectivity in landscapes should be the primary goal of reserve planning for dispersal and migration.
- (5) The area of forest in the province should be maintained. Forest practices need to ensure rapid reforestation of harvested or naturally disturbed areas with native and adaptive tree species mixes. Converting forested areas to other land uses should be resisted because of the additional pressures it places on species, water and carbon budgets.
- (6) Accelerated harvesting after large disturbances should be curbed with the intent of conserving biological legacies and system memory and to mitigate rapid carbon release from the landscape.

Stand-level practices

Where stands are harvested, variable retention methods should be applied with the intention to facilitate reforestation and mitigate losses of biodiversity, carbon and water quality. Harvested openings need to be large enough to provide variability, habitat attributes and a suitable environment for regeneration (single tree selection is often inadequate in many places). However, openings should also be small enough that forest edges are in close enough proximity to supply biological legacies and protection. Variable retention systems should consider:

- (1) Maintaining green (hub) trees, understory plants, dead and senescent trees (standing and down), coarse woody debris, forest floor, banks of seeds, buds and seedlings and other legacies in an effective distribution across disturbed stands.
- (2) Retaining live big old trees (broadleaves and conifers) in stands and across the landscape for the habitat they provide cavity-using vertebrates, fungal

- and microbial communities and the positive effects they have on nutrient, carbon and water cycling.
- (3) Retaining dead and dying trees (broadleaves and conifers). These should be retained in groups of trees that range in age and density to mitigate losses with disturbance and to provide future recruits when the core hubs die. To ensure a continuous supply of cavities, broadleaves (especially trembling aspen) should be retained in a range of conditions, especially old, unhealthy and dead trees, but also young and mid-aged trees.
 - (4) Reforesting disturbed areas as rapidly as possible to restore carbon sequestration capacity and reduce decomposition rates and hence carbon emission rates. This could involve under-planting prior to a planned disturbance.
 - (5) Encouraging natural regeneration and discouraging its removal from plantations through intensive silviculture practices.
 - (6) Protecting and conserving advance regeneration.
 - (7) Planting variable mixes of tree species that are appropriate for site- and landscape-level objectives. The tree species mixtures should include the range of conifer and broadleaf species that are native in the area, but also include a small proportion (perhaps 10 per cent) of species or genotypes predicted to migrate from warmer climates (e.g. from lower latitudes or elevations). They should also include species that are particularly at risk of being lost.
 - (8) Planting at variable densities and compositions, following natural microsite patterns that are favourable for survival and growth.
 - (9) Regenerating broadleaf stands, whether for habitat, timber, carbon sequestration or future cavity resources, at higher stand densities than conifer or mixed stands, as occurs in nature. High density stands will not only sequester more carbon, but will facilitate natural self-thinning, producing higher quality stems for cavity nesters or timber.
 - (10) Allowing a large proportion of regenerating trees to reach old-age.
 - (11) Avoiding soil degradation. Where soil is degraded or forest floor or coarse woody debris has been removed, it should be restored across openings.
 - (12) Avoiding domestic grass-seeding or introduction of exotic weeds that have the potential to reduce regeneration potential and degrade habitat quality.
 - (13) Using intensive silviculture practices such as fertilization, brushing or pruning with caution. These treatments often have unintended side-effects and fertilizers and herbicides in particular are carbon-expensive and pollutants to the environment.

Forest governance

The forests of British Columbia are largely owned by the people of the province and the activities of forest managers are governed by a collection of laws, regulations and policies with networks, connection memories and redundancies that rival the complexity of a forest ecosystem. This governance system has accumulated layers since the first Forest Act was enacted in 1912 and has witnessed the political interests of numerous governments over the last century with surprising resiliency.

At its heart lies the principle of the forest as a supplier of wood to be exploited for the benefit of the population, but with safeguards for renewal of the commodity over time and protection for non-wood based services provided by the forest. Transforming this system from one that is commodity-based to one that recognizes and manages forests as complex adaptive systems presents a major challenge. Legislation will be required that gives higher priority to maintaining forest cover for conservation of critical ecosystem services, including carbon storage, biodiversity and water than to supplying wood to mills. It will also be required to provide a coherent framework for adaptive forest management at scales from broad climatic regions to forest stands, rather than provide a licence for corporations to manage forests piecemeal in the interests of their shareholders. In the principles of complex adaptive systems, it will entail transforming governance from large top-down tentures to grass-roots community-based responsibilities.

While a transformation might seem improbable, in 1995 the then government of the province passed a Forest Practices Code Act that provided for stewardship of the forest based on an ethic of respect for the land and balancing economic, productive, spiritual, ecological and recreational values of forests to meet the economic social and cultural values of peoples and communities. And the Canadian Council of Forest Ministers, in the same era, supported criteria and indicators for sustainable management of forests based on the conservation of biological diversity, the maintenance of ecosystem condition and productivity, the conservation of soil and water resources and the maintenance of forest contributions to global ecological cycles. Political changes in Canadian society have stranded these first steps towards acknowledging the complexity of forest ecosystems and the values that they provide humanity, but they demonstrate that the task is not impossible.

Summary

Local and cross-scale interactions between organisms and their environment underpin self-organization in forest ecosystems; these interactions are commonly played out through interconnected biological networks. Interacting networks, or meta-networks, are thus important agents of complex adaptive systems; they are comprised of nodes and links in a scale-free structure through which matter and energy flow, thus creating and maintaining structure, function and adaptability. In this chapter, we showed that mycorrhizal networks interact with other networks of trees and plants, pathogenic fungi and cavity nesting birds and small mammal communities, resulting in self-organization and resilience of the ecosystem. Once interior Douglas-fir seeds are dispersed and germinate, local competitive and facilitative interactions between component networks results in self-organization and emergence of higher order structures and functions in a meta-network. The heterogeneity of the ecosystem is compounded by the variability of weather, climate and disturbances characteristic of interior Douglas-fir forests. Management practices, climate change and interacting disturbances that stress or remove legacy hubs (old Douglas-fir trees, trembling aspen trees and woodpeckers) can reduce regeneration potential. Managing forests as complex adaptive systems through

conservation of key species and legacies (system memory), network structures and interacting hubs, will increase the adaptability of forests and reduce future losses in biodiversity and carbon stocks in the face of climate change.

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8 Complexity confronting tropical silviculturists

Francis Putz

Introduction

In addressing tropical silviculture as a complex adaptive socio-ecological system, it seems important to differentiate between what has been revealed by researchers or recommended by foresters from what is actually happening in the forest. Furthermore, such an analysis should be interdisciplinary, reflecting tight coupling of the mostly biophysical realms of silviculture and ecology with the socio-economic and political realms that have such large impacts on forests and forestry. Such analyses of coupled human and natural systems benefit from inputs from experts representing a wide variety of disciplines and consideration of the full range of driving and responding factors at a wide variety of temporal, spatial and hierarchical scales (Liu et al., 2007). Inputs from local researchers and practitioners are also critical lest important factors be overlooked or misconstrued. As a traditionally trained forest ecologist, North American and sole author of this chapter, I recognize limitations in my understanding of the social, economic and political dimensions of tropical forestry. That said, given the background on ecology of tropical forests provided in Chapter 3, background on complexity science provided in Chapters 1 and 2 and some possible applications to forest management provided in Chapter 14, plus the availability of many excellent reviews of silvicultural systems recommended for application in tropical forests (e.g. Bruning, 1996; Dawkins and Philip, 1998) and abundant literature on rural sociology and political ecology (e.g. Robbins, 2012), I feel secure in focusing on some of the factors that emerge from beyond forest boundaries but nevertheless confront tropical silviculture. To understand how these factors might influence tropical silviculture, I strive to differentiate between what is complicated (i.e. involves many components) from what is complex (i.e. uncertain and emergent), but the two are often difficult to distinguish.

Despite decades of efforts at reform and some notable exceptions, most tropical forests are simply logged with little regard to future production or other ecosystem values (Blaser et al., 2011). In other words, they are mostly exploited for timber, not managed. Voluntary third-party certification, in some cases reinforced by efforts of states to reign in timber industries, is having some positive impacts but discussions of managing tropical forests for resilience, biodiversity, or even sustained yields are still mostly academic. Instead, advocates for sound tropical