

Consequences for ectomycorrhizal fungi of the selective loss or gain of pine across landscapes

Justine Karst, Morgan J. Randall, and Catherine A. Gehring

Abstract: Altered disturbance regimes and novel introductions are causing rapid shifts in the distribution of pines (*Pinus* L.). The functionally obligate symbiosis between pines and ectomycorrhizal (EM) fungi dictates that shifts in the distribution of one partner will affect the distribution of the other. In this review, we examine evidence for three hypotheses. (1) The loss of photosynthates through stress or tree mortality decreases the abundance of EM fungi and selects for less carbon-demanding species. (2) Pine introductions initiate establishment of novel EM fungal communities. (3) The extent of shifts in EM fungal abundance and community composition is mediated by surrounding vegetation. We find support for these hypotheses though changes in EM fungal abundance are variable and context-dependent. We posit that the consequences of shifts in EM fungal abundance and community composition extend beyond the individual tree to the landscape; these changes may affect population dynamics of both symbionts, ecosystem processes, and the conservation and evolution of fungi. In addition to conducting baseline surveys to assess the distribution of EM fungi, increasing our understanding of their function, morphology, propagation, and controls on host-specificity, and shifts would also assist in predicting the trajectory of ecosystems following the loss or gain of pine.

Key words: climate change, disturbance, drought, ecosystems, fire, fungi, insect outbreaks, invasion, *Pinus*.

Résumé : Les régimes de perturbation modifiés et les nouvelles introductions sont responsables des déplacements rapides de la distribution des pins (*Pinus* L.). La symbiose fonctionnelle obligée entre les pins et les champignons ectomycorhizes (EM) signifie que des changements dans la distribution d'un partenaire affectera la distribution de l'autre. Dans cet article de revue, les auteurs examinent les données qui soutiennent trois hypothèses. (1) La perte de photosynthats à cause du stress ou de la mortalité des arbres diminue l'abondance des champignons EM et sélectionne les espèces à demande plus faible en carbone. (2) L'introduction du pin initie l'établissement de nouvelles communautés d'EM fongiques. (3) L'étendue des changements d'abondance des EM fongiques et la composition de la communauté passent par l'intermédiaire de la végétation environnante. Les auteurs ont trouvé un appui à ces hypothèses à travers le fait que les changements d'abondance des EM fongiques sont variables et dépendent du contexte. Ils postulent que les conséquences de ces déplacements sur le plan de l'abondance des EM fongiques et de la composition de la communauté vont au delà de l'arbre individuel vers l'écosystème ; ces changements peuvent affecter la dynamique de la population des deux symbiotes, les processus de l'écosystème et la conservation et l'évolution des champignons. En plus de réaliser des estimations de référence afin d'évaluer la distribution des EM fongiques, il est nécessaire de mieux comprendre leur fonction, leur morphologie, leur propagation et les contrôles de la spécificité à un hôte et des déplacements, afin de prédire la trajectoire des écosystèmes à la suite d'une perte ou d'un gain en pin. [Traduit par la Rédaction]

Mots-clés : changement climatique, perturbation, sécheresse, écosystèmes, feu, champignons, infestation d'insectes, invasion, *Pinus*.

Introduction

Pines (genus *Pinus* L.) comprise a diverse, economically important taxon of species distributed throughout the northern hemisphere, and introduced widely in the southern hemisphere (Richardson et al. 2007). Through relatively rapid range expansions and contractions, immense changes are occurring in the distribution of pines worldwide (Richardson et al. 2007). Of 111 *Pinus* species (Price et al. 1998), at least 19 are alien invaders in the southern hemisphere (Richardson 1998b) and another third are threatened across the world (Richardson et al. 2007). Mortality rates in western North American pines have increased over the past 200 years (van Mantgem et al. 2009) and have also been documented in Asia and Europe (Allen et al. 2010). Commercial plantations and ornamental introductions of pines have been the main cause of conifer

invasions in South Africa, Australia, New Zealand, and South America (Simberloff et al. 2010). The consequences of these losses and gains of pine across landscapes have complex economic, ecological, and cultural implications (Richardson 1998a; Richardson et al. 2007).

Though climate is an important factor underlying the distribution of pines, plant traits may also affect the ability of pines to expand into new regions or their propensity to be lost from others. For instance, time to reproduction, intervals between large seed crops, and relative growth rates predict pine invasiveness (Grotkopp et al. 2002; Rejmanek and Richardson 1996). These life history traits can also be modified by root-colonizing symbiotic fungi, i.e., ectomycorrhizal (EM) fungi. EM fungi co-diversified with the evolution of pines, approximately 200 million years ago (Tedersoo et al. 2010) and their presence often results in increased

Received 28 March 2014. Accepted 6 October 2014.

J. Karst. Department of Renewable Resources, University of Alberta, 442 Earth Sciences Building, Edmonton, AB T6G 2E3, Canada.

M.J. Randall. College of Biological Science, University of Guelph, Guelph, ON N1G 2W1, Canada.

C.A. Gehring. Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011-5640, USA.

Corresponding author: Justine Karst (e-mail: justine@karst.ca).

survival and growth of their hosts (Smith and Read 2008). Pines, in particular, host a rich assemblage of EM fungi and, based on contemporary evidence, form functionally obligate associations with fungi exhibiting a range of host specificity (Molina et al. 1992; Smith et al. 2009). The obligate nature of the association suggests that the loss or gain of pine across landscapes will be inextricably linked to EM fungi — shifts in the distribution of one partner will ultimately affect the distribution of the other.

A variety of ecological agents may cause rapid shifts in the distribution of pines. Intentional or inadvertent introductions have resulted in invasions by pine on several continents and islands, most notably those in the southern hemisphere (Richardson 1998b). Altered disturbance regimes involving fire, drought, temperature stress, and insect outbreaks have resulted in the extirpation of pines at regional scales (Allen et al. 2010; Anderegg et al. 2013; Meddens et al. 2012). These gains (invasion) and losses (selective mortality as a result of altered disturbance regimes) have cascading effects on the remaining ecosystem (e.g., Kurz et al. 2008; Richardson 1998b). Accumulating evidence indicates that the loss or gain of pines on the landscape also impacts the abundance, composition, and functioning of EM fungi — this is no surprise given the intimate and dependent relationship between tree hosts and fungi.

In this review, we examine the effects of the selective loss or gain of pines from the landscape on the local response of ectomycorrhizas, i.e., the presence, species composition, diversity and abundance of EM fungi. Specifically, we bring together evidence to examine three hypotheses. (1) The loss of photosynthates, a key source of energy synthesized by host trees and used by EM fungi, results in decreased abundance of EM fungi and a shift in community composition. We predict this shift will often be towards less carbon-demanding species because tree mortality and stress can reduce photosynthates available for EM fungi. (2) Pine introductions initiate establishment of novel EM fungal communities; EM fungi vary in dispersal ability, host preference, and environmental tolerance, limiting their natural distribution. (3) The extent of shifts in fungal abundance and community composition is mediated by surrounding vegetation. The matrix of vegetation — or its absence — following the loss or gain of pine may promote or impede changes in the EM fungal community depending on the extent of host specificity of EM fungi and their tolerance to the altered abiotic and biotic conditions of the disturbed stand.

To examine our first hypothesis, we begin the review by considering disturbances resulting in rapid mortality of pine including extreme drought, fire, and insect-caused mortality. In the absence of other EM hosts, the loss of pines should decrease abundance of EM fungi and as a result, cause a shift in community composition. Subsequently, we review the effects of host physiological stress caused by drought, insects, and parasites on EM fungi, as these types of stress can be precursors to tree mortality. Though pines remain present, the potential reduction of photosynthates with stress may select for less carbon-demanding fungi, consistent with our first hypothesis. Intentional or inadvertent introductions are examined in the third section where the extent of co-dispersal between EM fungi and pines provide a test of our second hypothesis that introduction of pines initiates the establishment of novel fungal communities. In each of these three sections, we first describe shifts in the abundance of EM fungi, followed by changes in their community composition and diversity. To examine our third hypothesis, throughout the review, we consider the importance of the surrounding vegetation, particularly the mycorrhizal associations of the matrix vegetation and their host specificity to EM fungi. We end by examining the mechanisms and implications of changes in EM abundance and community composition while identifying major gaps in our understanding of EM ecology.

Community responses of EM fungi to the loss of pine from landscapes

Many species of pine are adapted to disturbance such as fire, drought, and insect outbreaks; however, with climate change, these types of disturbances are predicted to increase in frequency, scale, and severity (Allen et al. 2010; Moritz et al. 2012; Sturrock et al. 2011). In this section, we test our first hypothesis that the loss of hosts associated with pine mortality results in decreased abundance of EM fungi and shifts in community composition, presumably caused by the loss of photosynthates and (or) changes in soil conditions selecting for different fungal species.

Abundance

Given the projections for increasing fire activity across large portions of the planet (Moritz et al. 2012), it is important to gain a detailed understanding of both the extent and timing of EM fungal responses to wildfires of varying severity. Low-intensity fires may have only modest effects on EM fungi (e.g., Jonsson et al. 1999; Korb et al. 2004), therefore, we focused our literature review on more severe fires that resulted in loss of pines from forest stands (Table 1). Fire can affect EM fungi through mortality of host plants, but also by heating the soil, combustion of the organic layer, deposition of ash, and alteration of runoff from soil surfaces (Cairney and Bastias 2007). High-intensity fires that resulted in significant pine mortality negatively affected EM abundance in some studies but not others (e.g., Kutorga et al. 2012; Stendell et al. 1999; Torres and Honrubia 1997; Trusty and Cripps 2011). EM biomass was eight-fold lower in a *Pinus ponderosa* forest following a prescribed ground fire that destroyed the litter layer and killed numerous trees (Stendell et al. 1999). The abundance of EM sporocarps declined dramatically following a stand-replacing wildfire in *Pinus mugo* dominated forest (Kutorga et al. 2012). In contrast, EM colonization of planted or naturally re-establishing *Pinus albicaulis* seedlings did not vary between severely burned and unburned sites (Trusty and Cripps 2011). Some of this variation in response is likely owing to the proximity to living trees that serve as EM hosts, consistent with our third hypothesis, as well as to differences in the time elapsed since the fire.

In addition to fire, other disturbance agents may selectively remove pine from landscapes (Table 1). As a result of recent climate change, pine mortality due to drought, insect outbreaks, and disease has rapidly increased around the globe (Allen et al. 2010; Sturrock et al. 2011). The single study investigating large-scale mortality caused by extreme drought found that remaining individuals of *Pinus edulis* at high mortality sites had 34%–52% lower EM colonization than conspecifics at nearby low mortality sites (Swaty et al. 2004). Bark beetles have disturbed approximately 47 million hectares of pine forests in western North America (Raffa et al. 2008); both EM sporocarp production and fungal hyphae in soils decreased following high tree mortality (>80% pine killed) caused by mountain pine beetle (*Dendroctonus ponderosae*) (Treu et al. 2014). Stands with less beetle-induced tree mortality lost fewer species of EM fungi presumably due to the presence of EM hosts, consistent with our third hypothesis.

Community composition and diversity

High-severity fires that resulted in significant pine mortality also led to shifts in EM fungal communities. Effects on species richness and (or) diversity were variable but shifts in species composition were common (e.g., Kipfer et al. 2011; Rincón and Pueyo 2010) (Table 1). Colonization of roots was predominantly by resistant propagules in stands of *Pinus muricata* (Baar et al. 1999) and differences among species of propagules in sensitivity to high soil temperatures could contribute to shifts in fungal species composition. Studies along fire chronosequences provide important information about the duration of fire effects. In *Pinus sylvestris* stands, species richness recovered within 5 years of burning,

Table 1. Ectomycorrhizal (EM) fungal community shifts and functional responses to loss of pine.

<i>Pinus</i> species	Study	Mechanism of pine loss	Structural changes to EM fungal communities	Functional responses	Reference
<i>P. edulis</i>	Pinyon-juniper woodlands, southwest USA	Drought	Decrease in percent colonization and richness ^{a,c} ; community composition ^{a,c} changed	Decreased trunk growth	Swaty et al. 2004
<i>P. albicaulis</i>	<i>P. albicaulis</i> forest, Montana, USA	Severe fire	Fire did not alter EM colonization, but affected composition ^{a,d}	Not assessed	Trusty and Cripps 2011
<i>P. banksiana</i>	<i>P. banksiana</i> forest, Michigan, USA	Stand-replacing fire chronosequence	Fire effects on EM richness were short-lived; composition differed throughout chronosequence and was associated with nitrogen dynamics ^b	Not assessed	LeDuc et al. 2013
<i>P. halepensis</i>	<i>P. halepensis</i> forest, Spain	Stand-replacing fire	Fire did not alter EM colonization in a bioassay, but it altered species composition and increased sclerotia ^{a,d}	Not assessed	Torres and Honrubia 1997
<i>P. jeffreyi</i>	Old growth forest, California	Stand-replacing fire	Species of EM fungi varied in sensitivity to high soil temperature	Not assessed	Izzo et al. 2006
<i>P. mugo</i>	<i>P. mugo</i> forest, Lithuania	Stand-replacing fire	Fire altered abundance of sporocarps of EM species	Not assessed	Kutorga et al. 2012
<i>P. muricata</i>	<i>P. muricata</i> forest, California, USA	Stand-replacing fire	Post-fire EM community of seedlings resembled resistant propagule community ^{a,b,c,d}	Not assessed	Baar et al. 1999
<i>P. muricata</i>	<i>P. muricata</i> forest, California, USA	Stand-replacing fire	Fire altered EM community composition, increasing biomass of Ascomycota; ash had minimal effects on community ^{b,c}	Not assessed	Grogan et al. 2000
<i>P. pinaster</i>	<i>P. pinaster</i> forest, Spain	Severe wildfire	Sporocarp dry mass, EM sporocarp richness, and diversity declined with fire	Not assessed	Martín-Pinto et al. 2006
<i>P. pinaster</i>	<i>P. pinaster</i> forest, Spain	Fire of varying severity including high severity	Fire did not alter EM colonization, species richness or diversity, but severe fire altered composition ^{a,b,c}	Not assessed	Rincón and Pueyo 2010
<i>P. pinaster</i>	<i>P. pinaster</i> forest, Spain	Stand-replacing fire chronosequence	Richness decreased with time since fire though phylogenetic diversity increased; fire altered composition ^{b,d}	Not assessed	Rincón et al. 2014
<i>P. pinaster</i>	<i>P. pinaster</i> and oak forest, Portugal	Severe fires of different ages	Shorter fire return intervals decreased richness and altered composition ^{b,d}	Not assessed	Buscardo et al. 2011
<i>P. pinaster</i>	<i>P. pinaster</i> forest, Portugal	Wildfire chronosequence	EM richness recovered after 6 years, but composition remained different from unburned; repeated fire reduced potential for common mycorrhizal networks ^{b,d}	Not assessed	Buscardo et al. 2010
<i>P. ponderosa</i>	<i>P. ponderosa</i> forest, California, USA	Prescribed fire resulting in tree mortality	Fire reduced EM biomass eight-fold and also reduced community evenness; community patterns difficult to assess due to high diversity and spatiotemporal variability ^{a,c}	Not assessed	Stendell et al. 1999
<i>P. sylvestris</i>	<i>P. sylvestris</i> , Italy Switzerland	Stand-replacing fire chronosequence	Fire reduced richness and altered composition ^{a,b,d} of EM root tips; richness recovered after 15–18 years, but not composition	Not assessed	Kipfer et al. 2011
<i>P. sylvestris</i>	Plantation in Scotland	Fire of varying severity with high severity	Fire did not alter EM colonization, but reduced richness, especially severe fire ^{a,d}	Not assessed	MacKay 2004
<i>P. contorta</i>	Pine forests, western Canada	Insect, <i>Dendroctonus ponderosae</i>	Decrease in richness, number of EM sporocarps, and hyphal length in soils; shifts in community composition of sporocarps	Not assessed	Treu et al. 2014

^aDetermined by morphotyping.^bDetermined by DNA sequencing.^cDetermined by restriction fragment length polymorphisms (RFLP).^dTreatments were not replicated.

while species composition remained different from unburned stands across the entire 18-year chronosequence (Kipfer et al. 2011). By studying naturally regenerating mono-dominant stands of *Pinus banksiana* killed by stand-replacing wildfires over a 5–56 year period, LeDuc et al. (2013) showed that changes in EM fungal communities were strongly associated with increases in soluble organic nitrogen and free amino acid nitrogen in soil with time since fire. Several studies observed that ascomycete EM fungi dominated immediately after fire (e.g., Grogan et al. 2000), a shift quantified using phylogenetic analyses by Rincón et al. (2014). In disturbances where pine was killed and not replaced by other pine species (i.e., extreme drought and insect-caused mortality), richness of EM fungi decreased both above- and below-ground, and the community composition changed (Swaty et al. 2004; Treu et al. 2014) (Table 1). Though trees may remain standing, the effects of pine mortality caused by extreme drought or insect attack on the EM fungal community are effectively similar to those caused by high-intensity fire. That is, EM sporocarp production and below-ground abundance of EM fungi often decreases, in combination with a shift in the community composition.

Community responses of EM fungi to stressed pines at landscape scales

The widespread tree mortality of the past decade, including that of pines, has been related to drought and (or) temperature stress, often accompanied by insect outbreaks (Allen et al. 2010; Anderegg et al. 2013). The physiological mechanisms proposed to lead to tree mortality could influence EM associations. Drought reduces photosynthesis (Rennenberg et al. 2006), which could cause carbon starvation in trees (McDowell and Sevanto 2010) and limit the carbon available to fungal symbionts. Insect herbivory can alter either host plant photosynthetic or transport capacity, depending on the mode of feeding of the insect (e.g., Soltis et al. 2014; Zangerl et al. 2002). Studies of trees experiencing drought stress or reductions in carbon availability through herbivory or parasitism may provide important insights into the fate of EM fungi in the increasing number of forests that are prone to these stresses as climate changes (Allen et al. 2010).

Abundance

Evidence for decreased EM abundance with pine drought stress is equivocal (Table 2). Across field and laboratory studies examining the effect of drought stress on pines, shifts in EM colonization rates are variable (Bell and Adams 2004; Kennedy and Peay 2007; Kipfer et al. 2012; Meier et al. 1990; Runion et al. 1997; Swaty et al. 2004; Valdés et al. 2006). The responsiveness of EM fungi to drought may be mediated by soil properties (Gehring and Whitham 1994; Swaty et al. 1998), and the identity of fungi present. Pezizalean (Ascomycota) fungi, in particular, have been found to increase in abundance relative to other groups under drought stress (Gordon and Gehring 2011).

As with drought, herbivory, manual defoliation, and parasitism should also reduce EM abundance if carbon supply to fungal symbionts is reduced, consistent with our first hypothesis. However, similar to drought, the response of EM fungi is variable. Herbivory and defoliation have different impacts on EM colonization when comparing among several species of pine (Table 2) (Cullings and Hanely 2010; Del Vecchio et al. 1993; Gehring et al. 1997; Gehring and Whitham 1991; Kuikka et al. 2003; Pestaña and Santolamazza-Carbone 2011; Saravesi et al. 2008). Defoliation and carbon loss caused by mistletoe parasitism had no effect on EM abundance in *Pinus contorta* (Cullings et al. 2005) and led to increases in EM colonization in *Pinus edulis* (Mueller and Gehring 2006). The variability in response of EM abundance to damaged photosynthetic tissue of pines (Table 2) raises several important points for understanding the outcome. First, the response appears contingent on the gradient of stress experienced by pines. Second, colonization

rates alone could grossly underestimate abundance of EM fungi in soils. Rates of colonization should indicate abundance when species of EM fungi have little extramatrical mycelium, but many species of EM fungi possess emanating hyphae and (or) rhizomorphs which increase the volume of exploited soil (Agerer 2001). The distribution of emanating hyphae and EM tips can be drastically different, with largely unknown consequences for host plants (Anderson et al. 2014). Third, most trees are colonized by more than one EM fungal species so that shifts in EM abundance may only be observed when species lost to the stress of reduced carbon availability are not replaced by others. Shifts in community composition as a response to herbivory, parasitism, or drought could reflect interspecific differences in carbon requirements pointing to the importance of fungal species identity.

Community composition and diversity

EM fungal community shifts in relation to abiotic stress have been investigated less frequently than changes in EM abundance. Aside from one study (Bell and Adams 2004), drought consistently changes the community composition of EM fungi with an increase in ascomycete fungi (Table 2) (Gehring et al. 2014a; Gordon and Gehring 2011; Swaty et al. 2004). Similar to drought, shifts in species composition are frequently observed in response to herbivory, manual defoliation, and parasitism with community convergence towards ascomycete fungi (Table 2) (Gehring and Bennett 2009; Gehring et al. 2014b; Kuikka et al. 2003; Mueller et al. 2005; Pestaña and Santolamazza-Carbone 2011). This conclusion, however, is based on three pine species and must be tested on a broader suite of hosts. Notably, in agreement with our first hypothesis, colonization by high- and low-biomass morphotypes was differentially affected by manual defoliation of *P. sylvestris*. High-biomass morphotypes, i.e., tuberculate ectomycorrhizas with thick mantles and rhizomorphs, decreased with severe defoliation and low-biomass morphotypes (i.e., smooth ectomycorrhizas with little external mycelium) increased (Saikkonen et al. 1999). When timing of defoliation was considered, early- and middle-season defoliation significantly increased colonization of low-biomass morphotypes. High-biomass morphotypes were more frequent on roots of *P. sylvestris* when defoliation occurred late in the season, presumably because carbon was preferentially directed to elongation of new needles in spring rather than supporting high carbon demanding fungi (Saravesi et al. 2008).

Stress may lead to mortality, thus understanding how it changes the community composition of EM fungi is important for predicting outcomes of large-scale loss of pines from the landscape. Two mechanisms emerge as explaining shifts in the species composition of EM communities. First, those species able to withstand drought, defoliation or parasitism appear to require less carbon than those colonizing roots of unstressed pine. Pezizalean ascomycete fungi typically form ectomycorrhizas with thin mantles and few emanating hyphae (Tedersoo et al. 2006). High-biomass morphotypes, which produce thick mantles and emanating hyphae are thought to have greater carbon requirements than low-biomass morphotypes (Saikkonen et al. 1999). Second, some EM fungi may acquire small amounts of carbon from soil sources (Chapela et al. 2001; Talbot et al. 2008), which may enable them to withstand periods of stress. The ability to take advantage of alternative sources of carbon may confer a competitive advantage over other species of EM fungi. Interspecific competition among fungi for carbon is supported by recent studies showing how some pezizalean fungi thrive in comparison with other fungi in periods of water stress and herbivory (Gehring and Bennett 2009; Gordon and Gehring 2011). Functional differences among EM species in their carbon requirements and acquisition strategies may underlie community shifts with potential consequences that extend beyond the individual tree to the landscape.

Table 2. Ectomycorrhizal (EM) fungal community shifts and functional responses to stressed pine.

<i>Pinus</i> species	Study	Stress	Structural changes to EM fungal communities	Functional responses	Reference
<i>P. edulis</i>	Pinyon-juniper woodlands, southwest USA	Drought	Decrease in richness ^{a,b} ; community composition ^{a,b} changed depending on genetic characteristics of tree hosts	Not assessed	Gehring et al. 2014a
<i>P. edulis</i>	Pinyon-juniper woodlands, southwest USA	Drought	Community composition ^{a,b,c} changed	Not assessed	Gordon and Gehring 2011
<i>P. taeda</i>	Greenhouse	Drought	No change in percent colonization	Not assessed	Meier et al. 1990
<i>P. sylvestris</i>	Growth chamber	Drought	No change in percent colonization	<i>Suillus granulatus</i> increased seedling growth more in moist than dry soils; no difference in root enzyme activity	Kipfer et al. 2012
<i>P. muricata</i>	Growth chamber	Drought	Decrease in percent EM root biomass	Response of seedlings to EM fungi depended on soil moisture	Kennedy and Peay 2007
<i>P. oaxacana</i>	Pine-oak forest in Sierra Norte region, Mexico	Drought	No change in percent colonization; decrease in EM root biomass and inoculum potential	Not assessed	Valdés et al. 2006
<i>P. pinaster</i> , <i>P. radiata</i>	12-year-old pine plantations, western Australia	Drought	Decrease in EM root length and sporocarp productivity	Altered activity of some but not all soil enzymes	Bell and Adams 2004
<i>P. palustris</i>	Growth chamber	Drought	Decrease in number of EM root tips; no change in community composition ^a	Not assessed	Runion et al. 1997
<i>P. edulis</i>	Pinyon juniper woodlands southwest, USA; growth chamber	Dwarf mistletoe <i>Arceuthobium divaricatum</i> parasitism	Increase in percent colonization and inoculum potential; altered community composition ^{a,b,c}	Decrease in shoot growth; higher seedling establishment under infected canopies	Mueller and Gehring 2006
<i>P. edulis</i>	Pinyon-juniper woodlands southwest, USA	Herbivory by sap-feeding scale insect <i>Matsucoccus acalyptus</i>	No change in richness ^{a,b,c} ; change in community composition ^{a,b,c}	Not assessed	Gehring and Bennett 2009
<i>P. edulis</i>	Pinyon-juniper woodlands southwest, USA	Herbivory by <i>Dioryctria albovittella</i> moths	Community composition and richness ^{a,b,c} similar between moth removal and moth susceptible trees	Not assessed	Sthultz et al. 2009
<i>P. sylvestris</i>	Boreal forest, northern Finland	Manual defoliation	No change in proportion of EM fungal biomass in roots ^d or percent colonization; shift in community composition ^a to low-biomass morphotypes	Not assessed	Saikkonen et al. 1999
<i>P. pinaster</i>	Pine forests, Spain	Manual defoliation	Decrease in percent colonization, richness ^{a,b} and diversity ^{a,b} ; no change in sporocarp abundance, richness or diversity	Reduced tree growth	Pestaña and Santolamazza-Carbone 2011
<i>P. sylvestris</i>	Botanical Gardens of the University of Oulu, Finland	Manual defoliation	No change in colonization; altered community composition ^{a,b}	Not assessed	Saravesi et al. 2008
<i>P. contorta</i>	Lodgepole pine stands, Yellowstone National Park, USA	Dwarf mistletoe parasitism	No change in percent colonization; decrease in richness ^{a,b,c} and diversity ^{a,b,c} ; altered community composition ^{a,b,c}	Not assessed	Cullings et al. 2005
<i>P. edulis</i>	Pinyon-juniper woodlands, southwest USA	Drought stress, herbivory by <i>D. albovittella</i> moths and simulated herbivory	Decrease in percent colonization	Not assessed	Gehring and Whitham 1995
<i>P. edulis</i>	Pinyon-juniper woodlands southwest USA; greenhouse	Drought stress, herbivory by <i>D. albovittella</i> moths	Decreased percent colonization depending on soil type	Decrease in pine seedling growth	Gehring and Whitham 1994
<i>P. edulis</i>	Pinyon-juniper woodlands, southwest USA	Herbivory of sap-feeding scale insect <i>M. acalyptus</i>	Decrease in percent colonization	Not assessed	Del Vecchio et al. 1993
<i>P. edulis</i>	Pinyon-juniper woodlands, southwest USA	Herbivory by <i>D. albovittella</i> moths	Decrease in percent colonization	Not assessed	Gehring and Whitham 1991

^aDetermined by morphotyping.^bDetermined by DNA sequencing.^cDetermined by restriction fragment length polymorphisms.^dErgosterol content analysis.

Community responses of EM fungi to the gain of pines on landscapes

Introductions of pine through plantations has occurred in South Africa, Australia, and New Zealand for at least a century. Recently, nearly 4 million hectares have been planted with approximately 20 species of pine across Argentina, Chile, Brazil, and Uruguay (Simberloff et al. 2010). The extent of co-dispersal of pines and EM fungi is likely unappreciated because reports of established plantations in South America lag behind those for introductions in other regions of the southern hemisphere. Based on trends from these earlier introductions, imminent changes to EM fungal communities are likely to ensue with invasion of pines in South America.

Abundance

Little is known on how pine invasion impacts the abundance of EM fungi in soils; however, the limited data available on EM inoculum potential suggests that the composition of surrounding vegetation and species used to assay EM fungi in soils is important (Table 3). Inoculum potential is a commonly used measure for the efficacy of a substrate in providing EM fungal propagules for root colonization. Where exotic pines have established in initially non-forested landscapes (e.g., grasslands, heathlands), EM inoculum potential decreases with distance from pine stands (Bahram et al. 2013; Collier and Bidartondo 2009; Salomon et al. 2011; Thiet and Boerner 2007). Where exotic pines have established in already forested landscapes, trends are equivocal, demonstrating the importance of the existence and identity of matrix vegetation, consistent with our third hypothesis. EM inoculum potential was lower (Baohanta et al. 2012), higher (Nuñez et al. 2009), or the same (Dehlin et al. 2008) between exotic pine stands and adjacent native forest. While we have some information on the effects of pine invasion on EM inoculum potential, missing are data on actual abundance of EM fungi in soils. EM fungi present as hyphae are not necessarily those present as sporocarps or EM root tips (Anderson et al. 2014; Hynes et al. 2010; Kjølner 2006). Determining the extent of hyphae is also difficult, complicating measures of changes in the abundance of EM fungi with pine invasion. This information is critical as EM hyphae are important for host acquisition of soil resources, the formation of common mycorrhizal networks, and their presence and activity affects a variety of ecosystem properties such as carbon storage (Chapela et al. 2001) and mineral weathering (Landeweert et al. 2001).

Community composition and diversity

In support of our second hypothesis, the majority of reports of pine invasion suggest that EM hosts co-disperse with EM fungi, initiating the establishment of novel fungal communities (Table 3). EM fungi associated with invasive pine tend to be non-native (Dickie et al. 2010). In the majority of cases, EM fungal communities of invading pine tend to be species poor and different from those present in native forests (Table 3) (Baohanta et al. 2012; Barroetaveña et al. 2007, 2010; O'Hanlon and Harrington 2012b; Salomon et al. 2011). Dispersal limitation and lack of compatible EM fungi has, in some cases, limited the spread of pine in novel regions (Collier and Bidartondo 2009; Nuñez et al. 2009). In rare cases, the composition of EM fungal communities may remain similar following pine invasion if pines form new associations with local mycobionts (Bahram et al. 2013; Trocha et al. 2012). In these cases, both richness and composition of EM fungal communities are similar between invaded and native soils. The ability of pines to overcome the loss of their native fungal symbionts and form novel associations will depend on specificity between partners and the distribution and abundance of EM fungi in the introduced habitat (Dickie et al. 2010).

Pine invasion may affect EM fungal communities directly and (or) indirectly. Shifts in EM fungal abundance or community com-

position may occur directly when exotic EM fungi co-disperse with pine hosts, which then become part of the local mycoflora. These EM fungi can persist for decades after initial planting of their hosts (Sawyer et al. 2001). Co-dispersal has likely been facilitated by humans — many plant species have been transported to novel environments with intact root systems in soils (Vellinga et al. 2009) or provisioned with inoculum (Ruehle and Marx 1979). The ubiquitous distribution of fungi has been increasingly questioned as evidence builds for dispersal limitation in EM fungi (Peay et al. 2010; Talbot et al. 2014; Thiet and Boerner 2007), suggesting that the spread of EM fungi spatially coincides with that of their hosts. This kind of co-introduction has potentially removed dispersal limitation for a large, but unknown, number of fungal species.

Changes in EM fungal communities with the introduction of pines may also occur indirectly through changes to chemical and physical properties of soils deriving from the introduction of pines. Pine litter is high in secondary compounds (e.g., terpenoids and (or) phenolic compounds), which can affect soil chemistry, litter decomposition, nutrient cycling, and carbon sequestration. One of the most pronounced changes to soils following pine introductions is acidification (Berthrong et al. 2009). In addition to altering soil chemical characteristics, pine introductions to novel landscapes may also alter physical properties of soils, including soil bulk density and hydrological processes (Farley et al. 2005; Olszewska and Smal 2008). Given that EM fungi are sensitive to fine-scale soil conditions, it is likely that the introduction of pine to landscapes supporting EM vegetation may cause a shift in the composition of indigenous EM fungi through soil modifications. Though it is recognized that trees can indirectly affect EM fungi through soil modifications via canopy inputs (Dickie et al. 2006), this has not been investigated in systems invaded by pines. Litter produced by pines can suppress EM fungal growth (Koide et al. 1998; Rose et al. 1983), reduce EM fungal species richness (Baar 1996, 1997; Baar and De Vries 1995; Baar and Kuyper 1998; Cullings et al. 2003; De Vries et al. 1995), and alter their function (Cullings et al. 2010).

Implications

Changes in EM fungal abundance

More research is required to quantify changes in the abundance of EM fungi occurring in soils in response to the gain or loss of pines. Changes in EM abundance, measured as inoculum potential, suggest that shifts in the distribution of pines may have consequences for the population dynamics of both symbionts. Reduction in pine population size owing to extreme drought, as observed in *Pinus edulis*, may result in reduced inoculum availability, inhibiting re-colonization of pines under improved climate conditions. On landscapes where pine is newly introduced, limited EM inoculum can hinder the spread of non-native pines (Table 3) (Nuñez et al. 2009). The situation is more complicated if EM hosts are present in pine-invaded regions as the specificity between pines and EM fungi becomes important. Mature conspecifics are important sources of EM inoculum for establishing pine seedlings (Haskins and Gehring 2005) and understanding pine regeneration in native and non-native regions requires an understanding of the availability of EM fungal associates and their host specificity.

Without replacement by other EM hosts, the loss of pine and the subsequent loss or decrease of EM fungi at a landscape level may also affect ecosystem processes, such as carbon and nutrient cycling. Exclusion of EM fungi increases the rate of pine litter decomposition (Gadgil and Gadgil 1971) and colonization by EM fungi can increase root decomposition of pine depending on the fungus (Koide et al. 2011). In addition to effects on decomposition, the presence of EM fungi can also induce the production of phenolics, decreasing fungal pathogens in roots (Sylvia and Sinclair

Table 3. Ectomycorrhizal (EM) fungal community shifts and functional responses to pine invasion.

Exotic or invasive <i>Pinus</i> species	Invaded ecosystem	Age of invaded site (years)	Structural changes to EM fungal communities	Functional changes to invaded ecosystem	Reference
<i>P. radiata</i> , <i>P. patula</i> , <i>P. pinaster</i> , <i>P. taeda</i>	Subalpine shrublands and grasslands, Hawai'i	<50	Decreased richness with distance from plantation ^b	Not assessed	Hynson et al. 2013
<i>P. sylvestris</i> , <i>P. taeda</i> , <i>P. nigra</i> , <i>P. eldarica</i>	Hyrcaunium forests, northern Iran	>25	Decreased richness ^{a,b} and percent colonization, depending on distance to native forest; most EM fungal species were shared between pines and native trees	Not assessed	Bahram et al. 2013
<i>P. patula</i>	Highland sclerophyllous forest, Madagascar	~80	Decreased percent colonization for <i>Uapaca bojeri</i> seedlings; altered community composition ^{a,b,c}	Phosphorus leaf content, shoot biomass, and root biomass of <i>U. bojeri</i> seedlings lowered	Baohanta et al. 2012
<i>P. sylvestris</i>	Oak forest, Ireland	~300	Altered community composition ^{a,b,c} ; no change in richness	Not assessed	O'Hanlon and Harrington 2012a
<i>P. sylvestris</i>	Oak and ash forest, Ireland	~300	Altered sporocarp community composition ^{a,b,c} ; no change in richness	Not assessed	O'Hanlon and Harrington 2012b
<i>P. ponderosa</i>	Nursery, Argentina	25–45	Pine seedlings colonized by taxa found in nurseries worldwide, no native EM fungi present ^{a,b,c}	Not assessed	Barroetaveña et al. 2010
<i>P. ponderosa</i>	Grassland and shrublands, Argentina	17–22	Decrease in percent colonization and richness ^a ; altered community composition ^a	Not assessed	Salomón et al. 2011
<i>P. contorta</i> , <i>P. ponderosa</i>	Isla Victoria, Argentina	>70	Percentage of pine seedlings colonized and EM richness ^{a,b,c} dependent on distance to pine plantations	Increased pine seedling establishment	Nuñez et al. 2009
<i>P. sylvestris</i>	Lowland heathlands, England	Unknown	Richness ^b and proportion of EM seedlings increased	EM seedlings had more biomass than non-EM seedlings	Collier and Bidartondo 2009
<i>P. contorta</i>	<i>Nothofagus solandri</i> stands, New Zealand	~60	No change in percent colonization of pines	Increased nematode abundance	Dehlin et al. 2008
<i>P. virginiana</i>	Serpentine grassland and barrens, USA	>80	Decreased colonization of pine seedlings grown in soils collected from barrens compared with seedlings grown in soils collected from oak forest	Not assessed	Thiet and Boerner 2007
<i>P. ponderosa</i>	Patagonian Andes, Argentina	Unknown	Richness of sporocarps decreased	Not assessed	Barroetaveña et al. 2007
<i>P. nigra</i>	Managed tree plots, Poland	~35	Change in richness dependent on host taxa and tissue structure (sporocarp versus EM roots) ^{a,b}	Not assessed	Trocha et al. 2012
<i>P. contorta</i>	<i>Nothofagus solandri</i> forests converted to grasslands, New Zealand	~60	Community composition altered ^{a,b,c}	Not assessed	Dickie et al. 2010
<i>P. caribaea</i>	Forests of Seychelle islands	~40	Community composition altered ^{a,b}	Not assessed	Tedersoo et al. 2007
<i>P. radiata</i>	Highlands of Northern Andes, Ecuador	10–25	Sporocarp productivity increased; richness decreased ^{a,b,c}	Loss of soil carbon after conversion of grasslands to exotic pine plantations	Chapela et al. 2001

^aDetermined by morphotyping.^bDetermined by DNA sequencing.^cDetermined by restriction fragment length polymorphism.

1983), and modifying the dominant form of nitrogen present in pine ecosystems (Northup et al. 1995). It has been recently suggested that competition between EM fungi and decomposer microbes for organic nitrogen causes the accumulation of carbon at the ecosystem scale (Averill et al. 2014).

Changes in EM fungal community composition and diversity

One of the most consistent findings from studies examining the consequences of both loss and gain of pines is a shift in EM fungal community composition. Changes in species composition are important from multiple perspectives. First, they have implications for the conservation and evolution of EM fungi. Some species of fungi may expand their range in the case of invasion, or be locally or even regionally extirpated in the case of pine mortality. Unfortunately, such changes are difficult to quantify because EM fungal distributions are rarely well known due to their cryptic life forms and the lack of past monitoring (Dahlberg et al. 2010). If fungal species with particular suites of traits are more likely to persist as the distribution of their hosts shift, evolutionary trajectories could be altered. For example, forests worldwide are considered vulnerable to drought (Choat et al. 2012), which may select for EM fungi that reproduce hypogeously (belowground) or that rely more extensively on asexual reproduction (e.g., the ascomycete genus *Cenococcum* (Spatofora et al. 2012; Trappe 1964)).

Second, EM fungi are taxonomically and functionally diverse so that changes in community composition are likely to have consequences for host plants. Species of EM fungi vary in attributes such as hyphal exploration, carbon cost to host plants, enzymatic activities, N fixation, and ability to utilize organic forms of nitrogen and phosphorus (Landeweert et al. 2001; Lilleskov et al. 2011; Paul et al. 2007; Tedersoo et al. 2006, 2012). As a result of these differences, EM fungi are not equivalent mutualists (Egger and Hobbitt 2004; Kipfer et al. 2012). However, communities of EM fungi may function similarly through the aggregation of interspecific functional differences across EM fungal species (Jones et al. 2010; Rineau and Courty 2011; Talbot et al. 2014). Recognizing that most hosts are colonized by more than one species of EM fungi will be important in addressing the functional consequences for hosts of shifts in the composition of EM fungi.

Third, variation in EM fungal species composition may affect not only host plant performance, but also ecosystem processes. For example, species of EM fungi that form mycelial mats appear to be more efficient at mobilizing nutrients from minerals than species of EM fungi that do not (Landeweert et al. 2001). Likewise, variation among EM fungi in the chemical composition of the EM roots influences their subsequent decomposition with likely impacts on carbon and nitrogen cycling (Fernandez and Koide 2012). The addition of *Suillus* species along with *Pinus radiata* dramatically reduced soil carbon storage in Ecuadorian grasslands (Chapela et al. 2001). Though historic research emphasized consequences of EM fungi for host performance, new methodological developments (e.g., enzymatic profiling, stable isotope analysis, oligonucleotide fingerprinting of rRNA genes) have facilitated the inquiry on the role of EM fungi in ecosystem function.

Future directions

We propose five directions guiding future research on the consequences for EM fungi of the selective loss or gain of pine across landscapes. Though we focus on the response of EM fungi to shifts in pine, these proposed lines of inquiry are applicable to understanding the consequences of shifts in the distribution of any EM host. (1) First, there is poor understanding of the functioning of EM fungi. Our review of the literature yielded few studies addressing functional responses to shifts in EM fungal abundance and community composition. This lack of information makes it difficult to predict the trajectory of an ecosystem following the loss (extirpation) or gain of pine. For example, understanding the deg-

radation abilities of EM fungi and how they vary with the soil environment, host identity and function, and in the presence of other EM fungi will be critical information for assessing how plant communities respond to rapid shifts in the distribution of pines. Investigating variation in carbon acquisition and sequestration is an important component to this avenue of research. (2) Second, the magnitude of shifts in the species composition of EM fungi, to some extent, depends on host specificity and the ability of EM fungi to form novel associations with other hosts. Shared compatibility among host species for EM symbionts influences the ability of pines to invade new locations and also which EM fungi will be lost upon their selective mortality. Though this need for information was documented over 20 years ago (Molina et al. 1992), we still know surprisingly little about the controls of specificity between pines and EM fungi (Smith et al. 2009), and the mechanisms underlying host shifts. (3) In addition to increasing our understanding of controls on host specificity and shifts, we also need more information on how EM fungi spread and propagate. Specifically, the consequence of shifts in reproduction mode (sexual to asexual) for fungal diversity and EM community function is poorly understood. (4) While DNA sequences have uncovered a substantial amount of cryptic diversity in EM fungi, the morphology and life history traits of the species making up these sequences cannot be overlooked. For instance, knowing the amount and distribution of tissue possessed by a species is useful towards predicting fungal responses to changes in photosynthate inputs by their hosts. Knowledge of the extent of intraspecific variation in the function of EM fungi may also be important. Although rarely compared, functional variation within a species of EM fungi can be similar to that among EM fungal species (Johnson et al. 2012). How different species or isolates of fungi explore and forage for nutrients in soils has consequences for hosts, but also for nutrient cycling. (5) Finally, to assess changes in the distribution of fungi requires baseline surveys and monitoring. Traditional surveys have relied on sporocarp surveys because the belowground, cryptic lifestyle of EM fungi has presented an obstacle to monitoring (Dahlberg et al. 2010). As mentioned previously, patterns in sporocarp distribution and diversity do not necessarily represent those belowground. Thus, monitoring could include a combination of sporocarp surveys and molecular techniques to detect not only the presence (DNA-based) but also activity of fungi (RNA-based). These proposed avenues of research will help inform our understanding of the response of EM fungi to rapid shifts in the distribution of pine.

The available data indicates that pines and their EM fungi are tightly linked — shifts in the distribution of host trees coincide with changes in EM fungal communities in the affected landscape. Pine distributions are changing dramatically owing to human impacts of climate change and planting outside their range. Needed now is more knowledge about the fungi with which pines associate, especially their functioning and biology to predict the future of both symbionts.

Acknowledgements

J.K. was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Grant and M.J.R. was supported by an NSERC Undergraduate Student Research Award. C.A.G. acknowledges funding provided by the National Science Foundation (grant DEB0816675) and Science Foundation Arizona.

References

- Agerer, R. 2001. Exploration types of ectomycorrhizae - a proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza*, **11**(2): 107–114. doi:10.1007/s005720100108.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of

- drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* **259**(4): 660–684. doi:10.1016/j.foreco.2009.09.001.
- Anderegg, W.R.L., Kane, J.M., and Anderegg, L.D.L. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change*, **3**(1): 30–36. doi:10.1038/nclimate1635.
- Anderson, I.C., Genney, D.R., and Alexander, I.J. 2014. Fine-scale diversity and distribution of ectomycorrhizal fungal mycelium in a Scots pine forest. *New Phytol.* **201**(4): 1423–1430. doi:10.1111/nph.12637. PMID:24345261.
- Averill, C., Turner, B.L., and Finzi, A.C. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature*, **505**(7484): 543–545. doi:10.1038/nature12901. PMID:24402225.
- Baar, J. 1996. The ectomycorrhizal flora of primary and secondary stands of *Pinus sylvestris* in relation to soil conditions and ectomycorrhizal succession. *J. Veg. Sci.* **7**(4): 497–504. doi:10.2307/3236298.
- Baar, J. 1997. Ectomycorrhizal root growth in Scots pine stands in response to manipulation of litter and humus layers. *Mycorrhiza*, **7**(2): 89–94. doi:10.1007/s005720050167.
- Baar, J., and De Vries, F.W. 1995. Effects of manipulation of litter and humus layers on ectomycorrhizal colonization potential in Scots pine stands of different age. *Mycorrhiza*, **5**(4): 267–272. doi:10.1007/bf00204960.
- Baar, J., and Kuyper, T.W. 1998. Restoration of aboveground ectomycorrhizal flora in stands of *Pinus sylvestris* (Scots pine) in The Netherlands by removal of litter and humus. *Restor. Ecol.* **6**(3): 227–237. doi:10.1046/j.1526-100X.1998.00635.x.
- Baar, J., Horton, T.R., Kretzer, A.M., and Bruns, T.D. 1999. Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. *New Phytol.* **143**(2): 409–418. doi:10.1046/j.1469-8137.1999.00452.x.
- Bahram, M., Kóljalg, U., Kohout, P., Mirshahvaladi, S., and Tedersoo, L. 2013. Ectomycorrhizal fungi of exotic pine plantations in relation to native host trees in Iran: evidence of host range expansion by local symbionts to distantly related host taxa. *Mycorrhiza*, **23**(1): 11–19. doi:10.1007/s00572-012-0445-z. PMID:22592855.
- Baohanta, R., Thioulouse, J., Ramanankierana, H., Prin, Y., Rasolomampianina, R., Baudoin, E., Rakotoarimanga, N., Galiana, A., Randriambanona, H., Lebrun, M., and Duponnois, R. 2012. Restoring native forest ecosystems after exotic tree plantation in Madagascar: combination of the local ectotrophic species *Leptolena bojeriana* and *Uapaca bojeri* mitigates the negative influence of the exotic species *Eucalyptus camaldulensis* and *Pinus patula*. *Biol. Invasions*, **14**(11): 2407–2421. doi:10.1007/s10530-012-0238-5.
- Barroetaveña, C., Cázares, E., and Rajchenberg, M. 2007. Ectomycorrhizal fungi associated with ponderosa pine and Douglas-fir: a comparison of species richness in native western North American forests and Patagonian plantations from Argentina. *Mycorrhiza*, **17**(5): 355–373. doi:10.1007/s00572-007-0121-x. PMID:17345105.
- Barroetaveña, C., Pildain, M.B., Salomón, M.E.S., and Eberhart, J.L. 2010. Molecular identification of ectomycorrhizas associated with ponderosa pine seedlings in Patagonian nurseries (Argentina). *Can. J. For. Res.* **40**(10): 1940–1950. doi:10.1139/X10-135.
- Bell, T.L., and Adams, M.A. 2004. Ecophysiology of ectomycorrhizal fungi associated with *Pinus* spp. in low rainfall areas of Western Australia. *Plant Ecol.* **171**(1-2): 35–52. doi:10.1023/B:VEGE.0000029372.78102.9d.
- Berthrong, S.T., Jobbágy, E.G., and Jackson, R.B. 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. *Ecol. Appl.* **19**(8): 2228–2241. doi:10.1890/08-1730.1. PMID:20014590.
- Buscardo, E., Rodríguez-Echeverría, S., Martín, M.P., De Angelis, P., Pereira, J.S., and Freitas, H. 2010. Impact of wildfire return interval on the ectomycorrhizal resistant propagules communities of a Mediterranean open forest. *Fungal Biol.* **114**(8): 628–636. doi:10.1016/j.funbio.2010.05.004. PMID:20943174.
- Buscardo, E., Freitas, H., Pereira, J.S., and De Angelis, P. 2011. Common environmental factors explain both ectomycorrhizal species diversity and pine regeneration variability in a post-fire Mediterranean forest. *Mycorrhiza*, **21**(6): 549–558. doi:10.1007/s00572-011-0363-5. PMID:21301892.
- Cairney, J.W.G., and Bastias, B.A. 2007. Influences of fire on forest soil fungal communities. *Can. J. For. Res.* **37**(2): 207–215. doi:10.1139/x06-190.
- Chapela, I.H., Osher, L.J., Horton, T.R., and Henn, M.R. 2001. Ectomycorrhizal fungi introduced with exotic pine plantations induce soil carbon depletion. *Soil Biol. Biochem.* **33**(12-13): 1733–1740. doi:10.1016/S0038-0717(01)00098-0.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., and Zanne, A.E. 2012. Global convergence in the vulnerability of forests to drought. *Nature*, **491**(7426): 752–755. doi:10.1038/nature11688. PMID:23172141.
- Collier, F.A., and Bidartondo, M.I. 2009. Waiting for fungi: the ectomycorrhizal invasion of lowland heathlands. *J. Ecol.* **97**(5): 950–963. doi:10.1111/j.1365-2745.2009.01544.x.
- Cullings, K., and Hanely, J. 2010. Dwarf mistletoe effects on soil basidiomycete community structure, soil fungal functional diversity, and soil enzyme function: Implications for climate change. *Soil Biol. Biochem.* **42**(11): 1976–1981. doi:10.1016/j.soilbio.2010.07.018.
- Cullings, K.W., New, M.H., Makhija, S., and Parker, V.T. 2003. Effects of litter addition on ectomycorrhizal associates of a lodgepole pine (*Pinus contorta*) stand in Yellowstone National Park. *Appl. Environ. Microbiol.* **69**(7): 3772–3776. doi:10.1128/AEM.69.7.3772-3776.2003. PMID:12839743.
- Cullings, K., Raleigh, C., and Vogler, D.R. 2005. Effects of severe dwarf mistletoe infection on the ectomycorrhizal community of a *Pinus contorta* stand in Yellowstone Park. *Can. J. Bot.* **83**(9): 1174–1180. doi:10.1139/b05-100.
- Cullings, K., Ishkhanova, G., Ishkhanov, G., and Henson, J. 2010. Induction of saprophytic behavior in the ectomycorrhizal fungus *Suillus granulatus* by litter addition in a *Pinus contorta* (Lodgepole pine) stand in Yellowstone. *Soil Biol. Biochem.* **42**(7): 1176–1178. doi:10.1016/j.soilbio.2010.03.010.
- Dahlberg, A., Genney, D.R., and Heilmann-Clausen, J. 2010. Developing a comprehensive strategy for fungal conservation in Europe: current status and future needs. *Fungal Ecol.* **3**(2): 50–64. doi:10.1016/j.funeco.2009.10.004.
- Dehlin, H., Peltzer, D.A., Allison, V.J., Yeates, G.W., Nilsson, M.C., and Wardle, D.A. 2008. Tree seedling performance and below-ground properties in stands of invasive and native tree species. *N.Z. J. Ecol.* **32**(1): 67–79.
- Del Vecchio, T.A., Gehring, C.A., Cobb, N.S., and Whitham, T.G. 1993. Negative effects of scale herbivory on the ectomycorrhizae of juvenile pinyon pine. *Ecology*, **74**(8): 2297–2302. doi:10.2307/1939582.
- De Vries, B.W.L., Jansen, J., Van Dobben, H.F., and Kuyper, Th.W. 1995. Partial restoration of fungal and plant species diversity by removal of litter and humus layers in stands of Scots pine in the Netherlands. *Biodivers. Conserv.* **4**(2): 156–164. doi:10.1007/BF00137782.
- Dickie, I.A., Oleksyn, J., Reich, P.B., Karolewski, P., Zytkowski, R., Jagodzinski, A.M., and Turzanska, E. 2006. Soil modification by different tree species influences the extent of seedling ectomycorrhizal infection. *Mycorrhiza*, **16**(2): 73–79. doi:10.1007/s00572-005-0013-x. PMID:16322987.
- Dickie, I.A., Bolstridge, N., Cooper, J.A., and Peltzer, D.A. 2010. Co-invasion by *Pinus* and its mycorrhizal fungi. *New Phytol.* **187**(2): 475–484. doi:10.1111/j.1469-8137.2010.03277.x. PMID:20456067.
- egger, K.N., and Hibbett, D.S. 2004. The evolutionary implications of exploitation in mycorrhizas. *Can. J. Bot.* **82**(8): 1110–1121. doi:10.1139/b04-056.
- Farley, K.A., Jobbágy, E.G., and Jackson, R.B. 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. *Global Change Biol.* **11**(10): 1565–1576. doi:10.1111/j.1365-2486.2005.01011.x.
- Fernandez, C.W., and Koide, R.T. 2012. The role of chitin in the decomposition of ectomycorrhizal fungal litter. *Ecology*, **93**(1): 24–28. doi:10.1890/11-1346.1. PMID:22486083.
- Gadgil, R.L., and Gadgil, P.D. 1971. Mycorrhiza and litter decomposition. *Nature*, **233**(5315): 133. doi:10.1038/233133a0. PMID:16063238.
- Gehring, C., and Bennett, A. 2009. Mycorrhizal fungal-plant-insect interactions: the importance of a community approach. *Environ. Entomol.* **38**(1): 93–102. doi:10.1603/022.038.0111. PMID:19791601.
- Gehring, C.A., and Whitham, T.G. 1991. Herbivore-driven mycorrhizal mutualism in insect-susceptible pinyon pine. *Nature*, **353**(6344): 556–557. doi:10.1038/353556a0.
- Gehring, C.A., and Whitham, T.G. 1994. Comparisons of ectomycorrhizae on pinyon pines (*Pinus edulis*, Pinaceae) across extremes of soil type and herbivory. *Am. J. Bot.* **81**(12): 1509–1516. doi:10.2307/2445327.
- Gehring, C.A., and Whitham, T.G. 1995. Duration of herbivore removal and environmental stress affect the ectomycorrhizae of pinyon pines. *Ecology*, **76**(7): 2118–2123. doi:10.2307/1941686.
- Gehring, C.A., Cobb, N.S., and Whitham, T.G. 1997. Three-way interactions among ectomycorrhizal mutualists, scale insects, and resistant and susceptible pinyon pines. *Am. Nat.* **149**(5): 824–841. doi:10.1086/286026. PMID:18811251.
- Gehring, C., Flores-Rentería, D., Sthultz, C.M., Leonard, T.M., Flores-Rentería, L., Whipple, A.V., and Whitham, T.G. 2014a. Plant genetics and interspecific competitive interactions determine ectomycorrhizal fungal community responses to climate change. *Mol. Ecol.* **23**: 1379–1391. doi:10.1111/mec.12503. PMID:24118611.
- Gehring, C.A., Mueller, R.C., Haskins, K.E., Rubow, T.K., and Whitham, T.G. 2014b. Convergence in mycorrhizal fungal communities due to drought, plant competition, parasitism, and susceptibility to herbivory: consequences for fungi and host plants. *Front. Microbiol.* **5**. doi:10.3389/fmicb.2014.00306.
- Gordon, G.J., and Gehring, C.A. 2011. Molecular characterization of pezizalean ectomycorrhizas associated with pinyon pine during drought. *Mycorrhiza*, **21**(5): 431–441. doi:10.1007/s00572-010-0349-8. PMID:21191620.
- Grogan, P., Baar, J., and Bruns, T.D. 2000. Below-ground ectomycorrhizal community structure in a recently burned bishop pine forest. *J. Ecol.* **88**(6): 1051–1062. doi:10.1046/j.1365-2745.2000.00511.x.
- Grotkopp, E., Rejmánek, M., and Rost, T.L. 2002. Toward a causal explanation of plant invasiveness: Seedling growth and life-history strategies of 29 pine (*Pinus*) species. *Am. Nat.* **159**(4): 396–419. doi:10.1086/338995. PMID:18707424.
- Haskins, K.E., and Gehring, C.A. 2005. Evidence for mutualist limitation: the impacts of conspecific density on the mycorrhizal inoculum potential of woodland soils. *Oecologia*, **145**(1): 123–131. doi:10.1007/s00442-005-0115-3. PMID:15891858.
- Hynes, M.M., Smith, M.E., Zasoski, R.J., and Bledsoe, C.S. 2010. A molecular survey of ectomycorrhizal hyphae in a California *Quercus-Pinus* woodland. *Mycorrhiza*, **20**(4): 265–274. doi:10.1007/s00572-009-0281-y. PMID:19826841.
- Hynson, N.A., Merckx, V.S.F.T., Perry, B.A., and Treseder, K.K. 2013. Identities and distributions of the co-invading ectomycorrhizal fungal symbionts of exotic

- pinus in the Hawaiian Islands. *Biological Invasions*, **15**(11): 2373–2385. doi:10.1007/s10530-013-0458-3.
- Izzo, A., Canright, M., and Bruns, T.D. 2006. The effects of heat treatments on ectomycorrhizal resistant propagules and their ability to colonize bioassay seedlings. *Mycological Research*, **110**: 196–202. doi:10.1016/j.mycres.2005.08.010.
- Johnson, D., Martin, F., Cairney, J.W.G., and Anderson, I.C. 2012. The importance of individuals: intraspecific diversity of mycorrhizal plants and fungi in ecosystems. *New Phytol.* **194**(3): 614–628. doi:10.1111/j.1469-8137.2012.04087.x. PMID:22489902.
- Jones, M.D., Twieg, B.D., Ward, V., Barker, J., Durall, D.M., and Simard, S.W. 2010. Functional complementarity of Douglas-fir ectomycorrhizas for extracellular enzyme activity after wildfire or clearcut logging. *Funct. Ecol.* **24**(5): 1139–1151. doi:10.1111/j.1365-2435.2010.01699.x.
- Jonsson, L., Dahlberg, A., Nilsson, M.C., Zackrisson, O., and Karen, O. 1999. Ectomycorrhizal fungal communities in late-successional Swedish boreal forests, and their composition following wildfire. *Mol. Ecol.* **8**(2): 205–215. doi:10.1046/j.1365-294x.1999.00553.x.
- Kennedy, P.G., and Peay, K.G. 2007. Different soil moisture conditions change the outcome of the ectomycorrhizal symbiosis between *Rhizopogon* species and *Pinus muricata*. *Plant Soil*, **291**(1-2): 155–165. doi:10.1007/s11104-006-9183-3.
- Kipfer, T., Moser, B., Egli, S., Wohlgemuth, T., and Ghazoul, J. 2011. Ectomycorrhiza succession patterns in *Pinus sylvestris* forests after stand-replacing fire in the Central Alps. *Oecologia*, **167**(1): 219–228. doi:10.1007/s00442-011-1981-5. PMID:21468664.
- Kipfer, T., Wohlgemuth, T., van der Heijden, M.G.A., Ghazoul, J., and Egli, S. 2012. Growth response of drought-stressed *Pinus sylvestris* seedlings to single- and multi-species inoculation with ectomycorrhizal fungi. *PLoS ONE*, **7**(4). doi:10.1371/journal.pone.0035275.
- Kjøller, R. 2006. Disproportionate abundance between ectomycorrhizal root tips and their associated mycelia. *FEMS Microbiol. Ecol.* **58**(2): 214–224. doi:10.1111/j.1574-6941.2006.00166.x. PMID:17064263.
- Koide, R.T., Suomi, L., Stevens, C.M., and McCormick, L. 1998. Interactions between needles of *Pinus resinosa* and ectomycorrhizal fungi. *New Phytol.* **140**(3): 539–547. doi:10.1046/j.1469-8137.1998.00293.x.
- Koide, R.T., Fernandez, C.W., and Peoples, M.S. 2011. Can ectomycorrhizal colonization of *Pinus resinosa* roots affect their decomposition? *New Phytol.* **191**(2): 508–514. doi:10.1111/j.1469-8137.2011.03694.x. PMID:21418224.
- Korb, J.E., Johnson, N.C., and Covington, W.W. 2004. Slash pile burning effects on soil biotic and chemical properties and plant establishment: Recommendations for amelioration. *Restor. Ecol.* **12**(1): 52–62. doi:10.1111/j.1061-2971.2004.00304.x.
- Kuikka, K., Härmä, E., Markkola, A., Rautio, P., Roitto, M., Saikkonen, K., Ahonen-Jonnarth, U., Finlay, R., and Tuomi, J. 2003. Severe defoliation of scots pine reduces reproductive investment by ectomycorrhizal symbionts. *Ecology*, **84**(8): 2051–2061. doi:10.1890/02-0359.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., and Safranyik, L. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature*, **452**(7190): 987–990. doi:10.1038/nature06777. PMID:18432244.
- Kutorga, E., Adamonytė, G., Iršenaite, R., Juzenas, S., Kasparavičius, J., Markovskaja, S., Motiejūnaitė, J., and Treigienė, A. 2012. Wildfire and post-fire management effects on early fungal succession in *Pinus mugo* plantations, located in Curonian Spit (Lithuania). *Geoderma*, **191**: 70–79. doi:10.1016/j.geoderma.2012.02.007.
- Landeweert, R., Hoffland, E., Finlay, R.D., Kuyper, T.W., and van Breemen, N. 2001. Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. *Trends Ecol. Evol.* **16**(5): 248–254. doi:10.1016/S0169-5347(01)02122-X. PMID:11301154.
- LeDuc, S.D., Lilleskov, E.A., Horton, T.R., and Rothstein, D.E. 2013. Ectomycorrhizal fungal succession coincides with shifts in organic nitrogen availability and canopy closure in post-wildfire jack pine forests. *Oecologia*, **172**(1): 257–269. doi:10.1007/s00442-012-2471-0. PMID:23053232.
- Lilleskov, E.A., Hobbie, E.A., and Horton, T.R. 2011. Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. *Fungal Ecol.* **4**(2): 174–183. doi:10.1016/j.funeco.2010.09.008.
- MacKay, J. 2004. Effect of burning on the mycorrhizal fungi of Scots pine *Pinus sylvestris* at Boat of Garten, Inverness-shire, Scotland. *Conserv. Evidence*, **1**: 20–22.
- Martín-Pinto, P., Vaquerizo, W., Peñalver, F., Olaiola, J., and Oria-de-Rueda, J.A. 2006. Early effects of a wildfire on the diversity and production of fungal communities in Mediterranean vegetation types dominated by *Cistus ladanifer* and *Pinus pinaster* in Spain. *For. Ecol. Manage.* **225**(1-3): 296–305. doi:10.1016/j.foreco.2006.01.006.
- McDowell, N.G., and Sevanto, S. 2010. The mechanisms of carbon starvation: how, when, or does it even occur at all? *New Phytol.* **186**(2): 264–266. doi:10.1111/j.1469-8137.2010.03232.x. PMID:20409181.
- Meddens, A.J.H., Hicke, J.A., and Ferguson, C.A. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecol. Appl.* **22**(7): 1876–1891. doi:10.1890/11-1785.1. PMID:23210306.
- Meier, S., Grand, L.F., Schoeneberger, M.M., Reinert, R.A., and Bruck, R.I. 1990. Growth, ectomycorrhizae and nonstructural carbohydrates of loblolly pine seedlings exposed to ozone and soil-water deficit. *Environ. Pollut.* **64**(1): 11–27. doi:10.1016/0269-7491(90)90092-Q. PMID:15092304.
- Molina, R., Massicotte, H.B., and Trappe, J.M. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In *Mycorrhizal functioning*. Edited by M.F. Allen. Chapman and Hall, New York. pp. 357–423.
- Moritz, M.A., Parisien, M.-A., Batllori, E., Krawchuk, M.A., Van Dorn, J., Ganz, D.J., and Hayhoe, K. 2012. Climate change and disruptions to global fire activity. *Ecosphere*, **3**(6). doi:10.1890/es11-00345.1.
- Mueller, R.C., and Gehring, C.A. 2006. Interactions between an above-ground plant parasite and below-ground ectomycorrhizal fungal communities on pinyon pine. *J. Ecol.* **94**(2): 276–284. doi:10.1111/j.1365-2745.2006.01105.x.
- Mueller, R.C., Sthultz, C.M., Martinez, T., Gehring, C.A., and Whitham, T.G. 2005. The relationship between stem-galling wasps and mycorrhizal colonization of *Quercus turbinella*. *Can. J. Bot.* **83**(10): 1349–1353. doi:10.1139/b05-105.
- Northup, R.R., Yu, Z.S., Dahlgren, R.A., and Vogt, K.A. 1995. Polyphenol control of nitrogen release from pine litter. *Nature*, **377**(6546): 227–229. doi:10.1038/377227a0.
- Núñez, M.A., Horton, T.R., and Simberloff, D. 2009. Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology*, **90**(9): 2352–2359. doi:10.1890/08-2139.1. PMID:19769113.
- O'Hanlon, R., and Harrington, T.J. 2012a. Macrofungal diversity and ecology in four Irish forest types. *Fungal Ecol.* **5**(5): 499–508. doi:10.1016/j.funeco.2011.12.008.
- O'Hanlon, R., and Harrington, T.J. 2012b. Similar taxonomic richness but different communities of ectomycorrhizas in native forests and non-native plantation forests. *Mycorrhiza*, **22**(5): 371–382. doi:10.1007/s00572-011-0412-0. PMID:21947779.
- Olszewska, M., and Smal, H. 2008. The effect of afforestation with Scots pine (*Pinus sylvestris* L.) of sandy post-arable soils on their selected properties. I. Physical and sorptive properties. *Plant Soil*, **305**(1-2): 157–169. doi:10.1007/s11104-008-9537-0.
- Paul, L.R., Chapman, B.K., and Chanway, C.P. 2007. Nitrogen fixation associated with *Suillus tomentosus* tuberculate ectomycorrhizae on *Pinus contorta* var. *latifolia*. *Ann. Bot.* **99**(6): 1101–1109. doi:10.1093/aob/mcm061.
- Peay, K.G., Garbelotto, M., and Bruns, T.D. 2010. Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. *Ecology*, **91**(12): 3631–3640. doi:10.1890/09-2237.1. PMID:21302834.
- Pestaña, M., and Santolamazza-Carbone, S. 2011. Defoliation negatively affects plant growth and the ectomycorrhizal community of *Pinus pinaster* in Spain. *Oecologia*, **165**(3): 723–733. doi:10.1007/s00442-010-1760-8. PMID:20842382.
- Price, R., Liston, A., and Strauss, S. 1998. Phylogeny and systematics of *Pinus*. In *Ecology and biogeography of Pinus*. Edited by D.M. Richardson. University Press, Cambridge, U.K. pp. 49–68.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience*, **58**(6): 501–517. doi:10.1641/B580607.
- Rejmanek, M., and Richardson, D.M. 1996. What attributes make some plant species more invasive? *Ecology*, **77**(6): 1655–1661. doi:10.2307/2265768.
- Rennerberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R.S., and Gessler, A. 2006. Physiological responses of forest trees to heat and drought. *Plant Biol.* **8**(5): 556–571. doi:10.1055/s-2006-924084. PMID:16773557.
- Richardson, D. 1998a. Ecology and biogeography of *Pinus*. University Press, Cambridge, U.K.
- Richardson, D.M. 1998b. Forestry trees as invasive aliens. *Conserv. Biol.* **12**(1): 18–26. doi:10.1046/j.1523-1739.1998.96392.x.
- Richardson, D.M., Rundel, P.W., Jackson, S.T., Teskey, R.O., Aronson, J., Bytnerowicz, A., Wingfield, M.J., and Procheş, Ş. 2007. Human impacts in pine forests: Past, present, and future. *Annu. Rev. Ecol. Syst.* **38**: 275–297. doi:10.1146/annurev.ecolsys.38.091206.095650.
- Rincón, A., and Pueyo, J.J. 2010. Effect of fire severity and site slope on diversity and structure of the ectomycorrhizal fungal community associated with post-fire regenerated *Pinus pinaster* Ait. seedlings. *For. Ecol. Manage.* **260**(3): 361–369. doi:10.1016/j.foreco.2010.04.028.
- Rincón, A., Santamaria, B.P., Ocaña, L., and Verdú, M. 2014. Structure and phylogenetic diversity of post-fire ectomycorrhizal communities of maritime pine. *Mycorrhiza*, **24**(2): 131–141. doi:10.1007/s00572-013-0520-0. PMID:23955264.
- Rineau, F., and Courty, P.E. 2011. Secreted enzymatic activities of ectomycorrhizal fungi as a case study of functional diversity and functional redundancy. *Ann. For. Sci.* **68**(1): 69–80. doi:10.1007/s13595-010-0008-4.
- Rose, S.L., Perry, D.A., Pilz, D., and Schoeneberger, M.M. 1983. Allelopathic effects of litter on the growth and colonization of mycorrhizal fungi. *J. Chem. Ecol.* **9**(8): 1153–1162. doi:10.1007/BF00982218. PMID:24407807.
- Ruehle, J.L., and Marx, D.H. 1979. Fiber, food, fuel, and fungal symbionts. *Science*, **206**(4417): 419–422. doi:10.1126/science.206.4417.419. PMID:17809357.
- Runion, G.B., Mitchell, R.J., Rogers, H.H., Prior, S.A., and Counts, T.K. 1997. Effects of nitrogen and water limitation and elevated atmospheric CO₂ on ectomycorrhiza of longleaf pine. *New Phytol.* **137**(4): 681–689. doi:10.1046/j.1469-8137.1997.00865.x.
- Saikkonen, K., Ahonen-Jonnarth, U., Markkola, A.M., Helander, M., Tuomi, J., Roitto, M., and Ranta, H. 1999. Defoliation and mycorrhizal symbiosis: a

- functional balance between carbon sources and below-ground sinks. *Ecol. Lett.* **2**(1): 19–26. doi:10.1046/j.1461-0248.1999.21042.x.
- Salomon, M.E.S., Barroetavena, C., and Rajchenberg, M. 2011. Do pine plantations provide mycorrhizal inocula for seedlings establishment in grasslands from Patagonia, Argentina? *New For.* **41**(2): 191–205. doi:10.1007/s11056-010-9220-1.
- Saravesi, K., Markkola, A., Rautio, P., Roininen, M., and Tuomi, J. 2008. Defoliation causes parallel temporal responses in a host tree and its fungal symbionts. *Oecologia*, **156**(1): 117–123. doi:10.1007/s00442-008-0967-4. PMID:18236083.
- Sawyer, N.A., Chambers, S.M., and Cairney, J.W.G. 2001. Distribution and persistence of *Amanita muscaria* genotypes in Australian *Pinus radiata* plantations. *Mycol. Res.* **105**: 966–970. doi:10.1016/S0953-7562(08)61953-x.
- Simberloff, D., Nunez, M.A., Ledgard, N.J., Pauchard, A., Richardson, D.M., Sarasola, M., Van Wilgen, B.W., Zalba, S.M., Zenni, R.D., Bustamante, R., Pena, E., and Ziller, S.R. 2010. Spread and impact of introduced conifers in South America: lessons from other southern hemisphere regions. *Austral Ecol.* **35**(5): 489–504. doi:10.1111/j.1442-9993.2009.02058.x.
- Smith, M.E., Douhan, G.W., Fremier, A.K., and Rizzo, D.M. 2009. Are true multi-host fungi the exception or the rule? Dominant ectomycorrhizal fungi on *Pinus sabiniana* differ from those on co-occurring *Quercus* species. *New Phytol.* **182**(2): 295–299.
- Smith, S.E., and Read, D.J. 2008. *Mycorrhizal symbiosis*. 3rd ed. Academic Press, U.K.
- Soltis, N., Gomez, S., Leisk, G., Sherwood, P., Preisser, E., Bonello, P., and Orians, C. 2014. Failure under stress: the effect of the exotic herbivore *Adelges tsugae* on biomechanics of *Tsuga canadensis*. *Ann. Bot.* **113**(4): 721–730. doi:10.1093/aob/mct286. PMID:24335663.
- Spatafora, J.W., Owensby, C.A., Douhan, G.W., Boehm, E.W.A., and Schoch, C.L. 2012. Phylogenetic placement of the ectomycorrhizal genus *Cenococcum* in Gloniaceae (Dothideomycetes). *Mycologia*, **104**(3): 758–765. doi:10.3852/11-233. PMID:22453119.
- Stendell, E.R., Horton, T.R., and Bruns, T.D. 1999. Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. *Mycol. Res.* **103**: 1353–1359. doi:10.1017/S0953756299008618.
- Sthultz, C.M., Whitham, T.G., Kennedy, K., Deckert, R., and Gehring, C.A. 2009. Genetically based susceptibility to herbivory influences the ectomycorrhizal fungal communities of a foundation tree species. *New Phytol.* **184**(3): 657–667. doi:10.1111/j.1469-8137.2009.03016.x. PMID:19761493.
- Sturrock, R.N., Frankel, S.J., Brown, A.V., Hennon, P.E., Kliejunas, J.T., Lewis, K.J., Worrall, J.J., and Woods, A.J. 2011. Climate change and forest diseases. *Plant Pathol.* **60**(1): 133–149. doi:10.1111/j.1365-3059.2010.02406.x.
- Swaty, R.L., Gehring, C.A., Van Ert, M., Theimer, T.C., Keim, P., and Whitham, T.G. 1998. Temporal variation in temperature and rainfall differentially affects ectomycorrhizal colonization at two contrasting sites. *New Phytol.* **139**(4): 733–739. doi:10.1046/j.1469-8137.1998.00234.x.
- Swaty, R.L., Deckert, R.J., Whitham, T.G., and Gehring, C.A. 2004. Ectomycorrhizal abundance and community composition shifts with drought: predictions from tree rings. *Ecology*, **85**(4): 1072–1084. doi:10.1890/03-0224.
- Sylvia, D.M., and Sinclair, W.A. 1983. Phenolic compounds and resistance to fungal pathogens induced in primary roots of Douglas-fir seedlings by the ectomycorrhizal fungus *Laccaria laccata*. *Phytopathology*, **73**(3): 390–397. doi:10.1094/Phyto-73-390.
- Talbot, J.M., Allison, S.D., and Treseder, K.K. 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. *Funct. Ecol.* **22**(6): 955–963. doi:10.1111/j.1365-2435.2008.01402.x.
- Talbot, J.M., Bruns, T.D., Taylor, J.W., Smith, D.P., Branco, S., Glassman, S.I., Erlanson, S., Vilgalys, R., Liao, H.-L., Smith, M.E., and Peay, K.G. 2014. Endemism and functional convergence across the North American soil mycobiome. *Proc. Natl. Acad. Sci. U.S.A.* **111**(17): 6341–6346. doi:10.1073/pnas.1402584111. PMID:24733885.
- Tedersoo, L., Hansen, K., Perry, B.A., and Kjoller, R. 2006. Molecular and morphological diversity of peizizalean ectomycorrhiza. *New Phytol.* **170**(3): 581–596. doi:10.1111/j.1469-8137.2006.01678.x. PMID:16626478.
- Tedersoo, L., Suvi, T., Beaver, K., and Koljalg, U. 2007. Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native *Vateriaopsis seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpiniaceae) to the introduced *Eucalyptus robusta* (Myrtaceae), but not *Pinus caribea* (Pinaceae). *New Phytologist*, **175**(2): 321–333. doi:10.1111/j.1469-8137.2007.02104.x.
- Tedersoo, L., May, T.W., and Smith, M.E. 2010. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. *Mycorrhiza*, **20**(4): 217–263. doi:10.1007/s00572-009-0274-x. PMID:20191371.
- Tedersoo, L., Naadel, T., Bahram, M., Pritsch, K., Buegger, F., Leal, M., Kõljalg, U., and Põldmaa, K. 2012. Enzymatic activities and stable isotope patterns of ectomycorrhizal fungi in relation to phylogeny and exploration types in an afro-tropical rain forest. *New Phytol.* **195**(4): 832–843. doi:10.1111/j.1469-8137.2012.04217.x. PMID:22758212.
- Thiet, R.K., and Boerner, R.E.J. 2007. Spatial patterns of ectomycorrhizal fungal inoculum in arbuscular mycorrhizal barrens communities: implications for controlling invasion by *Pinus virginiana*. *Mycorrhiza*, **17**(6): 507–517. doi:10.1007/s00572-007-0123-8. PMID:17356853.
- Torres, P., and Honrubia, M. 1997. Changes and effects of a natural fire on ectomycorrhizal inoculum potential of soil in a *Pinus halepensis* forest. *For. Ecol. Manage.* **96**(3): 189–196. doi:10.1016/S0378-1127(97)00058-3.
- Trappe, J.M. 1964. Mycorrhizal hosts + distribution of *Cenococcum graniforme*. *Lloydia*, **27**(2): 100.
- Treu, R., Karst, J., Randall, M., Pec, G., Cigan, P., Simard, S.W., Cooke, J., Erbiling, N., and Cahill, J. 2014. Decline of ectomycorrhizal fungi following a mountain pine beetle epidemic. *Ecology*, **95**: 1096–1103. doi:10.1890/13-1233.1. PMID:24933827.
- Trocha, L.K., Kažucka, I., Stasińska, M., Nowak, W., Dabert, M., Leski, T., Rudawska, M., and Oleksyn, J. 2012. Ectomycorrhizal fungal communities of native and non-native *Pinus* and *Quercus* species in a common garden of 35-year-old trees. *Mycorrhiza*, **22**(2): 121–134. doi:10.1007/s00572-011-0387-x. PMID:21573837.
- Trusty, P., and Cripps, C.L. 2011. Influence of fire on mycorrhizal colonization of planted and natural whitebark pine seedlings: ecology and management implications. In *The future of high-elevation five-needle white pines in Western North America: Proceedings of the High Five Symposium, 28–30 June 2010*. Edited by R. Keane. USDA FS, Rocky Mountain Research Station, Missoula, Mont. pp. 198–202.
- Valdés, M., Asbjørnsen, H., Gómez-Cárdenas, M., Juárez, M., and Vogt, K.A. 2006. Drought effects on fine-root and ectomycorrhizal-root biomass in managed *Pinus oaxacana* Mirov stands in Oaxaca, Mexico. *Mycorrhiza*, **16**(2): 117–124. doi:10.1007/s00572-005-0022-9. PMID:16322986.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. *Science*, **323**(5913): 521–524. doi:10.1126/science.1165000. PMID:19164752.
- Vellinga, E.C., Wolfe, B.E., and Pringle, A. 2009. Global patterns of ectomycorrhizal introductions. *New Phytol.* **181**(4): 960–973. doi:10.1111/j.1469-8137.2008.02728.x. PMID:19170899.
- Zangerl, A.R., Hamilton, J.G., Miller, T.J., Crofts, A.R., Oxborough, K., Berenbaum, M.R., and de Lucia, E.H. 2002. Impact of folivory on photosynthesis is greater than the sum of its holes. *Proc. Natl. Acad. Sci. U.S.A.* **99**(2): 1088–1091. doi:10.1073/pnas.022647099. PMID:11792866.