Mapping the potential mycorrhizal associations of the conterminous United States of America

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Abstract – Mycorrhizal associations are recognized as key symbioses in a changing world, yet our understanding of their geographic distribution and temporal dynamics remain limited. We combined data on mycorrhizal associations and historical dominant vegetation to map the pre-European Settlement mycorrhizal associations of the conterminous United States of America (USA). As a demonstration of the map's utility, we estimated changes in mycorrhizal associations due to urbanization, agriculture and the establishment of non-native species in two regions. We found that the conterminous USA was dominated by vegetation associated with arbuscular mycorrhizas, but that ~40% of vegetation types included multiple mycorrhizal associations. Shifting land use to agriculture and the introduction of non-native species in disproportionately affected ectomycorrhizas, as did urbanization. These preliminary results set a baseline for mycorrhizal biogeography of the USA and illustrate how synthesis of available data can help us understand the impact of anthropogenic changes on an important mutualism.

Keywords: anthropogenic change, geographic distribution, mutualism, mycorrhiza, pre-European settlement vegetation

Introduction

Most species of plants form mycorrhizas, symbiotic associations between roots and soil fungi in which photosynthate is traded for soil resources, including phosphorus, nitrogen and water (Smith and Read, 2008). Mycorrhizal associations are frequently mutualistic and can promote plant productivity, plant community diversity, and soil stability (van der Heijden et al., 1998, Wilson et al., 2009). Although all mycorrhizas have some features in common, there are distinct types that vary in morphology, function and the plant and fungal taxa involved. The arbuscular mycorrhizal (AM) symbiosis is an evolutionarily ancient one (Redecker 2000) involving a single phylum of fungi, the Glomeromycota, and a large number of terrestrial plant species including grasses, many crops and most species of tropical trees (Smith and Read 2008). By contrast, the ectomycorrhizal (ECM) symbiosis evolved repeatedly and recently among diverse lineages of fungi but is found primarily in woody perennial plants, albeit species that occupy large geographical areas, such as pines (Brundrett 2002). Ectomycorrhizal fungi evolved from saprotrophic fungi and some species retain the ability to obtain resources for host plants from the decay of organic matter. Members of some plant families such as the Salicaceae form both AM and ECM associations, but many plant species form one association or the other. Some genera in the family Ericaceae form arbutoid mycorrhizas (ABM), a morphologically distinct association involving some of the same fungi that form ECM (Brundrett 2002). Also less common than AM and ECM associations are the ericoid mycorrhizas (ERM), associations between mostly ascomycete fungi and some members of the Ericales. Ericoid mycorrhizal fungi are well known for their saprotrophic abilities, facilitating growth of their hosts in environments exceptionally low in nitrogen and phosphorus (Read 1996). Orchid mycorrhizas are unique in morphology and function - young orchids receive both energy and nutrients from partner fungi (Brundrett 2002).

These distinctive types of mycorrhizas are associated with the climatic and soil conditions that characterize the major terrestrial biomes (Read 1991). Arbuscular mycorrhizas dominate low-latitude biomes, ECM associations are common in temperate and boreal forests and ericoid mycorrhizas are abundant in the highest latitudes and elevations (Read and Perez-Moreno 2003). These distribution patterns are hypothesized to result from variation in the uptake and utilization of inorganic and organic forms of nutrients by AM, ECM and ERM mycorrhizas (Read 1991, 1994). Organic matter accumulates at high altitudes and latitudes due to cold temperatures and slow rates of litter decomposition. As a result, nitrogen and phosphorus are largely contained within organic compounds, conditions thought to favor mycorrhizal fungal associates with saprotrophic abilities (Read and Perez-Moreno 2003). Conversely, as latitude decreases, mean annual temperature increases along with decomposition rates and soil pH. These conditions are thought to favor AM fungi over ECM and ERM associations because of the efficiency of AM fungi at acquiring inorganic nutrients (Read 1991, 1994; Read and Perez-Moreno 2003). Subsequent work has supported many of these hypotheses (Smith and Read 2008) but also shown that AM fungi can take up organic nitrogen with variable consequences for host plant nutrition (Hodge and Storer, 2015). Research also indicates that ECM, but not AM, are able to increase P availability by mineral weathering (Landeweert et al., 2001; Taylor et al., 2009), and that ECM associations may represent a greater carbon cost to their hosts than AM associations (Smith and Read, 2008). The Mycorrhizal-Associated-Nutrient-Economy (MANE) framework was recently developed for ECM and AM fungi where they co-occur in temperate US forests (Phillips et al., 2013). It proposes and provides evidence in support of an inorganic nutrient economy for AM dominated plots and an organic nutrient economy for ECM dominated

plots with consequences for litter quality, dominant decomposer communities and soil processes like nitrification and carbon sequestration (Phillips et al., 2013).

Anthropogenic environmental changes are likely to influence mycorrhizal associations across the landscape. Nitrogen deposition results in higher availability of inorganic nitrogen and may stimulate the transition from heathland dominated by ERM to grassland dominated by AM symbioses (Aerts 1999; Heil and Diemont 1983). Many invasive plant species in the United States are non-mycotrophic or facultatively mycotrophic (Meinhardt and Gehring 2012; Owen et al., 2013; Pringle et al., 2009) and their increase due to human activities could reduce mycorrhizal associations, with potentially significant consequences for fungal diversity. Tree mortality in the southwestern United States has fallen disproportionately on ECM associated pines (Breshears et al., 2005; Mueller et al., 2005). In the United States, roughly 24% of the land area has been converted to agricultural land use and 23% of the non-converted lands have high levels of ecosystem alteration when compared to historic vegetation (Swaty et al., 2010). These changes in land use and ecosystem structure can have substantial effects on biodiversity across taxa from birds (McKinney 2002) to mammals (Badgley and Fox 2000) to understory plants (McKinney 2002). Due to the tight relationship between mycorrhizal fungi and their host plants, shifts in plant species composition due to anthropogenic change likely affect mycorrhizal fungi, and vice versa.

While the importance of mycorrhizal fungi to communities and ecosystems is now widely acknowledged, as is their responsiveness to anthropogenic change (Peay et al. 2010), few studies have examined mycorrhizal distributions at large spatial scales. Suz et al. (2015) described a research program focused on ECM fungi using the European forest monitoring network. In the eastern United States, shifts in ECM and AM trees at the landscape scale as a function of climate

change, nitrogen deposition and increased atmospheric CO₂ were recently documented using United States Forest Service Forest Inventory and Analysis (FIA) data (Lankau et al., 2015; Phillips et al., 2013). In this study, we combined historical dominant vegetation data generated by the LANDFIRE program (www.landfire.gov) with data on mycorrhizal associations from the literature to generate a map of the mycorrhizal associations of the lower forty eight states of the USA prior to European settlement. We use these data to provide a visual representation of the mycorrhizal associations in a large portion of the USA and to estimate the land area occupied by each of the five major types of mycorrhizal associations. The map we generate provides a historical baseline against which contemporary changes in vegetation and their associated mycorrhizas can be compared. We illustrate this function through two case-studies, the effect of agriculture and invasive species on the mycorrhizal associations of California and the effect of urbanization on the mycorrhizal associations of a portion of New York and New Jersey. A pre-European settlement map could also facilitate projections for the future in which rapid, large scale changes in vegetation due to disturbances such as drought (Clark et al. 2016) could alter dominant mycorrhizal associations with consequences for nutrient cycling, carbon storage, and plant-soil feedback dynamics. Additionally, understanding mycorrhizal dynamics may help identify areas most resilient to climate change. Our linkage of vegetation and mycorrhizal distribution data differs from that of Phillips et al. (2013) and Lankau et al. (2015) because of its historical perspective, its consideration of mycorrhizal associations other than AM and ECM, and its inclusion of the western United States, an area of diverse topography, vegetation and mycorrhizal associations.

Materials and Methods

We used the LANDFIRE program's Biophysical Settings descriptions and spatial dataset (www.landfire.gov, version 1.2.0) as the basis for our reconstruction of mycorrhizal associations in the United States prior to European Settlement. LANDFIRE's Biophysical Settings (BpS) dataset covers the entire United States (www.landfire.gov) but we have included only the conterminous US in our mapping for ease of visualization. The Biophysical Settings in LANDFIRE represent the vegetation that would have been dominant on a particular site just prior to major European settlement (ca 1800s) and includes comprehensive descriptions and linkage to disturbance models (www.landfire.gov, Rollins 2009). This dataset has been used in numerous peer reviewed papers from restoration planning (e.g. Haugo et al. 2015), wildfire assessment (e.g., Keane and Karau 2010), national vegetation departure analysis (e.g., Swaty et al. 2010), wildlife habitat modeling (e.g., Cushman et al. 2013) and management alternative modeling (e.g., Low et al. 2013) as it crosses all ownership boundaries, was consistently developed and has extensive descriptive material. The BpSs are named based on NatureServe's Ecological Systems (Comer 2003) and are an evolution of the LANDFIRE Environmental Site Potential (ESP) dataset (Rollins 2009). The ESP dataset represents the dominant climax vegetation that would have occurred on a site based on abiotic factors such as climate, soils, surficial geology and topography plus the competitive potential of native plants. Similar to other classifications such as habitat (Daubenmire 1968; Pfister et al., 1977) and plant associations (Henderson et al., 1989) the ESP dataset does not incorporate disturbances and mostly served as the foundation for the BpS dataset.

The Biophysical Settings dataset builds on the ESP data by incorporating estimated natural disturbance regimes such as fire, flooding and windthrow. State and transition models of

historic vegetation and descriptions of each of ~1,700 BpSs were developed between 2005 and 2009 in numerous modeling workshops and incorporated literature, expert opinion and local datasets (Blankenship et al., 2012). The models were developed in Vegetation Dynamics Development Tool (VDDT, www.essa.com) and are used to estimate the percentage of each succession class that would have occurred under natural disturbance regimes, and to provide the key inputs to LANDSUM (Keane et al., 2006) which was used to map disturbances. The mapped and modeled disturbances were then used to reclassify the ESP dataset to better represent ecosystem dynamics. For example the ESP dataset may map shade tolerant species such as Douglas fir (*Pseudotsuga menziesii*) on a site based on abiotic factors. If the site is modeled to have a frequent low-intensity fire, then the BpS would be mapped as having more fire-dependent species such as ponderosa pine (*Pinus ponderosa*). The disturbance models were merged with the ESP dataset to produce the BpS dataset. LANDFIRE spatial datasets are in grid (raster) format with 30m pixels. Each BpS has a description that includes sections on natural disturbances, the biophysical site description, geographic range and vegetation. While the BpSs represent ecosystems (not specific overstory species), one to eight dominant species were selected and listed by experts and represent the overstory (or shrubs or herbaceous, depending on the BpS) that would most characterize that BpS for mapping, and for on-the-ground identification.

We determined the mycorrhizal association(s) characteristic of the dominant species of each of 1698 BpSs using data from the literature, primarily previously published reviews by Wang and Qiu (2006) and Brundrett (2009). We searched for information by plant species, but used genus information when data for a species was not available. For 288 plant species, information on mycorrhizal association was not available within published reviews for either

species or genus. We searched the literature for these species individually and assigned a mycorrhizal association based on information from other published sources, usually from the plant species or genus, but sometimes from the plant subfamily or family. We could not find any information on species within two plant families, the Saururaceae and the Garryaceae.

Fortunately, members of these families were only found in a few of the BpSs.

We tabulated data for plants using the following mycorrhizal associations: arbuscular mycorrhizas (AM), ectomycorrhizas (ECM), arbutoid mycorrhizas (ABM), ericoid mycorrhizas (ERM) and orchid mycorrhizas (OM). Plants that have been examined for mycorrhizal associations and shown not to form them were designated nonmycorrhizal (NM). Most plant species formed only one type of mycorrhizal association, but some species were observed to form more than one, such as many members of the Salicaceae and Fagaceae that can form AM and ECM associations and were thus designated AM/ECM. If the literature suggested the plant species formed predominantly one type of association, but also occasionally formed a second type, the dominant type was indicated by uppercase letters and the subordinate by lower case letters (e.g., ECM/am for a species that generally forms ectomycorrhizas but also has been observed to form arbuscular mycorrhizas).

Once we determined the mycorrhizal association characteristic of each of the one to eight plant species present in a BpS using the literature, we characterized the BpS into one of thirty categories based on the relative abundance of mycorrhizal associations present. We used a similar system as described above using uppercase letters to indicate a relatively dominant mycorrhizal type and lowercase letters to indicate less common associations. For example, the dominant vegetation of the BpS called East Gulf Coastal Plain Northern Mesic Hardwood Slope Forest consists of four species of trees that form ECM associations and two species of tree that

form AM associations and is categorized as ECM/am. Many BpSs contained dominant species that all formed the same type of mycorrhizal association, particularly AM, while others had dominant plant species of multiple mycorrhizal types in varying relative abundances. The Southern Appalachian Montane Pine Forest and Woodland BpS had several overstory species of trees that formed ECM associations but also a species of understory shrub that forms ERM associations and another that forms AM associations and was thus designated ECM/am/erm. We acknowledge that our focus on the dominant species means that some BpSs have plant species with mycorrhizal associations that are not reflected in our categorization or the resulting map.

Once each BpS was assigned a mycorrhizal status in a spreadsheet, the spreadsheet was joined to the BpS grid in ArcMap 10.3 (Environmental Systems Resource Institute 2014). The resultant grids were exported to make the data joins permanent. All mycorrhizal maps were then made using the “mycorrhizal status” field. To represent the mycorrhizal communities in a way that was viewable by color impaired, we used Color Brewer (www.colorbrewer.org) to generate color palettes and legends, then tested maps for viewability in Vischeck (<http://www.vischeck.com/>).

To explore loss of mycorrhizal communities and to demonstrate the potential utility of the dataset, we coupled the 2012 LANDFIRE Existing Vegetation Type (EVT, version 1.3.0) dataset with our mycorrhizal data. The EVT data represents recent vegetation on a site and is mapped using predictive landscape models based on extensive (often user-supplied) field reference data, satellite imagery (e.g., LANDSAT), biophysical gradient layers, and classification and regression trees (see metadata at www.landfire.gov). As an illustration of the potential effects of agriculture, non-native plant species, and urbanization on mycorrhizal associations, we extracted then combined the BpS and EVT data for two areas, the state of

California and eastern New York/northeastern New Jersey. The eastern New York/New Jersey area was created manually in ArcMap 10.3 solely for illustrative purposes. For California we only used the agricultural and introduced species pixels and for the New York/New Jersey area we only used the urban pixels. The ArcMap database files were exported to Microsoft Excel then graphed using Pivot Tables.

Results

We classified 1698 BpSs into 30 mycorrhizal categories, with all but three categories consisting of multiple types of mycorrhizal associations. Most of these categories had two mycorrhizal types, but six categories included four types of mycorrhizas (Fig. 1). The large number of categories were created to distinguish among BpSs that had the same types of mycorrhizal associations, but differed in the abundance of those associations. More detailed categorizations could facilitate detection of change following European settlement. Although a species of orchid occurred in one BpS, their abundance was too low to appear on our map.

Aside from a few locations where vegetation density was low and thus not described in the LANDFIRE data base, a large proportion of the conterminous United States consisted of mycorrhizal vegetation (97.01%) prior to European settlement (Fig. 1). Arbuscular mycorrhizal associations dominated the US, occurring over 60% of the land area (Figs. 1, 2).

Ectomycorrhizal associations were also common, particularly in the eastern United States, montane areas of the western US and the oak woodlands of California (Figs. 1, 2). Roughly 43% of the US had multiple types of mycorrhizal associations most commonly some combination of ECM and AM associations (Fig. 1). These co-dominated areas included areas occupied by ECM overstory plants with an AM understory, AM grasslands with scattered ECM trees or plant

families that formed both AM and ECM associations such as the Salicaceae. Plants that do not form mycorrhizal associations occupied a slightly larger amount of the US land area than did ERM associated vegetation, but few of the 1698 vegetation types consisted entirely of nonmycorrhizal plants (Figs. 1, 2).

Areas of the US that tended to have the greatest variety of mycorrhizal associations were characterized by significant topographic and vegetation diversity. For example, Colorado and Utah have 18 different combinations of mycorrhizal associations (Fig 3). The large area in western Utah that is an approximately equal mix of NM and AM plants is associated with the Great Salt Lake and includes salt tolerant shrubs within the genus *Atriplex*. Members of this genus are classified within the subfamily Chenopodioideae of the Amaranthaceae, which tend to be nonmycorrhizal (Brundrett, 2009; Wang and Qiu, 2006). The eastern portion of Colorado is semi-arid grassland dominated by AM associations while the western portion of the state is heavily influenced by the Rocky Mountains, and contains vegetation types with a mix of mycorrhizal associations including ECM conifers, ERM shrubs such as *Vaccinium scoparium*, and ABM shrubs of the genus *Arctostaphylos* (Fig 3).

Agriculture and the introduction of non-native species have altered the abundance of plants that form a variety of types of mycorrhizal associations in California. Prior to European settlement, California had nearly one half of all of the mycorrhizal associations we described, with particularly significant land coverage by AM dominated and AM/ECM co-dominated vegetation (Fig 4). As of 2012, approximately 1.2 million hectares of land in California had been converted to agriculture since European settlement, with 450,000 ha in vineyards and orchards alone)(Fig 4). The largest single area affected by agriculture is the Central Valley of California, roughly 11 million ha of land where more than 200 crop species are grown (Fig 4)

(<http://ca.water.usgs.gov/projects/central-valley/about-central-valley.html>). Non-native plant species (not agricultural) also occupy significant land area in California, estimated at 203,000 ha in 2012. Changes in mycorrhizal associations due to these vegetation shifts would be most pronounced for AM/ECM vegetation (Fig 4), though NM vegetation, particularly salt-tolerant plants found in the southern portion of the Central Valley, would also be significantly altered (Fig 4).

Urbanization also dramatically alters vegetation with the potential to affect mycorrhizal associations as illustrated by the area including and surrounding New York City (Fig. 5). The area was dominated by vegetation that included ECM, ERM and AM fungi prior to European settlement. Approximately 570,000 ha of land area in that region is now urban including more than 450,000 ha of vegetation that was dominated by ectomycorrhizal associations (ECM, ECM/am, ECM/erm)(Fig. 5).

Discussion

Our system of categorizing the 1698 LANDFIRE pre-European settlement vegetation types into 30 different types of mycorrhizal associations allowed both dominant and less common mycorrhizal associations of an area to be visualized. We suggest that this detailed categorization provides a more complete picture of the diversity of mycorrhizal associations, and potentially unique species of fungi, historically present in an area. As with other studies of historical ecology, consideration of the pre-European settlement mycorrhizal associations can ensure that “management is grounded in the ecological patterns and processes that occur at a variety of temporal scales, including those beyond the scope of direct human observation (Wiens et al., 2012). For example, we were surprised that southern portion of the Central Valley of

California was historically dominated by nonmycorrhizal vegetation and may thus have had lower abundance and diversity of AM fungi than surrounding areas. Does that legacy persist after decades of growth of crops that form AM associations?

In addition, a map of pre-settlement mycorrhizal associations may have predictive value. For example, a change in a region from primarily woodland to urban can be expected to initiate a cascade of additional changes: forest fragmentation, airborne nutrient deposition, heat island effects, etc., perturbations that may co-vary or be spaced over time. These environmental variables in turn will likely initiate changes in vegetation and mycorrhizal associations. Thus, detected change can highlight regions of concern and suggest the need for monitoring, management, or investigation. As a practical illustration, the New Jersey pine barrens is notable for low pH and low N and P concentration in its water and soil. Urbanization and the nutrient enrichment of the water and aerial nitrogen deposition that accompanies urbanization (Hopkinson and Day, 1980) have profound effects on the vegetative communities adapted to low nutrient, low pH soil. Plant communities in areas of the barrens most affected by urbanization shift towards cosmopolitan, exotics, and neighboring biogeographic species with a notable loss of ericaceous species (Ehrenfeld, 1983) and presumably, a concomitant loss of ERM fungi. Wetland restoration and conservation efforts can be aided by knowing where potential depauperization of particular mycorrhizal types can be expected, as well as, where to obtain sources of inoculum from less affected areas.

The broad distribution of AM and ECM associations in the conterminous US is consistent with the predictions of Read's model of the prevalence of mycorrhizal associations based on biomes and their characteristics (Read 1991, 1994). The conterminous United States lies within the north temperate zone and consists largely of grassland, desert and deciduous forest biomes.

Grassland and desert biomes have low organic matter accumulation and predominantly inorganic forms of nitrogen and phosphorus, characteristics thought to favor dominance by AM fungi (Read 1994). LANDFIRE distinguishes more than 200 types of deciduous forest across the United States, with many of these consisting of AM and ECM associated vegetation as predicted (Read 1994). Recent studies of the mycorrhizal associations of eastern US forests using Forest Inventory and Analysis data are also broadly consistent with our findings, showing that both ECM and AM associations occur in many forests with ECM associations somewhat more prevalent in forests in the Northeast and Southeast than the midwest (Phillips et al. 2013). These similarities are important because Phillips et al. (2013) were able to describe forests quantitatively using measurements of basal area across species, while we were not.

The shift of vegetation in portions of California to agricultural crops and non-native plants likely has significant consequences for both nonmycorrhizal plants and those colonized by ECM fungi. Many of the crops commonly grown in California such as almonds, citrus, grapes and cereal grains (<http://ca.water.usgs.gov/projects/central-valley/about-central-valley.html>) form AM (Wang and Qui 2006), potentially increasing the land area dominated by this association, particularly in the formerly AM/ECM co-dominated northern portion of the Central Valley and the NM dominated areas to the south. A shift to dominance by AM associations does not convey the full picture of change in mycorrhizas with agriculture. The diversity and species composition of AM fungi found in association with native vegetation versus agricultural crops can vary substantially (Helgason et al. 1998), though impacts depend upon type of agriculture (Oehl et al. 2003) and other factors (Hijri et al. 2006; Verbruggen et al. 2012). Arbuscular mycorrhizal fungi associated with high fertilizer input agriculture may also function less mutualistically (Johnson 1993). Several of the non-native annual grass species that make up a

large portion of the invaded lands in California also form associations with AM fungi, resulting in little evidence of change across the landscape based on the maps we present. However, non-native plants are often associated with reductions in AM density (Vogelsang and Bever, 2009) and changes in species composition (Busby et al., 2013; Hawkes et al., 2006; Owen et al., 2013), that can have negative consequences for native plants (Owen et al., 2013). Although land use changes can swap a particular BPS for another with an identical mycorrhizal designation and are thus ‘silent’ when mapped, laying on additional map layers, such as “Agricultural”, “Disturbed” or “Invaded” can be used to highlight these changes and suggest hypotheses about AM diversity and function that can be tested.

Our results suggest that the dramatic shifts in vegetation with urbanization in the northeastern US may fall disproportionately on plants that form ECM associations. This finding is consistent with data showing that most of the core of urban areas is devoid of vegetation and that areas where vegetation remains tend to be characterized by low species diversity and a high percentage of alien ruderals and non-native ornamental species, often shrubs (McKinney 2002). These species are unlikely to be colonized by ECM fungi which are associated with long-lived woody perennials in a relatively small number of families (Brundrett 2009). Interestingly, detailed studies of the vegetation of New York City indicate that the city has lost ~43% of its native species, but also that only 22% of native woody plant species have been extirpated compared with 46% of herbaceous species (DeCandido et al., 2004). The loss of these potentially uncommon herbaceous species that are more likely colonized by AM than ECM fungi would not be shown on our map because of its emphasis on dominant vegetation, but their loss might alter AM fungal species diversity or composition as described above for agricultural land use change.

While the maps and associated data we generated in this study are valuable, they have significant limitations. First, we have not included maps of Hawaii and Alaska, states dominated by biomes (tropical forest and boreal forest/tundra, respectively) that are uncommon in the remainder of the USA. We are working to remedy this omission. Second, data on presence or type of mycorrhizal association was not available for all of the dominant plant species in the LANDFIRE database, likely introducing errors, particularly in situations where a plant family contains lineages that are mycorrhizal and nonmycorrhizal like the Papaveraceae (Brundrett, 2009). While the available data on mycorrhizal associations in the literature is impressive, key gaps remain. Third, we focused our efforts on the dominant vegetation, ignoring rare plant species and their potentially unique mycorrhizal associations. We already mentioned that orchid mycorrhizas were not included on our US map, but plants within the Monotropaceae that function as mycoheterotrophs were absent from the LANDFIRE data that we used. Fourth, while mapping types of mycorrhizal association is important because of their varying functions and the lineages of fungi they include, it is also important to map the distribution of species within each type of mycorrhizal association, a costly endeavor that has been carried out in a few recent studies (Bahram et al. 2015; Davison et al., 2015).

In conclusion, although the map we created has its limitations, it provides the first comprehensive image of the potential mycorrhizal associations of the conterminous USA prior to European settlement. The map and its associated data can provide a baseline for comparison of changes in mycorrhizal associations as vegetation distributions change due to climate change, deforestation, invasive species and other perturbations. Mycorrhizal fungi are important to population, community and ecosystem dynamics (Smith and Read 2008), and represent an important component of the biota worth better understanding and conserving (Lilleskov et al.

2011). Our next step is to use current vegetation data to create a 21st century map and also to use climate and species distribution models to map the potential mycorrhizal associations of the future. Both of the pre-European settlement and current vegetation datasets will ultimately be made publicly available. The approach we used also could be applied to other publicly available datasets that link organisms with plant hosts, including ultimately DNA sequences from repositories like GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>) that provide adequate metadata.

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Figure Legends

Figure 1. A map of the mycorrhizal associations of the conterminous United States prior to European settlement, reconstructed using the LANDFIRE Biophysical Settings vegetation database. Shown here by color are the distribution of thirty combinations of the main mycorrhizal associations: arbutoid (ABM), arbuscular (AM), ectomycorrhizal (ECM), ericoid (ERM), and non-mycorrhizal (NM). Orchid mycorrhizas (OM) are not shown. Uppercase letters in the legend indicate the dominant or co-dominant mycorrhizal association, while lower case letters refer to the subordinate association.

Figure 2. The distribution of each of four main mycorrhizal associations [arbutoid (ABM), arbuscular (AM), ectomycorrhizal (ECM), and ericoid (ERM)] and non-mycorrhizal plants (NM), prior to European settlement in the conterminous United States. The graph (lower middle panel) shows the estimated land surface area (hectares) in which each of these associations occurred.

Figure 3. Detail map of the states of Utah (left) and neighboring Colorado (right) showing the 18 mycorrhizal association types occurring there prior to European settlement. The large number of types of mycorrhizal associations is a result of the variety of topographical relief and vegetation diversity in the region. Extensive areas dominated by non-mycorrhizal plants can be seen in the saline soils of western Utah. Uppercase letters in the legend indicate the dominant or co-dominant mycorrhizal association type, while lower case letters refer to the subordinate association type. ABM, arbutoid; AM, arbuscular; ECM, ectomycorrhizal; ERM, ericoid; NM, non-mycorrhizal.

Figure 4. Detail map of the state of California prior to European settlement (left) and with post-settlement agricultural areas overlain in white (right). Most mycorrhizal association types have experienced losses in land area, plotted here logarithmically in the graph. Uppercase letters in the legend indicate the dominant or co-dominant type of mycorrhizal associations, while lower case letters refer to the subordinate type of association. ABM, arbutoid; AM, arbuscular; ECM, ectomycorrhizal; ERM, ericoid; NM, non-mycorrhizal.

Figure 5. Pre-settlement map (upper left) of northeastern New Jersey and the greater New York City area and the types of mycorrhizal associations in the region designated by color. The map, lower right, is overlain with areas designated as Developed. The graph shows mycorrhizal association types and losses in land surface area of each. Vegetated urban areas are characterized by a high percentage of alien ruderals and non-native ornamental species, often diverse, and perhaps in association with mycorrhizal fungal species of distant geographic origin. Uppercase letters in the legend indicate the dominant or co-dominant mycorrhizal association type, while lower case letters refer to the subordinate association type. ABM, arbutoid; AM, arbuscular; ECM, ectomycorrhizal; ERM, ericoid; NM, non-mycorrhizal.

Figure 1

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