

Testing the influence of land-use history and forest stand age on the distribution and abundance of parasitic plants at multiple scales

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Background

The herbaceous layer makes up over 80% of the plant biodiversity in Eastern Forests and includes a wide variety of life history adaptations (Spicer et al. 2020). Some species found on the forest floor do not conduct photosynthesis, but rather obtain carbon from other organisms. The category of non-photosynthetic plants includes both parasitic species and saprophytes, or plants that feed on dead material. Parasitic relationships may be formed with other vascular plant species or through mycoheterotrophy, a form of parasitism in which species obtain carbon through networks of mycorrhizal fungi (Furman and Trappe 1971, Bidartondo 2005, Leake and Cameron 2010). Some parasites of vascular plants also require the presence of fungal partners for successful establishment (Baird and Riopel 1986). Parasitic plants contribute to ground-layer biodiversity, support wildlife (Johnson et al. 1995), and are a useful model system for testing the influence of host and symbiont-limitation in forest succession.

Most deciduous forest in Eastern North America and Northern Europe is second-growth that has regrown after clearance for agriculture and subsequent abandonment (Williams 1989, Hermy and Verheyen 2007). It is therefore necessary to place our understanding of forest ecology in the context of land-use history (Foster et al. 2003). Land-use legacies shape the structure and composition of modern forests, and their effects may last for centuries (Motzkin et al. 1996, Dupouey et al. 2002). The ground floras of post-agricultural forests are typically homogeneous and species-poor relative to primary forest; this lack of diversity has been attributed to both inability of many herb species to travel long distances in short periods of time and environmental alterations that may prevent establishment (Verheyen et al. 2003, Hermy and Verheyen 2007, Holmes and Matlack 2018).

Although prior research on land-use history has contributed to understanding the roles of colonization and environmental gradients in community assembly after disturbance, previous studies have not addressed the relationship between land-use history and non-photosynthetic plants in temperate forests. Disturbance, including human land use, affects the hosts of non-photosynthetic plants. Forest clearance removes trees that provide carbon to parasitic plants either directly or through fungal networks. Landscape-scale migration and colonization of parasitic species has been linked to density of host tree species (Tsai and Manos 2010), which is strongly impacted by disturbances such as logging. Land use can also damage fungal partners of mycoheterotrophic species (Neher 1999, Chaer et al. 2009). Some non-photosynthetic species are described in the literature as being limited to old, minimally-disturbed forests (Johnson et al. 1995, Bergman et al. 2006, McAuliffe et al. 2018), and presence of hosts and established fungal networks may be an underlying driver for this habitat preference. It follows that recolonization of parasitic species in young stands is likely to be limited by lack of autotrophic and mycological associates following disturbance. If this is the case, distributions of non-photosynthetic plants in the landscape may reflect patterns of past land-use history.

I analyzed patterns of presence and abundance to improve our understanding of the ways land use history shapes distributions of forest understories. The goals of this project were to describe the influence of stand age and land-use history on distributions of non-photosynthetic plants to test for host and symbiont limitation during community assembly. I aimed to test the hypothesis that presence of suitable hosts limits recolonization of non-photosynthetic species in young forests; therefore, parasitic species will be limited to older stands and those without histories of intensive land use; alternatively, their presence and abundance may be most strongly linked to environmental gradients.

Research methods

I selected three target species for analysis: *Conopholis americana* (bear corn), *Epifagus virginiana* (beechnuts), and *Monotropa uniflora* (ghost pipe) (Figure 1). All three are common across northeastern North America, which allows for enough available data for statistical analysis. This set of species also includes a variety of life histories and parasitisms: two tree parasites (*C. americana*, a perennial, *E. virginiana*, an annual) and a mycoheterotroph (*M. uniflora*, perennial). In addition to the three original target species, I was able to collect usable data on two additional mycoheterotrophs: *Corallorhiza odontorhiza* and *Hypopitys monotropa*. *C. odontorhiza* is a perennial orchid that parasitizes ectomycorrhizal fungi and flowers in early Autumn; *H. monotropa* is a close relative of *Monotropa uniflora* and fellow member of the Ericaceae family.



Figure 1: Non-photosynthetic forest herb species selected for analysis: *Conopholis americana*, *Corallorhiza odontorhiza*, *Epifagus virginiana*, *Hypopitys monotropa*, and *Monotropa uniflora*

For analysis of regional-scale patterns of occurrence of parasitic species, I downloaded data from the Consortium of Northeast Herbaria, Consortium of Midwest Herbaria and iNaturalist for the three target species. Herbarium data was limited to georeferenced specimens collected in 1980 or later to focus on recent collections rather than historical populations that may no longer be extant. Datapoints from iNaturalist were collected from research-grade observations with GPS coordinates.

Specimen-based investigations are ongoing. This is the only project I have seen to use iNaturalist and specimen-based data to assess species distributions in the context of land-use history, and unforeseen difficulties have arisen with precision of the spatial data. Accuracy of GPS coordinates for most of the specimens is not sufficient for addressing questions of fine-scale land-use pattern. Accuracy within 100 meters, in many regions, could place the specimen in an entirely different land-use patch. Most coordinates for data gathered from iNaturalist are even less precise and removing them drastically limits the amount of data available for analysis. In the meantime, I opted to focus on collection and analysis of the field research funded by NEBC and final decisions on the feasibility of specimen-based land-use history research are still in progress.

Field data collection

I completed the field portion of this work in Athens County, Ohio. Other possible sites in the Allegheny Plateau in Pennsylvania were investigated, but logistical concerns and the need for site-to-site consistency led to limiting the work to one study area. Athens County is located in the unglaciated Allegheny Plateau and includes a high percentage of forest cover. Most forest is second-growth that has regrown after abandonment from agriculture, logging, or resource extraction, making it typical of much forest in Eastern North America. Topography in the study area is rugged and highly dissected, and plant community composition differs strongly by landscape position (Olivero and Hix 1998). This contrast allows for selection of sites across environmental gradients to test the roles of the environment in shaping species distributions, as well as allowing for the inclusion of sites likely to include the target species and their hosts, which are often found in different habitats.

The study design for the field portion of the project was a 40-site replicated chronosequence that included both moist valley sites and dry upper slope/ridgetop sites, with stands ranging in age from 40-60 to >130 years past canopy closure. Stands were sorted into age four classes, 40-60, 61-80, 80-110, and >130, using historical aerial photos (USDA Soil and Water Conservation Office, USGS Earth Explorer). Forests used for the chronosequence have recruited on land previously used for agriculture, but, due to contrasts between landscape positions, it was not possible to incorporate type of agriculture (plowed vs pasture) in the study design. Replication within age and landscape position combinations was essential to account for issues of site-to-site variation that occur in ecological studies. The final study design was: 2 landscape positions x 4 age classes x 5 replicates per combination = 40 sites.

I visited field sites in May, July, and October 2019 to survey for target species. Sites were surveyed for all parasitic species using a meandering walk sampling method. All flowering stems were counted. To assess host limitation, all oaks and beeches were counted and measured for diameter at breast height (DBH). Presence of lowbush blueberry was noted to account for presence of ericoid species that might predict presence or abundance of *Monotropa uniflora*. Aspect was described in the field, and site elevation was collected from topographic maps (www.mytopo.com).

Results

Conopholis americana: Presence is linked to older forests with large individual red and black oaks. Abundance is predicted most strongly by size of the largest host tree, with marginal influence of forest age (abundance increases with forest age) and landscape position (preference for uplands) (Figure 2a). Although abundance generally increases with forest age as the size of host trees increases through time, the largest populations are present in post-agricultural sites with large individual host trees that were present during active pasturing. This result indicates that land-use history influences *C. americana* through its impacts on host trees rather than the species directly. This influence can be positive if red and black oaks are retained as shade trees in pastures and allowed to grow large in the absence of competition, or negative if they are removed entirely.

Corallorhiza odontorhiza: Abundance is linked to stand age, high elevation, and total Fagaceae basal area, indicating responses to both environmental gradients and presence of host fungi. Unlike most other species in this project, Autumn coralroot is most abundant in younger forests (40-80 years) (Figure 2b). The relationships with disturbance observed here indicate that there is no one response of parasitic plants to land-use history.

Epifagus virginiana: Presence is predicted by the size of the largest American beech in a site. Like *C. americana*, the dominant factor controlling distributions of beechdrops appears to be the presence or absence of large beech trees. Because large beech trees are rarely found in young post-agricultural forests, this limits beechdrops to older forest sites (Figure 2c). Here the relationship with land-use history is mediated by its effects on the host species, supporting the hypothesis of symbiont-limitation.

Hypopitys monotropa: Abundance was greatest in old forests, south and west-facing slopes, and sites with high total basal area of trees in the Fagaceae family (Figure 2d). This species is limited to old oak forests on dry sites and does not return to post-agricultural forests for close to 80 years after canopy closure.

Monotropa uniflora: Presence is linked to aspect and high total Fagaceae basal area; this species is most likely to be present in forests with abundant oak and beech, a proxy measurement for availability of ectomycorrhizal fungi (Figure 2e). Drivers of abundance are complex and interactive, with forest age, landscape position, aspect, presence of lowbush blueberry, and total Fagaceae basal area, as well as many interactions between variables, predicting abundance.

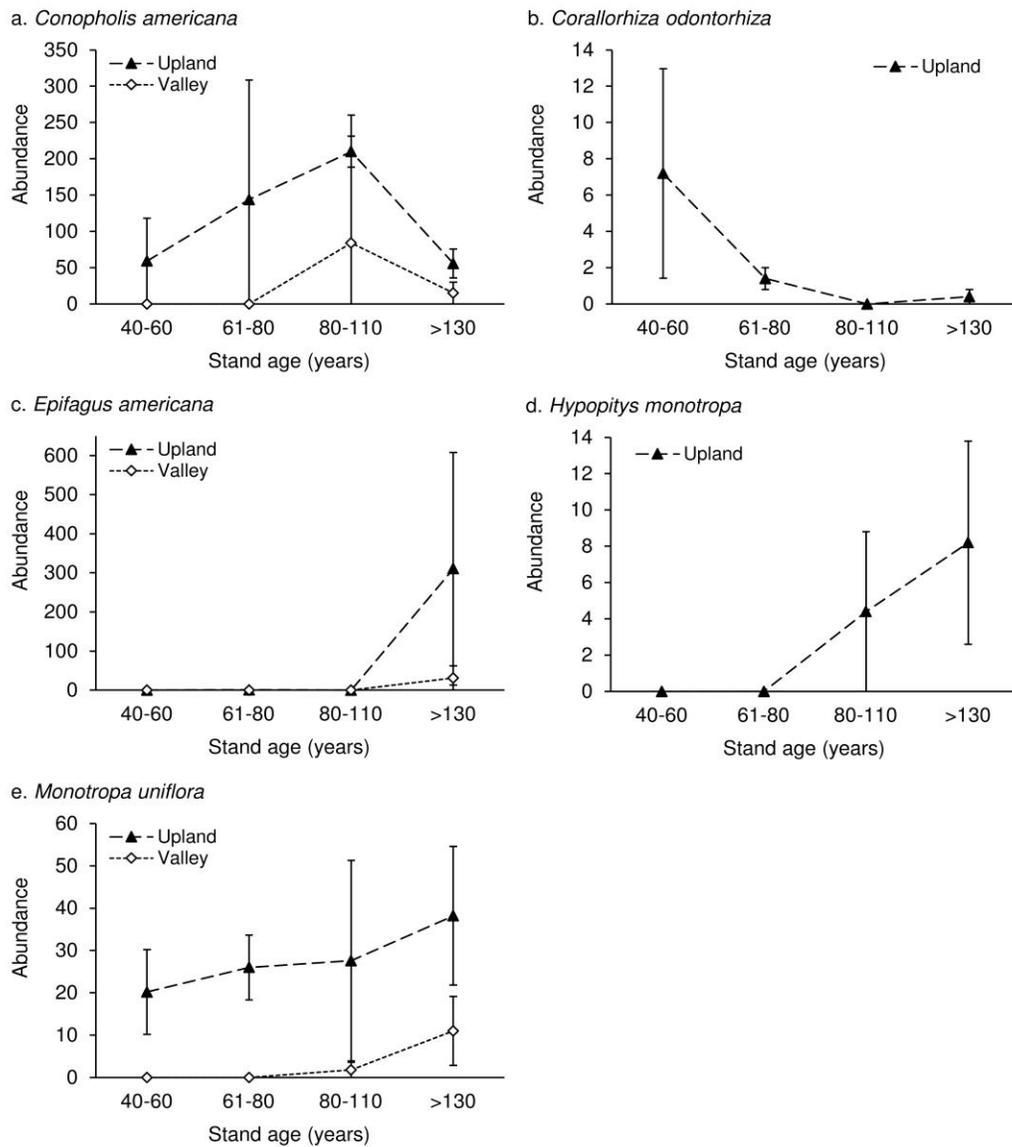


Figure 2: Abundance of parasitic species between landscape positions through time. Symbols indicate means, error bars represent standard errors. Figure 2a: *Conopholis americana* (bear corn); 2b: *Corallorhiza odontorhiza* (Autumn coralroot); 2c: *Epifagus virginiana* (beechdrops); 2d: *Hypopitys monotropa* (pinesap); 2e: *Monotropa uniflora* (ghost pipe).

Conclusions

Host availability and size emerged as the dominant process structuring distributions of parasitic plants. Distributions of many species do relate to forest age and land-use history; however, patterns and relationships are species-specific and often non-linear. The relative importance of host-limitation, environmental heterogeneity, and disturbance history vary by species, and reflect the life histories of both achlorophyllous species themselves and their hosts.

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Products:

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