

Using The Complexities Of Orchid Life Histories To Target Conservation Efforts

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While some orchids have likely always been rare, many orchid species that were once widespread are now also found in small fragmented populations. Declines of once widespread species are, in most cases, attributed to habitat loss and sometimes poaching (*e.g.*, Krupnick *et al.*, 2012). However, many of the very characteristics that make so many members of the Orchidaceae prone to being rare (and also so fascinating) may also be driving some of their susceptibility to decline. This is especially true among temperate orchids. Approximately 28% of the estimated 25,000+ species of orchids worldwide grow in the temperate zone and are terrestrial (*i.e.*, live in the soil rather than on trees; Gravendeel *et al.*, 2004). Conservation of these terrestrial species has proven to be especially challenging (*e.g.*, Swarts and Dixon, 2009; Stewart and Hicks, 2010). No terrestrial orchid has ever been de-listed as a result of conservation efforts and restoration is notoriously challenging (Stewart and Hicks, 2010; Zettler *et al.*, 2005).

Far from being overwhelming, we suggest that a better understanding of these challenges can be used to more clearly identify the threats to orchids and improve conservation and restoration success. Among the challenges represented by orchid biology is their dependence on other species. Orchids require two, often very specific, types of symbiotic associations to complete their life-cycle: association with pollinators to set seed and association with mycorrhizal fungi for seedlings to develop from those seeds (*e.g.*, Waterman and Bidartondo, 2008). These dependencies add to the complexity of orchid conservation, as orchid declines may be caused not by direct effects of any environmental factors on orchid growth, but rather by effects of those factors on one of the other species on which orchids depend (*e.g.*, Swarts and Dixon, 2009). Dependence on other species, each of which has its own set of required conditions, also means that orchids are particularly sensitive to a wide range of habitat changes (those that affect either set of associated species plus those that affect the orchid directly) and so are often among the first to disappear when the environment changes or is degraded. For this reason, orchids make excel-

lent indicators of ecosystem health. This integration of many aspects of ecosystem health also means that it is necessary to broaden the scope of factors considered to affect orchid populations to include both pollinator and mycorrhizal species and the factors that affect them in order to develop effective conservation and restoration plans.

The intricate and often very specialized relationships between orchids and their pollinators have long attracted attention. More than any other group of plants, orchids have evolved complex, often deceptive, systems to attract and interact with pollinators (e.g., Waterman and Bidartondo, 2008). Although some orchids are pollinated by many species, a side effect of pollination system complexity has been to limit the number of pollinator species that can successfully accomplish pollination. For example, the threatened cowhorn orchid (*Cyrtopodium punctatum*) in Florida requires a particular native bee (*Centris errans*) to successfully form seeds (Pemberton and Liu, 2008). However, *C. errans* requires host plants, which the orchid flowers mimic, that no longer co-occur with the few remaining wild populations. As a result, the orchids rarely produce seeds. Although the extensive over collection that made this once-common orchid rare is no longer such a threat, unless remaining plants can produce seeds, their recovery is unlikely. This finding led Pemberton and Liu (2008) to recommend that pollinator host plants, which grow nearby in different habitats, be planted in the vicinity of remaining native *C. punctatum* populations. This offers an excellent example of how the complexities of orchid biology can produce unique solutions for their conservation.

In addition to often depending on specific pollinators for successful seed set, all orchids also require fungi, often specific fungi, in order for their seeds to germinate. Orchid seeds are minute and include little or no nutrient reserves to support seedling development, so they require an external source of nutrients to support early development (Rasmussen, 1995). During the protocorm stage (from seed germination until they produce their first leaf), orchids rely entirely on mycorrhizal fungi, which they digest, for all nutrition. While many epiphytic orchids produce leaves very soon after germination, the protocorm stage of terrestrial orchids often lasts from several months to several years before a first leaf is produced (e.g., Rasmussen and Whigham, 1998). Without appropriate host fungi, orchid populations cannot recruit new members. Because the fungi most orchids associate with are almost invisible and require DNA sequencing for identification, the fungi needed by many orchids are unknown (e.g., McCormick *et al.*, 2012). Even when host fungi have been identified, the conditions needed for them to persist and flourish are almost never known. It is clear that some orchids are dependent upon fungi that are free-living decomposers in the soil, while others associate with fungi that are also connected to other plants, especially trees, and still others associate with plant pathogens or parasites of other fungi (Rasmussen, 1995). As habitats change, fungal com-

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munities also change and orchids may lose fungi upon which they depend for their survival, but what drives changes in fungal communities is often unknown. McCormick *et al.* (2006) found that drought can cause orchids to lose their host fungi, forcing them to switch to new fungi when wetter conditions return, suggesting that future climate change scenarios that include increased frequency and duration of drought may bode poorly for orchids. Partly because the conditions that support mycorrhizal fungus growth are poorly understood, no orchid conservation plans to date include improvement of conditions for growth of host fungi. However, this is poised to change.

McCormick *et al.* (2012) found that orchids require not just that their host fungi be present, but also that they be abundant. This is the first time it has been shown that the abundance of host fungi is important for their ability to support orchids and leads to several possibilities for environmental modifications that support host fungi to help conserve orchid populations. While it seems obvious that host fungus abundance would have implications for orchid growth, it is very difficult to figure out how abundant particular fungi are when an amount of soil the size of a lima bean can contain 150 or more species of fungi. McCormick *et al.* (2012) also found that amendments of chipped wood increased the abundance of some (though not all) orchid host fungi and in some cases host fungi collected locally could be introduced with seeds to support germination. While this has been informally tried for many years, such as when orchids are transplanted with a block of surrounding soil, it often fails when fungi are introduced to an environment where they cannot thrive (such as a garden). This emphasizes that knowledge about the ecological requirements of orchid host fungi is as important as knowledge about the fungus itself. Both elements need to be known to efficiently conserve orchids.

In addition to fungi required for seed germination, many orchids supplement their nutrition throughout their lifecycle by digesting their mycorrhizal fungi, especially in times of stress (McCormick *et al.*, 2006). However, all species except those that have no green leaves also fix carbon through photosynthesis. The life cycles of many terrestrial orchids also include periods lasting for one to several years when the plants are physiologically active but do not produce any aboveground tissues during an entire growing season. These periods are referred to as vegetative dormancy and high rates of dormancy have been associated with declining populations in many orchids (*e.g.*, Mehrhoff, 1989; Shefferson *et al.*, 2003). While dormant, orchids are thought to rely completely on their mycorrhizal fungi for nutrition (*e.g.*, Wells, 1967; Shefferson *et al.*, 2001; Reintal *et al.*, 2010), though this has not yet been demonstrated. The fungi used by many orchids for support during dormancy and times of stress may be the same as those needed for germination or they may involve other species, as McCormick *et al.* (2004) found for *Tipularia discolor* and Zettler and Piskin (2011) found for *Platanthera leucophaea*.

Determining which factors are acting on partner species in addition to those factors directly affecting orchids may seem daunting. However, direct effects, pollinators, and mycorrhizal fungi influence orchid population dynamics by acting primarily at different stages in orchid life histories (Figure 1, page 19). Therefore observing orchid population dynamics can be used to determining where conservation efforts could most effectively be focused. For example, pollinators affect seed set, but have limited or no effect on other life stages so to conserve an orchid that had healthy plants that flowered frequently but rarely set seed, managers might need to determine whether pollinator services were sufficient and possibly work to increase pollinator abundance. In contrast, mycorrhizal fungi dominate in determining the transition from seeds to protocorms and in support of dormant plants. Some direct factors also disproportionately affect different life stages. For example, light availability may strongly affect success of emergent, photosynthetic plants, but have little effect on protocorms or dormant plants. If an orchid produces numerous seedlings but adult plants grow slowly or many have extended dormant periods, light may be a limiting factor at the population level.

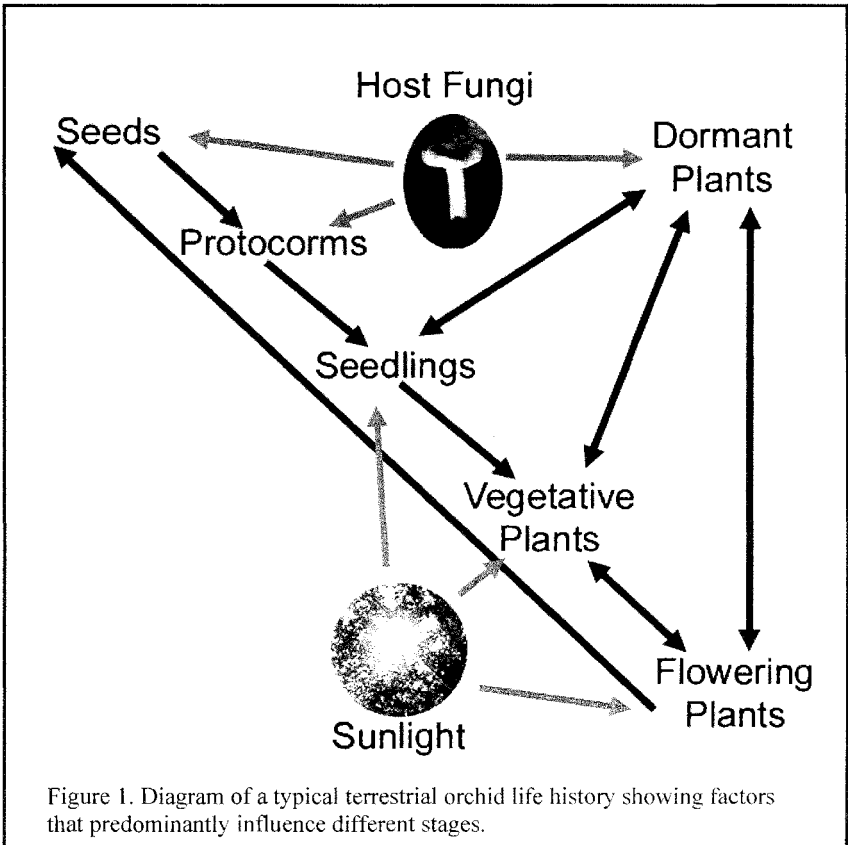


Figure 1. Diagram of a typical terrestrial orchid life history showing factors that predominantly influence different stages.

We decided to use the extent to which different life stages contribute to population decline in a threatened orchid to try to identify the most critical factors driving decline of *Isotria medeoloides* in the mid-Atlantic area. *Isotria medeoloides*, the small-whorled pogonia (back cover), is considered one of the most endangered orchids in the United States. Originally distributed up and down the east coast of the U.S., it is now restricted to a few moderate size populations in New England and widely scattered, very small, populations running south to northern Georgia, with a couple of very small outlier populations as far west as Missouri and Ontario, Canada. This distribution is thought to represent a northern migration since the retreat of glaciers approximately 18,000 years ago (Stone *et al.*, 2012) and so might suggest a decline of southern populations as a simple result of climate warming since the last glacial maximum, but even many northern populations seem to be declining. We have examined 14 *I. medeoloides* populations at two sites in the mid-Atlantic area since 2007, documenting emergence or dormancy, size, and reproductive status of all plants each year. In these populations, we found that high rates of plants entering dormancy, combined with low rates of re-emergence after dormancy, were the main drivers of population decline. We also observed low rates of fruit production, though these are most likely also driven by plant nutrition, rather than lack of pollinators, because *I. medeoloides* is largely self pollinating and is able to form fruit even in the absence of pollinators. Each year, approximately half of all vegetative plants and 1/3 of flowering plants that had emerged the previous year failed to appear above-ground, presumably entering dormancy. These rates of dormancy were similar to those found by Mehrhoff (1989) in declining populations and were much higher than he found in populations characterized as stable. Likely drivers of plants entering dormancy are factors that affect plant condition and nutrition, such as decreased light availability, altered hydrology, or insufficient fungal contribution to plant nutrition. We found that *I. medeoloides* that became dormant were very likely to remain so for multiple years, much longer than the dormancy duration observed in a stable population in New Hampshire (Cairns, 1999). This suggested that multiple stages in *I. medeoloides*' life history (nutrition of both emergent and dormant plants) were driving population declines so we focused on identifying factors disproportionately affecting those stages.

In a recent study, Brumback *et al.* (2011) found that increasing available light increased *I. medeoloides* seedling persistence and also decreased the likelihood of plants becoming dormant. This suggested that light might have a strong effect on nutrition of photosynthetic plants. However, other studies that attempted to increase light availability to *I. medeoloides* have met with either population declines or crashes. A possible explanation for why some canopy thinning attempts successfully increase population growth, while others have the opposite effect, might be the impact of thinning on the mycorrhizal fungi hosting *I. medeoloides*.

While most orchids associate primarily with decomposer fungi belonging to the genera *Tulasnella* and *Ceratobasidium* (e.g., McCormick *et al.*, 2004), we have identified *I. medeoloides* mycorrhizal host fungi as members of the genera *Russula* and *Lactarius* in the Russulaceae, a family of obligately ectomycorrhizal fungi. These fungi all require associations with trees and their abundance is likely driven by the health of their host trees. In the mid-Atlantic, the major potential host trees for ectomycorrhizal fungi are oaks (*Quercus* spp.), hickories (*Carya* spp., and beech (*Fagus grandifolia*), along with pines (*Pinus* spp.). We are currently working to determine exactly which of the potential host trees support the mycorrhizal fungi needed by *I. medeoloides* and what factors affect their abundance. This implies that management to conserve *I. medeoloides* may need to promote trees that host the mycorrhizal fungi needed by the orchids. It also implies that canopy thinning will need to target shrubs and trees that are not supporting the orchid host fungi. Removal of host trees could have disastrous effects on *I. medeoloides* populations.

While light is likely to be the primary supporter of emergent plants, mycorrhizal fungi are the primary supporters of seed germination, protocorms, and dormant plants and also increase stress tolerance of emergent plants. A deficit of mycorrhizal fungi would result in low seed germination and longer dormancy durations. We have observed no seed germination in seed packets over the five years of our study. However, population modeling indicates seedlings are being recruited into the populations, albeit at low rates, suggesting that either our current seed packet design in some way prohibits formation of mycorrhizal associations, that seed germination is episodic and we have not yet observed the appropriate conditions, or that years of seed weathering are required before germination can occur. We are currently working to solve this mystery.

Eighty-five percent of individuals that were dormant remained dormant the following year. This finding is nearly identical to the percentage of plants that Mehrhoff (1989) found remained dormant in declining populations. We have identified two possible causes for plants remaining dormant, one of which involves interactions with mycorrhizal fungi and the other is a direct effect on the plant. First, plants might fail to initiate an emergent bud as a result of insufficient nutrition. Second, they might initiate a bud that was subsequently damaged and unable to recover. Individual plants nearly always produce only one bud per year so the loss of a bud that had formed should result in dormancy the next growing season. To distinguish between these two factors, we tracked bud development and emergence in all emergent and a subset of dormant plants in our study populations. We found that 99% of plants that produced an overwintering bud emerged the following year, suggesting that persistent dormancy resulted from failure to initiate a bud, rather than bud damage. This, in turn, pointed to insufficient nutrition during dormancy as the cause of protracted dormancy in our study populations, as few of the plants that entered dormancy

have re-emerged during our study. Because dormant plants are thought to rely almost exclusively on their fungi for nutrition, factors that negatively influence either fungi or the interaction between the orchid and its fungi could influence both high rates of entering dormancy and also low rates of re-emergence after dormancy. It is also possible that plants we have identified as being dormant for extended periods of time have died. Five years of observation is not long enough to distinguish dead and dormant plants, but even plants that we have seen re-emerge have been dormant for longer than average in a stable New Hampshire population (Cairns, 1999).

Results from our study of *I. medeoloides* suggest that differentiating between factors affecting different parts of the orchid life cycle and using an analysis of which parts of the life cycle are driving population declines can be used to pinpoint conditions that need to be improved to support orchid recovery. For *I. medeoloides*, our study indicated that growing conditions, including nutritional support of emergent plants, most likely driven by light, and support of dormant plants, attributed to mycorrhizal fungi, must be examined to understand factors contributing to population declines. We are currently working to independently assess the effects of light availability and abundance of host fungi in these declining mid-Atlantic orchid populations.

Acknowledgments

The research on *Isotria medeoloides* has been supported by grants from the National Park Service and by a collaborative effort between SERC scientists and staff at Prince William Forest Park and Fort A.P. Hill. We greatly acknowledge the contributions of Paul Petersen at Prince William Forest Park and the staff at Fort A.P. Hill, especially Jason Applegate, Robert Floyd, and Kristine Brown. Other SERC staff involved in the *Isotria* research are Jay O'Neill and Liza McFarland. The volunteer efforts of Zoe Smith, Chelsea Kieffer and Jim Pilotte are also appreciated.

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