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Division of Biology and Biomedical Sciences

Evolution, Ecology, and Population Biology

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Regional Rarity: Consequences of Dispersal Limitation and Strategies for Reintroduction

by

Steven James Kroiss

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Abstract of the Dissertation

Regional rarity: consequences of dispersal limitation and strategies for reintroduction

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Steven James Kroiss

Doctor of Philosophy in Evolution, Ecology and Population Biology

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Professor Barbara Schaal, Chair

Understanding factors that limit species distributions within restored habitats has been a longstanding goal of restoration ecology, particularly with respect to differences between rare and widespread species. Numerous mechanisms have been proposed to contribute to rarity, including species traits, propagule limitation, ecological requirements, and population level processes such as demographic and environmental stochasticity. Yet, our understanding of species rarity remains limited since few studies have examined how these factors act in concert. This dissertation examines how these mechanisms may interact to influence the distribution and population establishment of plant species in restored xeric glades in the Missouri Ozarks (USA). First, I used a trait analysis of species in restored glades to determine whether traits related to niche breadth, persistence, or dispersal ability are related to species distributions. The results from this study suggest that several traits may interact to allow species to become widespread in this restored xeric habitat, including habitat specialization of open canopy environments, perennial or clonal life histories, and adaptations to arid conditions such as short plant height. To follow up these observations, I experimentally tested the degree to which propagule limitation, competitive environment (competitors present, burned, or removed), and abiotic stress (precipitation of typical dry, average and wet years) differentially limit the seedling establishment of 32 rare versus widespread species. I found that rare species established as well as widespread species in all treatments, suggesting that dispersal, rather than differences in stress tolerance or competitive ability, is the predominant limiting force for species distributions. This suggests that propagule introductions may be sufficient to increase rare species distributions. To examine how the success of propagule introduction might be influenced by propagule pressure (i.e., a single large versus several small introductions) versus habitat management during introduction (i.e., creating favorable conditions for seedling establishment), I conducted a meta-analysis with demographic modeling. My results indicate that habitat management during introduction has a much greater effect on long-term population establishment compared to propagule pressure. In summary, this dissertation demonstrates the importance of dispersal for limiting species distributions in restored habitats and also provides recommendations on how to best reintroduce rare species.

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Epigraph

"Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare, and, as I believe, the future success and modification of every inhabitant of this world." – Charles Darwin, *On the Origin of Species*.

"[Science] is really nothing more than a search for ultimate simplicity, but so far all we have is a kind of elegant messiness."
— Bill Bryson, *A Short History of Nearly Everything*

Introduction

Understanding factors that limit species presence within communities has been a longstanding goal of ecology (Darwin 1859, Gaston 1994), especially in terms of factors that govern differences in the relative rarity and commonness between species. While some species are widespread and abundant, others are rare and narrowly distributed. Numerous mechanisms have been proposed to contribute to rarity including species traits, propagule limitation, and specialized ecological requirements (Gaston 1994). These factors are proposed to influence species distributions by influencing dispersal and colonization of new habitat patches as well as establishment and maintenance of persistent populations (Murray et al. 2002, Myers and Harms 2009, Myers 2010). Less appreciated in the literature is the potential role of demographic and environmental stochasticity for limiting species establishment and occupancy. Propagule arrival and habitat suitability do not guarantee establishment, as colonizing propagules may be few in number, making incipient populations extremely susceptible to random fluctuations in vital rates and the environment (e.g., rainfall, fire, etc.). These chance factors may act as a "demographic gauntlet" to limit or prevent species establishment even if conditions are suitable for growth and survival overall. Consequently, ensuring species establishment in some habitats may require more propagules than are likely to ever naturally arrive. Here, I employ observational, experimental and simulation-based studies to examine factors that may contribute to regional rarity in a restored habitat as well as examine reintroduction strategies that may contribute to successful population establishment of rare species.

In the first chapter of this dissertation, I examine how species traits related to dispersal mechanism, habitat association, and life form may be important for contributing to local abundance and regional occupancy in a restored habitat. Factors that contribute to habitat degradation, such as invasive species or alterations to natural disturbance regimes, can cause local extinctions of characteristic flora and fauna (Huxel and Hastings 1998). Species traits might determine whether or not a species goes locally extinct when the habitat is altered (Figure 1 A,B), and whether or not a species can recolonize if the habitat is restored (Figure 1 C). Thus, these traits may determine whether or not a species is widespread or infrequent in the landscape (Ehrlén and van Groenendael 1998, Maurer et al. 2003). Traits important for allowing species to persist in altered habitats (Figure 1 A) or colonize and establish post-restoration (Figure 1 C-E) may include: (1) environmental niche breadth (Ellisa et al. 2007), (2) long life spans (MacArthur and Wilson 1967, Vellend et al. 2006) and/or clonal propagation (Wilcock and Neiland 2002), which allow individuals to persist for long time periods, (3) stress tolerance, especially in edaphically limited xeric habitats, and (4) seed dispersal mode and size, which may provide an advantage for colonizing suitable habitats (Burrows 1975, Bakker et al. 1996, Mabry 2004). Studies have shown that plant traits can influence the relative frequency of species in the landscape (Eriksson 1997, 1998, Ehrlén and van Groenendael 1998, Eriksson and Kiviniemi 1999, Jakobsson and Eriksson 2000, Zobel et al. 2000, Maurer et al. 2003), but they are typically restricted to undisturbed mesic habitats, and these patterns have rarely been examined in restored habitats (but see Maurer et al., 2003; Pywell et al., 2003). Understanding how traits are associated with species distributions in restored areas may provide vital information for land managers on why some species fail to establish in restored habitats.

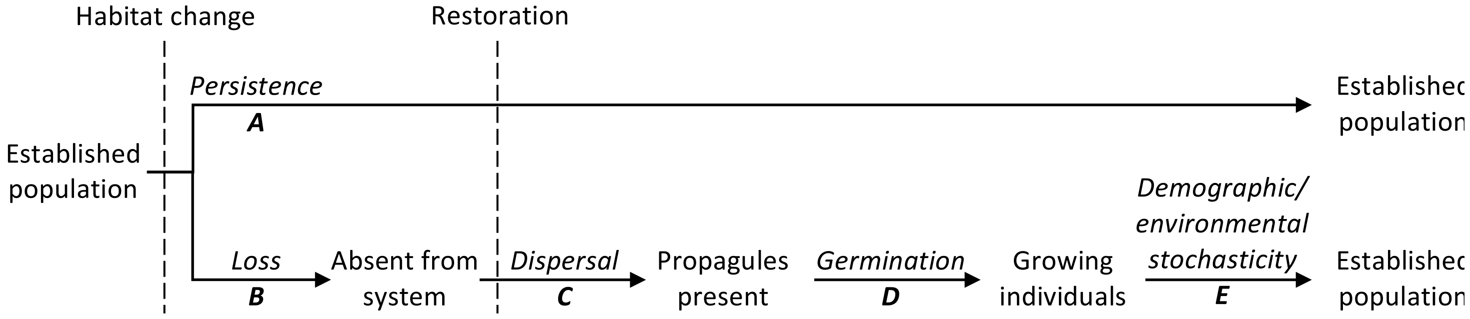

Figure 1. Factors that may limit the persistence and establishment of species.

Plant communities that develop on Missouri Ozark glades are an excellent system in which to test ideas concerning establishment limitation due to their island-type nature, distinct habitat boundaries and restoration history. Glades are open, unforested areas containing herbaceous plant communities growing on shallow rocky soils (Lawless et al. 2006) and can range in area from a few square meters to 1.2 km^2. In Missouri glades, the most common type of substrate is dolomite or a dolomite and limestone mix and as such we restrict ourselves to discussing only these types of glades. Glades typically occur on southwest facing hill slopes where solar irradiation is high and droughty conditions dominate in summer and autumn. The intense aridity in these habitats, which support such species as cacti, aloe, tarantulas, scorpions and numerous lizards, has drawn frequent comparisons to desert systems in the southwest as . These glades harbor a diverse flora with several species endemic to the Ozark region.

Glade coverage in Missouri pre-European settlement is estimated to have been 500,000 acres and now is thought to be less than 400,000 acres although the vast majority has been heavily invaded by cedars (Nelson 2005). Fire is a key component in these systems as it prevents woody encroachment by cedars (Guyette and McGinnes 1982). Historic fire frequency estimated from burn scars is thought to have been at least once every 3.2-4.3 years before 1879 (Nelson 2005). While cedars are often assumed to have been an important element of glade systems, early land survey records indicate that eastern red cedars were essentially restricted to bluffs where fires were absent (Nelson 2005). Glades also suffered from decades of overgrazing, allowing soil erosion as well as removal of chaff and debris, thereby limiting fire frequency. The combination of overgrazing and cessation of fire allowed for extensive invasion of cedars and other woody species, thereby decreasing glade area and possibly limiting dispersal due to changes in matrix structure. In the 1980s, land managers and conservationists began efforts to remove cedars from glades in order to preserve the remaining plant diversity. Restoration efforts include cedar removal and frequent burning, but almost never incorporate active re-seeding as these communities are allowed to re-establish from remaining vegetative individuals, the seed bank, and natural dispersal.

In Chapter Two, I employ an experimental approach to examine the degree to which an entire community of rare and widespread species may differ in their requirements for population establishment. Numerous studies have shown that the distribution of species within their range can be limited by abiotic factors such as edaphic conditions (Potvin 1993), biotic factors such as competitive environment (Sousa 1984), propagule limitation when insufficient numbers of propagules arrive at potential sites (Lockwood et al. 2005), and microsite limitation when recruitment is limited to spatially or temporally rare environmental conditions (Eriksson and Ehrlén 1992). Despite this extensive research base, little is understood about the mechanisms causing the majority of species to be rare while a few others are widespread (Bevill and Louda 1999). Several non-exclusive reasons have been proposed to explain this phenomenon by proposing that (1) rare species may be more limited by propagule availability than widespread species, (2) rare species are poorly adapted to the abiotic environment in context, or (3) rare species are poor competitors that rely upon spatially or temporally rare recruitment opportunities in which competitive interactions with established vegetation are reduced (Davis and Pelsor 2001, Drake et al. 2006). By examining whether or not these limiting factors systematically vary between rare and widespread species, I sought to contribute to the understanding of ecological theory as well as provide critical recommendations for the conservation and restoration of rare species. To examine the role of abiotic, biotic, and propagule limitation for limiting species distributions, I seeded 32 rare and widespread species into a restored Missouri Ozark glade habitat within a fully factorial experiment in which I manipulated the abiotic precipitation regime and the competitive environment.

In Chapter Three, I employed a modeling approach to examine how environmental context and introduction methodology may interact to influence the success of population establishment for a restored population. Restoration ecologists generally assume that habitat management and performing multiple introductions (Lockwood et al. 2005, Simberloff 2009) facilitates the successful establishment of a new population of a species, particularly in habitats with suboptimal environmental conditions and high temporal variation. However, the relative importance of each of these factors for different species and habitats has never been addressed. Furthermore, recent reviews of plant population reintroductions (Godefroid et al. 2011) suggest that the majority of introduced populations tend to fail, often for unknown reasons. Given the frequent use of propagule introductions as a restoration strategy (Brudvig and Mabry 2008, Godefroid et al. 2011), it is critical to understand what factors contribute most to successful population establishment. To examine this issue, I compiled published matrix population models for numerous species and populations and used demographic modeling to examine the relative importance of (1) habitat suitability and stochasticity, (2) the number of introduction events while keeping total numbers of propagules constant (i.e., a single large versus several small introductions) and (3) the role of introducing propagules in a favorable environment for seedling recruitment (i.e., timing the *first* introduction to coincide with a "good" year for seedling survival versus a randomly selected year) for affecting long-term population establishment. These models provide key insights into the role of site selection and introduction methodology for facilitating the success of propagule introductions.

This dissertation demonstrates the importance of morphological and functional traits, propagule availability, and abiotic and biotic factors for contributing to rare and widespread species distributions in restored habitats. Furthermore, this dissertation provides recommendations on how to maximize the success of rare species propagule introductions for the purposes of restoration. By putting species occupancy into a framework of traits, experimental establishment, propagule availability and introduction method, this dissertation contributes to a greater understanding of establishment limitation, patterns of biodiversity, and restoration ecology.

Works Cited

Bakker, J., P. Poschlod, R. J. Strykstra, R. M. Bekker, and K. Thompson. 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45:461-490.

Bevill, R. L., and S. M. Louda. 1999. Comparisons of related rare and common species in the study of plant rarity. Conservation Biology 13:493-498.

Brudvig, L. a., and C. M. Mabry. 2008. Trait-Based Filtering of the Regional Species Pool to Guide Understory Plant Reintroductions in Midwestern Oak Savannas, U.S.A. Restoration Ecology 16:290-304.

Burrows, F. M. 1975. Wind-borne seed and fruit movement. New Phytologist 75:405-418.

Darwin, C. 1859. The origin of species by means of natural selection. John Murray, London, UK.

Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421-428.

Drake, J., K. Drury, D. Lodge, A. Blukacz, N. Yan, and G. Dwyer. 2006. Demographic stochasticity, environmental variability, and windows of invasion risk for Bythotrephes longimanus in North America. Biological Invasions 8:843-861.

Ehrlén, J., and J. van Groenendael. 1998. The trade-off between dispersability and longevity-an important aspect of plant species diversity. Applied Vegetation Science 1:29.

Ellisa, C. J., B. J. Coppinsa, T. P. Dawsonb, and M. R. D. Seaward. 2007. Response of British lichens to climate change scenarios: Trends and uncertainties in the projected impact for contrasting biogeographic groups. Biological Conservation 140:217-235.

Eriksson, A. 1998. Regional distribution of Thymus serpyllum: Management history and dispersal limitation. Ecography 21:35-43.

Eriksson, O. 1997. Colonization dynamics and relative abundance of three plant species (Antennaria dioica, Hieracium pilosella and Hypochoeris maculata) in dry semi-natural grasslands. Ecography 20:559-568.

Eriksson, O., and J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91:360-364.

Eriksson, O., and K. Kiviniemi. 1999. Site occupancy, recruitment and extinction thresholds in grassland plants: an experimental study. Biological Conservation 87:319-325.

Gaston, K. J. 1994. Rarity. Chapman and Hall, London, UK.

Godefroid, S., C. Piazza, G. Rossi, S. Buord, A.-D. Stevens, R. Aguraiuja, C. Cowell, C. W. Weekley, G. Vogg, J. M. Iriondo, I. Johnson, B. Dixon, D. Gordon, S. Magnanon, B. Valentin, K.

Bjureke, R. Koopman, M. Vicens, M. Virevaire, and T. Vanderborght. 2011. How successful are plant species reintroductions? Biological Conservation 144:672-682. Elsevier Ltd.

Guyette, R. P., and E. A. McGinnes. 1982. Fire history of an Ozark glade in Missouri. Transactions of the Missouri Academy of Science 16:85-93.

Huxel, G. R., and A. Hastings. 1998. Population size dependence, competitive coexistence and habitat destruction. Journal of Animal Ecology 67:446-453.

Jakobsson, A., and O. Eriksson. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos 88:494-502.

Lawless, P. J., J. M. Baskin, and C. C. Baskin. 2006. Xeric limestone prairies of Eastern United States : Review and synthesis. Botanical Review 72:235-272.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20:223-8.

Mabry, C. M. 2004. The number and size of seeds in common versus restricted woodland herbaceous species in central Iowa, USA. Oikos 107:497-504.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, N.J.

Maurer, K., W. Durka, and J. Stöcklin. 2003. Frequency of plant species in remnants of calcareous grassland and their dispersal and persistence characteristics. Basic and Applied Ecology 4:307-316.

Murray, B. R., P. H. Thrall, a. M. Gill, and A. B. Nicotra. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. Austral Ecology 27:291-310.

Myers, J. A. 2010. Ecological assembly of high-diversity plant communities: dispersal, competition, and environmental filtering in longleaf pine savannas. Louisiana State University.

Myers, J. A., and K. E. Harms. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. Ecology Letters 12:1250-60.

Nelson, P. 2005. The Terrestrial Natural Communities of Missouri. Missouri Natural Areas Committee, Jefferson City, MO.

Potvin, M. 1993. Establishment of native grass seedlings along a topographic/moisture gradient in the Nebraska Sandhills. American Midland Naturalist 130:248-261.

Pywell, R. F., J. M. Bullock, D. B. Roy, L. Warman, K. J. Walker, L. I. Z. Warman, and P. Rothery. 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40:65-77.

Simberloff, D. 2009. The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and 40:81-102.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology, Evolution, and Systematics 15:353-391.

Vellend, M., K. Verheyen, H. Jacquemyn, A. Kolb, H. V. Calster, G. Peterken, and M. Hermy. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87:542-548.

Wilcock, C., and R. Neiland. 2002. Pollination failure in plants: why it happens and when it matters. Trends in plant science 7:270-7.

Zobel, M., M. Otsus, J. Liira, M. Moora, T. Mols, S. Ecology, and N. Dec. 2000. Is Small-Scale Species Richness Limited by Seed Availability or Microsite Availability? Ecology 81:3274-3282.

Chapter 1

Plant traits associated with regional occupancy and local abundance in a restored habitat

Abstract

While some species are widespread and abundant, others are narrowly distributed and regionally rare. Observed differences in abundance and occupancy rates may be heavily influenced by species traits, but few studies have examined these relationships in restored areas and almost none have made comparisons between mesic and xeric habitats. Traits that may allow species to persist locally or disperse into restored habitats include: breadth of habitat tolerances, length of life spans, dispersal mode, and seed size. To determine whether plant traits related to persistence or dispersal ability explain species abundance and occupancy patterns in a restored habitat, I surveyed 32 plant communities in restored Ozark glades (Missouri, USA). I used a generalized estimating equation approach with AIC model selection to assess the extent to which the variance in species occupancy and abundance could be explained by a composite of the aforementioned species traits. This analysis identified several traits may be important for explaining species abundance and occupancy in restored glades: habitat specialization on bright environments, perennial or clonal life histories, short plant height, and unassisted modes of dispersal. The results of this study provide several important implications for the future of restoration efforts. Habitat specialists tend to be more widespread and abundant than generalists, indicating glade restorations have been relatively successful. These results suggest that regionally rare glade specialists may benefit from assisted colonization, as successful establishment is likely in restored glades in which they are currently absent. Third, these results suggest that while relationships between persistence traits and regional distribution may be generalizable between mesic and xeric habitats, traits related to niche breadth and stress tolerance may not be.

Introduction

Understanding factors that limit the abundance and distribution of species at different spatial scales has been a longstanding goal of ecology (Gaston 1994). Studies that have explored how local abundance and regional distribution are associated with plant species niche breadth and traits have shown that while traits associated with species distribution tend to be variable (Murray et al. 2002), species with traits related to broad environmental tolerances, competitive ability, and dispersal ability tend to be more abundant (Eriksson 1997, Ehrlén et al. 1998, Eriksson and Kiviniemi 1999, Jakobsson and Eriksson 2000, Zobel et al. 2000, Maurer et al. 2003). These studies are primarily restricted to relatively undisturbed mesic habitats such as forests and grasslands such that only a few studies have explored these relationships in restored habitats (Maurer et al. 2003, Pywell et al. 2003). This is surprising since ecological restoration is a trillion dollar global activity; most restoration projects aim to restore native biodiversity, and understanding how traits are associated with species distributions in these systems could shed light on the reasons why some species fail to colonize and establish in restored habitats. For example, if species with poor dispersal traits are rare in restored habitats, this would suggest that propagule introductions could be a useful management strategy. Further, few studies focus on xeric ecosystems (but see Lavergne et al. 2003) despite their widespread, global distribution. Results from mesic systems might not be generalizable to xeric systems, if, for example, traits related to stress tolerance are more important than those that relate to competitive ability.

What are the general categories of traits that may be important?

Several types of species traits may be important for success in terms of local abundance and regional occupancy within restored habitats and these traits are not necessarily the same as those important for success in undisturbed habitats. This is evidenced by the fact that habitats that have been severely degraded and restored often have distinct differences in species assemblages compared to undisturbed habitats (Seabloom and van der Valk 2003). Habitat degrading forces, such as invasive species or shifts in disturbance regimes, can lead to shifts in local species abundances and even local extinctions for species that are unable to tolerate or persist through the degradation (Huxel and Hastings 1998). The ability to tolerate or persist during the temporarily unfavorable conditions may be mediated by factors such as niche breadth (i.e., breadth of environmental tolerances) or persistence ability (e.g., perennial life form or clonality). Once the habitat has been restored, species can establish via colonization or direct reintroduction or remain absent. The ability to colonize and establish within a habitat following restoration may be mediated by traits such as dispersal mode or seed size. Furthermore, the traits important for success in restored habitats may depend on the edaphic conditions of the site (e.g., mesic or xeric). For example, stress tolerance may be more important for success than persistence or dispersal ability in xeric sites. Below, I outline three broad categories of functional and morphological traits related to niche breadth, persistence ability, and dispersal ability that may correlate with species abundance and occupancy patterns in restored habitats. I also outline why some traits important for species distribution may depend on the edaphic conditions in the restored habitat.

Niche breadth

In undisturbed mesic habitats, plant species with broad environmental tolerances tend to be more widespread than more specialized species (Thompson et al. 1999, Kolb and Diekmann 2005, Kolb et al. 2006). In restored habitats, broad environmental tolerances may be especially important in restored habitats as they may allow species to persist within the focal habitat during its degraded time (Ellis et al. 2007) and thus be more abundant and widespread post-restoration. Furthermore, habitat generalists may be able to persist in habitats adjacent to those degraded, giving them a dispersal advantage following restoration. Important metrics of niche breadth could include both the range of habitat types a species can occupy as well as the range of light environments a species can occupy. This latter factor is especially relevant in systems for which the habitat degradation results in invasion of species that change the light availability such as invasions of woody plants into grasslands (Briggs et al. 2005, Báez and Collins 2008).

In contrast to mesic restored habitats, niche breadth might be negatively correlated with species abundance and distribution in xeric restored habitats as extreme habitat conditions such as low water availability may more strongly limit plant growth and reproduction than habitat degrading factors such as invasive species. This may be especially relevant if the habitat-degrading factors are not evenly distributed across the habitat of interest. For example, invasive species may not be able to invade the most extreme microsites within xeric habitats, leaving some areas relatively undisturbed (Melbourne et al. 2007). Thus, habitat specialists of open canopy environments (e.g., grasslands or rocky outcrops) may have a greater ability to persist within degraded xeric habitats and thus be more abundant and widespread post-restoration than species with broad niche breadth. More studies on non-mesic systems are needed in order to understand how the relationship between niche breadth and species distributions differs across sites with different environmental conditions and ecological history; this study provides the first examination of these patterns in a restored xeric ecosystem.

Persistence traits

Traits that could increase persistence ability during the time that a habitat is degraded may include perennial life histories, clonal propagation, and short plant height. Long life spans may allow individuals to persist for long time periods even if conditions are temporarily unfavorable (MacArthur and Wilson 1967, Warner and Chesson 1985, Vellend et al. 2006). Clonal propagation can allow species to continue to reproduce even when population sizes are low (Wilcock and Neiland 2002), and to establish new populations from a single individual. Plant height has been shown to be a proximate correlate for stress tolerance and competitive ability (Grime 1979). Tall species are predicted to have higher competitive ability in benign habitats, whereas short species are better able to tolerate low water availability (Rösch et al. 1997, Westoby 1998, Lavergne et al. 2003).

Dispersal traits

Dispersal characteristics may be important for allowing species to recolonize restored habitats. Along with small seed size, assisted modes of dispersal such as animal or wind dispersal have been shown to significantly increase habitat occupancy in undisturbed habitats (Burrows 1975, Bakker et al. 1996, Mabry 2004). Dispersal ability has also been shown to limit species distribution at a local scale, even on the order of a few meters (Primack and Miao 1992). Thus, assisted dispersal or small seed size may allow species to quickly expand their population size within newly restored sites.

Objectives

To examine how niche breadth and species traits may be correlated with local abundance and regional occupancy in a restored xeric habitat, I examined the distributions of plant species in restored herbaceous communities that develop on dolomite substrates of glades in the Missouri Ozarks (USA) and examined how plant traits may explain species distributions. The aim of this study is to determine whether ecological niche breadth, persistence traits and dispersal traits are associated with species' occupancy and abundance in a restored xeric habitat. Because species traits and distributions (e.g. regional occupancy) may be influenced by evolutionary history, I examine this issue by incorporating phylogenetic relationships into my analyses.

Methods

Study system

To assess whether plant traits may be associated with rarity in restored habitats, I chose dolomite glades (hereafter referred to as glades) in Missouri, USA as my study system. Glades are an ideal habitat in which to study species distributions because of their discrete habitat boundaries, island-like distribution, and restoration history. Glades are typically small (0.05-2 km^2) island-like herbaceous plant communities occurring on rocky outcrops within a closed canopy forest matrix. These habitats are highly xeric, typically occurring on south or west-facing hill slopes where shallow, rocky soils overlay dolomite or limestone bedrock (Nelson 2005). Glades are sometimes referred to as xeric upland prairies because the plant community is characterized by drought tolerant species typically found in prairies and dry grasslands from the American southwest (Lawless et al. 2006). Dolomite glades are distributed throughout the Ozark region from central Missouri to northern Arkansas, but share functional similarities (i.e., community composition, soil depth, xeric conditions, open canopy, etc.) to rocky outcrop habitats and glades in the American southeast and rocky barren communities around the world (Baskin and Baskin 1999, Nelson 2005). From historical accounts and burn scars, pre-European settlement fire frequencies, estimated to be once every three to seven years, prevented woody tree and shrub invasion into glades (Guyette and McGinnes 1982). Fire suppression in the last 100-200 years in Missouri has allowed fire intolerant species trees, primarily native eastern red cedars (*Juniperus virginiana*), to expand their local distributions from areas with low fire frequency, such as cliffs to glades and surrounding habitats, into adjacent glades (Guyette and McGinnes 1982, Nelson 2005). Cedar invasion into glades reduces habitat area and light availability, leading to severe degradation and loss of endemic and characteristic glade flora and fauna (Nelson and Ladd 1983, Nelson 2005). Restoration efforts to remove cedars and reinstate historic burn regimes were initiated in the 1980s and are ongoing. However, glade restoration efforts focus almost entirely on habitat improvements, with almost no re-introductions of species that went locally extinct. This assumes that all plant species currently found in glades either persisted through the degradation event or dispersed there naturally.

Regional occupancy and abundance

To assess regional occupancy and local abundance of glade species, I surveyed 32 restored glades from eastern and central Missouri from July-September 2010 (Table S1). This summer sampling methodology did not allow me to sample early senescing species such as spring ephemerals, which may introduce some bias into my analyses. In particular, the absence of spring ephemerals is likely to reduce the number of annuals and tall species from my analyses. However, in glade habitats there tend to be relatively few spring ephemerals (<5-10% of the plant community; Nelson 2005; Yatskievych 2006) suggesting that my results are robust to the exclusion of these species. I selected glades that were restored between 5-20 years ago (mean restoration age ~13 years) and that were no larger than two hectares. All but six pairs of glades were spaced at least 1.6km apart to limit pseudoreplication of glade sites. I measured species abundance and occupancy within each glade using a sampling grid and random walk design.

Grids were randomly placed within glades and consisted of 25 1m^2 quadrats in a square pattern in which each quadrat was separated by 4m in each direction from another quadrat. Each grid was located so that no quadrat was closer than 1.5m from the edge of the glade-forest boundary. Some glades did not allow for a square grid design and as such the sampling grid was shifted to be as close to square as possible. The number of grids used to sample a glade depended on the size of the habitat: glades <1500m^2 had one grid, glades 1500-10,000m^2 had 2 grids, and glades >10,000m^2 had 4 grids. After each grid was surveyed, I walked throughout the glade to search for rare species not found in the quadrats until no new species were found for 20 minutes. If a species was found outside of the surveyed grids, I defined its abundance as 0.01. I defined species occupancy as the proportion of glades occupied and defined abundance as the average proportion of quadrats occupied per glade when a species was present.

Traits

For 108 total species that occurred in the 32 glade, I obtained seven morphological and functional trait data relating to niche breadth, dispersal and persistence characteristics from the Flora of Missouri (Yatskievych 2006), USDA Plants Database (USDA and NRCS 2012), Kew's Seed Information Database (Kew Royal Botanic Gardens 2008) and Prairie Moon Nursery (Prairie Moon Nursery 2012) (Table S2). The number of habitat associations for each species was collected from the Flora of Missouri (Yatskievych 2006). These habitat associations largely come from herbarium specimens and surveys by natural historians in which they describe the dominant plant community in which a species can be found. I assigned a light index to each habitat association based on methods from Brudvig and Mabry (2008). Light indeces ranged from one (a closed canopy habitat such as a bottomland forest) to ten (an open canopy habitat such as a glade). I calculated the range of light coefficients for each species as the range from the minimum to maximum light indices for the habitats with which they are associated. I calculated a mean light coefficient for the light indices for each species. I categorized species life history as short-lived (annual or biennial), non-clonal perennial, and clonal perennial. I defined height as the maximum from the literature as maximum plant height is good predictor of a species potential competitive ability (Grime 1979). Seed weight was taken as the mean from the literature. I defined assisted dispersal as dispersal by vertebrate animals or the wind based on documentation in the literature. I classified animal dispersal based upon the presence of burs or hooks for dispersal on the coats of animals, or fleshy fruits for internal dispersal. I classified wind dispersal for seeds with wings or a pappus, or for seeds ≤0.5mm in size that could be dispersed by the wind without other obvious dispersal structures (Flinn and Vellend 2005, Brudvig and Mabry 2008).

Phylogeny

I restricted my analyses to native forbs for which I could obtain data for all of the traits listed above (n=108). I constructed a phylogeny for these species using Phylomatic (Webb and Donoghue 2005) which uses the Angiosperm super tree constructed by Davis et al. (2004). I then hand resolved relationships based on recent studies for Apocynaceae (Fishbein et al. 2011), Asteraceae (Jansen et al. 1991, Karis 1995, Noyes and Riesberg 1999, Clevinger and Panero 2000, Schmidt and Schilling 2000, Urbatsch et al. 2000, Selliah and Brouillet 2008, Vaezi and Brouillet 2009), Boraginaceae (Langstrom and Chase 2002, Weigend et al. 2009), Fabaceae (Doyle et al. 2000, Kajita et al. 2001, Wojciechowski et al. 2004), Lamiales (Wagstaff et al. 1998, Olmstead et al. 2001, Wortley et al. 2005, Bennett and Mathews 2006, Schäferhoff et al. 2010, Bräuchler et al. 2010), and Malpighiales (Wurdack and Davis 2009). I treated nodes with less than 80% support as soft polytomies and set all branch lengths equal to one. The composite phylogeny is presented in Figure S1.1a and S1.1b.

Analyses

To control for the effect of evolutionary history on species traits (Harvey and Pagel 1991, Harvey et al. 1995), I used generalized estimating equations (GEE; Paradis and Claude 2002) to analyze the effect of traits on species local abundance and regional occupancy separately. GEE incorporates phylogenetic relatedness as a correlation matrix into the framework of general linear modeling. Two important benefits of GEE are that the response variable can follow a non-normal distribution and GEE can incorporate multiple categorical and continuous traits as additive or interactive effects in the same model. I conducted both univariate and multivariate analyses for all possible combinations of trait variables up to models with two main effects and a two-way interaction. For the multivariate analyses, I excluded all variables not significant in the univariate trait analysis. I assessed pairwise relationships between traits using non-parametric tests. I used Spearman's rank correlation coefficient for associations between two continuous traits, Kruskal-Wallis's H for associations between a continuous and a categorical trait, and Fisher's exact test for two categorical traits. Model selection was assessed using the quasi-likelihood information criterion (QIC) (Pan 2001). Gaussian error distribution was used for the range of light coefficients, mean light coefficient, square root transformed maximum height, log transformed seed weight, and life history. Binomial error distribution was used for dispersal mode. All statistical analyses were implemented in R version 2.13.0 (R Development Core 2012) using the package APE version 2.7-2 (Paradis et al. 2004, Paradis 2006).

Results

Niche breadth

Results from the univariate trait models indicated that local abundance and regional occupancy were significantly associated with several metrics related to niche breadth (Table 1.1). Species with fewer habitat associations tended to be more locally abundant (P<0.001) than species with broader habitat associations, but the number of habitat associations was not related to regional occupancy. Species with narrower ranges of light coefficients and higher mean light coefficients (i.e., specialists of open canopy environments) tended to have higher local abundance (P<0.001 and P<0.001 respectively) and higher regional occupancy (P=0.004 and P=0.001 respectively).

Persistence traits

All traits related to persistence were significantly associated with local abundance and regional occupancy (Table 1.1). Non-clonal perennials tended to have higher local abundance than short-lived and clonal species (P=0.002), whereas clonal species tended to have higher regional occupancy than short-lived and non-clonal perennials (P=0.043). Plant height was negatively associated with local abundance (P<0.001) and regional occupancy (P=0.004).

Dispersal traits

Results from the univariate trait associations suggested that dispersal traits may be more important for local abundance rather than regional occupancy (Table 1.1). Seed weight was not associated with local abundance or regional occupancy. Contrary to my predictions, unassisted modes of dispersal were associated with higher local abundance (P=0.001), but were not associated with regional occupancy.

Multivariate models and model comparisons

The most parsimonious models for local abundance include the univariate models of number of habitat associations, range of light coefficients, mean light coefficient, dispersal mode, and height along with three multivariate models (Table 1.2). The multivariate models indicate significant interactions between the range of light coefficients with plant height (P=0.029) and dispersal mode (P=0.007). In these cases, species with narrow ranges of light coefficients (i.e., specialists of particular light environments), with short plant height, and unassisted modes of dispersal tend to be more locally abundant in restored glades than species with contrasting traits. The multivariate models also indicated a significant interaction between mean light coefficient and dispersal mode (P=0.017) such that species with high mean light coefficients (i.e., bright environments) with unassisted modes of dispersal tend to be more abundant than species with contrasting traits.

The most parsimonious models for regional occupancy include the range of light coefficients, mean light coefficient, height, and three multivariate models (Table 1.2). The multivariate models include significant interactions between the range of light coefficients and life history (P=0.024) and height (P=0.037). In the first case, short-lived species have a more negative association between the range of light coefficients and regional occupancy than clonal and non-clonal perennials. In the second case, species with narrower ranges of light coefficients and shorter plant height tended to have higher regional occupancy than species with contrasting traits. The multivariate models also indicate a significant interaction between mean light coefficients and height (P<0.001) such that species with higher mean light coefficients and short plant height tended to have higher regional occupancy than species with contrasting traits.

Correlations between traits and abundance and occupancy

I found several significant correlations between trait variables (Table 1.3). The number of habitat associations was positively correlated with the range of light coefficients (Spearman's $\rho=0.53$, $P<0.001$) and plant height (Spearman's $\rho=0.38$, $P<0.001$), dispersal mode (Kruskal-Wallis $H=3.10$, $P_{corr}=0.078$), and negatively correlated with mean light coefficient (Spearman's $\rho=-0.24$, $P=0.014$). The range of light coefficients was positively correlated with plant height (Spearman's $\rho=0.27$, $P=0.005$), negatively correlated with mean light coefficient (Spearman's $\rho=-0.72$, $P<0.001$), and seed weight (Spearman's $\rho=-0.18$, $P=0.06$) and correlated with life history (Kruskal-Wallis $H=5.57$, $P_{corr}=0.06$). Clonal species tended to have broader ranges of light coefficients than non-clonal perennials and short-lived species. Seed weight was significantly correlated with dispersal mode (Kruskal-Wallis $H=15.47$, $P_{corr}<0.001$) and life-history (Kruskal-Wallis $H=10.53$, $P_{corr}=0.005$). Species with unassisted modes of dispersal tended to have heavier seeds than species with assisted dispersal, which is in line with well-established relationships between seed weight and dispersal ability (Westoby et al. 1996). Clonal species had smaller seeds than short-lived or non-clonal perennials. Dispersal was significantly associated with life-history (Fisher's Exact Test $P_{corr}=0.007$). Short-lived and non-clonal perennials tended to have unassisted modes of dispersal while clonal species tended to have assisted modes of dispersal. Furthermore, I found a significant correlation between regional habitat occupancy and local abundance (Spearman's $\rho=0.53$, $P<0.001$).

Discussion

The results from this study demonstrate that plant traits related to niche breadth, persistence and dispersal ability are associated with local abundance and regional occupancy within restored glades, and that some of these relationships are qualitatively different from those found in mesic systems. Further, significant interactions between traits on species abundance and distribution suggests that there are numerous ways for species to be successful following the restoration of a xeric habitat. These findings are likely to have important implications for conservation and restoration efforts of other xeric habitats such as rocky outcrops and glades in the American southeast and other widely distributed rocky barren communities around the world.

Niche breadth associations with local abundance and regional occupancy

Species that tended to specialize on open canopy environments (i.e., narrow range of light coefficients and high mean light coefficients) tended to be more locally abundant and regionally widespread than more generalized species. In terms of the functional habitat types a species could occupy, habitat specialists were more locally abundant than generalists, but specialists and generalists did not differ in their regional occupancies. This suggests that habitat specialization may influence persistence and dispersal ability as well as allow specialist species to more quickly establish larger populations post restoration in the highly xeric conditions found in restored glades. For example, habitat specialists may have been better able to persist than generalists throughout the habitat degradation in extremely shallow soil areas within glades where cedar trees were unable to invade and the canopy remained open. These results contrast with studies that have found that habitat generalists tend to be more abundant and widespread than specialists in mesic undisturbed habitats (e.g., Thompson et al. 1999, Vellend et al. 2006) and restored mesic grasslands (Pywell et al. 2003). These differences suggest that the relative success of habitat specialists versus generalists in restored areas may depend on the degree of stress (e.g., mesic versus xeric) experienced in the habitat of interest relative to the surrounding landscape. The relative success of habitat specialists versus generalists may depend on the extent to which the habitat degradation altered the abiotic properties of the habitat and the ease with which they can be restored. In the case of glades, invasion by eastern red cedars may have had few long lasting effects on soil properties, especially in the shallowest soil areas of glades that cedars could not invade, thereby granting habitat specialists of bright environments a competitive advantage over generalists in restored glades. Thus, the ease with which glades were restored may have been a major factor allowing habitat specialists to achieve higher abundance post-restoration than habitat generalists.

Persistence traits associated with abundance and occupancy

Species with long life spans such as clonal and non-clonal perennials tended to have higher local abundance and regional occupancy than annuals and biennials. These findings are consistent with studies conducted in more mesic undisturbed habitats (Maurer et al. 2003, Vellend et al. 2006). This is expected if long-lived species have higher persistence probability during periods of degradation in which recruitment conditions are temporarily unfavorable or if they are less reliant on habitat disturbances such as fires for recruitment (Belsky 1992). Contrary to our predictions, non-clonal perennials had higher local abundance than clonal perennials. This might be explained by the higher seed production of non-clonal perennials compared to clonal species (Kolb and Diekmann 2005). Amongst the perennial species, clonal species had higher regional occupancy than non-clonal species, which is likely due to the increased persistence ability of clonal species in degraded habitats (Pywell et al. 2003). Furthermore, the multivariate analyses revealed that the occupancy of long-lived species is less affected by their range of light coefficients than the occupancy of short-lived species. This suggests that habitat specialization for long-lived species may be less critical for persistence in degraded glades than for short-lived species as habitat specialization and long life spans may be two different ways of persisting in degraded glades.

Another trait that may influence persistence ability is the presence and longevity of a seed bank (Warner and Chesson 1985). Unfortunately, data for the presence or absence of seed banks as well as seed bank longevity are typically lacking for large numbers of species making, the inclusion of this trait difficult for studies of species distributions. Other studies that have explored the relationship between seed bank presence and species distribution are rare. One study that included seed bank presence showed that seed banks significantly influenced patch occupancy (Dupre and Ehrlen 2002). Future efforts should be made to include seed bank information into studies of species distributions.

Shorter plant species tended to have higher local abundance and regional occupancy than taller plants, which contrasts with results from studies done in more mesic undisturbed habitats (Murray et al. 2002, Kolb and Diekmann 2005). In xeric systems such as restored glades, short plant height may be advantageous for increasing water stress tolerance (Westoby 1998). Thus, shorter species may have been more likely to persist than taller species in the areas within glades with shallow, rocky soils that were not invaded by cedars. Short height may also have been advantageous for avoiding grazing because many glades were used as pastures periodically for cattle during the last 100-200 years (Nelson 2005). Shorter species may also have been better able to establish large populations in restored glades since short height may be advantageous for increasing water stress tolerance in the predominantly xeric conditions within this habitat. Multivariate analyses indicated that height interacts with niche breadth traits such that shorter plants that are specialists of high light environments tend to have higher local abundance and regional occupancy in restored glades than species with contrasting traits. These species may have been particularly well adapted to persist and re-establish populations in restored glades.

Dispersal traits associated with abundance and occupancy

Seed weight was not associated with either local abundance or regional occupancy. This trait has received mixed support in the literature as a factor affecting species distributions, suggesting that it may depend on the spatial configuration of the habitats of interest (Thompson et al. 1999, Murray et al. 2002, Maurer et al. 2003, Mabry 2004). In my system, small seed size may not offer much if any advantage for dispersal into restored glades because these systems are often highly isolated and small in size.

Contrary to my predictions and numerous previous studies (reviewed in Murray et al. 2002), dispersal mode was not associated with regional occupancy, but species with unassisted modes of dispersal tended to have higher local abundance than species with animal or wind dispersed seeds. This result was surprising as assisted modes of dispersal are typically associated with higher local and regional dispersal ability than unassisted modes of dispersal. However, relationships between dispersal mode and local and regional distribution have also received mixed support in the literature (Thompson et al. 1999, Jakobsson and Eriksson 2000, Murray et al. 2002, Vellend et al. 2006). One possible explanation for my results is that dispersal mode may not have a large effect on regional persistence or dispersal, but if a species with unassisted modes of dispersal were able to persist in a restored glade, it may have greater numbers of seeds that stay within a glade that are available for increasing local population size post-restoration. Indeed, the multivariate models indicate that dispersal mode and niche breadth traits interact with local abundance, supporting this idea. Species that are specialists of high light environments (i.e., those with narrow ranges of light coefficients and high mean light coefficients) and have unassisted modes of dispersal tend to be more locally abundant in restored glades than species with contrasting traits. These types of species may have had both an advantage for persisting in glades due to their stress tolerant nature as well as an advantage for quickly increasing abundance post-restoration due to their ability to focus their seed dispersal to sites within the locality.

Relationships between trait variables

Several traits tended to co-vary, suggesting inherent physiological relationships or trade-offs between niche breadth, persistence ability, and dispersal ability. First, I found support for the positive association between local abundance and regional occupancy, which matches trends in undisturbed habitats (Gaston 1994, but see Kolb et al. 2006). This suggests that traits important for influencing local abundance are also likely to be important for influencing regional occupancy, and was indeed the predominant trend within our trait analysis. Second, relationships between the number of habitat associations and the range of light coefficients with dispersal mode, seed weight, height and life history suggests that habitat generalization may be partially due to increased dispersal ability, increased competitive ability, and clonal growth form. For example, species with small, wind dispersed seeds and tall plant height may be able to disperse to a wider variety of habitat types and also better compete within mesic habitats compared to species with contrasting traits (Grime 1979). These inherent relationships may then partially explain the individually significant associations of habitat breadth, height, and life history with local abundance and regional occupancy in restored glades. Third, the association of clonal species with small seed weight and assisted modes of dispersal was surprising because it is contrary to theoretical trade-offs between dispersal ability and longevity (Ehrlén and van Groenendael 1998). However, clonal species may produce fewer seeds than non-clonal species (Vallejo-Marín et al. 2010). This double benefit of increased persistence and dispersal ability may partially explain the significant associations of these individual traits with occupancy and abundance.

Summary

The results from this study suggest that there are numerous ways to be successful in terms of local abundance and regional occupancy in this restored xeric habitat, including: habitat specialization of bright environments, perennial or clonal life histories, traits that are advantageous in stressful environments such as short plant height, and unassisted modes of dispersal. Mesic systems and this xeric system show similar relationships between species abundance and occupancy and life-history and seed size, but differ entirely in the relationships between species abundance and occupancy and habitat breadth, plant height and dispersal mode. These differences emphasize the important role that the environmental context and the ecological history can have with regard to which species traits may be most successful (Murray et al. 2002). In this case, the highly xeric nature of these habitats are likely to have caused habitat specialization and short plant height to have been critical for allowing certain species to persist and re-establish populations in these restored systems. In addition, the small, island-like nature and restoration history of glades may have caused unassisted modes of dispersal to have been important for allowing certain species to maintain more propagules within sites and establish large populations after the restoration.

Recommendations for future glade management

These results bode well for future glade management and restoration for two main reasons. First, they suggest that glade restorations have been relatively successful in terms of restoring habitat conditions since specialists are more abundant than generalists. Second, these results suggest that regionally rare glade specialists that are of conservation concern may be able to successfully establish in restored glades in which they are currently absent. This idea is supported by anecdotal reports from a few glade restorations that have successfully established regionally rare species through seed introductions (personal communication Trager). While natural dispersal may eventually allow these species to re-establish over long time periods, dispersal between patches may be extremely rare due to habitat destruction, degradation and isolation. Thus, active propagule introduction may be necessary to restore regionally rare species.

I suggest that future management efforts should focus on increasing the abundance and distribution of the few glade specialists that are locally and regionally rare, including tall species such as *Manfreda virginica* and *Silphium laciniatum*, and short-lived species such as *Buchnera americana* or *Sabatia angularis*. Propagule introductions for several of these species in particular has been highly successful at establishing populations in a few restored glades (personal communication Trager). If facilitated dispersal is undesirable or cost or time prohibitive, restoration activities could be focused on improving habitat in degraded glades in which these species are currently present.

Concluding remarks

Developing hard and fast rules that guide restoration efforts based on species traits is a tantalizing goal, but this and other recent studies (Murray et al. 2002) suggest this goal may not be straightforward. This study suggests that the relationship between persistence traits and species distributions may be generalizable between mesic and xeric habitats, but traits related to niche breadth and stress tolerance may not be. Future studies are needed to determine the extent to which these trait associations are or are not generalizable across other mesic and xeric restored habitats. Finally, experimental tests that assess the degree to which competition, stress and dispersal limit the establishment of rare versus widespread species may aid in the understanding of rarity and for making future management recommendations.

Trait	**Predicted relationship**	**Abundance**	**Occupancy**
Number of habitat associations	-	-0.015***	n.s.
Range of light coefficients	-	-0.015**	-0.017**
Mean light coefficient	+	0.030*	0.040**
Life history	+ (clonal and non-clonal perennials)	E*	E**
Height	-	-0.022***	-0.015**
Seed weight	-	n.s.	n.s.
Dispersal mode	+ (assisted)	- 0.67**	n.s.

Table 1.1. Results from univariate trait analyses. The predicted relationships represent the direction of association between the trait of interested and local abundance and regional occupancy. Significance values as follows: n.s.>0.10, †P<0.10, *P<0.05, **P<0.01, ***P<0.001,. E, significant estimates not shown for traits with more than one category.

Dependent variable	**Predictor variables in the model**	**ΔQIC**
Abundance	Range of light**	0
	Mean light***	0.17277
	Dispersal mode**	0.8242
	Range of light*, dispersal mode***, interaction**	1.19296
	Height***	1.40927
	Mean light†, dispersal mode, interaction*	1.51619
	Number of habitats***	1.53093
	Range of light**, height**, interaction*	1.95294
Occupancy	Range of light**	0
	Range of light*, life history*, interaction*	0.34651
	Mean light**	0.96188
	Mean light***, height***, interaction***	0.99216
	Height**	1.18717
	Range of light**, height*, interaction*	1.81443

Table 1.2. Most parsimonious univariate and multivariate models. Only models with ΔQIC < 2 with traits that were significantly related to species distribution in the univariate analyses are shown. Significance values are the same as in Table 1.1.

	Abundance	Range of light	Mean light	Life- history	Height	Seed weight	Dispersal mode
Occupancy^1	0.545***						
Number of habitats^1		0.531***	-0.235*		0.383***	-0.139	
Range of light^1			-0.724***		0.266**	-0.181†	
Height^1			-0.160			0.111	
Mean light^1						0.089	
Seed weight^2				10.534**			15.467***
Number of habitats^2				4.017			3.103†
Range of light^2				5.570†			0.210
Height^2				1.565			1.220
Dispersal mode^3				**			

Table 1.3. Correlations between trait variables. Values represent: ^{1}Spearman's rank correlation, ^{2}Kruskal-Wallis's H, ^{3}Fisher's exact test. P-values are as indicated in Table 1.1.

Works Cited

Bakker, J., P. Poschlod, R. J. Strykstra, R. M. Bekker, and K. Thompson. 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45:461-490.

Baskin, J. M., and C. C. Baskin. 1999. Cedar glades of the southeastern United States. Pages 206-219 *in* R. C. Anderson, J. S. Fralish, and J. M. Baskin, editors. Savannas, barrens and rock outcrop plant communities of North America. Cambridge University Press, New York, NY, USA.

Belsky, A. J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. Journal of Vegetation Science 3:187-200.

Bennett, J. R., and S. Mathews. 2006. Phylogeny of the parasitic plant family Orobanchaceae inferred from phytochrome A. American Journal of Botany 93:1039-1051.

Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. BioScience 55:243. American Institute of Biological Sciences.

Brudvig, L. a., and C. M. Mabry. 2008. Trait-Based Filtering of the Regional Species Pool to Guide Understory Plant Reintroductions in Midwestern Oak Savannas, U.S.A. Restoration Ecology 16:290-304.

Bräuchler, C., H. Meimberg, and G. Heubl. 2010. Molecular phylogeny of Menthinae (Lamiaceae, Nepetoideae, Mentheae)--Taxonomy, biogeography and conflicts. Molecular Phylogenetics and Evolution 55:501-23. Elsevier Inc.

Burrows, F. M. 1975. Wind-borne seed and fruit movement. New Phytologist 75:405-418.

Báez, S., and S. L. Collins. 2008. Shrub invasion decreases diversity and alters community stability in northern Chihuahuan Desert plant communities. PloS one 3:e2332. Public Library of Science.

Clevinger, J. A., and J. L. Panero. 2000. Phylogenetic analysis of Silphium and subtribe Engelmanniinae (Asteraceae: Heliantheae) based on ITS and ETS sequence data. American Journal of Botany 87:565-572.

Davies, T. J., T. G. Barraclough, M. W. Chase, P. S. Soltis, D. E. Soltis, and V. Savolainen. 2004. Darwin’s abominable mystery: Insights from a supertree of the angiosperms. Proceedings of the National Academy of Sciences of the United States of America 101:1904-1909.

Doyle, J. J., J. A. Chappill, C. D. Bailey, and T. Kajita. 2000. Towards a comprehensive phylogeny of legumes: Evidence from rbcL sequences and non-molecular data. Advances in Legume Systematics:1-20.

Dupre, C., and J. Ehrlen. 2002. Habitat configuration, species traits and plant distributions. Journal of Ecology 90:796-805.

Ehrlén, J., and J. van Groenendael. 1998. The trade-off between dispersability and longevity-an important aspect of plant species diversity. Applied Vegetation Science 1:29.

Ellis, C. J., B. J. Coppins, T. P. Dawson, and M. R. D. Seaward. 2007. Response of British lichens to climate change scenarios: Trends and uncertainties in the projected impact for contrasting biogeographic groups. Biological Conservation 140:217-235.

Eriksson, A. 1998. Regional distribution of Thymus serpyllum: Management history and dispersal limitation. Ecography 21:35-43.

Eriksson, O. 1997. Colonization dynamics and relative abundance of three plant species (Antennaria dioica, Hieracium pilosella and Hypochoeris maculata) in dry semi-natural grasslands. Ecography 20:559-568.

Eriksson, O., and K. Kiviniemi. 1999. Site occupancy, recruitment and extinction thresholds in grassland plants: an experimental study. Biological Conservation 87:319-325.

Fishbein, M., D. Chuba, C. Ellison, R. J. Mason-Gamer, and S. P. Lynch. 2011. Phylogenetic Relationships of Asclepias (Apocynaceae) Inferred from Non-coding Chloroplast DNA Sequences. Systematic Botany 36:1008-1023.

Flinn, K. M., and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3:243-250.

Gaston, K. J. 1994. Rarity. Chapman and Hall, London, UK.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, UK.

Guyette, R. P., and E. A. McGinnes. 1982. Fire history of an Ozark glade in Missouri. Transactions of the Missouri Academy of Science 16:85-93.

Harvey, P. H., and M. D. Pagel. 1991. The comparatve method in evolutionary biology. Oxford University Press, Oxford, UK.

Harvey, P. H., A. F. Read, and S. Nee. 1995. Why ecologists need to be phylogenetically challenged. Journal of Ecology 83:535-536.

Huxel, G. R., and A. Hastings. 1998. Population size dependence, competitive coexistence and habitat destruction. Journal of Animal Ecology 67:446-453.

Jakobsson, A., and O. Eriksson. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos 88:494-502.

Jansen, R. K., H. J. Michaels, and J. D. Palmer. 1991. Phylogeny and character evolution in the Asteraceae based on chloroplast DNA restriction site mapping. Systematic Botany 16:98-115.

Kajita, T., H. Ohashi, Y. Tateishi, C. D. Bailey, and J. J. Doyle. 2001. rbcL and legume phylogeny , with particular reference to Phaseoleae , Millettieae , and allies. Systematic Botany 26:515-536.

Karis, P. O. 1995. Cladistics of the subtribe Ambrosiinae (Asteraceae: Heliantheae). Systematic Botany 20:40-54.

Kew Royal Botanic Gardens. 2008. Seed Information Database (SID) Version 7.1. http://data.kew.org/

Kolb, A., F. Barsch, and M. Diekmann. 2006. Determinants of local abundance and range size in forest vascular plants. Global Ecology and Biogeography 15:237-247.

Kolb, A., and M. Diekmann. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. Conservation Biology 19:929-938.

Langstrom, E., and M. W. Chase. 2002. Tribes of Boraginoideae (Boraginaceae) and placement of Antiphytum , Echiochilon , Ogastemma and Sericostoma : A phylogenetic analysis based on atpB plastid DNA sequence data. Plant Sytematics and Evolution 234:137-153.

Lavergne, S., E. Garnier, and M. Debussche. 2003. Do rock endemic and widespread plant species differ under the Leaf–Height–Seed plant ecology strategy scheme? Ecology Letters 6:398-404.

Lawless, P. J., J. M. Baskin, and C. C. Baskin. 2006. Xeric limestone prairies of Eastern United States : Review and synthesis. Botanical Review 72:235-272.

Mabry, C. M. 2004. The number and size of seeds in common versus restricted woodland herbaceous species in central Iowa, USA. Oikos 107:497-504.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, N.J.

Maurer, K., W. Durka, and J. Stöcklin. 2003. Frequency of plant species in remnants of calcareous grassland and their dispersal and persistence characteristics. Basic and Applied Ecology 4:307-316.

Melbourne, B. a, H. V. Cornell, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. L. Freestone, R. J. Hall, S. Harrison, A. Hastings, M. Holland, M. Holyoak, J. Lambrinos, K. Moore, and H. Yokomizo. 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecology Letters 10:77-94.

Murray, B. R., P. H. Thrall, a. M. Gill, and A. B. Nicotra. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. Austral Ecology 27:291-310.

Nelson, P. 2005. The Terrestrial Natural Communities of Missouri. Missouri Natural Areas Committee, Jefferson City, MO.

Nelson, P. W., and D. Ladd. 1983. Preliminary report on the identification, distribution, and classification of Missouri glades. Pages 59-76 *in* C. L. Kucera, editor. Proceedings of the seventh North American Prairie Conference. Southwest Missouri State University, Springfield, Missouri.

Noyes, R. D., and L. H. Riesberg. 1999. ITS sequence data support a single origin for North American Astereae (Asteraceae) and reflect deep geographic divisions in Aster S.L. American Journal of Botany 86:398-412.

Olmstead, R. G., C. W. DePamphilis, A. D. Wolfe, N. D. Young, W. J. Elisons, and P. A. Reeves. 2001. Disintegration of the Scrophulariaceae. American Journal of Botany 88:348-361.

Pan, W. 2001. Model selection in estimating equations. Biometrics 57:529-34.

Paradis, E. 2006. Analysis of phylogenetics and evolution with R. Springer, New York, NY, USA.

Paradis, E., and J. Claude. 2002. Analysis of comparative data using generalized estimating equations. Journal of Theoretical Biology 218:175-185.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of Phylogenetics and Evolution in R language. Bioinformatics 20:289-290.

Prairie Moon Nursery. 2012. Online catalogue. http://www.prairiemoon.com/

Primack, R. B., and S. L. Miao. 1992. Dispersal can limit local plant distribution. Conservation Biology 6:513-519.

Pywell, R. F., J. M. Bullock, D. B. Roy, L. Warman, K. J. Walker, L. I. Z. Warman, and P. Rothery. 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40:65-77.

R Development Core. 2012. R: A language and environment for statistical computing. Vienna, Austria.

Rösch, H., M. W. Van Rooyen, and G. K. Theron. 1997. Predicting competitive interactions between pioneer plant species by using plant traits. Journal of Vegetation Science 8:489-494.

Schmidt, G. J., and E. E. Schilling. 2000. Phylogeny and biogeography of Eupatorium (Asteraceae: Eupatorieae) based on nuclear ITS sequence data. American Journal of Botany 87:716-726.

Schäferhoff, B., A. Fleischmann, E. Fischer, D. C. Albach, T. Borsch, G. Heubl, and K. F. Müller. 2010. Towards resolving Lamiales relationships: insights from rapidly evolving chloroplast sequences. BMC evolutionary biology 10:352.

Seabloom, E. W., and A. G. van der Valk. 2003. Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: Implications for restoration. Wetlands 23:1-12.

Selliah, S., and L. Brouillet. 2008. Molecular phylogeny of the North American eurybioid asters (Asteraceae, Astereae) based on the nuclear ribosomal internal and external transcribed spacersThis paper is one of a selection of papers published in the Special Issue on Systematics Research. Botany 86:901-915.

Thompson, K., K. J. Gaston, and S. R. Band. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. Journal of Ecology 87:150-155.

Trager, J. 2011. Personal communication. Shaw Nature Preserve, Gray Summit, MO, USA.

USDA, and NRCS. 2012. The PLANTS Database. http://plants.usda.gov

Urbatsch, L. E., B. G. Baldwin, and M. J. Donoghue. 2000. Phylogeny of the coneflowers and relatives (Heliantheae: Asteraceae) based on nuclear rDNA internal transcribed spacer (ITS) sequences and chlorplast DNA restriction site data. Systematic Botany 25:539-565.

Vaezi, J., and L. Brouillet. 2009. Phylogenetic relationships among diploid species of Symphyotrichum (Asteraceae: Astereae) based on two nuclear markers, ITS and GAPDH. Molecular Phylogenetics and Evolution 51:540-53. Elsevier Inc.

Vallejo-Marín, M., M. E. Dorken, and S. C. H. Barrett. 2010. The ecological and evolutionary consequences of clonality for plant mating. Review of Ecology 41:193-213.

Vellend, M., K. Verheyen, H. Jacquemyn, A. Kolb, H. V. Calster, G. Peterken, and M. Hermy. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87:542-548.

Wagstaff, S. J., L. Hickerson, R. Spangler, P. A. Reeves, and R. G. Olmstead. 1998. Phylogeny in Labiatae s . 1 ., inferred from cpDNA sequences. Plant Sytematics and Evolution 209:265-274.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: A field guide to the storage effect. The American Naturalist 125:769-787.

Webb, C. O., and M. J. Donoghue. 2005. Phylomatic. http://phylodiversity.net/phylomatic/

Weigend, M., M. Gottschling, F. Selvi, and H. H. Hilger. 2009. Marbleseeds are gromwells--systematics and evolution of Lithospermum and allies (Boraginaceae tribe Lithospermeae) based on molecular and morphological data. Molecular Phylogenetics and Evolution 52:755-68. Elsevier Inc.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199:213-227.

Westoby, M., M. Leishman, J. Lord, H. Poorter, and D. J. Schoen. 1996. Comparative ecology of seed size and dispersal. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 351:1309-1318.

Wilcock, C., and R. Neiland. 2002. Pollination failure in plants: why it happens and when it matters. Trends in plant science 7:270-7.

Wojciechowski, M. F., M. Lavin, and M. J. Sanderson. 2004. A phylogeny of legumes (Leguminosae) based on analysis of the plastid matK gene reolves many well-supported subclades within the family. American Journal of Botany 91:1846-1862.

Wortley, A. H., P. J. Rudall, D. J. Harris, and R. W. Scotland. 2005. How much data are needed to resolve a difficult phylogeny?: case study in Lamiales. Systematic Biology 54:697-709.

Wurdack, K. J., and C. C. Davis. 2009. Malpighiales phylogenetics: Gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. American Journal of Botany 96:1551-70.

Yatskievych, G. 2006. Steyermark’s Flora of Missouri. Missouri Botanical Garden Press, St. Louis, MO.

Zobel, M., M. Otsus, J. Liira, M. Moora, T. Mols, S. Ecology, and N. Dec. 2000. Is Small-Scale Species Richness Limited by Seed Availability or Microsite Availability? Ecology 81:3274-3282.

Chapter 2

Propagule availability rather than competition or stress limits the establishment of rare species in a restored system

Abstract

Understanding factors that limit species occupancy of rare versus widespread species within restored habitats has been a longstanding goal of ecology. Several hypotheses have been put forward to explain differences in habitat occupancy, including that (1) rare species may be more limited by propagule availability than widespread species, (2) rare species may require abiotic conditions for recruitment that are spatially or temporally rare (e.g., years with above average rainfall), or (3) rare species may be poor competitors such that they can effectively compete only when competition with established vegetation is reduced (e.g. after fires or disturbances). I tested these hypotheses for a large suite (n=32) of rare versus widespread plant species in a restored habitat to assess the factors most limiting seedling establishment. Restored Ozark glades in Missouri, USA are highly fragmented prairie-like habitats dominated by competitive grasses, periodic fires, and summer droughts. I manipulated abiotic stress by simulating rainfall regimes typical of dry, average, and wet years and manipulated competition through burning, hand-removing unseeded competitors, and leaving some plots as unmanipulated controls. The fully factorial experiment was conducted under 45 rain-out shelters in a restored glade in St. Louis, MO, USA. Seedlings were censused bimonthly for percent survival. The effects of regional occupancy and treatment on percent survival and seedling growth were assessed using a Bayesian modeling approach with Markov chain Monte Carlo simulations. Results from this establishment experiment provide strong evidence that rare species distributions in this habitat are primarily limited by propagule availability, as rare species established as well or better than widespread species across all treatments. Furthermore, the effects of precipitation and competitive environment modified the degree of establishment success. In the rainfall treatments, drier conditions reduced seedling survival equally for all species, regardless of regional occupancy. When competition was reduced via controlled burning or hand clipping, seedling survival for all species was relatively high. Future management practices for this highly fragmented restored system should consider increasing opportunities for rare species establishment through facilitated dispersal and controlled burns.

Introduction

Broad issue

The distribution of species within their range can be limited by abiotic factors (e.g., edaphic conditions), biotic factors (e.g., interspecific interactions), or recruitment limitation (Eriksson and Ehrlén 1992, Turnbull et al. 2000, Moore and Elmendorf 2006, Clark et al. 2007, Zimmermann et al. 2008, Myers and Harms 2009). When recruitment is limited, one of two processes may limit plant recruitment: propagule limitation, whereby insufficient numbers of propagules arrive within suitable sites (Eriksson and Ehrlén 1992, Turnbull et al. 2000, Nathan and Muller-Landau 2000, Clark et al. 2007); and microsite limitation, whereby recruitment through the particularly vulnerable seedling stage is limited to spatially or temporally rare environmental conditions (Harper 1977, Clark and Macklin 1998, Nathan and Muller-Landau 2000, Ejrnæs et al. 2006). Seed addition experiments have been widely employed to show that plant populations are often limited by propagule numbers (reviewed in Clark et al. 2007) and that, at the community level, seed additions can lead to an overall increase in species diversity (Burke and Grime 1996, Tilman 1997, Zobel et al. 2000, Foster and Tilman 2003, reviewed in Myers and Harms 2009). However, the effect of seed additions are also highly variable and may be influenced by the biotic and abiotic conditions of the site, as well as the traits of the species being studied (Moles and Westoby 2002). Furthermore, the relative influence of abiotic, biotic, and recruitment limiting factors may vary between different species within a community (Moore and Elmendorf 2006).

All communities are characterized by a few very widespread/common species and many narrowly distributed/rare species (e.g., McGill et al. 2007). However, the mechanisms underlying why some species are more common and others particularly rare remain poorly understood (Bevill and Louda 1999). Regionally rare species may be so for three nonexclusive reasons which are described in more detail below: (1) because they are more limited by propagule availability than more common species, (2) because they are less well-adapted to the abiotic environment of the habitat of interest, or (3) because they are inferior competitors that take advantage of spatial-temporal windows created by the absence of more common species (Davis and Pelsor 2001, Drake et al. 2006). Understanding how these factors influence the recruitment of common and rare species will not only provide important information for basic understanding in ecology, but will provide practical recommendations for restoration ecology, which focuses on enhancing the recruitment of rare species. In this study, I provide some of the first evidence to explicitly examine how abiotic, biotic and recruitment limiting factors interact to differentially limit the distribution of a large assemblage of rare and widespread species.

Propagule availability

Many studies have shown that species distributions can be severely limited by propagule availability (e.g., Primack and Miao 1992, Ehrlén and Eriksson 2000, Myers and Harms 2009, Brudvig et al. 2011), even on the scale of a few meters. Although an explicit comparison of propagule limitation among a large suite of rare versus widespread species has not been conducted, several factors suggest that rare species may be more propagule limited than widespread species. First, species traits such as seed size or dispersal mode influences dispersal ability and rarity (Burrows 1975, Bakker et al. 1996, Mabry 2004), although important counterexamples exist (Murray et al. 2002, Munzbergova 2004, Kroiss chapter 1). Second, by being more regionally abundant, widespread species produce more propagules and thus should be less recruitment limited. Regardless of the mechanism, "escaping the state of rarity" (Gaston 1994) may be extremely difficult for regionally rare species, especially within the context of currently increasing levels of habitat isolation and fragmentation (Munzbergova 2004, Kolb and Diekmann 2005).

Stress tolerance

If a species is less well adapted to a particular set of environmental conditions (e.g., a generalist occurring outside of its favored habitats), it will be expected to be rarer in those habitats, and it might be able to establish more successfully if the habitat conditions become more favorable. For example, for edaphically limited communities, such as in xeric habitats, common species might be those that are more tolerant of low moisture stress conditions, and rare species might be those that require higher soil moisture (Lavergne et al. 2003). Thus, seedling recruitment in rare species might be limited to years with above average moisture availability (Potvin 1993, Lauenroth et al. 1994). Indeed, in a previous study (Chapter 1), I found that regionally widespread species within xeric glade communities tended to have traits related to stress tolerance such as short height and also tended to be habitat specialists of open canopy environments.

Competitive ability

Competition with established vegetation can also hamper seedling recruitment (Sluis 2002, Pywell et al. 2004, Huddleston and Young 2004, Zimmermann et al. 2008), and if rare species are less well adapted to a particular environment, they might also be more strongly influenced by competition from better-adapted species. Thus, it might be expected that rarer species in a particular habitat type are more strongly influenced by competitive interactions than more common species (Grime 1979). Recruitment of rare species might thus benefit from disturbances such as fire, grazing, or mowing that temporarily decrease the competitive dominance of established vegetation and thereby increase recruitment opportunities (Old 1969, Foster and Gross 1997, Martin and Wilsey 2006, Zimmermann et al. 2008). Fire is of particular interest within the context of rarity and habitat restoration because its suppression has been implicated as one of the main causes of losses in species diversity in many natural communities (Leach and Givnish 1996), and its reintroduction in the context of restoration often increases diversity by facilitating rare species establishment (Duncan et al. 2008, Godefroid et al. 2011). However, the few studies that have experimentally tested competitive differences between rare and widespread species (e.g., Rabinowitz et al. 1984, Aplet and Laven 1993, Snyder et al. 1994, Walck et al. 1999, Lloyd et al. 2002) have found mixed support for competitive differences between rare and widespread species. Furthermore, these studies have typically been restricted to a few species or were conducted ex-situ, making broad inferences between competitive ability and regional distribution difficult.

Objectives

To assess whether the establishment of rare species may differ from those of widespread species as a result of propagule limitation, stress tolerance and/or competitive ability, I seeded

32 species that differed in their regional occupancy within Ozark glade ecosystems into a recently restored but depauperate glade near St. Louis, MO, USA. Glades are rocky outcrop communities that occur on shallow xeric soils throughout the Ozark region of Missouri, USA (see 'Study System' below). I subjected each species to a fully factorial experiment in which I manipulated the precipitation regime and competitive environment (through burning and competitor removal) within a restored glade in order to test the relative roles of propagule availability, stress, and competitive environment on the recruitment of these species. There are three non-mutually exclusive outcomes possible from this experiment: (1) rare species may establish in all treatments equally well compared to widespread species, suggesting that their distribution is limited by propagule availability; (2) rare species may establish better in certain competition or stress treatments, suggesting that their distribution is limited by competitive ability or stress tolerance; and (3) rare species may fail to establish even when conditions are manipulated to be favorable (high moisture or low competition) suggesting that they are unable to establish in currently unoccupied habitats. To account for potential effects of evolutionary relatedness on species occupancy or response to treatments, I incorporate phylogenetic relationships into all of my analyses.

Methods

Study system

Rocky outcrop glades occur throughout the Ozarks of the USA as edaphically harsh (xeric) communities within a matrix of a more mesic forested ecosystem. In this study, I restricted analyses to glades that developed on dolomite bedrock, which is the most common substrate of glades in the region of study (east-central Missouri). Dolomite glades are typically small (0.05-2 km^2), open-canopy habitats that develop on south or west-facing hill slopes where shallow, rocky soils overlay dolomite and limestone bedrock (Nelson 2005). Because of their shallow, rocky soil and intense sun exposure, glades are highly xeric and tend to be dominated by drought tolerant herbaceous species commonly found in dry prairies and grasslands in the American southwest (Lawless et al. 2006). Historically, frequent fires (~3-7 year intervals; Guyette and McGinnes 1982) precluded woody species from invading this habitat, but for the last 100-200 years, European settlers have actively suppressed fires throughout the region. This allowed the native eastern red cedar (*Juniperus virginiana*) to expand its local distribution into glades, leading to reductions in habitat area, light availability, and losses of characteristic glade flora and fauna (Nelson and Ladd 1983, Nelson 2005). In the 1980s, restoration efforts began to remove the cedars and reinstate historic fire regimes. While these efforts have been successful at restoring habitat conditions, many characteristic glade species remain regionally rare.

Regional occupancy data

To assess the regional occupancy of glade plant species, I surveyed 32 restored glades across eastern and central Missouri, USA in 2010 (see Chapter 1). For a full description of the survey methods, see Chapter 1; for the purposes of this chapter, I defined the regional occupancy of each species as the proportion of the surveyed glades it occupied.

Selection of species

I selected 32 forb species (Table S2.1) for this experiment based on their occurrence in my regional surveys, recommendations from area naturalists, and availability of seeds from local (Missouri, USA) seed distributors. I focused on forbs because they comprise the dominant proportion of species in glade communities (92% of the herbaceous plant species versus 8% grasses) and are the predominant focus of conservation and restoration efforts. As much as possible, I selected species that varied widely in their regional occupancy and that were widely dispersed across the eudicot phylogeny. In two cases (*Manfreda virginica* and *Clematis fremontii*), seeds were unavailable from local seed distributors and thus were collected from nearby glade sites. Two species (*Clematis fremontii* and *Talinum calycinum*) failed to germinate in the greenhouse or in any experimental treatment. Further inspection suggested that seed viability might have been particularly low for both of these species due to self-incompatible breeding issues in the source populations and/or pathogen attack. Both of these species were removed from any further analyses. I also removed any species from the analyses that failed to establish in more than 5 of the 45 plots (*Castilleja coccinea, Dodecatheon meadia, Lobelia spicata,* and *Pycnanthemum tenuifolium*). These species had the smallest seeds of all the species in the experiment and the seeding rate that I used is may have been insufficient to generate sufficient seedling numbers. In all, 26 species were included in the analyses.

Phylogeny

To account for potential effects of evolutionary history on species distributions and responses to experimental treatments, I constructed a phylogeny for the species used in this experiment (Supplemental Figure S2.1) using Phylomatic (Webb and Donoghue 2005), which uses the Angiosperm super tree constructed by Davis et al. (2004). I then hand resolved relationships based on recent studies for Asteraceae (Jansen et al. 1991, Karis 1995, Noyes and Riesberg 1999, Clevinger and Panero 2000, Schmidt and Schilling 2000, Urbatsch et al. 2000, Selliah and Brouillet 2008, Vaezi and Brouillet 2009), Fabaceae (Doyle et al. 2000, Kajita et al. 2001, Wojciechowski et al. 2004), Lamiales (Wagstaff et al. 1998, Olmstead et al. 2001, Wortley et al. 2005, Bennett and Mathews 2006, Schäferhoff et al. 2010, Bräuchler et al. 2010), and Malpighiales (Wurdack and Davis 2009). I treated nodes with less than 80% support as soft polytomies. I assigned branch lengths using the BLADJ function in the Phylocom program, version 4.2 (Webb et al. 2008) and molecular and fossil dates from Wikström et al. (2001).

Experimental design and treatments

To examine how rare and widespread species might differ in terms of propagule limitation or their response to competition and stress, I manipulated the moisture availability and competitive regime in a fully factorial experimental design within a restored dolomite glade at Tyson Research Center in Eureka, MO USA. Cedars were removed and the herbaceous community burned approximately 10 years (~2002) prior to this experiment. This glade was chosen because it is edaphically similar to the glades in my regional survey, but only one of the seeded species was present (*Rudbeckia missouriensis*, which is ubiquitous across restored glades).

There were a total of 9 treatment levels (3 precipitation levels x 3 competitor levels), each of which was replicated five times for a total of 45 plots. Each of the nine treatment combinations was spatially aggregated into one of five blocks that were randomly located within the glade. Prior to experimental manipulations, seeds for each species were placed in humid, cold storage (4^{o}C) for at least four weeks and then hand scattered into each plot in January 2011. Seeding density was held constant at 200 seeds for each species.

I manipulated precipitation at three levels to mimic mean weekly precipitation patterns of typical dry, average, or wet years by using rainout shelters designed to partially reduce ambient precipitation, yet minimize light interference. Each shelter was 2m by 2m in area with an interior 0.25m buffer to account for edge effects, leaving an area of 1.5m x 1.5m for experimental manipulation (Figure 2.1). Each shelter was 0.76m in height and built with a 10% grade on flat ground. The roofing material consisted of clear corrugated greenhouse roofing (LEXAN corrugated polycarbonate sheets; 90% light transmission) that was cut into 12.7cm wide strips that were spaced 4.5cm apart on top of each shelter frame. This design reduced ambient precipitation levels by 75%. Precipitation runoff was collected from each shelter and discarded off-site to prevent precipitation from one shelter from entering downhill plots.

To determine low, ambient, and high precipitation treatment levels, I used precipitation data for the last 30 years (1980-2010) from the nearest weather station (Valley Park, MO, USA; Station ID 238561). Target weekly precipitation for each treatment was calculated by using polynomial function fitting and AIC model selection in ZunZun (ZunZun.com 2012) for all 30 years, the 5 driest and 5 wettest years based on total growing season precipitation. I then monitored weekly precipitation amounts from May 9 to September 30, 2011 by calculating the mean weekly ambient precipitation recorded with a RainWise Electronic Recording Rain Gauge (resolution of 0.25mm, accuracy of 0.5%) and two Tru-Chek Direct-Reading Rain Gauges located at the experimental site, which allowed me to calculate the amount of precipitation received in each plot by reducing the precipitation amount per unit area by 75% (the amount of plot area covered by greenhouse roofing slats). Plots were then supplemented weekly with irrigation via hand watering to achieve their weekly target precipitation. In effect, plots in the dry treatment received 51% and plots in the average treatment received 73% of the amount of water that the wet treatment received.

I manipulated competition at three levels by burning in early spring, removing competitors with continuous hand clipping, or leaving as untouched controls (see below for further details). Plots in the burn treatment were burned in late February 2011 with a propane flamethrower. Plots in the competitor removal plot were removed of duff (mostly from grasses) to increase light availability at the soil surface, and unseeded vegetation was subsequently hand clipped and removed every 3 weeks during the growing season (mid April – September). The clipped, unseeded vegetation was predominantly composed of native grasses (e.g., *Bouteloua curtipendula*) and to a lesser degree native perennial forbs (e.g., *Rudbeckia missouriensis*) as glade habitats have very few non-native species.

Data collection

Plots were censused in May, July, and October to assess seedling germination, death and survival for each seeded species. Each plot was divided into a 5x5 grid for sampling. During each census, seedlings with at least one true leaf were identified to species and then mapped so that the fate of each seedling could be followed. I defined the number of established seedlings per species as the total number of seedlings alive up through the third census. I defined the proportion of seedlings that established as the number of seedlings alive per species per plot in the final census divided by the total number of seeds per species (200). At the end of the growing season (November), up to 5 seedlings per species per plot were subsampled for seedling size. To distribute the subsampling evenly across the plot, I divided the total number of seedlings per species per plot into quintiles and sampled the median individual of each quintile starting in the downhill left cell (when looking uphill) and proceeding in a serpentine fashion uphill through the 25 grid cells. For example, if a species had 100 seedlings in a plot, the 10th, 30th, 50th, 70th, and 90th individuals were censused. As a proxy for fitness, I measured the longest leaf for plants with a rosette growth form and total plant height for species with upright growth forms.

Data analysis

To determine the effect of regional occupancy and treatment interactions on seedling establishment, I used a Bayesian approach with Markov chain Monte Carlo (MCMC) simulation using the MCMCglmm package, version 2.16, (Hadfield 2010) to estimate the posterior distributions of model parameters and to test for significance. This approach was chosen because it is amenable to model comparison (DIC scores), multiple random effects, non-standard distributions (e.g., Poisson hurdle models), and allows the incorporation of phylogenetic relatedness. I performed six analyses described below.

To assess the overall treatment effects on the establishment of all species regardless of regional occupancy, in the first model, I analyzed the main treatment effects and interactions on seedling establishment. The predictor variables were the treatment effects (competition and precipitation treatments). The response variable was the number of seedlings per species per plot that were alive at the end of the experiment (hereafter referred to as establishment). Species, experimental block, and seed weight were included as random effects. Because the data were highly zero-inflated due to plots in which particular species failed to establish, I used Poisson hurdle models that model all zeros in a logistic regression, and non-zeros in a truncated Poisson (Welsh et al. 1996). Hurdle models were chosen over other types of zero-inflated models (e.g., zero-inflated Poisson or mixture models) that can be more difficult to interpret. This two-part hurdle modeling procedure allowed me to estimate the probability that a species was present and then, given that it was present, estimate the mean number of seedlings within a plot. Because residual variance cannot be calculated for a binary trait (e.g., seedlings present or not present), I fixed residual variance for that parameter to 1.

To assess the effect of occupancy and potential interactions with treatments on seedling establishment, in the second model, I analyzed the effect of treatment in combination with regional occupancy on seedling establishment. This model was built similarly to the first model, with the exception that the regional occupancy for each species and potential interactions with treatments were included as predictor variables.

To assess the individual relationships between occupancy and treatment effect size within each factorial treatment combination, in the third model, I analyzed the relationship between treatment effect size and regional occupancy on seedling establishment by building separate models for each potential treatment comparison. The effect size was calculated as the log response ratio of the mean proportion of seedlings establishing between treatments (i.e., the number of seedlings per species per plot that were alive at the end of the experiment divided by the number of seeds per species per plot = x/200). Two species, *Camassia scilloides* and *Physostegia virginiana*, were not present in enough of the treatments to accurately calculate effect sizes and so they were removed from this analysis. For these models, I included the effect size as the response variable, treatment and regional occupancy as the predictor variables, and species and seed weight as random effects. I weighted each effect size measurement by its inverse variance. I assumed normal error distributions for the response ratios.

To assess treatment effects in terms of seedling size regardless of regional occupancy, in the fourth model, I analyzed the effect of treatment on seedling size Z-values. Because seedling sizes represent different measurements on different species (e.g., height versus longest leaf), I transformed size measurements into Z-values. To do this, I calculated Z-values (Z) for each species in each plot as the difference between mean seedling size for that species within a plot

(Y_i) and the total mean seedling size for that species across all plots (Y) and then standardized this by the standard deviation of seedling size for that species(s).

$$Z = \frac{Y_i - \bar{Y}}{s}$$

The Z-value was coded as the response variable, treatment as the predictor variable, and species and seed weight as random effects. Species included in the model, weighting, prior specification, and error distributions were similar to model three.

To assess the effect of occupancy and any potential interactions with treatments, in the fifth model, I analyzed the effect of treatment in combination with regional occupancy on seedling size Z-values. This model was built similarly to the fourth model, with the exception that the regional occupancy for each species and potential interactions with treatments were included as predictor variables.

To assess the individual relationships between occupancy and treatment effect size within each factorial treatment combination in terms of seedling size, in the sixth model, I analyzed the relationship between regional occupancy and seedling size treatment effect sizes. These models were similar to the third set of models, except that the response variable was the log response ratio of the mean seedling size.

I ran each of the models for 600,000 MCMC simulation iterations, with a burn-in period of 100,000 iterations and a thinning interval of 100, which resulted in 5000 posterior distribution samples for each model parameter estimate. I used flat, uninformative priors with a low degree of belief for all parameters in all analyses. I checked for convergence of model parameters by visual inspection of the MCMC iterations and by using the Raftery-Lewis diagnostic (Raftery and

Lewis 1992). Model estimates for all parameters represent means and 95% lower and upper credible intervals from the posterior distribution. P-values represent tests between model estimates in terms of the number of iterations in which one factor is greater or less than the other standardized by the total number of iterations.

Because species distributions (e.g. regional occupancy) and responses to experimental treatments may be influenced by evolutionary history, I ran each model with and without phylogenetic structure. In the former case, species were simply included as a random effect, while in the later, I included the full phylogeny into the analysis in which species relatedness is accounted for by a phylogenetic covariance matrix. I compared model fits using the deviance information criterion (DIC). Models with differences of DIC values >5 indicate that one model is a better fit. All analyses were conducted using R, version 2.15.0 (R Development Core 2012).

Results

Main treatment effects on seedling establishment

Analysis of treatment effects on the number of seedlings establishing indicated that the competition and precipitation treatments significantly affected seedling establishment (Figure 2.2, Table 2.1) when controlling for species identity, block effects, and seed weight. Results between all analyzed models with and without phylogeny were qualitatively similar and so I discuss results from models without phylogeny. Burning and removal of competitors increased establishment compared to the competitors present treatment (P=0.024 and <0.001 respectively), but establishment was highest in the competitor removal treatment. Establishment was highest in the treatments that simulated precipitation patterns in wet years compared to dry and average precipitation treatments (P=0.055), but there was no significant difference between dry and average precipitation treatments. There were also a few significant interactions between the competition and precipitation treatments. Within the competitors present treatment, seedling establishment was highest in the dry and wet precipitation treatments compared to the average treatment (P= 0.21 and 0.055 respectively).

Effects of regional occupancy and treatment on seedling establishment

Including species occupancy into the analysis of treatment effects on seedling establishment decreased model fit and partially changed treatment effect estimates, but also indicated that there were no significant positive relationships between regional occupancy on seedling establishment. Competitor removal increased seedling establishment compared to burning (P<0.001), but there was no significant difference between the burned and competitors present treatments. Establishment was higher in treatments that simulated precipitation in wet years compared to average precipitation treatments (P<0.001), but there was no significant difference between the dry and average precipitation treatments. While there was no main effect of regional occupancy on seedling establishment, there were significant two and three-way interactions between occupancy and treatments. Occupancy tended to be more negatively related to establishment in the competitors removed (P<0.001), competitors present (P=0.001), dry (P=0.036) and wet treatments (P=0.014) compared to the average and burned treatments. This relationship also tended to be positive within certain treatment combinations such as the competitors removed and dry treatment (P=0.008), competitors present and dry treatment (P=0.089), and the competitors removed and wet treatments (P=0.087). Despite these complex interactions, there were no individually significant relationships between regional occupancy and establishment within each of the nine treatment combinations (Figure 2.3).

Relationship between regional occupancy and treatment effect sizes on seedling establishment

Analysis of treatment effect sizes on seedling establishment indicated few significant relationships with regional occupancy. In terms of competition treatment effect sizes (Figure 2.4 and Supplemental Table S2.2), there was a positive relationship between regional occupancy and the effect size of burned versus competitors present treatments within the average precipitation treatments (P=0.028), but regional occupancy was negatively related to the effect size of competitors removed versus burned treatments within average precipitation treatments (P=0.013). In terms of precipitation treatment effect sizes (Figure 2.5 and Supplemental Table S2.3), there was a nearly significant positive relationship between regional occupancy and the effect size of average versus dry precipitation treatments within burned treatments (P=0.07), but regional occupancy was negatively related to the effect size of wet versus average precipitation treatments within burned treatments (P=0.009). All other relationships between regional occupancy and treatment effect sizes were non-significant.

Main treatment effects on seedling size

Results from the analysis of treatment effects on seedling size indicated that reducing competition through competitor removal increased seedling size (P=0.021), but neither burning nor any of the precipitation treatments had significant effects on seedling size (Figure 2.6 and Table 2.3). There were also no significant interactions between the precipitation and competition treatments on seedling size.

Interactive effects of regional occupancy and treatment effects on seedling size

Including species occupancy into the analysis of treatment effects on seedling size increased model fit and partially changed treatment effect estimates (Table 2.4). In this case, all treatment effects, including competitor removal, were not significant. There was also no significant main effect of regional occupancy on seedling size or any significant interactions between occupancy and treatments.

Relationship between regional occupancy and treatment effect sizes on seedling size

Analysis of treatment effect sizes on seedling establishment indicated few significant relationships with regional occupancy (Figures 2.7 & 2.8 and Supplemental Tables S2.4 & S2.5). Within comparisons of competition treatments on seedling size, the treatment comparisons (intercepts) were never significant. Occupancy was significantly related to the effect size of competition reduction in two cases. For average precipitation treatments, the effect size of seedling size tended to be positively related to regional occupancy for the competitor removal versus the competitors present comparison as well as the burned versus competitors present comparison, but these relationships were weakly significant (P=0.079 and 0.098 respectively, Figure 2.7).

Within comparisons of precipitation treatments on seedling size (Figure 2.8 and Supplemental Table S2.5), the treatment comparisons (intercepts) were only marginally significant in one case in which seedlings were larger in the average versus the dry treatments within the competitors present treatment (P=0.061). Regional occupancy was significantly related to the effect size of precipitation addition in two cases. Within the competitors present treatment, the effect size of seedling size tended to be negatively related to regional occupancy for the wet versus dry and the average versus dry treatment comparisons (P=0.054 and 0.016 respectively).

Discussion

Overall, the results from this experiment demonstrate that propagule limitation, rather than the abiotic or biotic environment, played an overriding role in determining the distribution of species in this system regardless of the regional occupancy of the species; 30 out of 32 species established in at least some plots, and 24 established in considerable numbers (25,250 germinants in total). However, establishment success was also modified by precipitation levels and competitors, suggesting a role for both abiotic and biotic factors in addition to propagule availability. Higher amounts of precipitation tended to increase seedling establishment of most species, as did disturbance from fire or competitor removal. Both disturbance (Belsky 1992, Seabloom et al. 2003, Zimmermann et al. 2008, Myers 2010) and precipitation effects (Potvin 1993, Zimmermann et al. 2008) on recruitment have been found in previous studies, but the effect sizes of precipitation tended to be smaller than those for competitor removal in both this and previous studies, suggesting a possible stronger role for competition rather than moisture limitation of recruitment. Further, competitor removal tended to have a larger effect on seedling establishment and growth than did burning, likely because fire acted as a "pulse" disturbance through a temporary increase in light availability at the soil surface, release of nutrients, and stimulation of germination (Old 1969, Williams et al. 2005) whereas the competitor removal treatment acted more as as a "press" disturbance through a perpetual reduction of competitive regime.

Relationship between occupancy and seedling establishment

Results from this experiment suggest that rare species may be more strongly limited by propagule availability than widespread species. This is evidenced by the fact that relationships between seedling establishment and regional occupancy were either not significant or tended to be negative, suggesting that rare species tended to establish as well or better than widespread species. This implies that propagule limitation may indeed be limiting the population establishment of the rare species in these restored habitats. Indeed, several anecdotal reports have demonstrated that seed introductions of rare species into restored glades have been quite successful at establishing populations (personal communication Trager). These results in combination with previous research (Primack and Miao 1992, Myers and Harms 2009, Brudvig et al. 2011) suggest that propagule limitation for rare species may be a widespread phenomenon, especially in restored areas.

This study also finds very little support for the idea that rare and widespread species might systematically differ in terms of seedling establishment or growth under different competition and water stress conditions. Instead, both rare and widespread species tended to respond similarly to burning, competitor removal, and increased precipitation. Only in a few cases did occupancy interact with treatment effect sizes, and these relationships were contradictory between treatment combinations, weak or only marginally significant. This suggests that rare species are not limited to establishing or growing in spatially or temporally rare environmental conditions such burned areas or years with high amounts of precipitation.

Experimental issues

While most species in this experiment established in almost every plot, six out of the thirty species (*Camassia scilloides*, *Castilleja coccinea, Dodecatheon meadia, Lobelia spicata,* and *Pycnanthemum tenuifolium, Symphyotrichum oolentangiense*) failed to establish in more than five plots. Establishment of these species could have been limited by specific ecological requirements that were not present in the experimental glade rather than propagule availability. I suggest, however, that this is unlikely for two reasons. First, the poor establishment of these species may in large part be due to their small seed size, which is positively correlated with establishment success in this and other studies (Moles and Westoby 2002). All but *C. scilloides* had the smallest seeds of all species in the experiment. Because of well-established physiological trade-offs between the number of seeds produced per plant and the size of seeds produced, these small seeded species may have been particularly disadvantaged in this experiment. Second, documentation from the literature and personal observation have shown that these species can occupy a wide variety of environmental conditions within glades and across other habitat types (Nelson 2005, Yatskievych 2006). Regardless, the species that failed to widely establish contain a diversity of regional occupancies and are not particularly biased towards rarity or widespreadness. This suggests that the findings of this study are robust to the failed establishment of these species.

While this experiment suggests that seedling establishment in this restored habitat is primarily limited by propagule availability, it should be noted that seedling establishment is not necessarily equivalent to population establishment. Only long-term studies that assess reproductive success and population growth rates can definitively determine the degree to which these species are limited by propagule availability. Due to the long life spans of several of these species, those results would not be obtainable for several years and are outside of the scope of this study. Despite these limitations, there are several reasons to expect that propagule limitation at the seedling stage may scale up to the population level. First, theory suggests that seedling recruitment is the most limiting stage of the life cycle since young seedlings are particularly prone to mortality from competition and moisture stress due to their lack of previously stored resources (Harper 1977). Second, several previous studies have shown that simple seed additions that establish as seedlings frequently become enduring populations (Werner 1977, Primack and Miao 1992).

What factors might influence propagule limitation?

While propagule availability appears to be a dominant limiting factor for species distributions, the exact mechanism remains unclear. Several hypotheses have been put forth to explain the mechanism causing stronger propagule limitation for rare versus widespread species. First, species traits such as dispersal mode, propagule size, propagule number and height of propagule release have all been proposed to influence dispersal ability and thus species distributions (Burrows 1975, Bakker et al. 1996, Mabry 2004), but the connection between these factors remains tenuous. In a review of studies examining the connection between traits and species distributions, Murray et al. (2002) found mixed support for the influence of traits on regional occupancy. The only trait that appeared to have some support was that of propagule number, since rare species tended to produce fewer total propagules than widespread species. In a trait analysis of species within restored glades (including the species used in this experiment), I found no relationship between regional occupancy and seed size or dispersal mode (Chapter 1). Munzbergova (2004) used an experimental approach, but found that dispersal ability did not correlate with the degree of propagule limitation. Second, broad habitat tolerance (i.e., niche breadth) may influence dispersal ability since habitat generalists may have a dispersal advantage via proximity to newly restored areas relative to habitat specialists. However, this trait has received mixed support in the literature (see Murray et al. 2002) and I found the opposite correlation: that habitat specialists tended to be more widespread in this system (Chapter 1). Third, regional distributions may be self-perpetuating to some degree through mass effects on dispersal. For example, species that are already regionally abundant or widespread may simply have greater numbers of propagules that are likely to colonize unoccupied sites. In this system, my trait analysis suggested that species that have long life spans (clonal and non-clonal perennials), are short, or are habitat specialists of open canopy environments tend to be more widespread (Chapter 1). These traits may have been important for allowing species to persist throughout the period of cedar invasion in which cedars preferentially invaded deep soil areas of glades leaving only the most shallow soil areas open for typical glade species. Thus, species that were better able to persist throughout the period of habitat degradation and remain relatively widespread may have also been better able to disperse to newly restored glades.

Management implications

As emphasized by the findings of this study, managing rare species distributions in restored habitats may require active propagule introductions. This fact is especially relevant to highly fragmented and isolated habitats like glades. Movement between habitat patches is likely to be extremely rare (Damschen et al. 2008), and successful population establishment may be even rarer due to demographic and environmental stochasticity. Propagule introductions are likely to be highly successful since this and other studies (Myers 2010, Brudvig et al. 2011) suggest that restored habitats are unlikely to be closed communities. Since competition and water stress also influence establishment, land managers should attempt to time seedling introductions to coincide with favorable environmental conditions (e.g., El Nino/La Nina years) or actively promote those conditions through controlled burning. If, however, active propagule introductions are undesirable, land managers should focus their efforts on restoring areas that currently contain regionally rare species. This may in turn increase the dispersal potential of rare species through mass effects.

Conclusions

This study provides strong evidence that propagule availability is the dominant limiting force for rare species distributions in this system, rather than differences among common and rare species in competitive response or stress tolerance. However, the competitive environment and amount of precipitation affected the degree of propagule limitation. These results are fairly surprising since classic ecological theory predicts that rare and widespread species should lie at opposite ends of the stress tolerance versus competitive ability trade-off spectrum (Grime 1979). While the particular mechanisms contributing to rarity may be idiosyncratic to individual species and habitats (Gaston 1994), propagule limitation is likely to play an increasingly important role in limiting species distributions due to anthropogenic increases in habitat loss, fragmentation and isolation as well as rapid global climate change. Within this context, assisted colonization may then become a crucial tool for increasing species distributions, especially for rare species (Seddon 2010).

Figure 2.1 – Panel A shows a rainout shelter with equally spaced slats of corrugated greenhouse roofing designed to decrease ambient precipitation by 75% and collect the excess in a bucket to prevent precipitation from flowing into downhill plots. Panel B illustrates the layout of a few of the structures. Panel C illustrates the propane flamethrower used to ignite plots and the burn box designed to limit fire spread. Panel D illustrates plot irrigation.

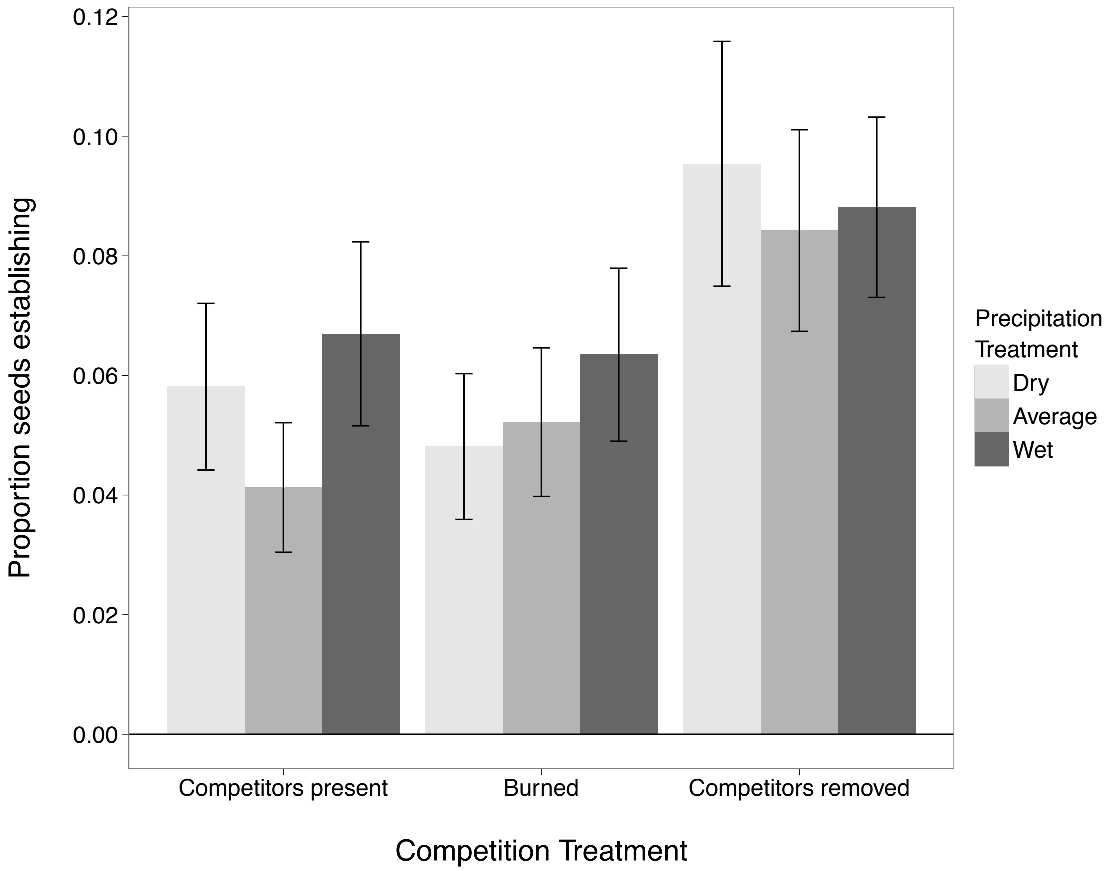

Figure 2.2 – Mean proportions of seeds establishing per species per plot (i.e., number of seedlings alive/200 sown seeds) across the treatment combinations. Error bars represent 95% confidence intervals.

	No phylogeny			**With phylogeny**		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
Intercept ($\text{Comp}_{\text{Burned}}$:$\text{Precip}_{\text{Average}}$)	**1.674**	**(0.919, 2.422)**	**0.002**	**1.636**	**(0.022, 3.187)**	**0.046**
$\text{Comp}_{\text{Removed}}$	**0.502**	**(0.292, 0.716)**	**<0.001**	**0.503**	**(0.298, 0.717)**	**<0.001**
$\text{Comp}_{\text{Competitors present}}$	**-0.268**	**(-0.49, -0.03)**	**0.024**	**-0.268**	**(-0.491, -0.03)**	**0.024**
$\text{Precip}_{\text{Dry}}$	-0.061	(-0.277, 0.156)	0.580	-0.062	(-0.277, 0.156)	0.580
$\text{Precip}_{\text{Wet}}$	**0.215**	**(-0.002, 0.435)**	**0.055**	**0.213**	**(0.001, 0.44)**	**0.055**
$\text{Comp}_{\text{Removed}}$:$\text{Precip}_{\text{Dry}}$	0.155	(-0.151, 0.439)	0.314	0.156	(-0.13, 0.451)	0.304
$\text{Comp}_{\text{Present}}$:$\text{Precip}_{\text{Dry}}$	**0.382**	**(0.062, 0.7)**	**0.021**	**0.387**	**(0.058, 0.684)**	**0.016**
$\text{Comp}_{\text{Removed}}$:$\text{Precip}_{\text{Wet}}$	-0.096	(-0.373, 0.214)	0.508	-0.093	(-0.384, 0.193)	0.542
$\text{Comp}_{\text{Present}}$:$\text{Precip}_{\text{Wet}}$	**0.312**	**(-0.02, 0.617)**	**0.055**	**0.318**	**(0.021, 0.636)**	**0.048**

Table 2.1 – Model one results showing mean parameter estimates and 95% credible intervals (CI) describing the relationship between the number of seedlings establishing per species per plot and the treatment effects with and without phylogeny. Random effects in this model are species, block and seed weight. DIC values for the models with no phylogeny and with phylogeny are 6482.082 and 6482.406 respectively. Significant relationships are bolded.

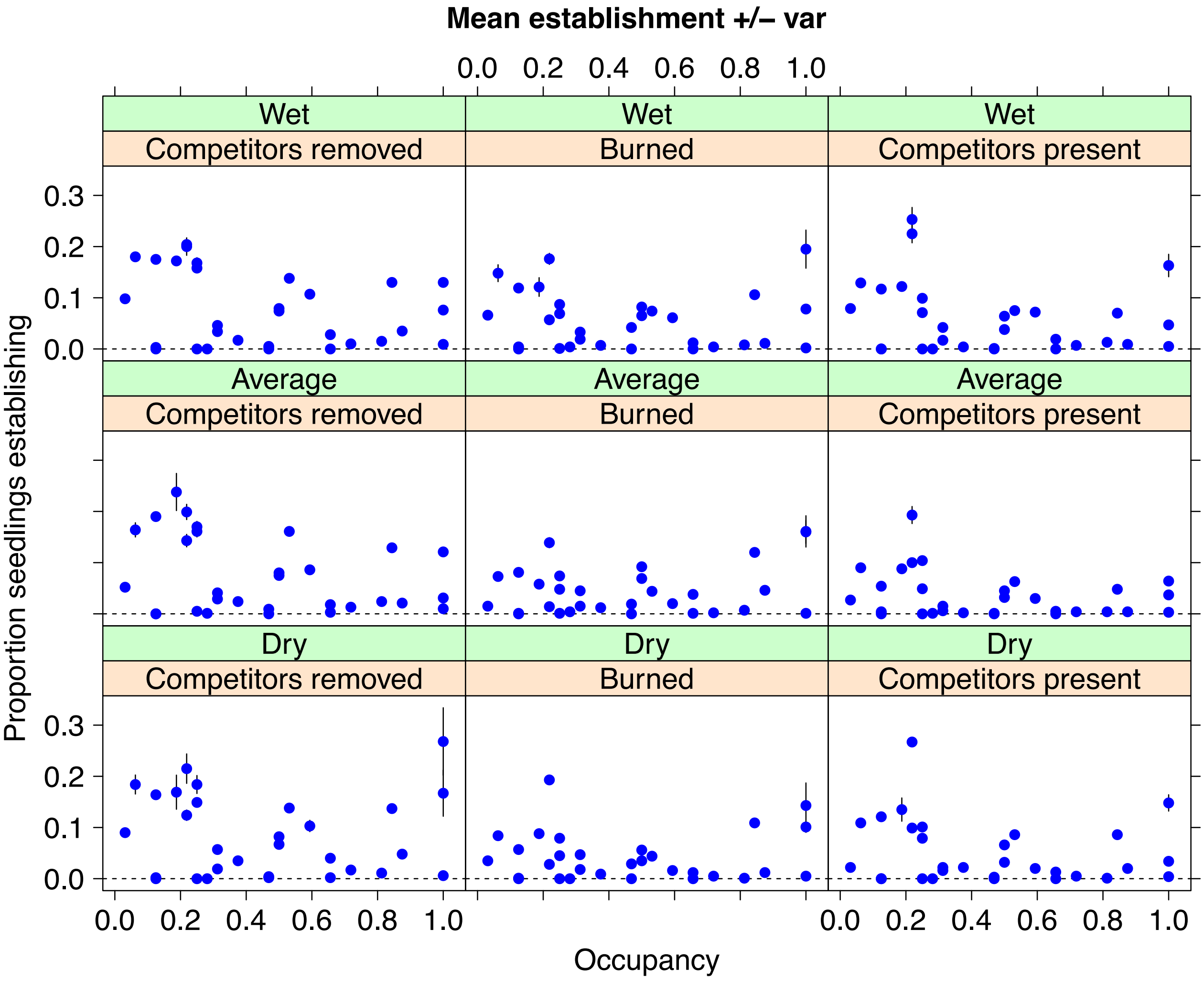

Figure 2.3 – The effect of regional occupancy on the proportion of seedlings establishing within each treatment combination. Points with error bars represent means and variances for each species. As there are no individually significant relationships between seedling establishment and regional occupancy, no model lines are depicted.

	No phylogeny			With phylogeny		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
Intercept	**1.616**	**(0.605, 2.609)**	**0.004**	**1.424**	**(-0.195, 3.103)**	**0.089**
Comp$_{Removed}$	**1.108**	**(0.704, 1.443)**	**<0.001**	**1.111**	**(0.759, 1.507)**	**<0.001**
Comp$_{Present}$	0.333	(-0.084, 0.711)	0.102	0.332	(-0.04, 0.742)	0.102
Precip$_{Dry}$	0.290	(-0.09, 0.676)	0.128	0.294	(-0.083, 0.697)	0.138
Precip$_{Wet}$	**0.633**	**(0.245, 1.006)**	**0.000**	**0.637**	**(0.249, 1)**	**0.001**
Occupancy	0.176	(-1.289, 1.658)	0.811	0.411	(-0.968, 1.638)	0.506
Comp$_{Removed}$:Precip$_{Dry}$	-0.412	(-0.929, 0.111)	0.118	-0.416	(-0.922, 0.125)	0.122
Comp$_{Present}$:Precip$_{Dry}$	-0.036	(-0.567, 0.519)	0.902	-0.036	(-0.561, 0.51)	0.902
Comp$_{Removed}$:Precip$_{Wet}$	**-0.473**	**(-0.988, 0.04)**	**0.074**	**-0.479**	**(-0.983, 0.024)**	**0.071**
Comp$_{Present}$:Precip$_{Wet}$	-0.048	(-0.615, 0.467)	0.848	-0.045	(-0.588, 0.506)	0.868
Comp$_{Removed}$:Occupancy	**-1.323**	**(-1.985, -0.639)**	**<0.001**	**-1.328**	**(-2.034, -0.677)**	**0.000**
Comp$_{Present}$:Occupancy	**-1.333**	**(-2.064, -0.589)**	**0.001**	**-1.328**	**(-2.135, -0.627)**	**0.001**
Precip$_{Dry}$:Occupancy	**-0.744**	**(-1.483, -0.078)**	**0.036**	**-0.754**	**(-1.468, -0.054)**	**0.038**
Precip$_{Wet}$:Occupancy	**-0.906**	**(-1.623, -0.232)**	**0.014**	**-0.908**	**(-1.633, -0.234)**	**0.012**
Comp$_{Removed}$:Precip$_{Dry}$: Occupancy	**1.221**	**(0.248, 2.169)**	**0.008**	**-1.215**	**(-2.68, 0.243)**	**0.108**
Comp$_{Present}$:Precip$_{Dry}$: Occupancy	**0.917**	**(-0.127, 1.941)**	**0.089**	**0.187**	**(-1.16, 1.544)**	**0.786**
Comp$_{Removed}$:Precip$_{Wet}$: Occupancy	**0.821**	**(-0.114, 1.747)**	**0.087**	**-0.206**	**(-1.645, 1.155)**	**0.773**
Comp$_{Present}$:Precip$_{Wet}$: Occupancy	0.784	(-0.209, 1.821)	0.136	-0.828	(-2.274, 0.63)	0.268

Table 2.2 - Model two results showing mean parameter estimates and 95% credible intervals (CI) describing the relationship between the number of seedlings establishing per species per plot and regional occupancy and treatment effects with and without phylogeny. Random effects in this model are species, block and seed weight. DIC values for the models with no phylogeny and with phylogeny are 6490.671 and 6490.088 respectively. Significant relationships are bolded.

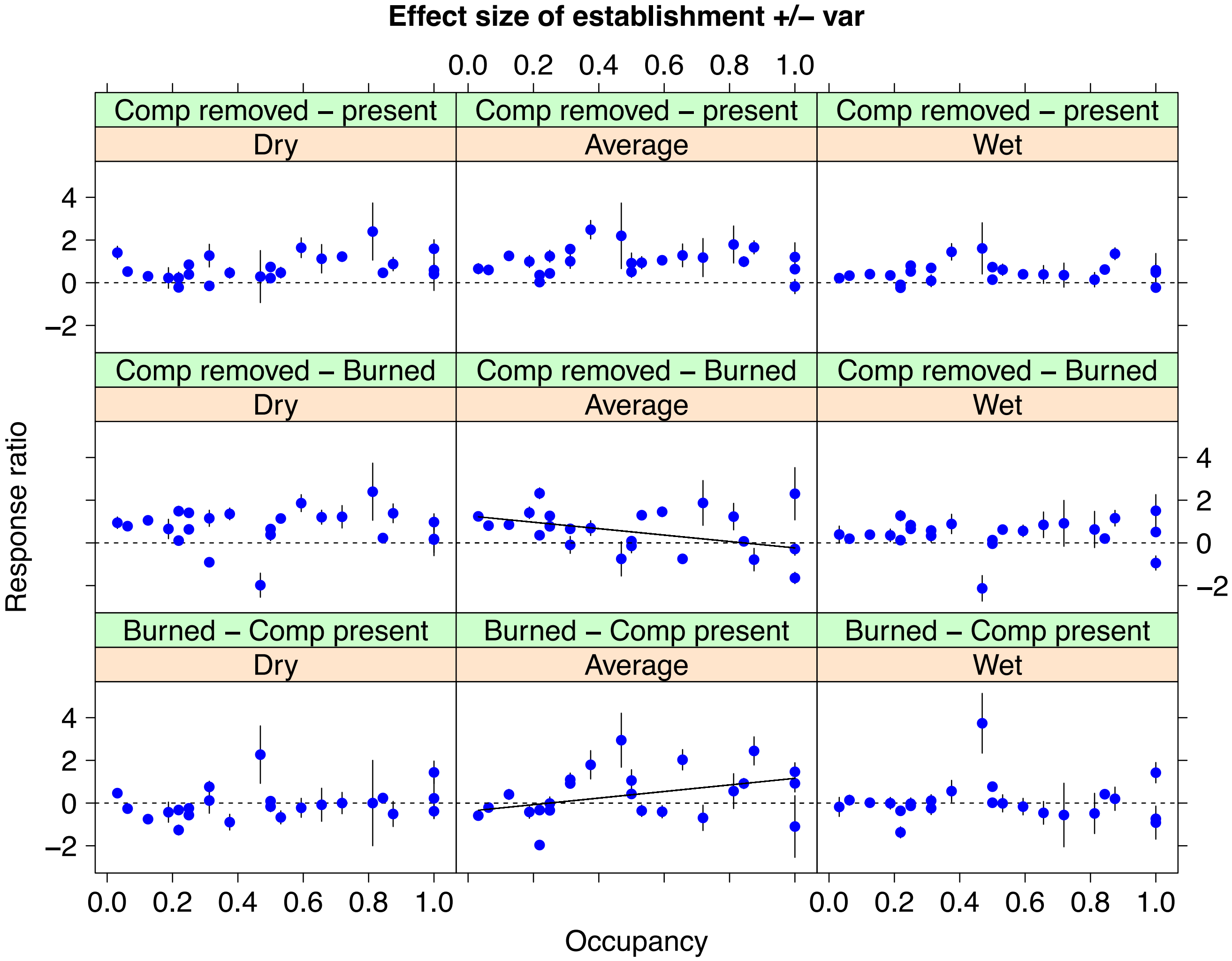

Figure 2.4 – The effect of regional occupancy on the log response ratio of seedling establishment between competition treatment comparisons within each factor of precipitation. Points with error bars represent means and variances for each species. Lines represent significant relationships from model three (Table 2.3).

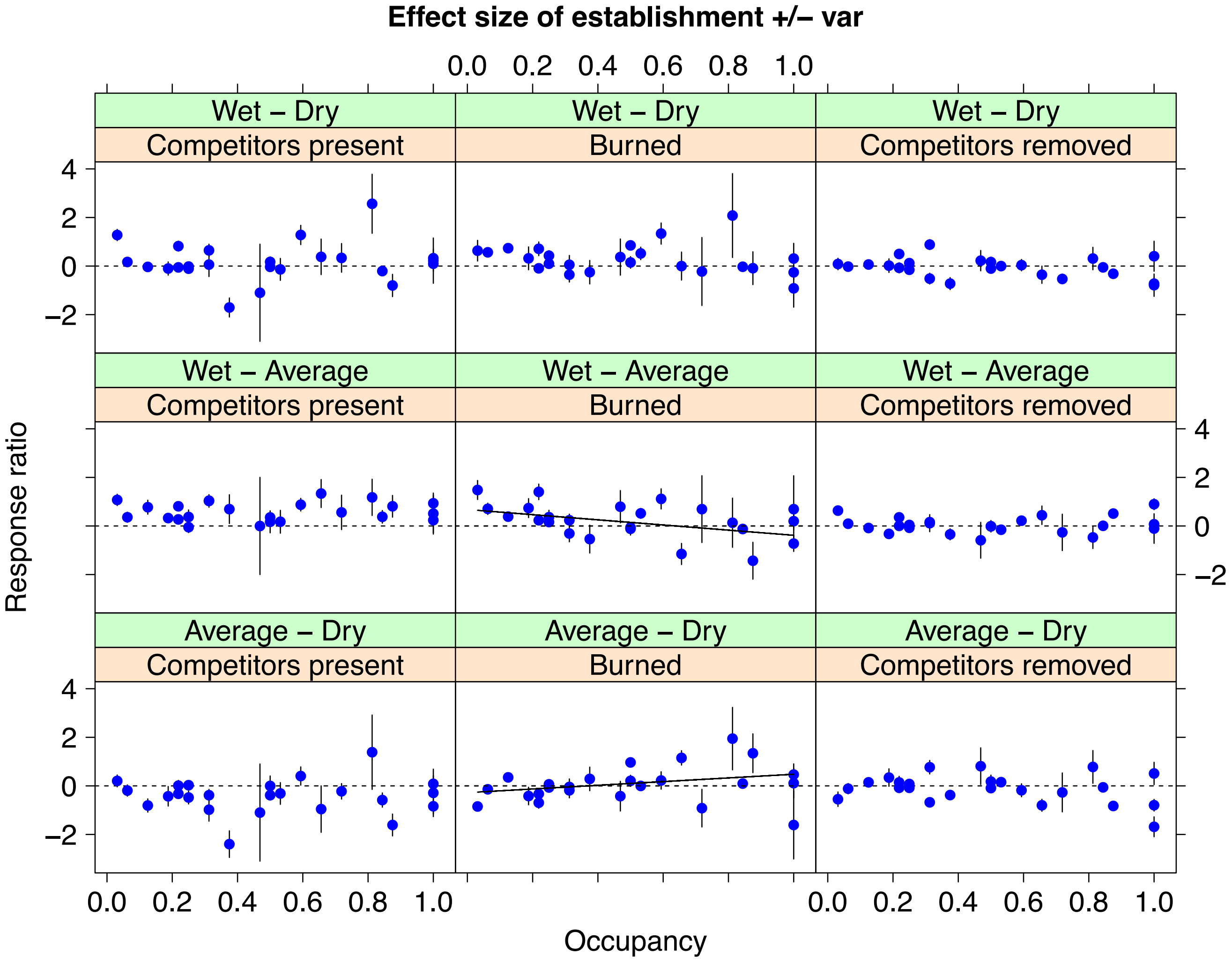

Figure 2.5 – The effect of regional occupancy on the log response ratio of seedling establishment between precipitation treatment comparisons within each factor of competition. Points with error bars represent means and variances for each species. Lines represent significant relationships from model three (Table 2.4).

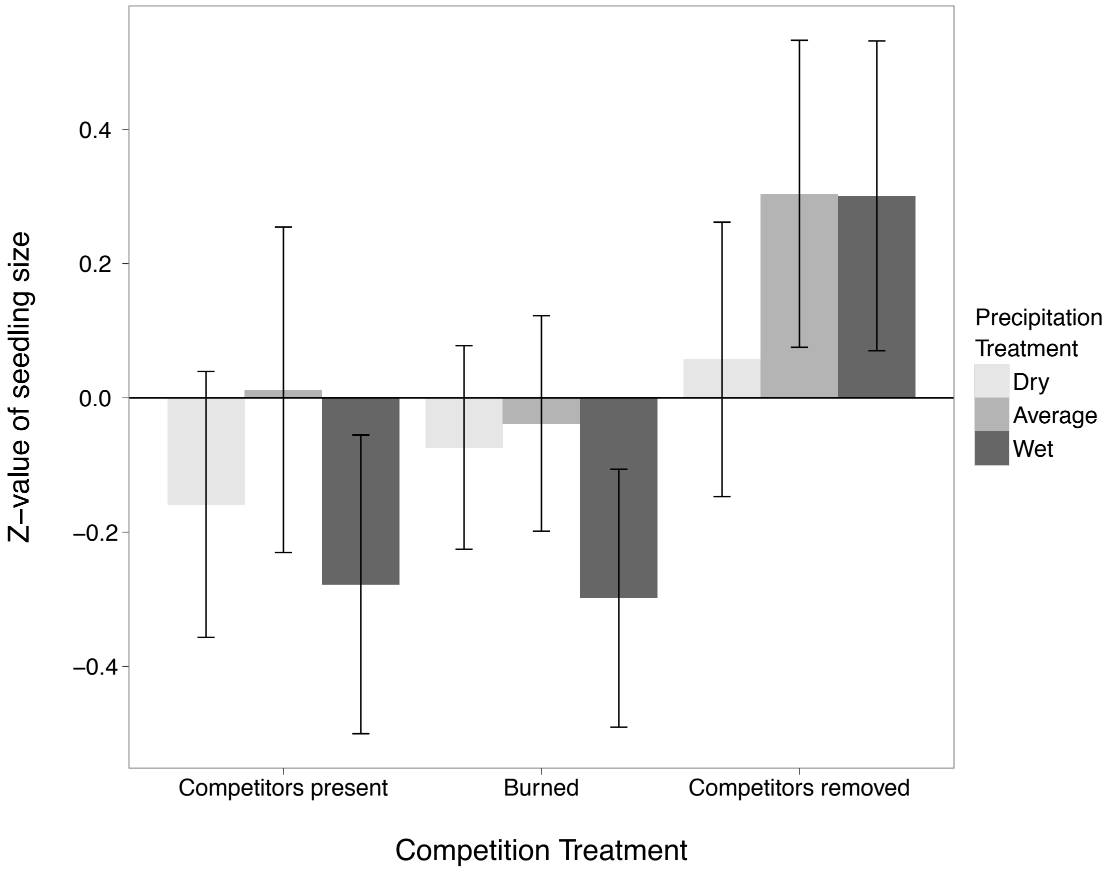

Figure 2.6 - Mean Z-values of seedling size per species per plot across the treatment combinations. Error bars represent 95% confidence intervals.

	No phylogeny			**With phylogeny**		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
(Intercept)	-0.219	(-0.504, 0.085)	0.150	-0.214	(-0.532, 0.091)	0.180
$\text{Comp}_{\text{Removed}}$	**0.421**	**(0.077, 0.792)**	**0.021**	**0.417**	**(0.06, 0.78)**	**0.023**
$\text{Comp}_{\text{Present}}$	-0.012	(-0.375, 0.364)	0.942	-0.014	(-0.38, 0.353)	0.930
$\text{Precip}_{\text{Dry}}$	-0.144	(-0.601, 0.333)	0.550	-0.139	(-0.609, 0.324)	0.561
$\text{Precip}_{\text{Wet}}$	-0.269	(-0.682, 0.138)	0.206	-0.268	(-0.705, 0.116)	0.217
$\text{Comp}_{\text{Removed}}\text{:Precip}_{\text{Dry}}$	0.043	(-0.532, 0.605)	0.880	0.043	(-0.504, 0.637)	0.877
$\text{Comp}_{\text{Present}}\text{:Precip}_{\text{Dry}}$	0.054	(-0.525, 0.627)	0.862	0.052	(-0.477, 0.681)	0.864
$\text{Comp}_{\text{Removed}}\text{:Precip}_{\text{Wet}}$	0.263	(-0.266, 0.802)	0.326	0.271	(-0.277, 0.797)	0.314
$\text{Comp}_{\text{Present}}\text{:Precip}_{\text{Wet}}$	-0.001	(-0.532, 0.495)	0.995	0.004	(-0.546, 0.497)	0.997

Table 2.3 - Model four results showing mean parameter estimates and 95% credible intervals (CI) describing the relationship between the mean z-values of seedling size per species and the treatment effects with and without phylogeny. Random effects in this model are species and seed weight. DIC values for the models with no phylogeny and with phylogeny are -82.65299 and -74.65299 respectively. Significant relationships are bolded.

	No phylogeny			**With phylogeny**		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
(Intercept)	-0.223	(-0.721, 0.275)	0.377	-0.214	(-0.707, 0.309)	0.410
Occupancy	0.013	(-0.879, 0.939)	0.980	0.013	(-0.879, 0.905)	0.969
$\text{Comp}_{\text{Removed}}$	0.213	(-0.411, 0.863)	0.502	0.215	(-0.423, 0.847)	0.514
$\text{Comp}_{\text{Present}}$	0.226	(-0.454, 0.918)	0.522	0.228	(-0.456, 0.892)	0.499
$\text{Precip}_{\text{Dry}}$	0.142	(-0.768, 0.986)	0.752	0.147	(-0.726, 1.042)	0.746
$\text{Precip}_{\text{Wet}}$	-0.270	(-1.119, 0.525)	0.529	-0.254	(-1.049, 0.584)	0.564
$\text{Occupancy:Comp}_{\text{Removed}}$	0.367	(-0.717, 1.462)	0.510	0.349	(-0.8, 1.387)	0.520
$\text{Occupancy:Comp}_{\text{Present}}$	-0.427	(-1.601, 0.726)	0.468	-0.426	(-1.545, 0.725)	0.467
$\text{Occupancy:Precip}_{\text{Dry}}$	-0.468	(-1.799, 0.951)	0.506	-0.466	(-1.941, 0.792)	0.492
$\text{Occupancy:Precip}_{\text{Wet}}$	-0.012	(-1.571, 1.578)	0.985	-0.031	(-1.598, 1.498)	0.971
$\text{Comp}_{\text{Removed}}\text{:Precip}_{\text{Dry}}$	-0.099	(-1.183, 0.945)	0.858	-0.113	(-1.172, 0.984)	0.834
$\text{Comp}_{\text{Present}}\text{:Precip}_{\text{Dry}}$	-0.502	(-1.587, 0.645)	0.381	-0.510	(-1.63, 0.598)	0.371
$\text{Comp}_{\text{Removed}}\text{:Precip}_{\text{Wet}}$	0.029	(-1.022, 1.051)	0.950	0.018	(-1.023, 1.068)	0.980
$\text{Comp}_{\text{Present}}\text{:Precip}_{\text{Wet}}$	-0.101	(-1.191, 0.966)	0.849	-0.115	(-1.201, 0.924)	0.816
$\text{Occupancy:Comp}_{\text{Removed}}\text{:Precip}_{\text{Dry}}$	0.236	(-1.387, 1.994)	0.784	0.264	(-1.407, 1.979)	0.765
$\text{Occupancy:Comp}_{\text{Present}}\text{:Precip}_{\text{Dry}}$	0.945	(-0.874, 2.656)	0.306	0.953	(-0.918, 2.688)	0.298
$\text{Occupancy:Comp}_{\text{Removed}}\text{:Precip}_{\text{Wet}}$	0.564	(-1.366, 2.395)	0.568	0.594	(-1.23, 2.545)	0.528
$\text{Occupancy:Comp}_{\text{Present}}\text{:Precip}_{\text{Wet}}$	0.192	(-1.698, 2.018)	0.828	0.214	(-1.734, 1.954)	0.806

Table 2.4 – Model five results showing mean parameter estimates and 95% credible intervals (CI) describing the relationship between mean Z-values of seedling size per species and regional occupancy and treatment effects with and without phylogeny. Random effects in this model are species and seed weight. DIC values for the models with no phylogeny and with phylogeny are -70.59529and -65.58518 respectively. Significant relationships are bolded.

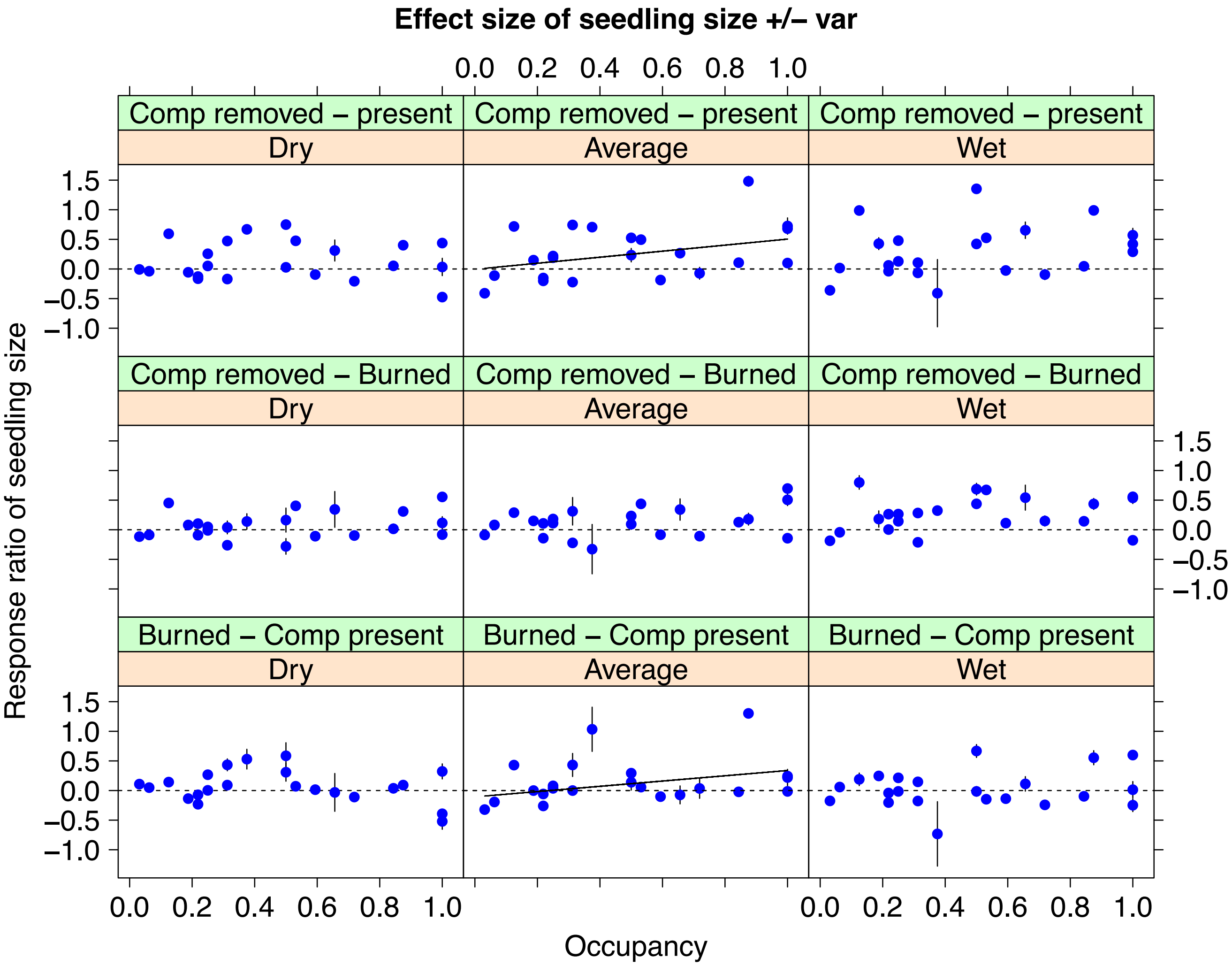

Figure 2.7 – The effect of regional occupancy on the log response ratio of seedling size between competition treatment comparisons within each factor of precipitation. Points with error bars represent means and variances for each species. Lines represent significant relationships from model six (Supplemental Table S2.4).

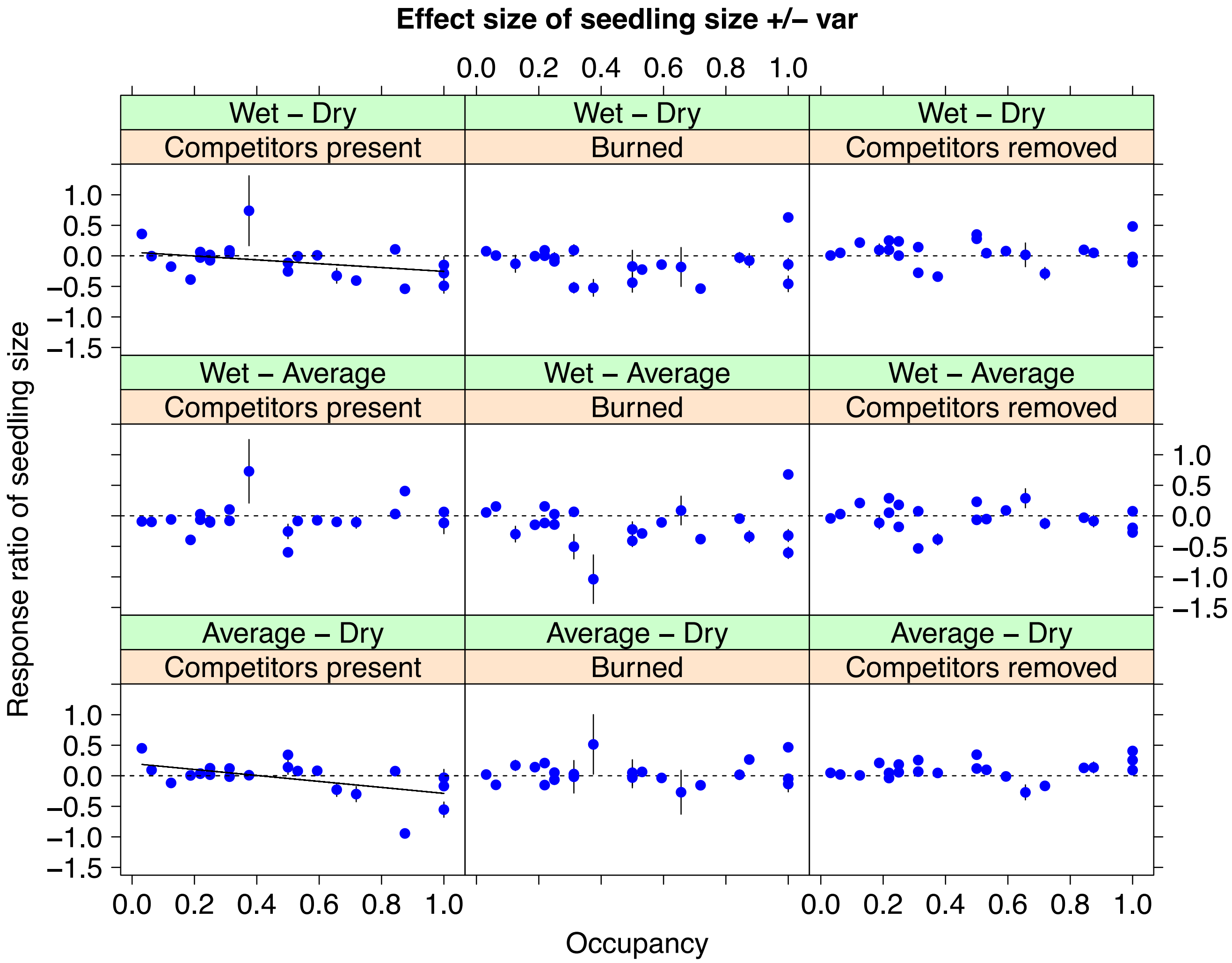

Figure 2.8 - The effect of regional occupancy on the log response ratio of seedling size between precipitation treatment comparisons within each factor of competition. Points with error bars represent means and variances for each species. Lines represent significant relationships from model six (Supplemental Table S2.5).

Works Cited

Adler, P.B., J. HilleRisLambers, J.M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95-104.

Aplet, G. H., and R. D. Laven. 1993. Relative performance of four Hawaiian shrubby plants (asteraceae) under greenhouse conditions with implications for rarity. Biological Conservation 65:15-21.

Bakker, J., P. Poschlod, R. J. Strykstra, R. M. Bekker, and K. Thompson. 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45:461-490.

Belsky, A. J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. Journal of Vegetation Science 3:187-200.

Bennett, J. R., and S. Mathews. 2006. Phylogeny of the parasitic plant family Orobanchaceae inferred from phytochrome A. American Journal of Botany 93:1039-1051.

Bevill, R. L., and S. M. Louda. 1999. Comparisons of related rare and common species in the study of plant rarity. Conservation Biology 13:493-498.

Brudvig, L., C. Mabry, and L. Mottl. 2011. Dispersal, not understory light competition, limits restoration of Iowa woodland understory herbs. Restoration Ecology 19:24-31.

Bräuchler, C., H. Meimberg, and G. Heubl. 2010. Molecular phylogeny of Menthinae (Lamiaceae, Nepetoideae, Mentheae)--Taxonomy, biogeography and conflicts. Molecular Phylogenetics and Evolution 55:501-23. Elsevier Inc.

Burke, M., and J. Grime. 1996. An experimental study of plant community invasibility. Ecology 77:776-790.

Burrows, F. M. 1975. Wind-borne seed and fruit movement. New Phytologist 75:405-418.

Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. The American Naturalist 170:128-42.

Clark, J., and E. Macklin. 1998. Stages and Spatial Scales of Recruitment Limitation in Southern Appalachian Forests. Ecological Monographs 68:213-235.

Clevinger, J. A., and J. L. Panero. 2000. Phylogenetic analysis of Silphium and subtribe Engelmanniinae (Asteraceae: Heliantheae) based on ITS and ETS sequence data. American Journal of Botany 87:565-572.

Damschen, E. I., L. a Brudvig, N. M. Haddad, D. J. Levey, J. L. Orrock, and J. J. Tewksbury. 2008. The movement ecology and dynamics of plant communities in fragmented landscapes. Proceedings of the National Academy of Sciences of the United States of America 105:19078-83.

Davies, T. J., T. G. Barraclough, M. W. Chase, P. S. Soltis, D. E. Soltis, and V. Savolainen. 2004. Darwin's abominable mystery: Insights from a supertree of the angiosperms. Proceedings of the National Academy of Sciences of the United States of America 101:1904-1909.

Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421-428.

Doyle, J. J., J. A. Chappill, C. D. Bailey, and T. Kajita. 2000. Towards a comprehensive phylogeny of legumes: Evidence from rbcL sequences and non-molecular data. Advances in Legume Systematics:1-20.

Drake, J., K. Drury, D. Lodge, A. Blukacz, N. Yan, and G. Dwyer. 2006. Demographic stochasticity, environmental variability, and windows of invasion risk for Bythotrephes longimanus in North America. Biological Invasions 8:843-861.

Duncan, R. S., C. Anderson, H. Sellers, and E. Robbins. 2008. The effect of fire reintroduction on endemic and rare plants of a southeastern glade ecosystem. Restoration Ecology 16:39-49.

Ehrlén, J., and O. Eriksson. 2000. Dispersal limitation and patch occupancy in forest herbs. Ecology 81:1667-1674.

Ejrnæs, R., H. Bruun, and B. Graae. 2006. Community assembly in experimental grasslands: suitable environment or timely arrival? Ecology 87:1225-1233.

Eriksson, O., and J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91:360-364.

Foster, B., and K. Gross. 1997. Partitioning the Effects of Plant Biomass and Litter on Andropogon Gerardi in Old-Field Vegetation. Ecology 78:2091-2104.

Foster, B., and D. Tilman. 2003. Seed limitation and the regulation of community structure in oak savanna grassland. Journal of Ecology 91:999-1007.

Gaston, K. J. 1994. Rarity. Chapman and Hall, London, UK.

Godefroid, S., C. Piazza, G. Rossi, S. Buord, A.-D. Stevens, R. Aguraiuja, C. Cowell, C. W. Weekley, G. Vogg, J. M. Iriondo, I. Johnson, B. Dixon, D. Gordon, S. Magnanon, B. Valentin, K. Bjureke, R. Koopman, M. Vicens, M. Virevaire, and T. Vanderborght. 2011. How successful are plant species reintroductions? Biological Conservation 144:672-682. Elsevier Ltd.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, UK.

Guyette, R. P., and E. A. McGinnes. 1982. Fire history of an Ozark glade in Missouri. Transactions of the Missouri Academy of Science 16:85-93.

Hadfield, J. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. Journal of Statistical Software 33.

Harper, J. L. 1977. Population biology of plants. Academic Press., London, UK.

Huddleston, R., and T. Young. 2004. Spacing and competition between planted grass plugs and preexisting perennial grasses in a restoration site in Oregon. Restoration Ecology 12:546-551.

Jansen, R. K., H. J. Michaels, and J. D. Palmer. 1991. Phylogeny and character evolution in the Asteraceae based on chloroplast DNA restriction site mapping. Systematic Botany 16:98-115.

Kajita, T., H. Ohashi, Y. Tateishi, C. D. Bailey, and J. J. Doyle. 2001. rbcL and legume phylogeny , with particular reference to Phaseoleae , Millettieae , and allies. Systematic Botany 26:515-536.

Karis, P. O. 1995. Cladistics of the subtribe Ambrosiinae (Asteraceae: Heliantheae). Systematic Botany 20:40-54.

Kolb, A., and M. Diekmann. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. Conservation Biology 19:929-938.

Lauenroth, W., O. Sala, and D. Coffin. 1994. The importance of soil water in the recruitment of Bouteloua gracilis in the shortgrass steppe. Ecological Applications 4:741-749.

Lavergne, S., E. Garnier, and M. Debussche. 2003. Do rock endemic and widespread plant species differ under the Leaf–Height–Seed plant ecology strategy scheme? Ecology Letters 6:398-404.

Lawless, P. J., J. M. Baskin, and C. C. Baskin. 2006. Xeric limestone prairies of Eastern United States : Review and synthesis. Botanical Review 72:235-272.

Leach, M. K., and T. J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. Science 273:1555-1558.

Lloyd, K., W. Lee, and J. Wilson. 2002. Competitive abilities of rare and common plants: comparisons using Acaena (Rosaceae) and Chionochloa (Poaceae) from New Zealand. Conservation Biology 16:975-985.

Mabry, C. M. 2004. The number and size of seeds in common versus restricted woodland herbaceous species in central Iowa, USA. Oikos 107:497-504.

Martin, L. M., and B. J. Wilsey. 2006. Assessing grassland restoration success: relative roles of seed additions and native ungulate activities. Journal of Applied Ecology 43:1098-1109.

McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Dornelas, B. J. Enquist, J. L. Green, F. He, A. H. Hurlbert, A. E. Magurran, P. a Marquet, B. a Maurer, A. Ostling, C. U. Soykan, K. I. Ugland, and E. P. White. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology letters 10:995-1015.

Moles, A. T., and M. Westoby. 2002. Seed addition experiments are more likely to increase recruitment in larger-seeded species. Oikos 99:241-248.

Moore, K. a, and S. C. Elmendorf. 2006. Propagule vs. niche limitation: untangling the mechanisms behind plant species' distributions. Ecology Letters 9:797-804.

Munzbergova, Z. 2004. Effect of spatial scale on factors limiting species distributions in dry grassland fragments. Journal of Ecology 92:854-867.

Murray, B. R., P. H. Thrall, a. M. Gill, and A. B. Nicotra. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. Austral Ecology 27:291-310.

Myers, J. A. 2010. Ecological assembly of high-diversity plant communities: dispersal, competition, and environmental filtering in longleaf pine savannas. Louisiana State University.

Myers, J. A., and K. E. Harms. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. Ecology Letters 12:1250-60.

Nathan, R., and H. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15:278-285.

Nelson, P. 2005. The Terrestrial Natural Communities of Missouri. Missouri Natural Areas Committee, Jefferson City, MO.

Noyes, R. D., and L. H. Riesberg. 1999. ITS sequence data support a single origin for North American Astereae (Asteraceae) and reflect deep geographic divisions in Aster S.L. American Journal of Botany 86:398-412.

Old, S. 1969. Microclimate, fire, and plant production in an Illinois prairie. Ecological Monographs 39:355-384.

Olmstead, R. G., C. W. DePamphilis, A. D. Wolfe, N. D. Young, W. J. Elisons, and P. A. Reeves. 2001. Disintegration of the Scrophulariaceae. American Journal of Botany 88:348-361.

Potvin, M. 1993. Establishment of native grass seedlings along a topographic/moisture gradient in the Nebraska Sandhills. American Midland Naturalist 130:248-261.

Primack, R. B., and S. L. Miao. 1992. Dispersal can limit local plant distribution. Conservation Biology 6:513-519.

Pywell, R. F., J. M. Bullock, K. J. Walker, S. J. Coulson, S. J. Gregory, and M. J. Stevenson. 2004. Facilitating grassland diversification using the hemiparasitic plant Rhinanthus minor. Journal of Applied Ecology 41:880-887.

R Development Core. 2012. R: A language and environment for statistical computing. Vienna, Austria.

Rabinowitz, D., J. Rapp, and P. M. Dixon. 1984. Competitive abilities of sparse grass species: means of persistence or cause of abundance. Ecology 65:1144-1154.

Raftery, A. E., and S. M. Lewis. 1992. One Long Run with Diagnostics : Comment : Chain Strategies for Markov Implementation. Statistical Science 7:493-497.

Schmidt, G. J., and E. E. Schilling. 2000. Phylogeny and biogeography of Eupatorium (Asteraceae: Eupatorieae) based on nuclear ITS sequence data. American Journal of Botany 87:716-726.

Schäferhoff, B., A. Fleischmann, E. Fischer, D. C. Albach, T. Borsch, G. Heubl, and K. F. Müller. 2010. Towards resolving Lamiales relationships: insights from rapidly evolving chloroplast sequences. BMC evolutionary biology 10:352.

Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications 13:575-592.

Seddon, P. 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. Restoration Ecology 18:796-802.

Selliah, S., and L. Brouillet. 2008. Molecular phylogeny of the North American eurybioid asters (Asteraceae, Astereae) based on the nuclear ribosomal internal and external transcribed spacersThis paper is one of a selection of papers published in the Special Issue on Systematics Research. Botany 86:901-915.

Sluis, W. 2002. Patterns of species richness and composition in re-created grassland. Restoration Ecology 10:677-684.

Snyder, K. M., J. M. Baskin, and C. C. Baskin. 1994. Comparative ecology of the narrow endemic Echinacea tennesseensis and two geographically widespread congeners: relative competitive ability and growth characteristics. International Journal of Plant Sciences 155:57-65.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81-92.

Trager, J. 2011. Personal communication. Shaw Nature Preserve, Gray Summit, MO, USA.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225-238.

Urbatsch, L. E., B. G. Baldwin, and M. J. Donoghue. 2000. Phylogeny of the coneflowers and relatives (Heliantheae: Asteraceae) based on nuclear rDNA internal transcribed spacer (ITS) sequences and chlorplast DNA restriction site data. Systematic Botany 25:539-565.

Vaezi, J., and L. Brouillet. 2009. Phylogenetic relationships among diploid species of Symphyotrichum (Asteraceae: Astereae) based on two nuclear markers, ITS and GAPDH. Molecular Phylogenetics and Evolution 51:540-53. Elsevier Inc.

Wagstaff, S. J., L. Hickerson, R. Spangler, P. A. Reeves, and R. G. Olmstead. 1998. Phylogeny in Labiatae s . 1 ., inferred from cpDNA sequences. Plant Sytematics and Evolution 209:265-274.

Walck, J., J. Baskin, and C. C. Baskin. 1999. Relative competitive abilities and growth characteristics of a narrowly endemic and a geographically widespread Solidago species (Asteraceae). American Journal of Botany 86:820-828.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098-2100.

Webb, C. O., and M. J. Donoghue. 2005. Phylomatic. http://phylodiversity.net/phylomatic/

Welsh, A. H., R. B. Cunningham, C. F. Donnelly, and D. B. Lindenmayer. 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. Ecological Modelling 88:297-308.

Werner, P. 1977. Colonization success of a “biennial” plant species: experimental field studies of species cohabitation and replacement. Ecology 58:840-849.

Wikström, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms: calibrating the family tree. Proceedings. Biological sciences / The Royal Society 268:2211-20.

Williams, P. R., R. a. Congdon, A. C. Grice, and P. J. Clarke. 2005. Germinable soil seed banks in a tropical savanna: seasonal dynamics and effects of fire. Austral Ecology 30:79-90.

Wojciechowski, M. F., M. Lavin, and M. J. Sanderson. 2004. A phylogeny of legumes (Leguminosae) based on analysis of the plastid matK gene reolves many well-supported subclades within the family. American Journal of Botany 91:1846-1862.

Wortley, A. H., P. J. Rudall, D. J. Harris, and R. W. Scotland. 2005. How much data are needed to resolve a difficult phylogeny?: case study in Lamiales. Systematic Biology 54:697-709.

Wurdack, K. J., and C. C. Davis. 2009. Malpighiales phylogenetics: Gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. American Journal of Botany 96:1551-70.

Yatskievych, G. 2006. Steyermark's Flora of Missouri. Missouri Botanical Garden Press, St. Louis, MO.

Zimmermann, J., S. I. Higgins, V. Grimm, J. Hoffmann, T. Münkemüller, and A. Linstädter. 2008. Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability. Journal of Ecology 96:1033-1044.

Zobel, M., M. Otsus, J. Liira, M. Moora, T. Mols, S. Ecology, and N. Dec. 2000. Is Small-Scale Species Richness Limited by Seed Availability or Microsite Availability? Ecology 81:3274-3282.

ZunZun.com. 2012. Online Curve and Surface Fitting. http://zunzun.com/

Chapter 3

Strategies for plant reintroductions: a meta-analysis of population establishment

Abstract

Plant propagule introductions and reintroductions are a commonly employed tool to aid in species conservation, yet literature reviews indicate that the vast majority of introduced populations fail to establish, and often for unknown reasons. Factors implicated in failed introductions include poor site conditions, environmental variation, lack of habitat management, and too few propagule introductions. However, there is a lack of understanding of the relative importance of these factors for contributing to population establishment. To examine this issue, I compiled published matrix population models and used demographic modeling to examine the relative importance of overall site conditions, environmental stochasticity, the number of introduction events given constant propagule number (i.e., a single large versus several small introductions) and the role of introducing propagules in a favorable environment for seedling recruitment (i.e., making the first introduction coincide with a "good" year for seedling vital rates versus a randomly selected year) for affecting long-term population establishment. Simulation results indicated that both greater site suitability (as measured by mean population growth rate) and environmental stochasticity (as measured by the standard deviation of population growth rate) were positively related to final population size. This may be in part due to correlations within our dataset between the mean and standard deviation in population growth rate. Simulation results also indicated that the effect of introducing propagules during a favorable environment for seedling recruitment was much greater on long-term population establishment than manipulations of propagule pressure. These results have important implications for management such as emphasizing the necessity of proper site selection, habitat preparation, and active site management during the early stages of plant reintroductions.

Introduction

Broad issue

Propagule introductions are often an essential component of rare species conservation strategies to overcome propagule limitation due to poor dispersal, low propagule availability, and habitat fragmentation and isolation (Primack and Miao 1992, Akeroyd and Jackson 1995, Montalvo et al. 1997, Ehrlén and Eriksson 2000, Myers and Harms 2009, Brudvig et al. 2011). Unfortunately, several recent reviews have shown that the vast majority of propagule reintroduction projects tend to fail (Williamson and Fitter 1996, Godefroid et al. 2011), and in many cases the reasons for failure remain unknown or poorly understood. Factors proposed to explain these previous failures include unsuitable restoration sites, lack of habitat management, and low propagule pressure (Bottin et al. 2007, Menges 2008, Godefroid et al. 2011). It is unclear how much each of these factors and their interactions contribute to population establishment. There is a need to improve our understanding of the dynamics of reintroduced populations and use this knowledge to make recommendations for these species, since seeds of rare species are often limiting (Guerrant et al. 2004, Godefroid et al. 2011). Further, a better understanding of why some populations establish and others fail when propagules arrive would contribute to a better basic understanding of population ecology and community assembly. Below, I describe how factors such as environmental conditions, management of site conditions and introduction methodology may interact to affect the success of propagule introductions.

Environmental conditions

If propagules are introduced to a site, one of the most basic factors limiting population establishment is the suitability of the habitat for contributing to positive population growth (Peterson and Vieglais 2001, Sutherst 2003, Drake et al. 2006). Optimal site selection by land managers is important, since more suitable conditions should lead to higher population growth rates and thus higher probabilities of establishment success. However, selecting sites for reintroductions can be challenging, especially for rare species, which often have narrow habitat requirements (Guerrant et al. 2004).

Propagule arrival and suitable site conditions do not guarantee population establishment since stochastic fluctuations in environmental conditions can lead to population declines in some years. Environmental stochasticity is particularly threatening immediately following propagule introduction since population sizes are small in number and primarily composed of seedlings, which are more vulnerable than older life history stages. Sites with highly favorable conditions and low environmental variation are expected to give populations the best chance for establishment and growth (Drake and Lodge 2004).

Habitat management and recruitment windows

If restoration ecologists understand the environmental variation of a habitat and the environmental drivers of population growth, then they might be able to capitalize on this knowledge to add propagules during a "recruitment window", thereby increasing the likelihood of population establishment (Davis and Grime 2000, Davis and Pelsor 2001, Drake et al. 2006). In cases where land managers have control over factors influencing seedling recruitment, such as controlled burning or mowing, or knowledge of periodic events, such as El Niño events or herbivore outbreaks, seed introductions should be timed to coincide with years that foster high seedling vital rates. A recent review by Godefroid et al. (2011) demonstrated that propagule introductions during years with some sort of habitat management (e.g., burning, irrigation, protection from herbivores, etc.) tended to have significantly higher rates of establishment success than those that did not. There is likely an interaction between the environmental conditions and the use of a recruitment window; populations that are associated with highly variable environments that have lower mean environmental suitability should benefit most from the recruitment window.

Number of introductions

While it is well established that increasing the total number of propagules increases establishment success (Lockwood et al. 2005, Drake and Lodge 2006, Simberloff 2009, Godefroid et al. 2011), less understood is the role of spreading out propagule introduction events across time. For example, introducing a set quantity of propagules across several years evenly rather than one single introduction (i.e., several small versus a single large introduction) might increase establishment success by minimizing the likelihood that all propagules are introduced during years with poor environmental conditions. However, we lack an understanding of the relative benefits of increasing the number of propagules versus the number of introduction events (Munzbergova et al. 2005, Simberloff 2009). The effect of increasing the number of introduction events, while keeping total number of propagules introduced constant, should benefit populations that are associated with highly variable environments that have lower mean environmental suitability.

Objectives

In order to examine the relative roles of environmental conditions, management of site conditions and introduction methodology, and their potential interactions on the success of propagule introductions, I employed a population projection modeling approach using previously published matrix population models from 161 populations of 49 plant species. This is a useful method for evaluating the role of environment and propagule introduction methods on the likelihood of population establishment because matrix population models incorporate information about the stage-structured demography of the species throughout its life cycle (i.e., the presence or absence of a seedbank, and time to reproductive age). For many species, demographic data has been collected for multiple years, representing multiple environmental conditions, and thus population projections through time included the effects of natural environmental variation. Such stochastic modeling can be used to project final population sizes after a set time period (e.g., 50 years) under different propagule introduction strategies.

The goal of this study is to quantify how the mean and variation in the environmental conditions, propagule introduction techniques (introducing propagules in one or in multiple years) and utilizing a recruitment window are likely to interactively influence population establishment success. Because species life histories, vital rates and population dynamics may be influenced by evolutionary history, I conducted my analyses in a phylogenetically controlled modeling framework (Burns et al. 2010). First, to determine the role of environmental suitability and stochasticity on population establishment, I examined the relationship of the mean and variation in population growth with final population size using one introduction event in a randomly selected year. Second, to determine the role of introducing propagules in a favorable environment for seedling recruitment, I examined the effect size (in terms of final population size) of introducing propagules during the best year for seedling vital rates (i.e., using a recruitment window) versus a randomly selected year. Third, to determine the role of multiple introductions on population establishment, I examined the effect of spreading out the introduction of a set number of propagules across different numbers of years. Finally, I examined the interactions between the different introduction methods as well as their interactions with mean and variation in population growth rate.

Methods

Study and species selection

To model the effect of population growth rate, variation in population growth rate, and different introduction strategies on population establishment, I combined a previously compiled database of plant demography studies collected by Ramula and colleagues (Burns et al. 2010, Buckley et al. 2010) with more recently published studies. I located studies by searching the ISI Web of Knowledge database for articles between 2008 and 2012 that included "demography", "plant", "populations", and "projection", "matrix", or "matrices" in the title, topic, abstract, or key words. I restricted my analyses to studies on native species (as defined by the author of each study) that contained at least three transition matrices per population to assess the effect of variation in population growth rates on population establishment. This compilation of demographic studies included 49 species with a total of 161 different populations (Supplemental Table S3.1). All of these demographic studies were on natural populations, since few reintroduced populations have multiple matrices that include information on all life stages (but see Bell et al. 2003, Colas et al. 2008). By using these natural populations, I am assuming that the introduced populations will experience similar mean and variance in vital rates as those of the established natural populations. Further, the natural populations provide appropriate data to ask the synthetic questions for this study about how introduction methods are expected to influence establishment success in species with different mean and variance in their population growth rates.

Phylogeny

To include the potential influence of evolutionary history on population dynamics, I constructed a phylogeny for these species (Supplemental Figure S3.1) using Phylomatic (Webb and Donoghue 2005), which uses the Angiosperm phylogeny built by Davies et al. (2004). I assigned branch lengths to the phylogeny with the BLADJ function in Phylocom, version 4.2 (Webb et al. 2008), using estimates of molecular and fossil dates from Wikström et al. (2001). I treated nodes with less than 80% support as soft polytomies.

Simulations

I modeled the effects of different introduction strategies on the final population size of each population with a custom built program in R using the following methods: First, I simulated environmental stochasticity by randomly selecting with equal probability one matrix within a study population for each of 50 years, and I kept this string of matrices constant for each iteration of the subsequent manipulations. This constituted the randomly selected first year for introduction treatment. I manipulated the number of introduction events by introducing a total of 100 seedlings into the population vectors in the first year, or evenly divided the seedlings between the first two, three, four or five years (i.e., one introduction represents 100 seedlings in year one, whereas 5 introductions represent 20 seedlings in each of the first five years). I chose to introduce 100 individuals because this is the median number of seedling transplants typically introduced from a meta-analysis of reintroductions (Godefroid et al. 2011). Individuals were introduced into the seedling stage or smallest, non-seedbank stage as defined by the author of each study. I manipulated the presence of a recruitment window by using the best matrix for the first year. The best matrix for a population is the one with the highest survivorship for the seedling stage class. I then projected population size for 50 years using standard matrix modeling methods (Morris and Doak 2002) by multiplying the population vector from the previous year by the matrix. I repeated this procedure for a total of 1000 iterations per population by selecting a new string of matrices for each iteration. This method allowed some declining populations to reach population sizes <1 which is unrealistic for natural populations, but comparisons of treatment effect sizes are still meaningful.

Calculation of variables

For each population, I calculated the population growth rate (log λ) for each matrix using methods from Caswell (2006). Positive log lambdas represent increasing population growth rates while negative log lambdas represent declining population growth rates. I calculated the mean deterministic population growth rate ($\log \lambda_{mean}$) by calculating the dominant eigenvalue of each matrix and then averaging these values. I also calculated the standard deviation of growth rates ($\sigma \log \lambda$) across these matrices. Final population size ($\log N_{t50}$) was calculated for each introduction strategy as the log transformed mean population size from the 1000 simulations.

To quantify the effect of the recruitment window, I calculated the effect size of final population size ($\log N_{t50}$) between the recruitment window and a randomly chosen first year using the log response ratio for each of the five different numbers of introduction events. To quantify the effect of the number of introduction events, I calculated the effect size of final population sizes between five introduction events and one introduction event using the log response ratio for both the randomly selected and best first introduction year.

Analyses

To assess the effect of population growth rate and introduction method on population establishment (as measured by projected population size in 50 years), I used a Bayesian approach with Markov chain Monte Carlo simulation (MCMC) using the MCMCglmm package (Hadfield 2010) implemented in R, version 2.15.0 (R Development Core 2012). This approach allowed me to incorporate multiple random effects of species and population, incorporate phylogenetic relatedness between species, and compare model fit using DIC scores.

To examine the effect of environmental suitability and stochasticity on the success of propagule introduction (as measured by projected population size in 50 years), I analyzed the effect of population growth rate ($\log \lambda_{mean}$) and standard deviation in population growth rate ($\sigma \log \lambda$) on final population size ($\log N_{t50}$) with one introduction in a randomly selected first year. Second, to test whether providing a recruitment window improved final population size, I analyzed the log response ratio of final population size between the best versus randomly selected year for seedling vital rates for each of the number of propagule introductions. Third, to test whether spreading propagule introductions over time improved final population size, I analyzed the log response ratio of final population size between five introductions and one introduction in response to whether or not the first introduction was during the best or a randomly selected year for seedling vital rates. Fourth, to examine the influence that mean and variation in population growth rates associated with an environment has on the importance of different types of introduction methodology, I analyzed the effect of population growth rate ($\log \lambda_{mean}$) and variation in population growth rate ($\sigma \log \lambda$) on the effect size of providing a recruitment window and the effect size of spreading out the number of introductions on final population size. For the analysis on the effect size of the recruitment window, I limited the analysis to only one introduction event. For the analysis on the effect size of the number of introductions, I conducted separate analyses for both the randomly selected first year and the best matrix for seedling vital rates. In all models, I included species and population as random effects.

I found a positive correlation between mean population growth rate and the standard deviation of population growth rate using Pearson's correlation coefficient and Spearman's rank correlation coefficient (see Results). In addition, I found outliers using methods from Hoeting et al. (1996) in the Bayesian Model Averaging (BMA) package version 3.15.1 (Raftery et al. 2012). To determine the effect of these outliers on model results, I reran the first set of models (final population size versus mean and standard deviation of population growth rates) after removing outliers. Finally, to determine if the standard deviation of population growth may have been particularly influenced by population growth rates that were extremely low (catastrophes) or high (bonanzas), I analyzed the effect of the minimum (multiplied by -1 to make negative population growth rates comparable to positive population growth rates) and maximum population growth rates on the standard deviation of population growth rate.

I ran each model for 600,000 MCMC iterations with a burn-in period of 100,000 iterations and a thinning interval of 100. This resulted in 5000 posterior distribution samples for each model parameter estimate. Flat, uninformative priors with a low degree of belief were used for all parameters in all analyses (mean=1 and variance=0.002) and normal error distributions were assumed for response variables. Convergence was checked using visual inspection of MCMC iterations and the Raftery-Lewis diagnostic (Raftery and Lewis 1992). Model estimates for all parameters represent means with 95% lower and upper credible intervals from the posterior distributions. P-values represent the proportion of tests in which a model parameter is greater or less than zero standardized by the total number of iterations.

I ran all analyses with and without the inclusion of phylogenetic structure by including species relatedness as a phylogenetic covariance matrix. Model fits were compared using DIC values. In all cases, either there was no difference in model fit between models with and without phylogeny (ΔDIC < 5), or models without phylogeny were preferred (ΔDIC > 5). As such, I only discuss results from models without phylogeny.

Results

Effect of mean and variation in population growth rate on final population size

Population growth rate and variation in population growth rate were significantly related to final population size (Figure 3.1 and Table 3.1). As predicted, population growth rate ($\log \lambda_{mean}$) was positively related to final population size ($\log N_{t50}$) (P-value < 0.001). Contrary to my predictions, variation in population growth rate ($\sigma \log \lambda$) was also positively related to final population size (P-value < 0.001). Analysis of correlations between the mean and standard deviation of population growth rate indicate that while there is evidence of a positive correlation (Pearson's r=0.200, P=0.011), this relationship is likely due to outliers since the Spearman's rank order correlation, which is non-parametric and less sensitive to outliers, is not significant (Spearman's ρ= 0.006, P= 0.937). However, the relationships between population growth rate and variation in population growth rate on final population size were qualitatively similar when outliers were removed (results not presented). Furthermore, I found that standard deviation in population growth rate was not more strongly influenced by population growth rates that were particularly low (catastrophes) or high (bonanzas) (Figure 3.2). Model results demonstrated that the minimum (multiplied by -1 to make slope positive) and maximum population growth rates were both associated with the standard deviation of growth rate (P<0.001), but the slopes were not significantly different.

Effect sizes of introduction methods

Analysis of the manipulation of recruitment conditions demonstrated that there was a large positive effect of creating a recruitment window (P<0.001; Figure 3.3; Table 3.2). On average, final population sizes after 50 years were approximately 45% larger between the best versus the randomly selected first year. However, this effect decreases as the number of propagule introductions increases (P<0.001).

Analysis of the number of propagule introductions indicated that introducing a fixed number of individuals across 5 years versus 1 year had no significant effect on final population size when the first year was randomly selected (Figure 3.3; Table 3.2). The effect of 5 introductions versus 1 introduction became significantly negative when the best matrix for seedling establishment was used for the first year (P<0.001).

Relationship between population growth rate and effect sizes

The effect sizes of introduction strategies on final population size depended on the mean and standard deviation of the growth rate of the population (Figure 3.4; Table 3.3). First, the effect size of selecting the best or randomly selecting a matrix in the first year was inversely related to mean population growth rates (P=0.002), but was not significantly related to the standard deviation of population growth rates. Second, the effect size of five versus one introductions within the randomly selected first year treatment and the best first year treatment were both inversely related to the mean and (P<0.001 and <0.001 respectively) and standard deviation of population growth rate (P=0.001 and 0.005 respectively).

Discussion

Effect of population growth rate on population size

As expected, populations that had higher average rates of population growth had higher projected population size in 50 years. If mean population growth rates are a reflection of the suitability of environmental conditions, it could be inferred that optimal site selection or management activities that focus on increasing long term environmental suitability should naturally lead to more successful population introductions. In a recent survey by Godefroid (2011), the second most often cited reason for reintroduction failure, after unknown factors, was incorrect site selection. This emphasizes the fact that without proper site selection, plant reintroductions will inevitably fail. When at all possible, great care should be taken to understand the biology of the species and its habitat requirements prior to reintroduction efforts to maximize the likelihood of successful population establishment. In my study, 61% of the populations had mean growth rates that indicated population decline based on the data collected in natural populations. This indicates that sites that allowed the establishment and growth of these natural populations at some point in the past are currently unsuitable or that they were censused during a stochastic period of temporary population decline. If this is indicative of the future challenges that restored populations will face, it suggests that habitat suitability is a moving target, and that it is important to restore as many populations as possible to give high probability of meta-population persistence.

Contrary to my expectations, increased variation in population growth rate was associated with increased projected population size. In most other studies, increased variation tends to decrease projected population size and the likelihood of successful establishment (e.g., Drake and Lodge 2004). My analyses also indicate that this relationship is unlikely to be due to outliers, significant correlations with mean population growth rates, or particularly high or low population growth rates (bonanzas and catastrophes). One alternative explanation for this result is that while there is limited evidence for a correlation between the mean and standard deviation in population growth rates, populations with low amounts of variation in growth rates are primarily declining populations. This may bias our analyses towards detecting a positive association between the standard deviation of population growth rates and final population size.

Effect sizes of introductions during a recruitment window

Creating a recruitment window for seedlings led to a 1.45 times larger projected population size. The magnitude of this effect is emphasized by the fact that manipulating only one year had such long-term consequences. This effect tended to decrease with the number of introductions, but this is not surprising since by design fewer seedlings are being introduced during that first best year for recruitment. These patterns suggest that whenever possible, land managers should focus their efforts on timing the early phases of propagule introductions to coincide with favorable recruitment environments such as heavily managed conditions. As evidenced by numerous experimental studies and reviews, this might include management activities such as removing competitors (Menges 2008), burning or irrigation (Zimmermann et al. 2008), or timing introductions to coincide with favorable weather patterns or biological cycles (Potvin 1993).

The effect size of the recruitment window was inversely related to mean population growth rate, and not related to variation in population growth rate. If mean population growth rates are a reflection of habitat suitability, it could be inferred that as overall environmental suitability increases, all matrices have reasonable seedling vital rates and the importance of choosing the best matrix for the first year decreases. In contrast, populations with low average growth rates may receive a relatively large benefit of a best first year that may allow them to increase in size temporarily. Thus, the importance of habitat management or the timing of introduction to coincide with recruitment windows may be most critical in less pristine habitats.

Effect size of the number of propagule introductions

Manipulations of the number of introduction events had no effect on final projected population size. Furthermore, this effect interacted with presence of a recruitment window such that increasing the number of introductions had a negative effect when the first year was manipulated to be favorable for seedling recruitment. As mentioned above, this is likely due to fewer seedlings being introduced during the best conditions for seedling recruitment. Thus, for a given number of propagules, these patterns argue for conducting fewer large rather than several small introductions through time, especially when land managers have some degree of control over the conditions for seedling recruitment. While few studies have examined the effect of the number of introduction events separately from the number of propagules introduced, other studies suggest that the number of introduction events may contribute to establishment success (reviewed in Simberloff 2009). For example, Veltman (1996) found that establishment for non-native bird species was highest when there were 10 or more introductions. However, these studies differ from ours in that they focus on the introduction of non-native species, in which those species are being introduced to multiple sites and from multiple source populations, which are likely to greatly increase the chances of population establishment success.

The effect size of the number of introductions tended to decrease with increasing means and variation in population growth rates. This relationship with mean population growth rate is likely caused by the fact that increasing the number of introductions delays the time it takes for the introduced propagues to reach a reproductive stage class and contribute numerically to population size through offspring production. For example, for populations that are increasing in size, greater numbers of propagule introductions will decrease the number of individuals initially available to contribute to population growth. Conversely, for declining populations, increasing the number of propagule introductions decreases the time over which introduced propagules have to die out. The cause for the positive relationship between the effect size of the number of introductions and the amount of variation in population growth rate is less clear. Based on population ecology theory (Tuljapurkar and Orzack 1980, Lande and Orzack 1988, Drake and Lodge 2004), I initially expected the opposite relationship – increasingly variable populations should benefit from a greater number of introduction events by bet hedging the probability of randomly catching a good year for seedling recruitment. The relationship I observed may be partially due to the fact that populations with low amounts of variation in population growth rate also happened to be declining.

Other factors that may affect population establishment

Several other species traits and introduction methods may influence the success of propagule introductions and should be explored in future studies. First, the age at first reproduction and generation time should tend to be inversely related to establishment success. Species that can reproduce shortly after recruitment will be able to more quickly create new propagules for recruitment. Second, the introduction of older life history stages such as seedlings or juveniles rather than seeds has been shown to increase the success of propagule introduction (Menges 2008, Godefroid et al. 2011). However, the effect size of introducing older propagules in comparison to habitat management and propagule pressure is not well understood. This effect size would be especially interesting to investigate because there is a significant increase in the cost and labor involved in introducing older plant life history stages. Despite this cost, it may be the best strategy for recruiting rare species since their seeds may be in limited supply (Guerrant and Kaye 2007, Menges 2008). Third, as evidenced by the pioneering work of Munzbergova et al. (2005), the spatial distribution of introductions may influence establishment success of entire meta-populations. This study employed a spatially explicit population modeling approach to assess the optimal meta-population reintroduction strategy by varying the number of habitats to which propagules were introduced and the number of seeds available. They found that as seed availability decreased, the introduction strategy that maximized total meta-population size tended to shift from introducting propagues to all potential introduction sites to introducting propagues to only a few of the largest sites.

Lack of phylogenetic signal

Including phylogenetic relatedness into my models always decreased model fit compared to models without phylogeny. This suggests that plant population growth rates and variation in growth rates are evolutionarily labile. While further resolution of the phylogenetic relationships between the species in this study may improve detectability of phylogenetic signal, previous studies have also found a similar lack of phylogenetic signal on life histories and plant vital rates (Burns et al. 2010, Buckley et al. 2010).

Model assumptions

The results of these models are contingent upon three key assumptions typical of population projection modeling. First, as discussed above, these models assume that natural, established populations and introduced populations will exhibit similar responses to manipulations of introduction methodology. Second, these models assume that population growth rates are independent of density and frequency (Adler 2007). In most cases, this is a reasonable assumption to make for negative density dependence since population sizes are small, at least initially. However, Allee effects may cause pollen limitation in newly introduced populations, but Allee effects are rarely incorporated into demographic models (but see Kirchner et al. 2006, Feldman and Morris 2011). Including Allee effects into our models would likely decrease final population size, particularly for multiple introductions. For example, increasing the number of propagule introductions along with decreasing the number of propagules introduced each year would likely decrease the number of individuals co-flowering, thereby reducing overall seed production if pollination and reproductive success is positively affected by flowering plant density (Wilcock and Neiland 2002). Third, these models assume that introduction of 100 seedlings is equally feasible for all species. This is not necessarily the case because some species are inherently difficult to transplant, especially if they have delicate root structures. Another way to interpret this assumption is that rather than transplanting 100 individuals, the propagule introduction introduces a sufficient number of seeds to produce 100 germinants. In this case, the number of seeds introduced will be highly species dependent due to differences in seed size, germination percentage, and environmental conditions (Moles and Westoby 2002).

Implications for management

My model results combined with previous research provide several practical recommendations for species conservation efforts that incorporate the creation of new populations through propagule introduction, reintroduction, or supplementation. First, optimal site selection that allows for positive population growth is critical because even the largest propagule introduction will eventually fail if habitat conditions are unsuitable. Observational and experimental studies should be undertaken to understand the habitat requirements of rare species so as to maximize the opportunity for habitat matching. Second, this study recommends that land managers focus their efforts on managing habitat conditions during propagule introduction or timing the introduction to coincide with favorable seedling recruitment environments rather than spreading out introduction events across numerous years. Third, as evidenced by the work of previous researchers (Lockwood et al. 2005, Robert et al. 2007, Godefroid et al. 2011) the number of propagules introduced should be maximized whenever possible. However, reviews of propagule introductions have shown that median introduction sizes are typically small in number: 830 seeds and 100 seedlings (Godefroid et al. 2011). These introduction sizes are relatively low compared to recommended introduction rates of 500-5000 individuals (Reed 2005, Godefroid et al. 2011). In situations when increasing propagule number is impractical or overly costly, such as for rare species, other introduction strategies that maximize success, such as introduction during favorable recruitment conditions, may be especially critical.

Conclusions

While establishing new populations for conservation may remain a costly and risky endeavor, this study provides several key recommendations on how to maximize the success of propagule introductions including optimal site selection, large propagule introductions, and habitat management and timing of propagule introduction to coincide with recruitment windows. In particular, this study argues for introducing propagules within suitable habitats in which the environment has been managed to create favorable recruitment environments over conducting multiple introductions. This is particularly important for rare species that may have extremely limited quantities of propagules. Future studies should be undertaken to experimentally verify the degree to which propagule pressure and habitat management interact to affect long-term success of population establishment.

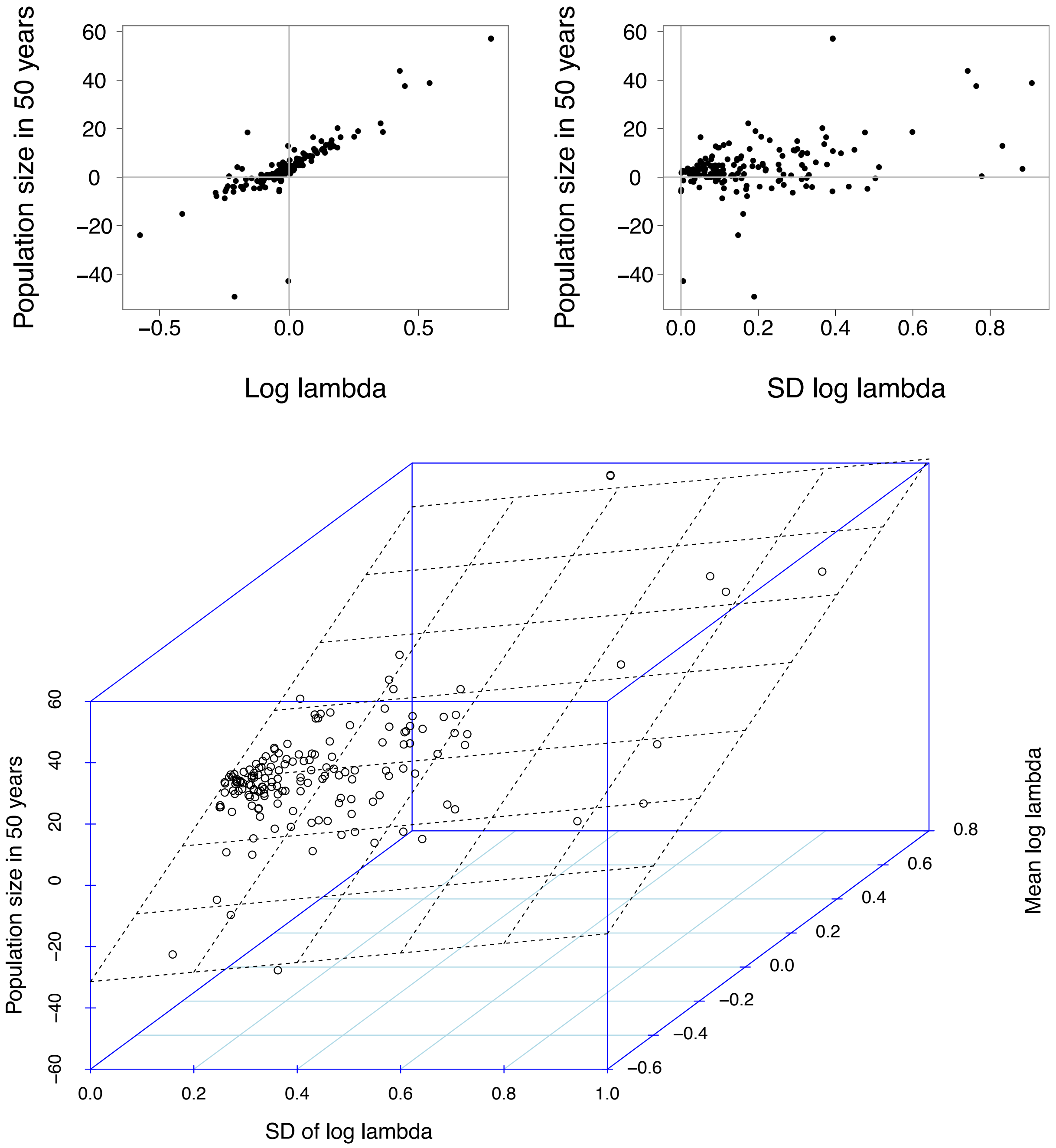

Figure 3.1 – Scatterplots of mean population growth (log λ_{mean}) and standard deviation of population growth rate (σ log λ) against final population size (log N_{t50}). The dashed plane in the bottom figure indicates results from the linear model.

	No phylogeny			With phylogeny		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
(Intercept)	**1.573**	**(0.169, 3.062)**	**0.032**	**1.605**	**(0.13, 3.162)**	**0.048**
Mean log lambda	**55.210**	**(50.008, 60.948)**	**<0.001**	**55.165**	**(50.015, 60.712)**	**<0.001**
SD log lambda	**15.450**	**(10.21, 20.975)**	**<0.001**	**15.473**	**(10.427, 20.334)**	**<0.001**
DIC	329.0259			334.9202		

Table 3.1 - Model one results showing mean parameter estimates and 95% credible intervals (CI) describing the relationship between final population size and the mean and standard deviation of population growth rates with and without phylogeny. Random effects in this model are species and population. DIC values for the models with no phylogeny and with phylogeny are 329.0259 and 334.9202 respectively. Significant relationships are bolded.

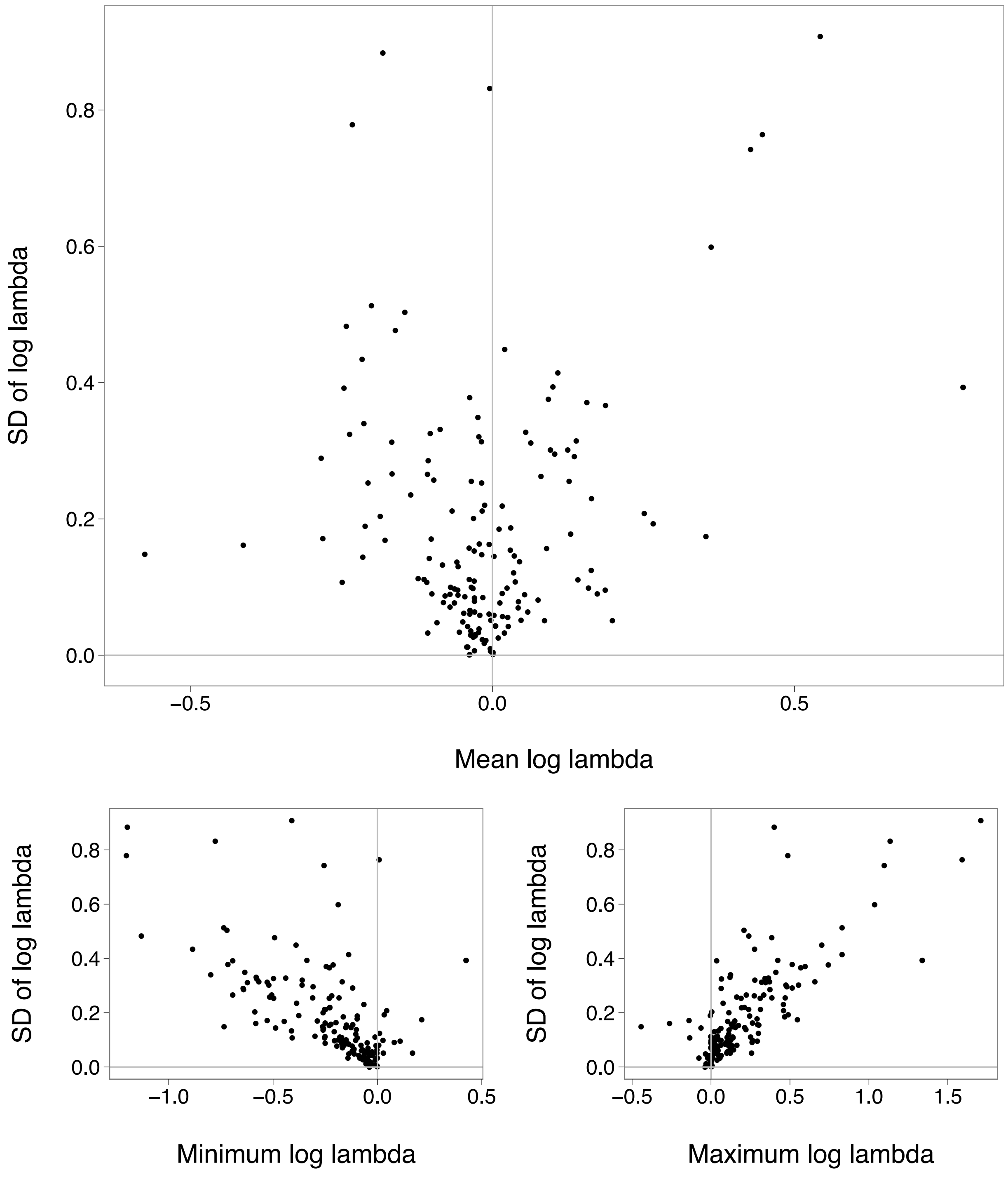

Figure 3.2 - Scatterplots of mean population growth (log λ_{mean}), minimum population growth rate(log λ_{min}), and maximum population growth rate (log λ_{max}),for each population against the standard deviation of population growth rate (σ log λ).

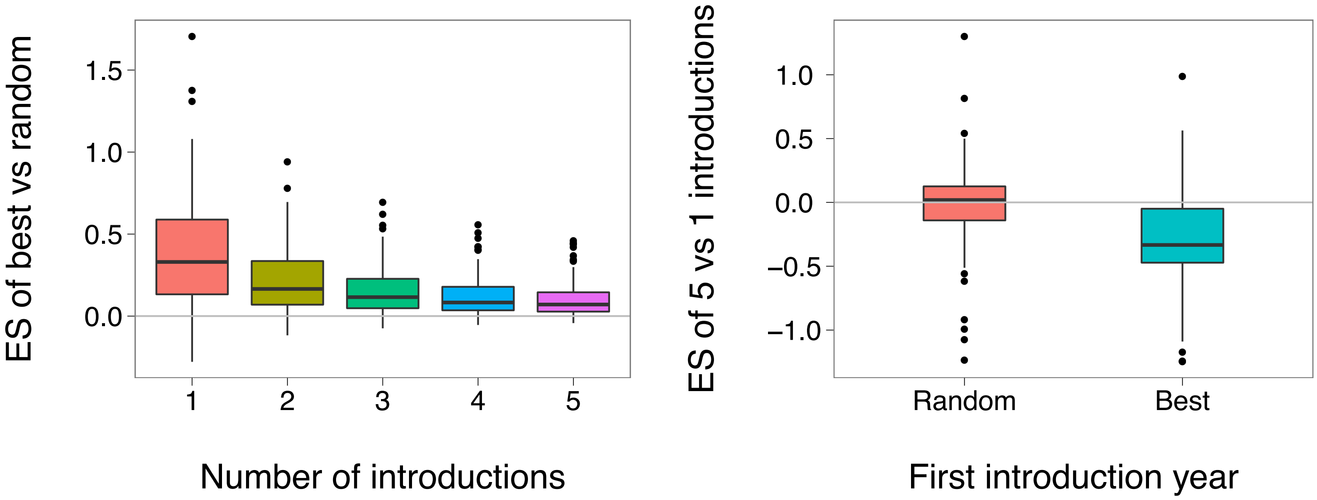

Figure 3.3 – Boxplots of introduction treatment effect sizes. The panel on the left indicates the log response ratio (ES) between final population sizes when the first year for propagule introduction used the matrix with the highest seedling vital rates versus a randomly selected year, and this is assessed across for each number of propagule introductions. The panel on the right indicates the log response ratio (ES) between final population sizes for five versus 1 introduction event, and this is assessed when the first introduction year is the matrix with the highest seedling vital rates and a randomly selected matrix. Horizontal bars indictate median values, box plots indicate the 25th and 75th percentiles, whiskers represent 1.5 times the inter quartile range (IQR), and dots represent outliers.

EFFECT SIZE OF BEST VS RANDOM FIRST YEAR

	No phylogeny			**With phylogeny**		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
ES of best vs random	**0.372**	**(0.331, 0.415)**	**<0.001**	**0.315**	**(0.184, 0.444)**	**<0.001**
Number of introductions	**-0.064**	**(-0.069, -0.058)**	**<0.001**	**-0.064**	**(-0.069, -0.059)**	**<0.001**
DIC	-1134.769			-1134.499		

EFFECT SIZE OF FIVE VS ONE INTRODUCTIONS

	No phylogeny			**With phylogeny**		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
ES for random	-0.019	(-0.083, 0.046)	0.541	0.043	(-0.143, 0.213)	0.629
ES for best	**-0.272**	**(-0.313, -0.234)**	**<0.001**	**-0.272**	**(-0.311, -0.232)**	**<0.001**
DIC	-67.66677			-66.52762		

Table 3.2 – Model two results showing mean parameter estimates and 95% credible intervals (CI) describing the relationship between introduction treatments with and without phylogeny. The top table indicates the effect of introducing propagules in the best matrix for seedling vital rates relative to a randomly selected matrix and then examines how this relationship relates to the number of introduction events. The bottom table indicates the effect of five versus one introduction event on final population size and then examines how this relationship relates to whether the first introduction event was for the best year for seedling vital rates or a randomly selected matrix. Random effects in this model are species and population. DIC values for the models with no phylogeny and with phylogeny are displayed below each table. Significant relationships are bolded.

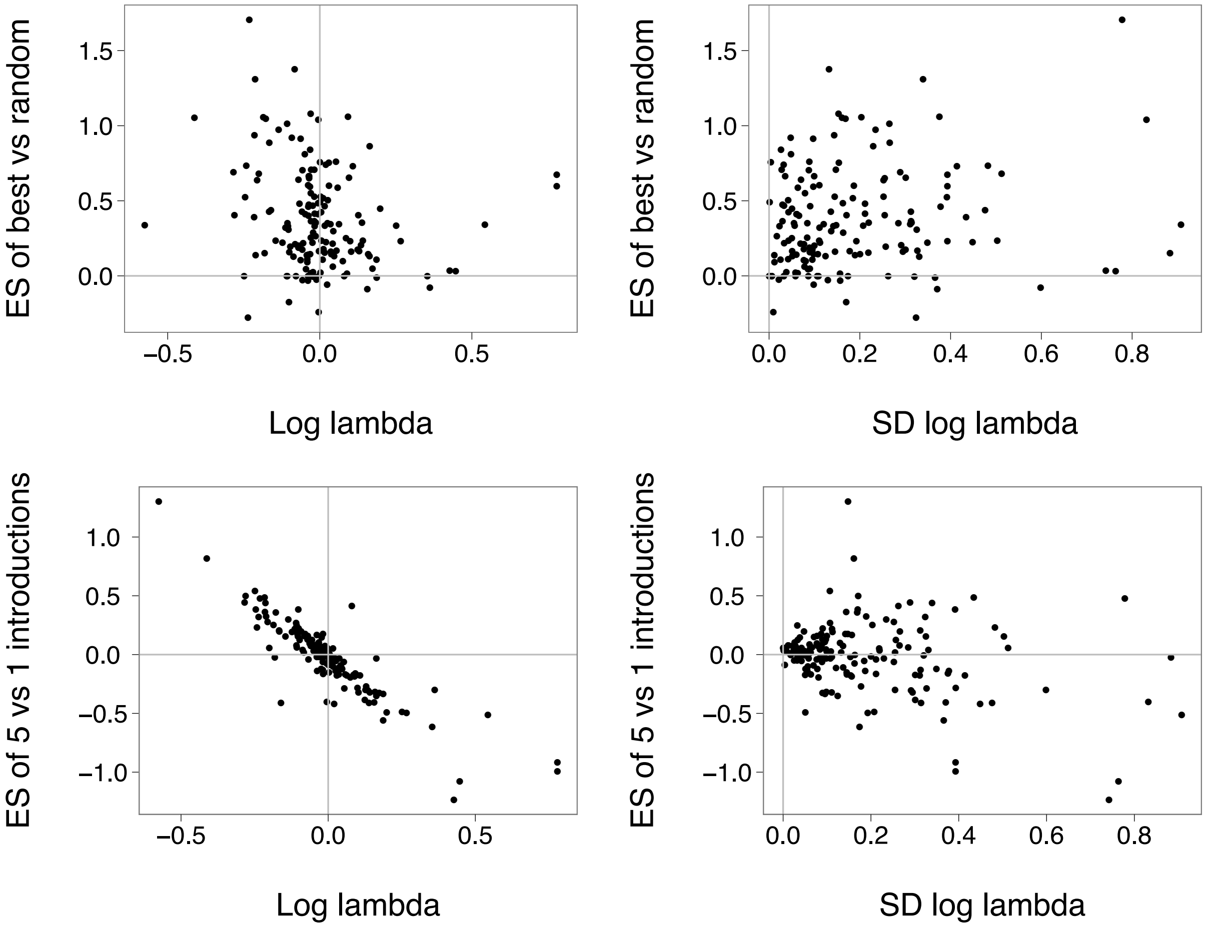

Figure 3.4 – Scatterplots of introduction treatment effect sizes relative to mean and standard deviation of population growth rate. Effect sizes (ES) of the best versus random first year are only displayed for 1 introduction. Effect sizes for 5 vs 1 introduction are only displayed for a randomly selected first matrix.

EFFECT SIZE OF BEST VS RANDOM FIRST YEAR WITH ONE INTRODUCTION

	No phylogeny			With phylogeny		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
(Intercept)	0.312	(0.223, 0.403)	<0.001	0.205	(-0.044, 0.446)	0.104
Mean log lambda	-0.484	(-0.794, -0.17)	0.002	-0.516	(-0.809, -0.211)	0.001
SD log lambda	0.235	(-0.075, 0.536)	0.135	0.232	(-0.083, 0.54)	0.150
DIC	-176.8324			-162.6744		

EFFECT SIZE OF FIVE VS ONE INTRODUCTIONS FOR A RANDOMLY SELECTED FIRST YEAR

	No phylogeny			With phylogeny		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
(Intercept)	0.014	(-0.019, 0.047)	0.402	0.014	(-0.036, 0.059)	0.534
Mean log lambda	-1.583	(-1.723, -1.453)	<0.001	-1.566	(-1.692, -1.428)	<0.001
SD log lambda	-0.216	(-0.34, -0.082)	0.001	-0.226	(-0.359, -0.104)	<0.001
DIC	-321.8374			-317.1156		

EFFECT SIZE OF FIVE VS ONE INTRODUCTIONS FOR THE BEST FIRST YEAR

	No phylogeny			With phylogeny		
Factor	**Parameter estimate**	**95% CI**	**P-value**	**Parameter estimate**	**95% CI**	**P-value**
(Intercept)	-0.220	(-0.292, -0.145)	<0.001	-0.143	(-0.328, 0.058)	0.146
Mean log lambda	-1.170	(-1.424, -0.93)	<0.001	-1.091	(-1.336, -0.851)	<0.001
SD log lambda	-0.356	(-0.607, -0.105)	0.005	-0.375	(-0.634, -0.13)	0.004
DIC	-214.1471			-209.5295		

Table 3.3 - Model three results showing mean parameter estimates and 95% credible intervals (CI) describing the relationship between treatment effect sizes and the mean and standard deviation of population growth rates with and without phylogeny. The top panel displays results from the model of the best versus a randomly selected first matrix with only one introduction. The bottom two panels display results from the models of the five versus one introduction when the first year is either randomly selected, or the best matrix respectively. Random effects in this model are species and population. DIC values for the models with no phylogeny and with phylogeny are displayed below each table. Significant relationships are bolded.

Works Cited

Adler, P.B., J. HilleRisLambers, J.M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95-104.

Akeroyd, J., and P. W. Jackson. 1995. A handbook for botanic gardens on the reintroduction of plants to the wild. Richmond (United Kingdom) : Botanic Gardens Conservation International.

Bell, T. J., M. L. Bowles, and A. K. Mceachern. 2003. Projecting the success of plant population restoration with viability analysis. Page *in* C. A. Brigham and M. W. Schwartz, editors. Population viability in plants: conservation, management, and modeling of rare plants. Springer.

Bottin, L., S. Le Cadre, A. Quilichini, P. Bardin, J. Moret, and N. Machon. 2007. Re-establishment trials in endangered plants: a review and the example of Arenaria grandiflora, a species on the brink of extinction in the Parisian region (France). Ecoscience 14:410-419. Centre d'etudes nordique, Universite Laval.

Brudvig, L., C. Mabry, and L. Mottl. 2011. Dispersal, not understory light competition, limits restoration of Iowa woodland understory herbs. Restoration Ecology 19:24-31.

Buckley, Y. M., S. Ramula, S. P. Blomberg, J. H. Burns, E. E. Crone, J. Ehrlén, T. M. Knight, J.-B. Pichancourt, H. Quested, and G. M. Wardle. 2010. Causes and consequences of variation in plant population growth rate: a synthesis of matrix population models in a phylogenetic context. Ecology Letters 13:1182-97.

Burns, J. H., S. P. Blomberg, E. E. Crone, J. Ehrlén, T. M. Knight, J.-B. Pichancourt, S. Ramula, G. M. Wardle, and Y. M. Buckley. 2010. Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. Journal of Ecology 98:334-344.

Caswell, H. 2006. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer Associates, Sunderland, MA.

Colas, B., F. Kirchner, M. Riba, I. Olivieri, A. Mignot, E. Imbert, C. Beltrame, D. Carbonell, and H. Fréville. 2008. Restoration demography: a 10-year demographic comparison between introduced and natural populations of endemic Centaurea corymbosa (Asteraceae). Journal of Applied Ecology 45:1468-1476.

Davies, T. J., T. G. Barraclough, M. W. Chase, P. S. Soltis, D. E. Soltis, and V. Savolainen. 2004. Darwin's abominable mystery: Insights from a supertree of the angiosperms. Proceedings of the National Academy of Sciences of the United States of America 101:1904-1909.

Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421-428.

Davis, M., and J. Grime. 2000. Fluctuating resources in plant communities: a general of invasibility theory. Journal of Ecology 88:528-534.

Drake, J., K. Drury, D. Lodge, A. Blukacz, N. Yan, and G. Dwyer. 2006. Demographic stochasticity, environmental variability, and windows of invasion risk for Bythotrephes longimanus in North America. Biological Invasions 8:843-861.

Drake, J., and D. M. Lodge. 2006. Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. Biological Invasions 8:365-375.

Drake, J. M., and D. M. Lodge. 2004. Effects of environmental variation on extinction and establishment. Ecology Letters 7:26-30.

Ehrlén, J., and O. Eriksson. 2000. Dispersal limitation and patch occupancy in forest herbs. Ecology 81:1667-1674.

Feldman, T. S., and W. F. Morris. 2011. Higher survival at low density counteracts lower fecundity to obviate Allee effects in a perennial plant. Journal of Ecology 99:1162-1170.

Godefroid, S., C. Piazza, G. Rossi, S. Buord, A.-D. Stevens, R. Aguraiuja, C. Cowell, C. W. Weekley, G. Vogg, J. M. Iriondo, I. Johnson, B. Dixon, D. Gordon, S. Magnanon, B. Valentin, K. Bjureke, R. Koopman, M. Vicens, M. Virevaire, and T. Vanderborght. 2011. How successful are plant species reintroductions? Biological Conservation 144:672-682. Elsevier Ltd.

Guerrant, E. O., K. Havens, and M. Maunder. 2004. Ex Situ Plant Conservation: Supporting Species Survival In The Wild (Google eBook). Page 504. Island Press.

Guerrant, E. O., and T. N. Kaye. 2007. Reintroduction of rare and endangered plants: common factors, questions and approaches. Australian Journal of Botany 55:362-370.

Hadfield, J. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. Journal of Statistical Software 33.

Hoeting, J., A. E. Raftery, and D. Madigan. 1996. A method for simultaneous variable selection and outlier identification in linear regression. Computational Statistics & Data Analysis 22:251-270.

Kirchner, F., A. Robert, and B. Colas. 2006. Modelling the dynamics of introduced populations in the narrow-endemic Centaurea corymbosa: a demo-genetic integration. Journal of Applied Ecology 43:1011-1021.

Lande, R., and S. Orzack. 1988. Extinction dynamics of age- structured populations in a fluctuating environment. Proceedings of the National Academy of Sciences of the United States of America 85:7418-7421.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20:223-8.

Menges, E. S. 2008. Restoration demography and genetics of plants: when is a translocation successful? Australian Journal of Botany 56:187-196.

Moles, A. T., and M. Westoby. 2002. Seed addition experiments are more likely to increase recruitment in larger-seeded species. Oikos 99:241-248.

Montalvo, A. M., S. L. Williams, K. J. Rice, S. L. Buchmann, C. Cory, S. N. Handel, G. P. Nabhan, R. Primack, and R. H. Robichaux. 1997. Restoration biology: a population biology perspective. Restoration Ecology 5:277-290.

Morris, W., and D. Doak. 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Sunderland, MA.

Munzbergova, Z., M. Milden, J. Ehrlen, and T. Herben. 2005. Population viability and reintroduction strategies: a spatially explicit landscape-level approach. Ecological Applications 15:1377-1386.

Myers, J. A, and K. E. Harms. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. Ecology Letters 12:1250-60.

Peterson, A., and D. Vieglais. 2001. Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. BioScience 51:363-371.

Potvin, M. 1993. Establishment of native grass seedlings along a topographic/moisture gradient in the Nebraska Sandhills. American Midland Naturalist 130:248-261.

Primack, R. B., and S. L. Miao. 1992. Dispersal can limit local plant distribution. Conservation Biology 6:513-519.

R Development Core. 2012. R: A language and environment for statistical computing. Vienna, Austria.

Raftery, A. E., and S. M. Lewis. 1992. One Long Run with Diagnostics : Comment : Chain Strategies for Markov Implementation. Statistical Science 7:493-497.

Raftery, A., J. Hoeting, C. Volinsky, I. Painter, and K. Y. Yeung. 2012. BMA package: Bayesian Model Averaging.

Reed, D. 2005. Relationship between population size and fitness. Conservation biology 19:563-568.

Robert, A., D. Couvet, and F. Sarrazin. 2007. Integration of demography and genetics in population restorations. Ecoscience 14:463-471. Centre d’etudes nordique, Universite Laval.

Simberloff, D. 2009. The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and 40:81-102.

Sutherst, R. W. 2003. Prediction of species geographical ranges. Journal of Biogeography 30:805-816.

Tuljapurkar, S., and S. Orzack. 1980. Population dynamics in variable environments: long-run growth rates and extinction. Theoretical Population Biology 18:314-342.

Veltman, C., S. Nee, and M. J. Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. American Naturalist 147:542-557.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098-2100.

Webb, C. O., and M. J. Donoghue. 2005. Phylomatic.

Wikström, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms: calibrating the family tree. Proceedings. Biological sciences / The Royal Society 268:2211-20.

Wilcock, C., and R. Neiland. 2002. Pollination failure in plants: why it happens and when it matters. Trends in plant science 7:270-7.

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology 77:1661-1666.

Zimmermann, J., S. I. Higgins, V. Grimm, J. Hoffmann, T. Münkemüller, and A. Linstädter. 2008. Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability. Journal of Ecology 96:1033-1044.

Dissertation Conclusion

The overarching goal of this dissertation was to examine potential mechanisms contributing to the relative rarity or regional occupancy of plant species in a restored habitat as well as provide recommendations for optimal reintroduction strategies. To these ends, I employed an observational study to examine traits associated with regional distribution, an experimental approach to examine potential factors limiting recruitment, and a population modeling approach to examine the importance of site conditions and method of introduction for contributing to population establishment success.

In Chapter One, to examine how niche breadth, persistence traits and dispersal traits may be associated with the local abundance and regional occupancy of species in a restored habitat, I conducted a regional survey of plant communities occurring within restored Ozark glade habitats in Missouri, USA. To control for the effect of evolutionary history on species traits, I incorporated phylogenetic relationships within the framework of generalized estimating equations to examine the relationship of species traits with local abundance and occupancy. Results from this analysis suggest that numerous plant traits may have been important for influencing species distributions in this restored xeric habitat including habitat specialization of open canopy environments, long-lived perennial or clonal life history strategies, short plant height which may be adaptive in xeric environments, and unassisted modes of dispersal. These results have several important implications for restoration and for understanding how species traits are associated with distribution. First, this analysis suggests that trait associations with species distribution may not be entirely generalizable between mesic and xeric habitats. In contrast to mesic habitats, I find that habitat specialization, short plant height and unassisted modes of dispersal are positively associated with abundance and occupancy. Habitat specialization and short plant height may have been vital for allowing species to persist and re-establish populations in the intensely xeric conditions in this restored habitat. Furthermore, unassisted modes of dispersal may have allowed species to maintain the majority of their propagules and establish large populations post-restoration within these small and isolated habitats. Second, this study suggests that restoration activities in this habitat have been highly successful at restoring site conditions since habitat specialists tend to be more abundant than generalists. Third, this suggests that introduction of propagules are likely to be successful at establishing new populations of species of conservation concern such as regionally rare habitat specialists. Indeed, assisted colonization may be necessary to overcome propagule limitation in this restored habitat due to the isolation between remaining glade patches.

In Chapter Two, to experimentally test whether the establishment of rare and widespread species differs in terms of propagule limitation, stress tolerance, and/or competitive ability, I seeded 32 rare and widespread species into a restored glade. I then experimentally manipulated the competitive environment and the amount of precipitation in a fully factorial design. To analyze the effect of the experimental treatments and regional occupancy on seedling recruitment and growth, I utilized a Bayesian approach with Markov chain Monte Carlo simulation that controlled for evolutionary relationships between species. The results from these models suggest that propagule limitation, rather than abiotic or biotic conditions, is the dominant limiting force for species distributions within this restored xeric habitat. Furthermore, there was little evidence to support my predictions that rare and widespread species differ in terms of recruitment limiting factors. While seedling recruitment increased from burning, competitor removal, and increased precipitation, all species tended to respond similarly regardless of regional occupancy. These results are surprising as classic ecological theory predicts that rare and widespread species should differ in terms of factors limiting their recruitment. This study also provides several important recommendations for restoration ecology and the future of restored glades. Given that rare species distributions appear to be primarily limited by propagule availability, land managers should consider assisted colonization as a management strategy for restoring species distributions. Since many restored habitats are highly isolated, natural colonization events are likely to be extremely rare, especially in the short term. In this setting, propagule introductions may be necessary to overcome propagule limitation for rare species. To maximize the success of propagule introductions, land managers should make every effort to increase opportunities for seedling establishment such as by conducting controlled burns. Alternatively, if assisted colonization is overly costly or undesirable, land managers should consider prioritizing conservation and restoration efforts on degraded habitats that contain species of conservation concern. This may increase the opportunity for natural dispersal events of rare species.

In Chapter Three, to examine how environmental suitability and stochasticity, management of site conditions, and number of introductions may interact to affect the success of propagule introductions, I employed a demographic modeling approach by collecting previously published matrix population models for native plant species. I simulated propagule introductions by introducing seedlings into the population vector, incorporated environmental variation by randomly selecting matrices for each year, and assessed the projected population size in 50 years. I assessed the effect of introducing propagules during favorable conditions for recruitment by either selecting the best matrix for seedling vital rates or a selecting a random matrix in the first year. I assessed the effect of the number of propagule introductions by spreading out a set number of propagules across multiple years. To analyze the effect of site conditions and introduction methodology on final population size, I utilized a Bayesian approach with Markov chain Monte Carlo simulation in a phylogenetically controlled framework. The results from this study indicate that overall site suitability and variation (as assessed by mean and standard deviation in population growth rates) are both positively related to final population size. While the former result was expected, the latter may be due to correlations between the mean and standard deviation in population growth rate within our dataset. This study also demonstrates that introducing seedlings during a favorable "recruitment window" has a much greater effect on the success of propagule introductions than do multiple introductions. Together, these results provide several important recommendations for restoration ecology. First, these results emphasize the importance of selecting suitable habitats for conducting propagule introductions since suboptimal sites are predisposed to failure. Second, these results emphasize the importance of creating favorable conditions for seedling recruitment during propagule introduction rather than conducting multiple introductions.

In all, this dissertation contributes to a broader understanding of factors limiting species distributions and suggests several strategies for their conservation and restoration. In particular, this study emphasizes the pervasive force that propagule limitation has played in limiting species distributions within a restored habitat. Propagule limitation is likely to play a critical role in many other habitats and contexts besides glade, especially given current rates of habitat destruction, isolation, and degradation as well as rapid global climate change. To overcome propagule limitation, assisted colonization may be necessary to increase rare native species distributions, increase local species richness, and preserve current levels of biodiversity. Propagule introductions are already suggested tools for conservation of at least one third of threatened and endangered species in the U.S. and this figure is only likely to increase in the future. Given this need for propagule introductions, this study recommends that land managers focus on optimal site selection and creating suitable habitat conditions for recruitment over increasing the number of propagule introduction events. Future research efforts should focus on understanding the degree to which propagule limitation is a generalizable limiting force in other restored habitats, especially for rare species. Furthermore, future propagule introductions should follow pilot studies that assess species habitat requirements as well as the factors most likely to contribute to recruitment and successful population establishment. Propagule introductions are likely to remain a risky and costly measure for species conservation, but hopefully the results from this dissertation will aid in maximizing the success of future conservation and restoration efforts.

Appendix A – Supplemental Material for Chapter 1

Site name	Latitude	Longitude
Blue Springs Creek Conservation Area	38.11415	-91.18835
Burnt Mill Cave Conservation Area	38.06290	-92.99352
Danville Conservation Area	38.86119	-91.51920
Danville Conservation Area	38.87364	-91.50631
Fiery Fork Conservation Area	38.08117	-92.93483
Ha Ha Tonka State Park	37.97995	-92.77014
Ha Ha Tonka State Park	37.97501	-92.76748
Indian Trail Conservation Area	37.71615	-91.38173
Johnson's Shut-Ins State Park	37.52480	-90.85500
Lake of the Ozarks State Park	38.05810	-92.58097
Lake of the Ozarks State Park	38.11397	-92.67113
Meramec State Park	38.19399	-91.11431
Meramec State Park	38.19427	-91.10798
Onondaga State Park	38.06231	-91.23460
Onondaga State Park	38.06251	-91.23722
Pea Ridge Conservation Area	38.06944	-90.99228
Private property[1]	38.5	-90.6
Private property[1]	38.4	-90.9
Private property[1]	38.4	-90.8
Private property[1]	38.4	-90.8
Private property[1]	37.1	-91.3
Private property[1]	38.1	-90.9
Reform Conservation Area	38.76830	-91.83476
Rocky Creek Conservation Area	37.08064	-91.37764
Shaw Nature Reserve	38.45671	-90.82879
Spring Creek Gap Conservation Area	38.14911	-91.79824
Spring Creek Gap Conservation Area	38.14681	-91.79581
St. Francois State Park	37.96944	-90.52881
St. Joe State Park	37.82503	-90.53287
Tyson Research Center	38.50769	-90.58628
Valley View Glades Natural Area	38.26441	-90.62172
Victoria Glades Conservation Area	38.20441	-90.55463

Table S1.1. List of glades surveyed with location info in decimal degrees. [1]Locations for glades on private property are fuzzed to the nearest tenth of a decimal degree.

Family	Species name	Occupancy	Abundance	Habitats	Light range	Life history	Height (cm)	Mean light	Dispersal	1000 Seed weight (g)
Scrophulariaceae	*Agalinis tenuifolia*	0.03	0.64	7	10	S	60	5.71	A	0.048
Liliaceae	*Allium stellatum*	0.31	0.08	4	7	C	45	6.50	U	1.890
Asteraceae	*Ambrosia artemisifolia*	0.19	0.02	18	8	S	120	7.72	A	3.990
Fabaceae	*Amorpha canescens*	0.66	0.09	9	6	NCP	90	8.00	A	2.000
Fabaceae	*Amphicarpa bracteata*	0.44	0.17	7	9	S	200	4.14	U	27.090
Ranunculaceae	*Anemone virginiana*	0.06	0.01	2	7	C	75	7.00	A	1.130
Apocynaceae	*Apocynum cannabinum*	0.56	0.03	17	10	C	100	6.82	A	1.100
Brassicaceae	*Arabis canadensis*	0.06	0.02	4	7	S	90	7.50	A	0.339
Asteraceae	*Arnoglossum plantagineum*	0.03	0.04	8	6	NCP	160	7.75	A	4.200
Apocynaceae	*Asclepias tuberosa*	0.19	0.02	8	6	NCP	90	8.00	A	6.800
Apocynaceae	*Asclepias verticillata*	0.56	0.05	8	9	NCP	60	7.13	A	2.200
Apocynaceae	*Asclepias viridiflora*	1.00	0.09	6	6	NCP	90	8.33	A	4.600
Apocynaceae	*Asclepias viridis*	0.19	0.01	4	3	NCP	60	9.00	A	6.620
Fabaceae	*Baptisia bracteata*	0.06	0.05	7	7	NCP	75	7.57	U	11.500
Lamiaceae	*Blephilia ciliata*	0.31	0.05	7	8	C	60	5.00	A	0.071
Scrophulariaceae	*Buchnera americana*	0.06	0.12	2	1	S	60	10.00	A	0.020
Fabaceae	*Cassia chamaecrista*	0.25	0.06	9	7	S	75	7.56	U	8.400
Fabaceae	*Cassia marilandica*	0.03	0.04	13	10	NCP	200	6.31	U	21.700
Scrophulariaceae	*Castilleja coccinea*	0.47	0.14	7	7	S	45	7.57	A	0.042
Asteraceae	*Cirsium altissimum*	0.13	0.04	9	10	S	250	6.67	A	4.650
Ranunculaceae	*Clematis fremontii*	0.09	0.12	1	1	NCP	45	10.00	U	12.853
Santalaceae	*Comandra umbellata*	0.44	0.18	5	9	C	25	6.80	A	89.122
Asteraceae	*Conyza canadensis*	0.06	0.05	11	7	S	250	8.09	A	0.070
Asteraceae	*Coreopsis lanceolata*	0.50	0.30	6	7	C	60	8.33	A	1.300
Asteraceae	*Coreopsis palmata*	0.47	0.10	8	6	C	90	7.88	A	1.990
Euphorbiaceae	*Croton monanthogynus*	1.00	0.42	5	3	S	40	9.20	U	5.660
Fabaceae	*Dalea purpurea*	1.00	0.24	9	6	NCP	90	7.78	U	3.200
Fabaceae	*Desmanthus illinoensis*	0.09	0.06	8	7	NCP	150	7.25	U	6.000
Fabaceae	*Desmodium obtusum*	0.03	0.02	7	9	NCP	105	7.29	A	2.537
Rubiaceae	*Diodia teres*	0.03	0.04	11	7	S	35	7.91	U	6.800
Primulaceae	*Dodecatheon meadia*	0.25	0.04	8	9	C	26	6.88	A	0.230
Asteraceae	*Echinacea paradoxa*	0.16	0.46	4	6	NCP	150	8.25	U	5.670

Family	Species name	Occupancy	Abundance	Habitats	Light range	Life history	Height (cm)	Mean light	Dispersal	1000 Seed weight (g)
Asteraceae	*Echinacea simulatat*	0.84	0.38	7	6	NCP	120	7.14	U	5.660
Asteraceae	*Erigeron strigosus*	0.41	0.06	10	7	S	70	7.70	A	0.070
Apiaceae	*Eryngium yuccifolium*	0.03	0.01	4	6	NCP	150	7.75	U	3.820
Asteraceae	*Eupatorium altissimum*	0.50	0.03	14	7	C	200	8.00	A	1.810
Asteraceae	*Eupatorium coelestinum*	0.03	0.01	10	10	C	100	6.70	A	0.081
Euphorbiaceae	*Euphorbia corollata*	0.81	0.28	6	7	C	100	7.83	A	3.790
Euphorbiaceae	*Euphorbia dentata*	0.41	0.13	6	6	S	60	8.17	U	5.400
Euphorbiaceae	*Euphorbia maculata*	0.28	0.11	10	7	S	45	7.20	U	0.230
Convolvulaceae	*Evolvulus nuttallianus*	0.19	0.30	3	6	NCP	15	7.00	U	4.950
Rosaceae	*Fragaria virginiana*	0.13	0.08	9	6	C	16	8.11	A	0.460
Rubiaceae	*Galium aparine*	0.13	0.04	17	10	S	100	7.00	A	8.900
Verbenaceae	*Glandularia canadensis*	0.47	0.06	8	7	NCP	45	6.88	U	0.817
Asteraceae	*Grindelia lanceolata*	0.06	0.01	8	7	NCP	150	7.75	U	0.700
Rubiaceae	*Hedyotis nigricans*	0.97	0.83	10	7	NCP	40	7.90	U	0.250
Asteraceae	*Helianthus hirsutus*	0.75	0.08	12	9	C	200	6.92	U	1.890
Asteraceae	*Helianthus occidentalis*	0.13	0.10	8	6	C	100	7.75	U	2.600
Boraginaceae	*Heliotropium tenellum*	0.94	0.43	2	1	S	35	10.00	U	1.543
Clusiaceae	*Hypericum sphaerocarpum*	0.56	0.33	7	7	C	70	7.29	U	0.710
Lamiaceae	*Isanthus brachiatus*	0.25	0.08	5	7	S	30	8.00	U	2.050
Asteraceae	*Kuhnia eupatorioides*	0.47	0.04	3	6	NCP	80	7.00	A	0.940
Fabaceae	*Lespedeza capitata*	0.34	0.04	11	7	NCP	120	7.55	A	2.900
Fabaceae	*Lespedeza hirta*	0.13	0.05	9	6	NCP	90	7.89	A	3.229
Asteraceae	*Liatris aspera*	0.56	0.17	10	7	C	180	7.50	A	2.100
Asteraceae	*Liatris cylindracea*	0.72	0.44	6	5	C	60	8.00	A	3.260
Linaceae	*Linum sulcatum*	0.75	0.11	3	7	S	70	7.00	U	0.675
Boraginaceae	*Lithospermum canescens*	0.72	0.09	12	9	NCP	40	6.92	U	2.817
Boraginaceae	*Lithospermum incisum*	0.03	0.10	7	4	NCP	40	8.57	U	12.620
Campanulaceae	*Lobelia spicata*	0.66	0.07	11	7	NCP	80	7.36	A	0.031
Malvaceae	*Malvastrum hispidum*	0.06	0.11	6	7	S	140	7.50	U	4.910
Asparagaceae	*Manfreda virginica*	0.22	0.12	2	7	NCP	240	7.00	U	7.159
Boraginaceae	*Mertensia virginica*	0.03	0.01	6	6	NCP	70	3.50	U	2.923
Nyctaginaceae	*Mirabilis nyctaginea*	0.25	0.11	6	7	NCP	120	7.00	U	5.000
Lamiaceae	*Monarda bradburiana*	0.06	0.03	8	8	C	50	5.75	A	0.810

Family	Species name	Occupancy	Abundance	Habitats	Light range	Life history	Height (cm)	Mean light	Dispersal	1000 Seed weight (g)
Lamiaceae	*Monarda fistulosa*	0.50	0.04	9	7	C	120	7.33	A	0.400
Onagraceae	*Oenothera macrocarpa*	0.53	0.17	6	7	NCP	60	8.33	A	5.130
Boraginaceae	*Onosmodium molle*	0.13	0.01	10	10	NCP	120	7.00	U	22.200
Cactaceae	*Opuntia humifusa*	0.16	0.02	8	6	C	8	8.13	A	29.990
Asteraceae	*Parthenium integrifolium*	0.25	0.14	8	6	C	100	7.63	U	3.080
Scrophulariaceae	*Pedicularis canadensis*	0.16	0.11	5	7	NCP	30	6.60	U	0.865
Scrophulariaceae	*Penstemon pallidus*	0.28	0.03	5	7	NCP	75	7.60	A	0.110
Lamiaceae	*Physostegia virginiana*	0.28	0.07	5	9	C	150	6.80	U	2.600
Fabaceae	*Psoralidium tenuiflorum*	0.59	0.09	4	3	NCP	90	9.00	U	26.160
Lamiaceae	*Pycnanthemum pilosum*	0.28	0.03	13	10	C	150	6.31	A	0.153
Lamiaceae	*Pycnanthemum tenuifolium*	0.13	0.07	13	9	C	80	7.46	A	0.070
Asteraceae	*Ratibida pinnata*	0.28	0.06	9	7	C	150	7.22	U	0.870
Asteraceae	*Rudbeckia missouriensis*	1.00	0.89	7	7	C	50	7.43	U	0.652
Acanthaceae	*Ruellia humilis*	1.00	0.65	7	6	NCP	55	7.43	U	5.452
Gentianaceae	*Sabatia angularis*	0.34	0.03	4	7	S	80	7.75	A	0.020
Asteraceae	*Silphium integrifolium*	0.56	0.02	12	7	C	200	7.42	A	30.650
Asteraceae	*Silphium laciniatum*	0.22	0.18	6	6	NCP	200	7.83	A	78.050
Asteraceae	*Silphium terebinthinaceum*	0.59	0.23	9	7	NCP	200	7.56	A	25.772
Liliaceae	*Sisyrinchium campestre*	0.63	0.14	5	9	C	30	7.40	A	0.460
Solanaceae	*Solanum carolinense*	0.09	0.01	5	4	C	90	7.20	A	2.440
Asteraceae	*Solidago altissima*	0.06	0.03	16	9	C	250	7.56	A	0.090
Asteraceae	*Solidago nemoralis*	0.66	0.14	11	7	C	100	7.27	A	0.300
Asteraceae	*Solidago ptarmicoides*	0.03	0.22	6	4	NCP	50	8.50	A	0.470
Asteraceae	*Solidago radula*	0.31	0.16	6	6	C	120	7.67	A	3.084
Asteraceae	*Solidago rigida*	0.25	0.18	11	7	NCP	150	8.00	A	0.900
Asteraceae	*Solidago ulmifolia*	0.34	0.05	10	9	NCP	120	6.30	A	0.190
Asteraceae	*Symphyotrichum laeve*	0.25	0.18	9	6	C	120	8.33	A	0.306
Asteraceae	*Symphyotrichum oblongifolium*	0.88	0.18	5	5	C	80	8.20	A	0.556
Asteraceae	*Symphyotrichum oolentangiense*	0.38	0.09	7	9	C	120	7.43	A	0.170
Asteraceae	*Symphyotrichum patens*	0.22	0.16	8	6	NCP	120	7.88	A	0.345
Asteraceae	*Symphyotrichum pilosum*	0.28	0.05	14	10	C	150	6.71	A	0.202
Asteraceae	*Symphyotrichum sericeum*	0.28	0.06	3	1	C	70	10.00	A	1.090

Family	Species name	Occupancy	Abundance	Habitats	Light range	Life history	Height (cm)	Mean light	Dispersal	1000 Seed weight (g)
Asteraceae	*Symphyotrichum urophyllum*	0.03	0.01	10	8	C	120	6.20	A	0.210
Portulacaceae	*Talinum calycinum*	0.09	0.19	3	5	NCP	7	8.00	A	0.426
Fabaceae	*Tephrosia virginiana*	0.03	0.01	6	10	NCP	60	6.33	U	11.340
Lamiaceae	*Teucrium canadense*	0.16	0.02	14	10	C	120	7.43	U	1.480
Commelinaceae	*Tradescantia virginiana*	0.03	0.01	5	7	C	90	5.00	U	2.873
Verbenaceae	*Verbena simplex*	0.50	0.07	9	7	NCP	75	8.22	U	0.806
Asteraceae	*Vernonia arkansana*	0.19	0.03	9	9	C	160	7.00	A	1.380
Asteraceae	*Vernonia baldwinii*	0.03	0.02	12	9	C	150	7.00	A	1.000
Violaceae	*Viola pedata*	0.63	0.36	10	7	C	15	7.20	A	0.929
Apiaceae	*Zizia aptera*	0.03	0.01	6	9	NCP	60	6.83	U	1.520
Apiaceae	*Zizia aurea*	0.25	0.03	11	10	NCP	110	5.73	U	2.350

Table S1.2. Species and trait data used in this study. Occupancy is the proportion of the 32 surveyed glades that a species occupied. Abundance is the mean proportion of quadrats in which a species occurred when it was present within a glade. Habitats refers to the number of habitat associations known for each species. Light range refers to the range of light environments a species is associated based on habitat light indexes. Life-history is classified as short-lived for annuals and biennials (S), clonal perennials (C), and non-clonal perennials (NCP). Height is the maximum recorded height. Light refers to the mean light coefficient and occurs on a scale from 1 representing shady environments to 10 representing bright environments. Dispersal is coded as assisted dispersal for bird, animal or wind dispersed seeds (A) or unassisted dispersal for species with primarily gravity dispersed seeds (U). Seed weight is the mean weight of an individual seed.

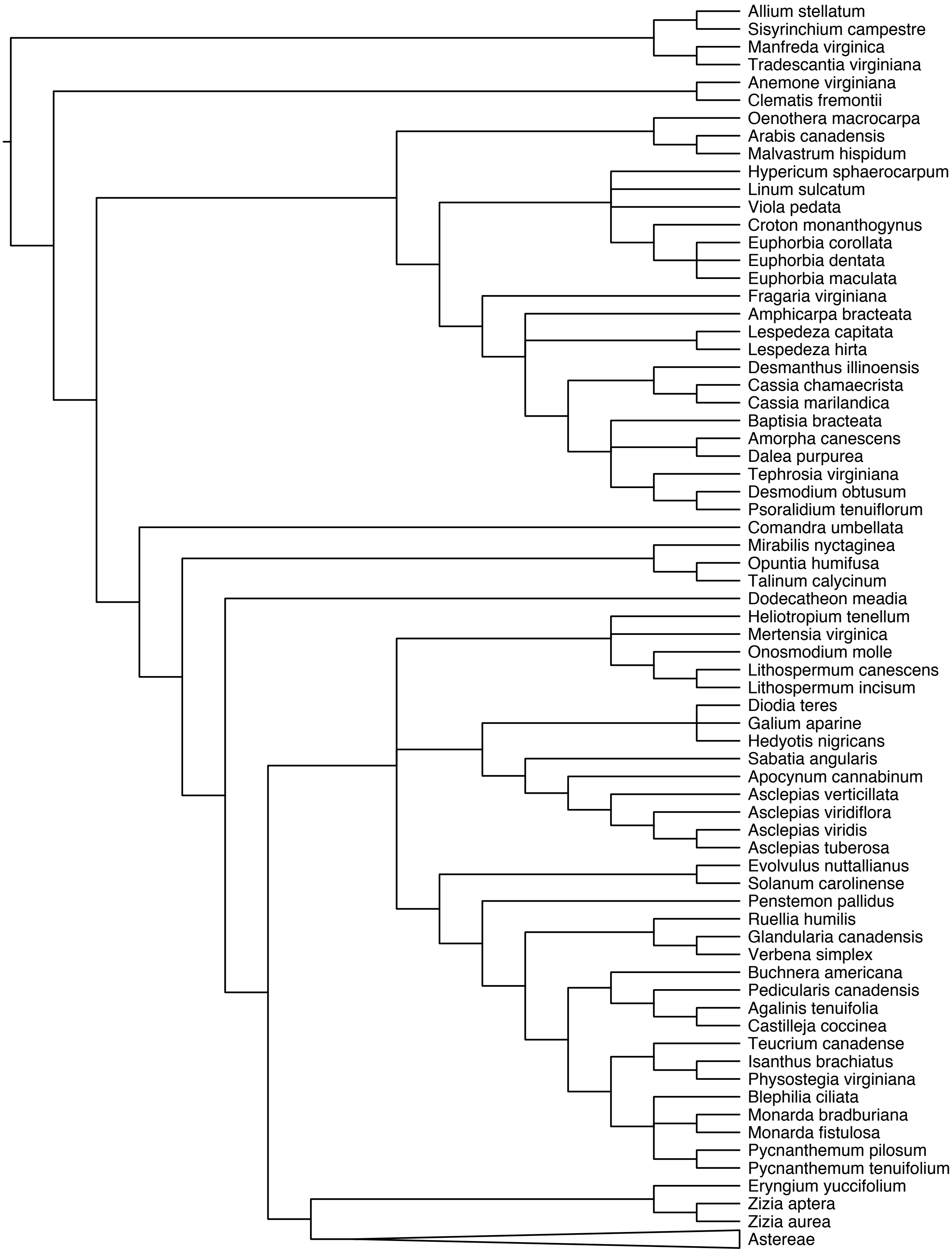

Figure S1.1a. Composite phylogeny of species used in trait analysis. Astereae clade continued in Figure S1.1.b

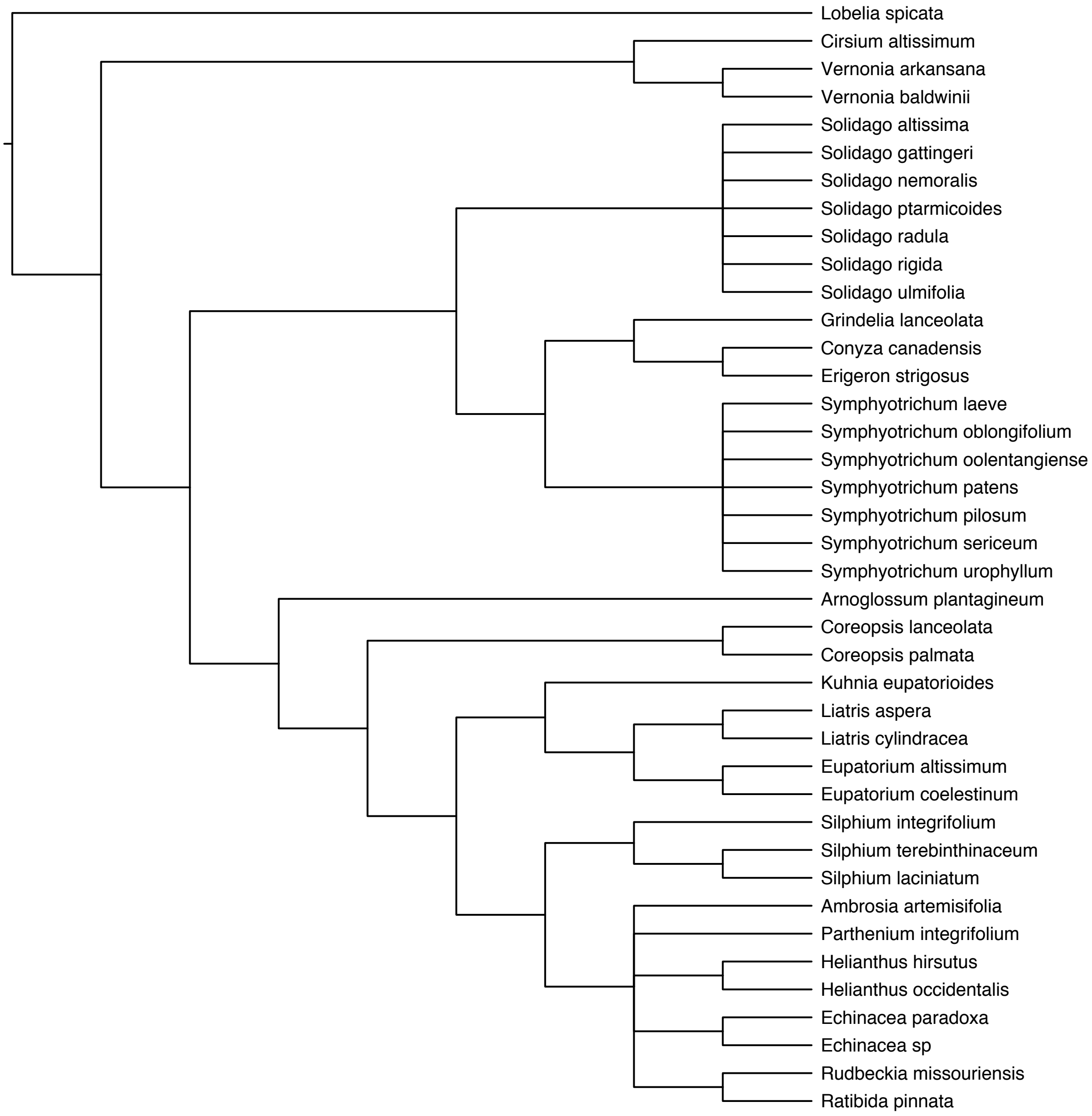

Figure S1.1b. Astereae clade continued from composite phylogeny in Figure S1.1a of species used in trait analysis.

Appendix B – Supplemental Material for Chapter 2

Species	Family	Mean local abundance	Regional occupancy	Habitats	Height (cm)	Seed weight (g)
Allium stellatum	Liliaceae	0.08	0.31	4	45	1.89
Asclepias tuberosa	Apocynaceae	0.02	0.19	8	90	6.80
Baptisia bracteata	Fabaceae	0.05	0.06	7	75	11.50
Camassia scilloides	Liliaceae	0.09	0.13	6	50	6.05
Cassia chamaecrista	Fabaceae	0.06	0.25	9	75	8.40
Castilleja coccinea	Scrophulariaceae	0.14	0.47	7	45	0.04
Coreopsis lanceolata	Asteraceae	0.30	0.50	6	60	1.30
Dalea purpurea	Fabaceae	0.24	1.00	9	90	3.20
Dodecatheon meadia	Primulaceae	0.04	0.25	8	26	0.23
Echinacea simulata	Asteraceae	0.38	0.84	7	120	5.66
Eryngium yuccifolium	Apiaceae	0.01	0.03	4	150	3.82
Euphorbia corollata	Euphorbiaceae	0.28	0.81	6	100	3.79
Glandularia canadensis	Verbenaceae	0.06	0.47	8	45	0.82
Helianthus occidentalis	Asteraceae	0.10	0.13	8	100	2.60
Liatris cylindracea	Asteraceae	0.44	0.72	6	60	3.26
Lobelia spicata	Campanulaceae	0.07	0.66	11	80	0.03
Manfreda virginica	Asparagaceae	0.12	0.22	2	240	7.16
Monarda fistulosa	Lamiaceae	0.04	0.50	9	120	0.40
Oenothera macrocarpa	Onagraceae	0.17	0.53	6	60	5.13
Parthenium integrifolium	Asteraceae	0.14	0.25	8	100	3.08
Physostegia virginiana	Lamiaceae	0.07	0.28	5	150	2.60
Pycnanthemum tenuifolium	Lamiaceae	0.07	0.13	13	80	0.07
Rudbeckia missouriensis	Asteraceae	0.89	1.00	7	50	0.65
Ruellia humilis	Acanthaceae	0.65	1.00	7	55	5.45
Silphium laciniatum	Asteraceae	0.18	0.22	6	200	78.05
Silphium terebinthinaceum	Asteraceae	0.23	0.59	9	200	25.77
Solidago gattingeri	Asteraceae	0.25	0.31	3	80	0.30
Solidago nemoralis	Asteraceae	0.14	0.66	11	100	0.30
Symphyotrichum oblongifolium	Asteraceae	0.18	0.88	5	80	0.56
Symphyotrichum oolentangiense	Asteraceae	0.09	0.38	7	120	0.17

Table S2.1. Species and trait data used in this study. Occupancy is the proportion of the 32 surveyed glades that a species occupied. Abundance is the mean proportion of quadrats in which a species occurred when it was present within a glade. Habitats refers to the number of habitat associations known for each species. Height is the maximum recorded height. Seed weight is the mean weight of 1000 seeds.

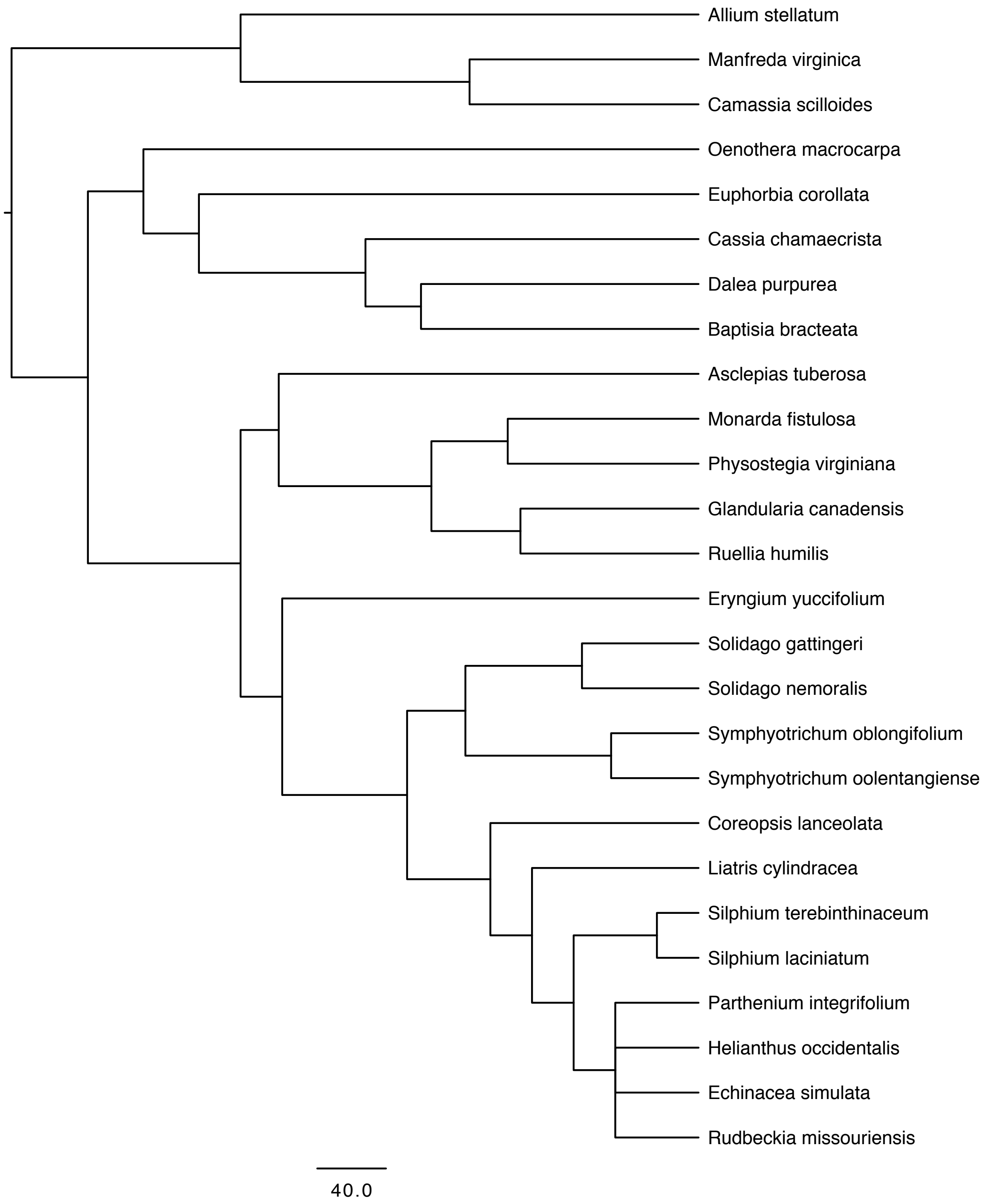

Figure S2.1 – A composite phylogeny for the species used in this experiment. Branch length units are in millions of years.

		No phylogeny			**With phylogeny**		
Model	**Factor**	**Model estimate**	**95% CI**	**P-value**	**Model estimate**	**95% CI**	**P-value**
Dry: Comp removed - Present	(Intercept)	0.304	(-0.113, 0.716)	0.15	0.271	(-0.191, 0.713)	0.236
	Occupancy	0.609	(-0.193, 1.399)	0.138	0.571	(-0.241, 1.364)	0.159
Dry: Comp removed - Burned	**(Intercept)**	**0.768**	**(0.193, 1.403)**	**0.02**	**0.694**	**(-0.003, 1.413)**	**0.064**
	Occupancy	-0.043	(-1.195, 1.031)	0.92	-0.245	(-1.247, 0.816)	0.623
Dry: Burned - Comp present	**(Intercept)**	**-0.438**	**(-0.81, 0.006)**	**0.039**	**-0.439**	**(-0.895, 0.004)**	**0.054**
	Occupancy	0.637	(-0.226, 1.443)	0.141	0.694	(-0.148, 1.516)	0.108
Avg: Comp removed - Present	**(Intercept)**	**0.873**	**(0.417, 1.361)**	**0**	**0.847**	**(0.318, 1.371)**	**0.003**
	Occupancy	0.126	(-0.725, 1.015)	0.766	0.071	(-0.82, 0.909)	0.866
Avg: Comp removed - Burned	**(Intercept)**	**1.269**	**(0.696, 1.898)**	**<0.001**	**1.286**	**(0.599, 1.965)**	**0.003**
	Occupancy	**-1.505**	**(-2.577, -0.325)**	**0.013**	**-1.57**	**(-2.629, -0.496)**	**0.007**
Avg: Burned - Comp present	(Intercept)	-0.384	(-1.094, 0.359)	0.287	-0.392	(-1.28, 0.477)	0.341
	Occupancy	**1.541**	**(0.134, 2.832)**	**0.028**	**1.5**	**(0.111, 2.764)**	**0.029**
Wet: Comp removed - Present	**(Intercept)**	**0.311**	**(-0.048, 0.665)**	**0.085**	0.287	(-0.118, 0.665)	0.14
	Occupancy	0.203	(-0.508, 0.848)	0.559	0.189	(-0.526, 0.853)	0.573
Wet: Comp removed - Burned	**(Intercept)**	**0.445**	**(-0.021, 0.854)**	**0.045**	**0.437**	**(0.017, 0.896)**	**0.052**
	Occupancy	-0.145	(-0.926, 0.63)	0.706	-0.137	(-0.881, 0.611)	0.715
Wet: Burned - Comp present	(Intercept)	-0.132	(-0.625, 0.332)	0.571	-0.155	(-0.625, 0.332)	0.525
	Occupancy	0.29	(-0.618, 1.166)	0.507	0.304	(-0.558, 1.182)	0.486

Table S2.2 - Model three results showing mean Model estimates and 95% credible intervals (CI) describing the relationship between the effect size of competition treatments on seedling establishment and regional occupancy with and without phylogeny. Each univariate model is separated with dashed lines. Random effects in this model are species and seed weight. Significant relationships are bolded.

		No phylogeny			**With phylogeny**		
Model	**Factor**	**Model estimate**	**95% CI**	**P-value**	**Model estimate**	**95% CI**	**P-value**
Comp present: Wet - Dry	(Intercept)	0.197	(-0.259, 0.652)	0.382	0.208	(-0.191, 0.713)	0.236
	Occupancy	-0.162	(-1.002, 0.776)	0.705	-0.145	(-0.241, 1.364)	0.159
Comp present: Wet - Avg	**(Intercept)**	**0.548**	**(0.127, 0.974)**	**0.012**	**0.543**	**(-0.003, 1.413)**	**0.064**
	Occupancy	0.095	(-0.704, 0.969)	0.818	0.081	(-1.247, 0.816)	0.623
Comp present: Avg - Dry	(Intercept)	-0.263	(-0.711, 0.2)	0.243	**-0.263**	**(-0.895, 0.004)**	**0.054**
	Occupancy	-0.264	(-1.097, 0.648)	0.542	-0.232	(-0.148, 1.516)	0.108
Burned: Wet - Dry	**(Intercept)**	**0.505**	**(0.083, 0.958)**	**0.023**	**0.492**	**(0.318, 1.371)**	**0.003**
	Occupancy	-0.496	(-1.343, 0.309)	0.238	-0.558	(-0.82, 0.909)	0.866
Burned: Wet - Avg	**(Intercept)**	**0.677**	**(0.282, 1.141)**	**<0.001**	**0.661**	**(0.599, 1.965)**	**0.003**
	Occupancy	**-1.061**	**(-1.902, -0.268)**	**0.009**	**-1.053**	**(-2.629, -0.496)**	**0.007**
Burned: Avg - Dry	(Intercept)	-0.279	(-0.687, 0.122)	0.17	-0.273	(-1.28, 0.477)	0.341
	Occupancy	**0.758**	**(-0.041, 1.617)**	**0.07**	**0.721**	**(0.111, 2.764)**	**0.029**
Comp removed: Wet - Dry	(Intercept)	0.163	(-0.197, 0.501)	0.358	0.171	(-0.118, 0.665)	0.14
	Occupancy	-0.466	(-1.117, 0.178)	0.16	-0.441	(-0.526, 0.853)	0.573
Comp removed: Wet - Avg	(Intercept)	-0.013	(-0.343, 0.305)	0.942	**-0.022**	**(0.017, 0.896)**	**0.052**
	Occupancy	0.178	(-0.415, 0.773)	0.546	0.176	(-0.881, 0.611)	0.715
Comp removed: Avg - Dry	(Intercept)	0.129	(-0.27, 0.52)	0.499	0.157	(-0.625, 0.332)	0.525
	Occupancy	-0.553	(-1.271, 0.187)	0.147	-0.53	(-0.558, 1.182)	0.486

Table S2.3 - Model three results showing mean Model estimates and 95% credible intervals (CI) describing the relationship between the effect size of precipitation treatments on seedling establishment and regional occupancy with and without phylogeny. Each univariate model is separated with dashed lines. Random effects in this model are species and seed weight. Significant relationships are bolded.

		No phylogeny			With phylogeny		
Model	**Factor**	**Model estimate**	**95% CI**	**P-value**	**Model estimate**	**95% CI**	**P-value**
Dry: Comp removed - Present	(Intercept)	0.135	(-0.132, 0.421)	0.301	0.117	(-0.23, 0.413)	0.446
	Occupancy	-0.061	(-0.57, 0.391)	0.78	-0.136	(-0.574, 0.353)	0.536
Dry: Comp removed - Burned	(Intercept)	-0.021	(-0.229, 0.166)	0.825	-0.012	(-0.24, 0.204)	0.888
	Occupancy	0.15	(-0.194, 0.525)	0.388	0.133	(-0.217, 0.487)	0.44
Dry: Burned - Comp present	(Intercept)	0.093	(-0.116, 0.31)	0.379	0.068	(-0.15, 0.316)	0.538
	Occupancy	-0.234	(-0.579, 0.173)	0.196	-0.249	(-0.616, 0.117)	0.174
Average: Comp removed - Present	(Intercept)	-0.005	(-0.327, 0.32)	0.976	-0.014	(-0.451, 0.38)	0.943
	Occupancy	**0.51**	**(-0.045, 1.123)**	**0.079**	0.411	(-0.187, 1.014)	0.16
Average: Comp removed - Burned	(Intercept)	0.041	(-0.155, 0.227)	0.633	0.037	(-0.161, 0.272)	0.696
	Occupancy	0.098	(-0.242, 0.463)	0.59	0.048	(-0.269, 0.39)	0.815
Average: Burned - Comp present	(Intercept)	-0.107	(-0.393, 0.209)	0.466	-0.106	(-0.463, 0.253)	0.526
	Occupancy	**0.445**	**(-0.109, 0.944)**	**0.098**	0.417	(-0.111, 0.904)	0.121
Wet: Comp removed - Present	(Intercept)	0.117	(-0.227, 0.491)	0.498	0.112	(-0.296, 0.488)	0.566
	Occupancy	0.381	(-0.267, 1.009)	0.215	0.366	(-0.256, 1.023)	0.242
Wet: Comp removed - Burned	(Intercept)	0.117	(-0.124, 0.351)	0.31	0.119	(-0.133, 0.391)	0.356
	Occupancy	0.224	(-0.187, 0.667)	0.288	0.211	(-0.18, 0.672)	0.313
Wet: Burned - Comp present	(Intercept)	-0.062	(-0.319, 0.175)	0.609	-0.043	(-0.324, 0.227)	0.724
	Occupancy	0.128	(-0.301, 0.579)	0.558	0.104	(-0.318, 0.533)	0.638

Table S2.4 - Model six results showing mean Model estimates and 95% credible intervals (CI) describing the relationship between the effect size of competition treatments on seedling size and regional occupancy with and without phylogeny. Each univariate model is separated with dashed lines. Random effects in this model are species and seed weight. Significant relationships are bolded.

		No phylogeny			**With phylogeny**		
Model	**Factor**	**Model estimate**	**95% CI**	**P-value**	**Model estimate**	**95% CI**	**P-value**
Comp present: Wet - Dry	(Intercept)	0.061	(-0.117, 0.241)	0.486	0.059	(-0.132, 0.25)	0.522
	Occupancy	**-0.315**	**(-0.63, 0.023)**	**0.054**	**-0.302**	**(-0.637, -0.003)**	**0.055**
Comp present: Wet - Avg	(Intercept)	-0.119	(-0.263, 0.036)	0.12	-0.115	(-0.271, 0.043)	0.144
	Occupancy	0.127	(-0.134, 0.386)	0.322	0.126	(-0.113, 0.393)	0.309
Comp present: Avg - Dry	**(Intercept)**	**0.201**	**(-0.001, 0.432)**	**0.061**	**0.201**	**(-0.033, 0.439)**	**0.092**
	Occupancy	**-0.489**	**(-0.91, -0.124)**	**0.016**	**-0.477**	**(-0.859, -0.073)**	**0.015**
Burned: Wet - Dry	(Intercept)	-0.085	(-0.376, 0.195)	0.556	-0.056	(-0.381, 0.271)	0.71
	Occupancy	-0.066	(-0.552, 0.48)	0.793	-0.056	(-0.561, 0.419)	0.814
Burned: Wet - Avg	(Intercept)	-0.052	(-0.302, 0.179)	0.662	-0.049	(-0.32, 0.202)	0.672
	Occupancy	-0.096	(-0.532, 0.333)	0.645	-0.092	(-0.496, 0.348)	0.656
Burned: Avg - Dry	(Intercept)	-0.035	(-0.235, 0.163)	0.72	-0.02	(-0.238, 0.207)	0.831
	Occupancy	0.21	(-0.139, 0.58)	0.237	0.233	(-0.127, 0.565)	0.183
Comp removed: Wet - Dry	(Intercept)	0.054	(-0.091, 0.216)	0.471	0.062	(-0.106, 0.219)	0.445
	Occupancy	0.077	(-0.201, 0.347)	0.552	0.098	(-0.175, 0.348)	0.443
Comp removed: Wet - Avg	(Intercept)	0.033	(-0.114, 0.176)	0.645	0.04	(-0.109, 0.206)	0.607
	Occupancy	-0.036	(-0.322, 0.22)	0.812	-0.033	(-0.308, 0.219)	0.83
Comp removed: Avg - Dry	(Intercept)	0.019	(-0.113, 0.146)	0.771	0.021	(-0.111, 0.165)	0.764
	Occupancy	0.136	(-0.127, 0.371)	0.274	0.14	(-0.096, 0.377)	0.231

Table S2.5 - Model six results showing mean Model estimates and 95% credible intervals (CI) describing the relationship between the effect size of precipitation treatments on seedling size and regional occupancy with and without phylogeny. Each univariate model is separated with dashed lines. Random effects in this model are species and seed weight. Significant relationships are bolded.

Appendix C – Supplemental Material for Chapter 3

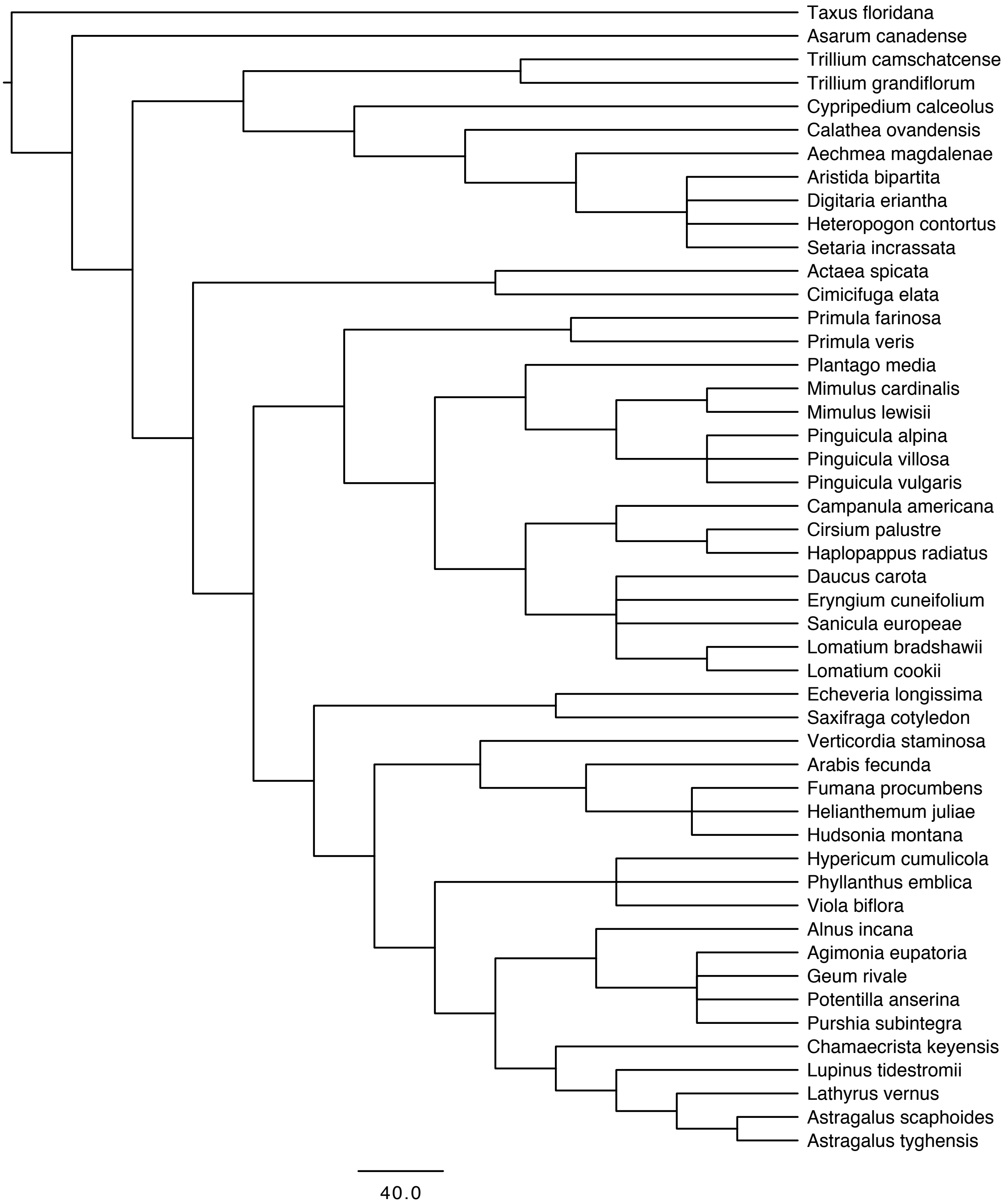

Figure S3.1 - A composite phylogeny for the species used in this experiment. Branch length units are in millions of years.

Species	**Family**	**Study**
Actaea spicata	Ranunculaceae	Froborg and Eriksson 2003
Aechmea magdalenae	Bromeliaceae	Ticktin and Nantel 2004
Agimonia eupatoria	Rosaceae	Kiviniemi 2002
Alnus incana	Betulaceae	Huenneke & Marks 1987
Arabis fecunda	Brassicaceae	Lesica and Shelly 1995
Aristida bipartita	Poaceae	O'Conner 1993
Asarum canadense	Aristolochiaceae	Damman and Cain 1998
Astragalus scaphoides	Fabaceae	Lesica 1995
Astragalus tyghensis	Fabaceae	Kaye and Pyke 2003
Calathea ovandensis	Marantaceae	Horvitz and Schemske 1995
Campanula americana	Campanulaceae	Wardle unpublished
Chamaecrista keyensis	Fabaceae	Liu et al. 2005
Cimicifuga elata	Ranunculaceae	Kaye and Pyke 2003
Cirsium palustre	Asteraceae	Ramula 2008
Cypripedium calceolus	Orchidaceae	Nicole et al. 2005
Daucus carota	Apiaceae	Verkaar and Schenkeveld 1984
Digitaria eriantha	Poaceae	O'Conner 1993
Echeveria longissima	Crassulaceae	Martorell 2007
Eryngium cuneifolium	Apiaceae	Menges and Quintana-Ascencio 2004
Fumana procumbens	Cistaceae	Bengtsson 1993
Geum rivale	Rosaceae	Kiviniemi 2002
Haplopappus radiatus	Asteraceae	Kaye and Pyke 2003
Helianthemum juliae	Cistaceae	Marrero-Gomez et al. 2002
Heteropogon contortus	Poaceae	O'Conner 1993
Hudsonia montana	Cistaceae	Gross et al. 1998
Hypericum cumulicola	Clusiaceae	Quintana-Ascencio et al. 2003
Lathyrus vernus	Fabaceae	Ehrlen and Eriksson 1995
Lomatium bradshawii	Apiaceae	Kaye et al. 2001
Lomatium cookii	Apiaceae	Kaye and Pyke 2003
Lupinus tidestromii	Fabaceae	Knight unpublished
Mimulus cardinalis	Phrymaceae	Angert 2006
Mimulus lewisii	Phrymaceae	Angert 2006
Phyllanthus emblica	Phyllanthaceae	Sinha and Brault 2005
Pinguicula alpina	Lentibulariaceae	Svensson et al. 1993
Pinguicula villosa	Lentibulariaceae	Svensson et al. 1993
Pinguicula vulgaris	Lentibulariaceae	Svensson et al. 1993
Plantago media	Plantaginaceae	Eriksson and Ove 2000
Potentilla anserina	Rosaceae	Eriksson 1988
Primula farinosa	Primulaceae	Lindborg and Ehrlen 2002
Primula veris	Primulaceae	Ehrlen et al. 2005
Purshia subintegra	Rosaceae	Maschinski et al. 2006
Sanicula europeae	Apiaceae	gustafsson unpublished unpublished
Saxifraga cotyledon	Saxifragaceae	Dinnetz and Nilsson 2002
Setaria incrassata	Poaceae	O'Conner 1993
Taxus floridana	Taxaceae	Kwit et al. 2004
Trillium camschatcense	Melanthiaceae	Tomimatsu and Ohara 2010
Trillium grandiflorum	Melanthiaceae	Knight 2004
Verticordia staminosa	Myrtaceae	Yates et al. 2007
Viola biflora	Violaceae	Evju et al. 2010

Table S3.1 – A list of the studies and species used in this analysis.