LINKING UNDERSTORY EVERGREEN HERBACEOUS DISTRIBUTIONS AND NICHE DIFFERENTIATION USING HABITAT-SPECIFIC DEMOGRAPHY AND EXPERIMENTAL COMMON GARDENS

by

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(Under the Direction of H. Ronald Pulliam)

ABSTRACT

The assumption that a 1:1 correspondence exists between a species' distribution and "suitable habitat," the ecological niche, is undermined by current theory – metapopulation, source/sink, dispersal limitation and remnant populations – and empirical evidence. Here I summarize dynamics where organisms are found in unsuitable habitat and are absent from suitable habitat. I then use evergreen understory herbaceous surveys across north- and south-facing aspects to investigate potential habitat suitability. The results, based on Bayesian generalized linear hierarchical models, indicate evergreen understory herbs occur less and perform worse on south-facing than north-facing slopes, and they likely are limited on south-facing slopes by low soil moisture combined with high temperatures in summer and high light combined with low temperatures in winter. I use habitat-specific demography for further insight into the suitable habitat of two understory evergreen herbs, *Hexastylis arifolia* and *Hepatica nobilis,* and the relationship between morphological trait differences and niche using Bayesian hierarchical models and simulations. The results suggest that *H. arifolia* and *H. nobilis* occur in declining populations in habitat made unsuitable habitat by declining levels of soil moisture. I also find that leaf traits have potential in predicting niche characteristics only when paired with demographic analysis. Since both survey and demography data of natural understory evergreen populations suggest that seasonal light, soil moisture and temperature explain a great deal of plant distribution and performance, I use experimental gardens with light and soil moisture manipulation to test these results. Experimental common gardens were established on north- and south-facing slopes in North Carolina and Georgia, and three understory evergreen species were transplanted into plots that included nested water augmentation and light suppression treatments. The plants responded to the environmental variables in a manner consistent with a guild that limited on south-facing slopes. Increased temperatures and light exposure and lower soil moisture generally led to decreased survival and growth and increased photoinhibition, and the responses varied among the three species. I conclude that the understory evergreen herbs often occur in unsuitable habitat, both at landscape and microsite scales, and performance and physiological responses to environmental variables provide better estimations of the species' niche than presence.

INDEX WORDS: Niche, suitable habitat, faux fitness, *Hexastylis arifolia*, *Hepatica nobili*s, *Goodyera pubescens*, habitat-specific demography, aspect, north- and south-facing slopes, understory, evergreen, herbaceous, population projection matrix models, Bayesian hierarchical models.

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INTRODUCTION

Ecologists cannot depend on a 1:1 correspondence between a species' distribution and "suitable habitat, " suitable habitat here defined as a location in the landscape containing the biotic and abiotic conditions conducive to demographic fitness (per capita birth > per capita death)—a.k.a., the ecological niche. Thus, in theory, a population can exist in habitat where it cannot reproduce at a sufficient rate for sustaining itself. In Chapter 1, I summarize instances where the evaluation of suitable habitat is confounded by (a) the presence of organisms in unsuitable habitat and (b) the absence of organisms in suitable habitat.

The remarkable shift in all plant communities across the boundaries of nonequatorial north- and south-facing slope aspects is one of the more striking and well-documented microclimate-correlated biotic transitions observed in nature; and the predominance of understory evergreen plants on north- versus south-facing slopes suggests a landscape-level dichotomy in habitat suitability. In the Northern Hemisphere, the surface of south-facing slopes orients toward the sun and thus receives a greater duration and intensity of the solar rays, resulting in a relatively warmer, drier microclimate. On a temporal scale, south-facing slopes inhabited by deciduous forests contain two environmental extremes: high temperatures and low soil moisture in summer; low temperatures and high light in winter. Each of these extremes create potentially stressful conditions for plants—particularly evergreen plants which must face both. The impact of aspect upon the distribution of understory evergreen herbs largely has been left unexplored—particularly with reference to summer and winter conditions. In chapter 2, I investigate whether (1) increased southerly aspect orientation correlates negatively with evergreen understory plant distribution; (2) environmental variables (summer and winter light, heat load) better predicts variance in evergreen distribution and performance than topographic position (aspect, slope and elevation) and (3) winter light best predicts evergreen understory plant distribution. In order to test these hypotheses, survey data were collected characterizing ten evergreen understory herbs and environmental and topographical conditions north- and south-facing slopes in the North Carolina mountains and Georgia piedmont. Bayesian hierarchical generalized linear models were used to estimate the relationship between distribution parameters and topographic and derived environmental variables.

While it is widely assumed that an organism's niche can be inferred from its presence or absence across environmental patches and gradients, the mere presence or short-term performance of a species cannot provide a robust delineation of the associated habitat suitability. Instead, I use population projection matrices in Chapter 3 to determine the trajectory of two understory herb populations, and investigate life stage transitions as a function of environmental variables for insight into suitable habitat. Furthermore, I investigate whether morphological trait differences between species correspond with niche differences. The objective of this chapter is to use demographic population matrices combined with extensive abiotic monitoring to map the niche for two understory evergreen herbs (*Hexastylis arifolia* and *Hepatica nobilis*), as well as determine the predictability of leaf and root traits for niche characteristics. Specifically, we ask: (1) What is the projected viability of nine *H. arifolia* and four *H. nobilis* populations? (2) What environmental variables best predict changes in λ and crucial vital rates (abundance, reproduction and growth)? (3) Do potential differences in morphological trait characteristics correspond with differences in demographic performance and suitable habitat? I use census data based on tracking more than 10,000 plants for six years to construct population matrix models both at pooled- and individual-population scales. I analyze this demographic data for population trends and use Bayesian hierarchical models to explore trends in vital rates as correlates of environmental variables such as light and soil moisture. These relationships are further explored in Bayesian hierarchical simulations with key life stage transitions modeled as a function of environmental variables.

Since both survey (Chapter 2) and demography (Chapter 3) data of natural understory evergreen populations suggest that seasonal light, soil moisture and temperature explain a great deal of plant distribution and performance, I use experimental gardens with light and soil moisture manipulation in Chapter 4 to test these results. Specifically, four questions were addressed: (1) What environmental variables best explain variation in understory evergreen herb vital rates? (2) Can abiotic (environmental) variables account for the observed limited distribution of understory evergreen herbs on south-facing slopes? (3) Do three phylogenetically distinct understory evergreen herbs respond similarly or in a species-specific manner in response to environmental gradients? Experimental common gardens were established on north- and south-facing slopes in North Carolina and Georgia, and 864 individuals of three understory evergreen species (*Hexastylis arifolia*, *Hepatica nobilis* and *Goodyera pubescens*) were randomly assigned in plots that included nested water augmentation and light suppression treatments.

CHAPTER 1

FAUX FITNESS: THE DISJUNCTION BETWEEN SPECIES DISTRIBUTION AND SUITABLE HABITAT

INTRODUCTION

A venerable goal in ecology has been, and will be, mapping species distributions and deriving the factors that explain those distributions; the growing possibility of global climate change and a potential re-alignment of suitable habitat makes this goal all the more crucial. Yet, predictive forays into the future might be hampered by an old assumption: the presence of an organism in a specific habitat identifies that habitat as suitable. A great deal of empirical and theoretical evidence suggests otherwise (Pulliam 1988; Matlack 1994; Eriksson 1996; Clark *et al.* 1998; Davis *et al.* 1998; Hanski 1998; Ehrlen & Eriksson 2000; Pulliam 2000; Peterson 2003; Guisan & Thuiller 2005; Murphy & Lovett-Doust 2007). While it is inarguably intuitive to assume that an organism occurs where habitat is suitable and is absent where it is not, this fails if we include a requirement that the organism not only survive, but reproduce at a sustainable rate. That is, suitable habitat must contain the biotic and abiotic conditions conducive to demographic fitness so that per capita birth > per capita death.

This review summarizes dynamics where correlative presence and/or abundance data—essentially that derived from standard survey methods—are confounded by (a) the presence of organisms in unsuitable habitat and (b) the absence of organisms in suitable habitat. Using this criterion, I identify four relatively common ecological dynamics where species distribution is not a reliable guide to suitable habitat. These are: (1) metapopulation, (2) dispersal limitation, (3) remnant population and (4) source/sink. For convenience and in order to highlight the common thread—the lack of a 1:1 correspondence between species distribution and suitable habitat—I summarize these dynamics with an inclusive term: *faux fitness*. While *faux fitness* applies to both plant and animal distributions, this review will center upon plants. The term encapsulates those scenarios where the mere presence or absence of a species gives a false indication of the suitability or unsuitability of the habitat. That the term includes "fitness," which is a word often used to designate the lifetime reproductive success of an organism, is not accidental. The fulcrum point between suitable and unsuitable habitat is not the ability of a species to live or even grow based on conditions in a certain habitat, but rather the ability for it to reproduce and replace itself based on niche conditions in that habitat.

Given the likelihood that global climate change, particularly increased temperature and major shifts in regional and seasonal precipitation (Davis & Zabinski 1992; Houghton *et al.* 2001; Matsui *et al.* 2004), will lead to increased change in species distributions (Pounds *et al.* 1999; Fitter & Fitter 2002; Cotton 2003; Parmesan & Yohe 2003; Root *et al.* 2003), *faux fitness* poses a problematic barrier in utilizing current presence or absence in predicting future plant distributions. Yet researchers use 'climate envelope' models based on current species distributions and their associated climate variables (often geographical, sometimes environmental, rarely both) to predict future distributions while largely minimizing or ignoring *faux fitness* (Beerling 1993; Huntley *et al.* 1995; Baker *et al.* 2000; Moody & Meentemeyer 2001; Peterson & Vieglais 2001; Welk *et al.* 2002; Peterson 2003; Skov & Svenning 2004; Thomas *et al.* 2004; Hamann & Wang 2006). In the final section of this review, I will critique the use of these model assumptions in light of *faux fitness* and suggest solutions for future analysis.

Faux fitness and niche theory

Early ecologists expected species to occur wherever their range of suitable environmental requirements occurred (Grinnell 1917, 1924). While Grinnell emphasized the role of the environment in defining the niche, Elton (1927) emphasized the role of the species and its impact on the environment (i.e. its place in the food web). While these concepts advanced the definition of the niche, Hutchinson (1957) established niche theory as a force in ecology with his quantification of niche space an n-dimensional hypervolume containing all points corresponding to environmental variables that support the organism's existence. These biotic and abiotic points (e.g. pH, prey size) correspond with environmental requirements, tolerances and interactions that allow the species to exist indefinitely. Hutchinson may have confused matters however, by splitting the niche into a fundamental niche (the hypervolume) and realized niche (the observed niche, reduced by interspecific competition). Hutchinson considered competitive exclusion as the mechanism behind the realized niche. Under competitive exclusion, two species utilizing a common resource cannot coexist (Gause 1934), which potentially excludes a lesser competitor from suitable habitat by a better competitor for that resource.

A great body of work has supported the theory that interspecific competition can limit the geographic distribution of a species (Clements *et al.* 1929; Grime 1973; Silander & Antonovics 1982; Tilman 1982; Fowler 1986; Wilson & Keddy 1986; Crawley 1997; Silvertown 2004). However, the extent to which competitive exclusion structures plant communities is still debated (Simberloff 1983; Goldberg *et al.* 1999; Hubbell 2001) and empirical demonstrations are somewhat lacking (Aarssen & Epp 1990; Silvertown 2004). Furthermore, a growing body of work suggests that positive interactions between species may have as much influence on shaping distributions as competition (Boucher 1985; Hoeksema & Bruna 2000; Bronstein *et al.* 2003;

Bruno *et al.* 2003; Freestone 2006). Rather than considering competition outside the fundamental niche, biotic interactions can be viewed as another dimension within Hutchinson's hypervolume (Pulliam 2000; Leathwick & Austin 2001; Chase & Leibold 2003; Araujo & Guisan 2006). Species not only respond to environmental variables, but influence the availability of those variables for themselves and interspecific competitors (Pulliam 2000). Therefore, here I consider the "niche" all abiotic *and* biotic interactions that that support the organism's existence in suitable habitat.

By measuring the biotic and abiotic variables that influence the demography of a species, the niche can be quantitatively calculated as the set of conditions that meet the minimum requirements of a species so that births outweigh deaths. This can be summarized demographically as habitat that supports a per capita population growth (λ) > 1.0, where λ is the finite rate of population increase ($N_{t+1} = \lambda N_t$), and $\lambda = 1$ indicates a population that exactly replaces itself. As a great deal of confusion reigns over the distinction between the terms 'niche' and 'habitat'; here I use habitat as a physical location containing the hypervolume of conditions demarcating the theoretical niche (Hutchinson 1957; Pulliam 2000; Chase & Leibold 2003; Kearney 2006). Thus, the niche is not a place in the environment but the set of limiting factors and "essential resources" (Tilman 1980; Tilman 1982; Tilman 1988) that determine demographic fitness (Figure 1.1). By extension, suitable habitat refers to locations that are within the species' niche ($\lambda > 1.0$) and unsuitable habitat falls outside the niche ($\lambda < 1.0$). *Faux fitness* occurs when the organisms fail to occur in suitable habitat ($\lambda > 1.0$) or when they occur in unsuitable habitat ($\lambda < 1.0$).

SPECIES ABSENT FROM SUITABLE HABITAT

Metapopulation

An ideal metapopulation acts as a “population of populations” where a network of local populations exist in a balance between extinction and colonization to create a greater regional population (Levins 1969, 1970) (Figure 1.2). The local populations inhabit discrete patches of suitable habitat within a matrix of unsuitable habitat, their only link via migration (Hanski 1998). In Levins’ model—analogous to population growth models except that it gives the rate of change in occupied patches (immigration and emigration) rather than population size (birth and death)—all unoccupied patches have an equal chance of colonization and all occupied patches have an equal chance of extinction. If local populations go extinct at different times, the extinct patches can be recolonized and the metapopulation persists.

The implication for species distribution is that extinction within the local populations is recurrent due to random events (Hanski 1997, 1998). Within the metapopulation as a whole, patches of suitable and unsuitable habitat should exist with the presence or absence of the species not acting as a definitive indication of either. This leads to a shifting mosaic of local populations linked through dispersal with only a fraction of suitable habitat occupied at any point (Husband & Barrett 1996). While any local patch has a recurrent risk of stochastic extinction (demographic, environmental or genetic), migration can rescue a local population from extinction and thereby prevent the extinction of the regional population (Brown & Kodric-Brown 1977; Hanski 1982).

In this framework, local population dynamics occur at a much faster time scale than regional dynamics (Hanski & Simberloff 1997); and extinction should be higher in the smaller, isolated local populations than the larger regional population (MacArthur & Wilson 1967).

Furthermore, birth and death rates likely affect local population dynamics while dispersal and recruitment affect regional population dynamics (Valverde & Silvertown 1997). This suggests, at a minimum, that scaling from local to regional scale may not be straightforward (Freckleton & Watkinson 2002). For example, environmental factors that promote local fitness might also constrain dispersal and recruitment (e.g., high soil moisture that supports reproduction but inhibits seed dispersers). This creates a dynamic where the environmental predictor has conflicting effects depending on the scale measured. Local populations may flourish with increased moisture while stochastic extinctions and increasingly inadequate dispersal leaves the regional population floundering.

Husband and Barrett (1996) and Freckleton and Watkinson (2002, 2003) have questioned the applicability of metapopulation dynamics for plant systems, and they argue that researchers often fail to test all assumptions that define a metapopulation. In reviewing the metapopulation literature, they conclude that much of it details local, patchy population dynamics scaled up to the regional level without addressing essential metapopulation components such as colonization and extinction or suitable habitat at the larger scale. It is widely accepted that plant distributions are patchy (Pickett & White 1985), but whether they form metapopulations hinges on whether individual populations are extinction prone and connected via emigration and immigration (Harrison 1991; Eriksson 1996; Husband & Barrett 1996; Freckleton & Watkinson 2002, 2003). Both of these dynamics are hard to measure (Husband & Barrett 1996; Freckleton & Watkinson 2002), but there is empirical evidence of metapopulation dynamics (Kadmon & Shmida 1990; Menges 1990; Valverde & Silvertown 1997). Hastings and Harrison (1994) suggest that the metapopulation concept has developed into a broader concept connoting any set of conspecific populations linked by dispersal. In this context, as outlined by Leibold et al. (2004), the demographic rates of local communities are driven by recognized species interactions such as competition while colonists drive interactions at the regional level. If dispersal is low, initial colonization events drive community structure while, if dispersal is high, the traditional metapopulation concept would better apply.

For the purpose of this *faux fitness* review, it is not necessary to redefine metapopulation semantics. In the metacommunity categories of both Freckleton and Watkinson (2002) and Leibold et al. (2004), a core framework remains: the dynamic nature of regional plant populations creates a mosaic of occupied and unoccupied suitable habitat. In this structure, both suitable and unsuitable habitats are difficult to recognize based simply on the presence or absence of individuals, and these dynamics can shift with time (Valverde & Silvertown 1997). In the discussion of *faux fitness*, this framework suggests that, in many cases, one can expect unoccupied patches of suitable habitat.

Limited dispersal

The ability to reach portions of the landscape where recruitment, growth and ultimately reproduction can occur is paramount for the persistence of a population. Dispersal lies at the heart of most modern theories of community dynamics and structure (Levins 1969, 1970; Ehrlen & Eriksson 2000; Pulliam 2000; Hubbell 2001). Limited dispersal is often the simplest and most parsimonious explanation for uninhabited suitable habitat (Figure 1.3). A dispersal-limited species is one whose landscape distribution is more strongly influenced by seed availability than habitat availability (Moore & Elmendorf 2006). If plants lack the capacity to disperse to disjunct habitats, those habitats may remain unoccupied no matter how suitable (Matlack 1994; Cain *et al.* 1998; Clark *et al.* 1998; Hubbell *et al.* 1999; Ehrlen & Eriksson 2000). This occurs both at the local scale, where suitable sites within a patch remain unoccupied, and at the regional scale, where suitable habitat within a novel community remains unoccupied. The successful introduction of plant seeds into unoccupied sites suggests dispersal limitation is widespread (Primack & Miao 1992; Tilman 1997; Ehrlen & Eriksson 2000; Turnbull *et al.* 2000; Zobel *et al.* 2000; McEuen & Curran 2006). It also implies that a substantial amount of suitable habitat remains unoccupied.

Species-level differences in fecundity, seed morphology and dispersal modes create unequal likelihoods that spatially proximate community members produce seeds that reach and colonize unoccupied space (Ribbens *et al.* 1994; Clark *et al.* 1998; Ehrlen & Eriksson 2000; McEuen & Curran 2004, 2006), though results in grasslands are mixed (Tilman 1997; Franzen & Eriksson 2003). Seed size, for example, appears to have strong influence upon seed dispersal and recruitment (Westoby *et al.* 1996; Clark *et al.* 1998; Eriksson & Jakobsson 1998; Ehrlen & Eriksson 2000; McEuen & Curran 2004, 2006). Larger seeds convey benefits in seedling establishment and survival; however, they are negatively correlated with dispersal distance (Tilman *et al.* 1994). Plants with smaller seeds produce greater numbers and cover more area, increasing the likelihood of striking upon suitable habitat; however, higher survival probability goes to the larger seeds, making more habitat area suitable. In conjunction with seed size, dispersal mode plays a major role in connecting seeds with suitable habitat. Plants with adaptations for dispersal by vertebrates and wind cover far more ground than those dispersed by invertebrates or gravity (Handel *et al.* 1981; Willson 1993; Matlack 1994; Brunet & von Oheimb 1998; Clark *et al.* 1998; Flinn & Vellend 2005; Moore & Elmendorf 2006).

The decrease in herbaceous richness from primary (relatively undisturbed) to secondary forests (once cleared) has been attributed to differing modes of dispersal among herbaceous species (Matlack 1994; Meier *et al.* 1995; Brunet & von Oheimb 1998; Singleton *et al.* 2001;

Mitchell *et al.* 2002; Harrelson & Matlack 2006). The growth of secondary forests creates suitable habitat for shade-tolerant herbaceous species which must migrate from extant populations (Matlack 1994; Bellemare *et al.* 2002). While many factors could explain the difference in herbaceous richness between primary and secondary forests, that it correlates negatively with distance to extant herbaceous communities suggests dispersal plays a large role (Kadmon & Pulliam 1993; Matlack 1994; Brunet & von Oheimb 1998; Bellemare *et al.* 2002; McEuen & Curran 2006). Furthermore, while forest herbs as a whole are not terribly effective dispersers (Brunet & von Oheimb 1998), many depend on ants (Beattie & Culver 1981; Handel *et al.* 1981; Giladi 2004, 2006; Moore & Elmendorf 2006). While dispersal distances are greater, and potentially more effective, with the presence of ant dispersers (Giladi 2004, 2006), but see (Mitchell et al. 2002), myrmecochores disperse excruciatingly slow (often < 1 m per year) (Heithaus *et al.* 1980; Cain *et al.* 1998; Giladi 2004). Not surprisingly, there is a dearth of ant-dispersed herbs in secondary forests (Mitchell et al. 2002). As most temperate forests are in some stage of recovery from clearing (Meier *et al.* 1995; Singleton *et al.* 2001; Bellemare *et al.* 2002), and considering the importance of species-specific dispersal competence in establishing and structuring forest communities (Matlack 1994; Clark *et al.* 1998; Ehrlen & Eriksson 2000), it is reasonable to conclude a considerable number of herbaceous species are in disequilibrium with their suitable habitat.

SPECIES PRESENT IN UNSUITABLE HABITAT

Source-sink dynamics

Just as species are absent from suitable habitat (e.g. metapopulation and dispersal limitation), species are often present in unsuitable habitat (Figure 1.4). In fact, a local population can persist indefinitely in unsuitable habitat ($\lambda < 1.0$) provided that its losses (death > birth) are mitigated by emigration from a population in suitable habitat ($\lambda > 1.0$) (Pulliam 1988, 2000). Across a landscape, a mosaic or gradient of environmental variables might occur at levels above and below the minimum threshold for reproduction. Within these discrete patches, a species replaces itself where resource levels are above the threshold (source) while failing to do so where resource levels are below (sink). Species persist in the sink habitats, however, if there is sufficient immigration (source emigration > sink mortality) from the source patches.

The source-sink dynamic, aka “mass effect” (Shmida & Ellner 1984; Kunin 1998; Leibold *et al.* 2004) can be viewed converse of metapopulation dynamics (Eriksson 1996). Whereas metapopulations depend on periodic dispersal within local populations to replace losses in suitable habitat, sink populations depend on periodic dispersal from extant populations to replace losses in unsuitable habitat. More importantly, in ideal metapopulations, the dispersal direction is reversible between local populations of equally suitable habitat while, in source-sink populations, dispersal is unidirectional from suitable to unsuitable habitat (Dias 1996). In as much as metapopulations likely exist at much larger, regional, scales, and contain multiple local subpopulations, they can be contrasted with source-sink dynamics which likely are more localized interacting subpopulations of different suitability. In both cases, the dynamic depends on dispersal to persist.

The ability to accurately detect a source-sink plant populations in nature remains challenging (Watkinson & Sutherland 1995; Dias 1996; Eriksson 1996; Pulliam 1996; Holt 1997; Mouquet *et al.* 2006). Furthermore, a sink habitat can be much larger than the source, making assessment of population dynamics misleading if the boundaries are cryptic (Pulliam 1988; Watkinson & Sutherland 1995). Regardless, there is extensive empirical evidence of source-sink plant populations, particularly among annuals and good dispersers (Shmida & Ellner

1984; Watkinson & Sutherland 1995; Dias 1996; Eriksson 1996; Pulliam 1996; Holt 1997; Mouquet *et al.* 2006).

Source-sink dynamics also muddy the relationship between species distribution and suitable habitat at the community level. Underlying most community ecology theory is the premise that the presence of a species indicates it has adaptations for local conditions and proximate interspecific species (Pulliam 2000), though neutral theory might be viewed as an exception (Hubbell 2001). Source-sink dynamics might increase a community's within-habitat diversity by augmenting the community with species for which the habitat is unsuitable via immigrants from suitable habitat. As long as the source population remains intact, this allows the local coexistence of many more species than could otherwise share the habitat. While source-sink dynamics might not act as a major structuring component of communities (Kunin 1998), a considerable portion of community membership may be in sink habitat (Pulliam 2000).

At the population or community level, source-sink theory severely weakens confidence in the premise that the mere presence of a species acts as an ironclad indicator of its suitable habitat. What appears as a generalist species due to a wide range of environmental tolerances might simply be a species spanning a source-sink boundary—an undetectable *faux fitness* border without knowledge of underlying demographic processes (e.g., λ). If the source-sink dynamic is widespread, and evidence suggests it is, a great deal of unsuitable habitat remains occupied.

Remnant populations

Remnant populations exist at the extreme end of dispersal limitation (Figure 1.5). Where dispersal limited populations in suitable habitat fail to reach unoccupied suitable habitat, remnant populations persist in unsuitable habitat that once was suitable. Eriksson (1996) defined remnant populations as systems of local populations with a declining growth rate ($\lambda < 1$) maintained by population inertia. Life history traits of certain species, such as long-lived plants with clonal propagation or extensive seed banks, buffer against extinction and can allow declining populations to withstand periods of unfavorable environmental conditions (Eriksson 1996). Remnant populations also may occur in habitat that has permanently shifted to unsuitable (e.g. succession or climate change) in a state of slow extinction.

Cloning allows the persistence of species in unsuitable habitat. Cloning is a widespread phenomenon in plant populations, and estimates from Europe and North America attribute a majority of herbaceous and shrub plant reproduction to cloning (Kanno & Seiwa 2004; Honnay & Bossuyt 2005). This appears to be a "waiting strategy" for weathering periods when suitable habitat becomes unsuitable (Tybjerg & Vestergaard 1992; Kudoh *et al.* 1999; Eckert 2002; Honnay & Bossuyt 2005). Clonal propagation likely makes some plant species more tolerant of environmental and demographic stochasticity, and might sustain small, isolated populations (Kanno & Seiwa 2004; Honnay & Bossuyt 2005). For example, there is evidence that perennial understory herbs shift from clonal to sexual reproduction as conditions grow favorable, such as increased light after changes in forest canopy (Whigham 1974; Tybjerg & Vestergaard 1992; Wijesinghe & Whigham 1997; Kudoh *et al.* 1999; Levine & Feller 2004) or vice versa when conditions become unfavorable (Honnay & Bossuyt 2005). While clonal reproduction allows short term population growth or maintenance ($\lambda > 1.0$), a population undergoing a long-term clonal phase may be unable to persist in light of environmental change due to lack of recombination via sexual reproduction. Gene flow can be further restricted if plants occur in dense, clonal patches, and pollen transfer is limited between ramets of a single genet (Charpentier 2002; Honnay & Bossuyt 2005).

Remnant persistence as a waiting strategy fails if habitat shifts permanently from suitable to unsuitable. This can occur at a local scale, such as long-lived, shade-intolerant plants that persist for decades after canopy closure during forest succession (Matlack 1994) or at a regional scale, such as long-lived, poor-dispersing plants at the trailing end of climate shifts (Svenning & Skov 2004). The forests of North America and Europe appear to be in such disequilibrium (Huntley 1990; Svenning & Skov 2004). Reconstruction of post-glacial tree distributions from pollen records suggest that forest communities shifted considerably since the Pleistocene glaciation, ~ 16 000 yr BP (Huntley 1990; Delcourt *et al.* 1993; Jackson & Overpeck 2000), and their current distribution lags behind their potential geographical ranges (Svenning & Skov 2004). Furthermore, maps of changing pollen patterns show a complex community history wherein each species responded differently to the climatic shifts, forming unique, metamorphosing community associations throughout time (Delcourt & Delcourt 1987; Prentice *et al.* 1991). The pollen record for herbaceous species is less extensive, but it appears they also fail to track climatic changes (Honnay *et al.* 2002; Skov & Svenning 2004) and clonal propagation increases near distribution boundaries (Dorken & Eckert 2001; Eckert 2002). For example, Pulliam *et al*. (in prep) showed that the perennial understory herb *Polygonatum biflorum* predominately reproduces clonally at the southern end of its range in the drier soils of the Georgia Piedmont, while it predominantly reproduces sexually in the moister soils of the North Carolina mountains.

A remnant population creates two temporary or permanent *faux fitness* scenarios: (1) plants that span the gradient from suitable to unsuitable habitat, or (2) plants that remain in unsuitable habitat and are absent from suitable habitat. In either case, plant presence and absence are poor indicators of the habitat suitability.

FAUX FITNESS THEORY AND ANALYSIS

Implications

The widespread occurrence of *faux fitness* in plant populations might tempt one to call into question the usefulness of the niche concept. If species can occur outside of suitable habitat, why use that framework at all? I would argue, however, that the appreciation of *faux fitness* increases our dependence on the niche concept as an organizing framework to discover both the occurrence and mechanisms of *faux fitness*. Instead, what might better be called into question is the measurement and assessment of the niche, not the theory. What appears to be lacking in niche and species distribution research are (1) consistent use of suitable habitat, environment and niche terminology, (2) an understanding of ecological theory as it relates to suitable habitat and species distributions and (3) appropriate data and/or statistical analysis of those data (Austin *et al.* 1990; Thomas & Kunin 1999; Pulliam 2000; Freckleton & Watkinson 2002; Chase & Leibold 2003; Leibold *et al.* 2004; Silvertown 2004; Mitchell 2005; Kearney 2006).

Climate envelope models

At present, there is probably as much literature criticizing climate envelope models as those utilizing or supporting them, with some doing both. Proponents suggest that matching current species distributions with correlated environmental or geographical variables (i.e. map species distribution data onto climate diagrams) in order to infer and predict future distributions under various climate change scenarios is a reasonable approach (Beerling 1993; Huntley *et al.* 1995; Baker *et al.* 2000; Moody & Meentemeyer 2001; Peterson & Vieglais 2001; Welk *et al.* 2002; Ackerly 2003; Peterson 2003; Skov & Svenning 2004; Thomas *et al.* 2004; Hamann & Wang 2006). Critics argue that the models fail to incorporate biotic interactions, dispersal limitation and evolutionary change (Davis *et al.* 1998; Vetaas 2002; Pearson & Dawson 2003; Guisan & Thuiller 2005; Hijmans & Graham 2006; Kearney 2006).

Often climate envelope models are touted as ecological niche models, but the users fail to incorporate or acknowledge the primary aspects of niche theory (Pearson & Dawson 2003; Kearney & Porter 2004; Guisan & Thuiller 2005; Kearney 2006). For example, current species distributions, without a doubt, reflect both biotic and abiotic influences and interactions, as well as all the exceptions attributable to *faux fitness*, yet the suitable habitat parameters in climate envelope models are almost universally topographic variables or abiotic proxies derived from topographical variables. This not only assumes a 1:1 match between suitable habitat and species distribution, but fails to acknowledge the inherent limitations of the predictions. The most serious of which is that the emergent abiotic variables and biotic interactions, such as competition and facilitation, vary both in time and space. Predictions based on climate envelopes may be very misleading if these interactions vary with climate change (Davis et al. 1998).

One of the common criticisms of climate envelope models is the failure to incorporate dispersal, or species-specific dispersal (Pearson & Dawson 2003). A well-parameterized species distribution model that is unable to distinguish between occupied and unoccupied sites may indicate a species that is propagule- rather than niche-limited (Moore & Elmendorf 2006). For example, for climate projection models to be accurate, one must assume that current species distributions and suitable habitat are close to equilibrium, but the known dispersal rate of herbs and trees is too slow to have reached current distributions from those during Pleistocene glacial (Cain *et al.* 1998; Clark *et al.* 1998). Species that only disperse meters per year have filled in thousands of kilometers north of southern glacial limits, which does not add up—even after 16,000 years (Pulliam 2000). This is known as Reid's Paradox, named after Clement Reid who first noted the discrepancy in 1899 (Clark et al. 1998). A “fat tail” dispersal curve where the skewed tail accounts for rare, long-distance dispersal events, was initially proffered as the best explanation for this phenomenon (Petit *et al.* 1997; Clark *et al.* 1998). Ackerly (2003) suggested that these dispersal rates are sufficient to keep the plants in equilibrium with suitable habitat over times scales of thousands of years, and there is some evidence that some species did rather well tracking Holocene changes in climate (Huntley *et al.* 1989; Johnson & Webb 1989). However, the “fat tail” of long-distance dispersal might not be dispersal after all. Molecular indicators suggest that rather than long-distance, post-glacial dispersal, *Fagus grandifolia* and *Acer rubrum* persisted in low-density populations within 500 km of the Laurentide Ice Sheet (McLachlan et al. 2005). This would signify that migration rates did not track climate change well at all, and for the assumption that plants can track suitable habitat to be met, some portion would have to already be there. Furthermore, a second alternative explanation is that indigenous humans, who extensively used and cultivated all modes of trees and herbs, quickly migrated into the post-glacial areas and may have acted as the mode of long-distance dispersal (Gilmore 1930; MacDougall 2003; McLauchlan 2003; Delcourt & Delcourt 2004).

Whether post-glacial vegetation tracks suitable habitat by hundreds, thousands or tens-of-thousands of years, the potential *faux fitness* gap is large enough that mapping current distributions, particularly if based upon geographic features, may not act as the best indicator of suitable habitat. If even a 100-year lag occurs between species distribution and suitable habitat shift due to climate change, it makes the predictability of climate models ineffective for the next century.

Measurement and analysis

The failure to consider *faux fitness* in climate envelope models is not just theoretical, but starts, literally and figuratively, from the ground up. This stems from (1) plant source data that fail to accurately address *faux fitness*, (2) insufficient habitat data that is incomplete or reflects geographical rather than environmental variables and (3) the interpretation of model output interpretation that overreaches the quality and scale of the input. The most frequent species distribution source data for climate envelope models comes from museum records or survey data (Hijmans & Graham 2006; Kearney 2006). While survey data surpasses museum data in capturing *faux fitness*, neither inspires great confidence (Guisan & Thuiller 2005; Mitchell 2005; Hijmans & Graham 2006). The shortcomings of simply using presence-only data should be obvious if considering *faux fitness*: it is highly plausible that a great number of plants can be found present in unsuitable habitat. Moreover, while the inclusion of absence improves the data, it is also highly plausible that a great number of plants are absent from suitable habitat. Presence-absence models thus contain two common types of error, those of commission (predicting a species where it does not occur) and those of omission (failing to predict a species where it does occur) (Guisan & Thuiller 2005).

Attempts at quantifying organism abundance/density and habitat attributes are based, generally, on correlation where a greater abundance or density implies more favorable habitat (Mitchell 2005). Instead, Pulliam (2000) suggested a straightforward and theoretically sound approach for measuring suitable habitat: “By measuring environmental conditions on the same sites where population growth rates are measured, ecologists can begin to determine what constitutes suitable and unsuitable habitat ... Furthermore, by coupling niche models with models of the physical environment, ecologists … may develop portable models of suitable habitat that allow them to predict the dynamics of species in places and times where they have not yet measured population dynamics.” Improved fitness data, such as per capita growth (λ) derived from demographic analysis, adds mechanism to predictive models. That is, rather than simply correlating increased abundance with soil moisture, including a mechanism such as reproduction gives an indication of performance as a function of soil moisture. In contrast with a habitat model approach, a mechanistic niche model begins with the fitness of the organism rather than its distribution (Beerling 1993; Kearney & Porter 2004; Hijmans & Graham 2006; Kearney 2006). This gives more useful response data which provides a stronger basis for predicting the relationship between climate and distribution (Beerling 1993; Kadmon & Pulliam 1993; Kadmon *et al.* 2003; Kearney & Porter 2004; Mitchell 2005; Hijmans & Graham 2006; Kearney 2006)

Toward this goal, experimental comparisons of physiological responses and fitness between habitats and in occupied and unoccupied space (e.g. experimental introductions to asses habitat suitability) would go along way toward elucidating distribution mechanisms and constructing predictive models (Ehrlen & Eriksson 2000, 2003; Moore & Elmendorf 2006). These mechanistic links are essentially useless, however, if lacking appropriate habitat data for association. Species-based measurements of basic environmental parameters such as temperature, pH, nutrients and light intensity are often lacking in demographic studies (Pulliam 2000). Furthermore, if one assumes that a niche is an attribute of an organism not an environment (Hutchinson 1957; Pulliam 2000; Chase & Leibold 2003; Kearney 2006), then basing ecological niche models solely on geographical parameters (e.g. topography) contradicts the underlying theory, and parameters based on geographic space can lead to inaccurate distributions in environmental space (Hijmans & Graham 2006). Direct and proximal parameters (e.g. precipitation, or better yet, soil moisture) should be used rather than indirect or distal predictors (e.g. altitude, latitude) (Austin 2002).

It must be acknowledged that the physiological, demographical and species-specific environmental data suggested here for correcting discrepancies in climate envelope models are neither readily available nor easy to obtain (Pearson & Dawson 2003; Guisan & Thuiller 2005; Mitchell 2005; Hijmans & Graham 2006). These data are labor, time and equipment intensive, on scales not conducive to rapid publication or graduate student intervals. Furthermore, while sometimes wildly incorrect, climate envelope models can provide coarse first approximations of potential climate change, particularly at the macro-scale (Pearson & Dawson 2003; Hijmans & Graham 2006). The relationship between species and their environment forms different spatial patterns at different scales in a hierarchical fashion: (1) at large scales and course resolution, climate is the dominant factor; (2) at local scales, the importance of topography and land-cover type increases; and (3) at small scales biotic interactions and microclimate dominate (Pearson & Dawson 2003; Guisan & Thuiller 2005). Applying climate envelope models at macro scales may override *faux fitness* and biotic interaction and provide course approximations of species distribution; however, predictive models do not perform well across regions and can falter when scaled up or down (Murphy & Lovett-Doust 2007).

The measure of functional plant traits have been suggested as an indirect approach for assessing plant fitness. Because functional traits such as leaf size react to environmental conditions in somewhat predictable ways, and these can act as a surrogate for fitness measures such as photosynthetic efficiency, they are viewed as a reasonable surrogate for fitness (Reich *et al.* 1997; Cornelissen *et al.* 2003; Reich *et al.* 2003; Stubbs & Wilson 2004; Wright *et al.* 2004; Poorter & Bongers 2006). Plant functional traits have even been suggested as core parameters valuable for scaling up to larger ecological processes such as distribution and community assembly (Shipley *et al.* 2006; Whitfield 2006). However, within-community and within-species variation in plant functional traits can be large, and this is often correlated with environmental gradients (Wright *et al.* 2004; Poorter & Bongers 2006; Ackerly & Cornwell 2007), yet consideration of *faux fitness* is largely absent or minimized. Thus, while the physiological and adaptive significance of plant functional trait variation for the species is emphasized, and implicit niche assumptions are made with no measure of demographic fitness, there has been insufficient consideration of plant functional trait distribution and suitable habitat. This is a glaring oversight of *faux fitness* dynamics and makes the scaling and predictability of plant functional traits questionable.

Conclusions

A large body of empirical and theoretical evidence undermines confidence in a 1:1 correlation between species distributions and suitable habitats, a trend here touted as *faux fitness*. The implications for scientific advancement and the application of ecological research are not small. While the awareness and acknowledgement of *faux fitness* dynamics continues to grow, the assumption that species distribution and suitable habitat are in equilibrium remains implicit and explicit in ecology. Overlooking *faux fitness* not only further confuses and muddles ecological niche theory, but a nebulous or contradictory body of work on potential species distributions confuses policymakers and nonscientists already dubious about science and climate change.

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FIGURES

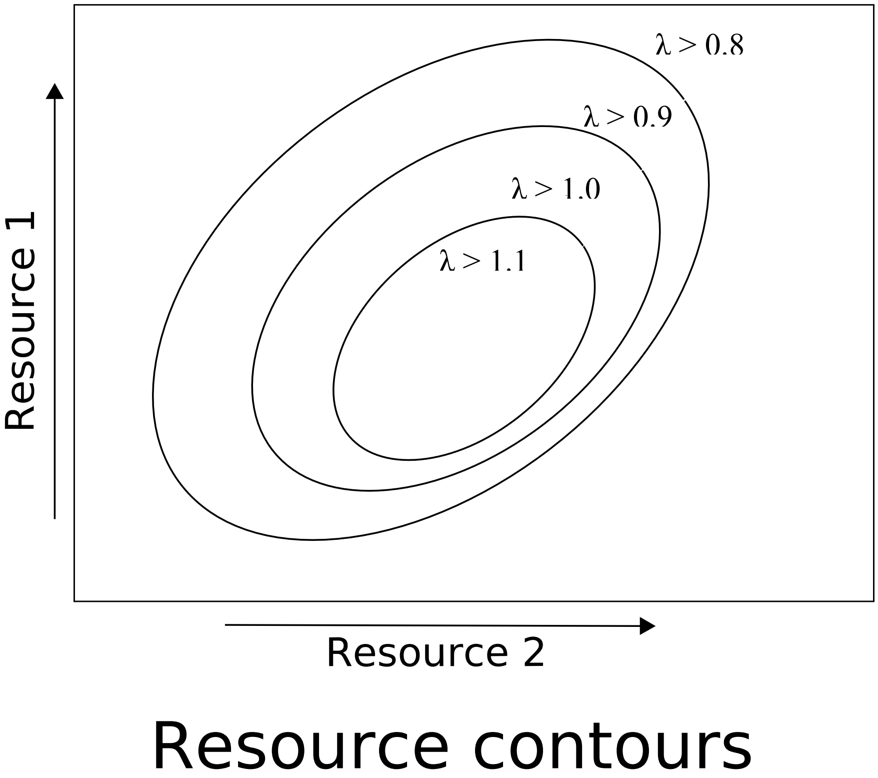
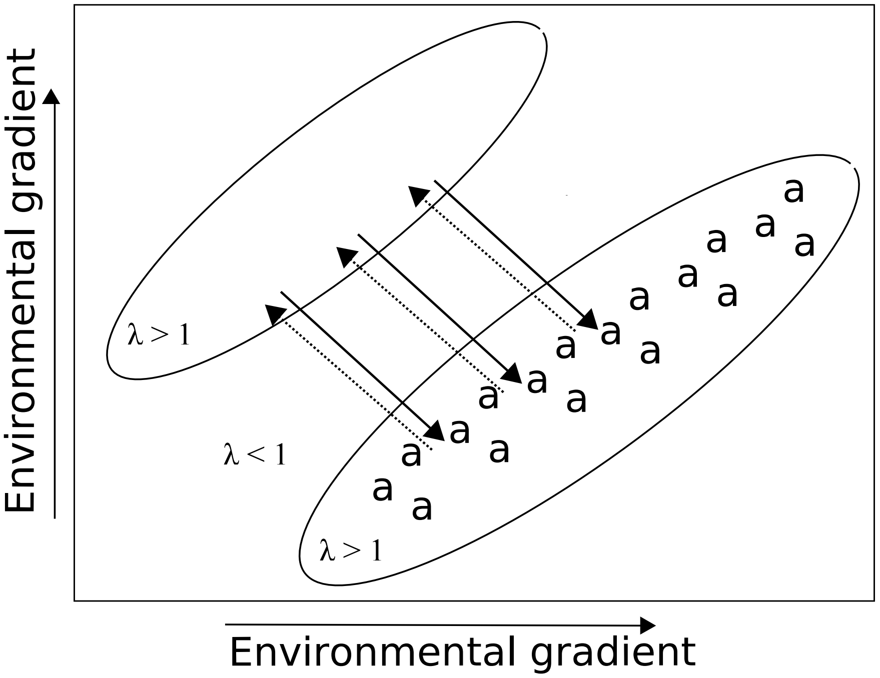


Figure 1.1. Map of the theoretical niche with contours of the per capita growth rate (λ) as predicted for two essential resources. Areas that fall within the contours where $\lambda > 1.0$ represent the minimum conditions needed for demographic fitness and areas that fall outside the range where $\lambda > 1.0$ represent unsuitable conditions.



Metapopulation

Figure 1.2. Recurrent localized extinctions due to environmental, demographic and genetic stochasticity leaves suitable habitat (λ > 1.0) as well as unsuitable habitat (λ < 1.0) unoccupied at any given time, but dispersal between local populations prevents extinction of the metapopulation as a whole (Levins 1969, 1970, Hanski 1982, 1998). Solid arrows represent dispersal into an extinct local population; dotted arrows represent potential reciprocal dispersal.

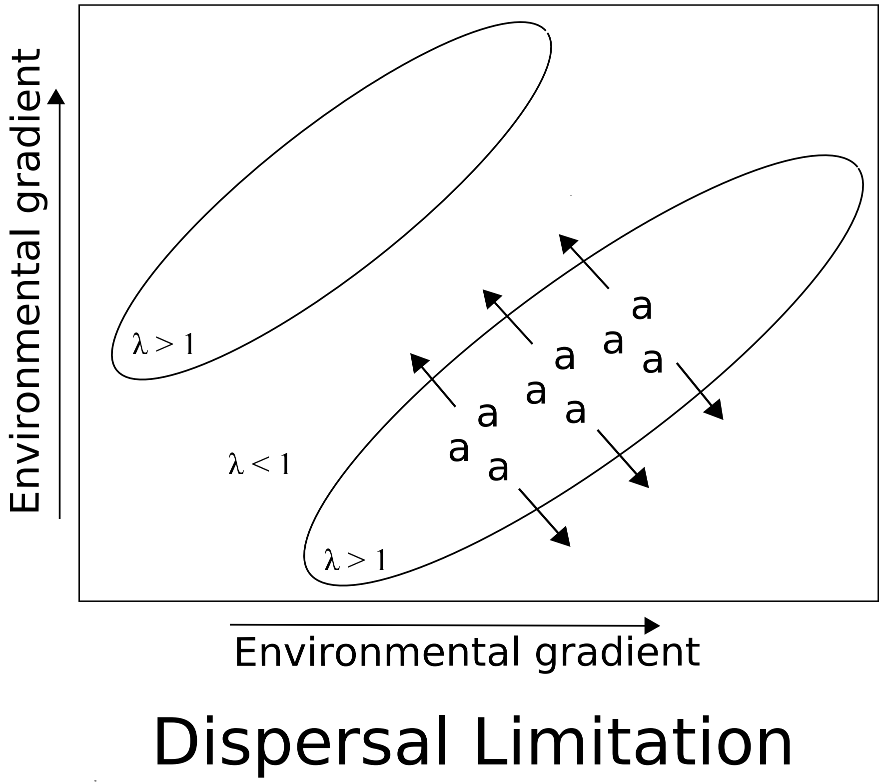


Figure 1.3. Suitable habitat (λ > 1.0) remains unoccupied due to the failure of propagules to reach it (Matlack 1994, Clark et al. 1998, Ehrlen and Erikkson 2000). Arrows represent dispersal.

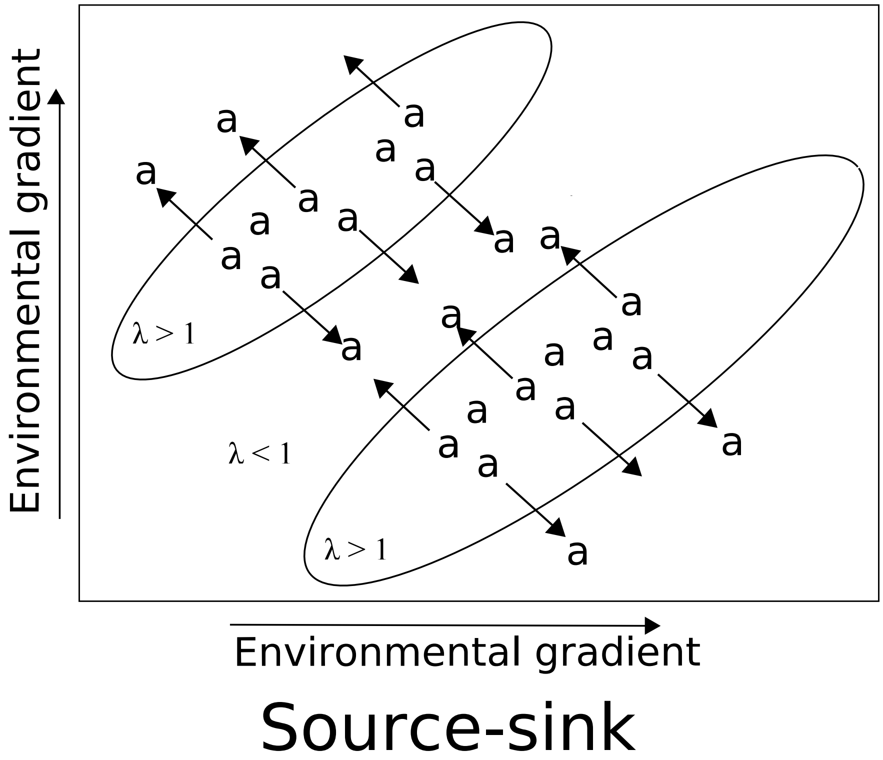


Figure 1.4. Species are present in unsuitable (sink) habitat (λ < 1.0), where they fail to reproduce at high enough rates to sustain the population. However, the population persists due to immigration from suitable (source) habitat (λ > 1.0). Arrows represent dispersal. (Pulliam 1988, 2000).

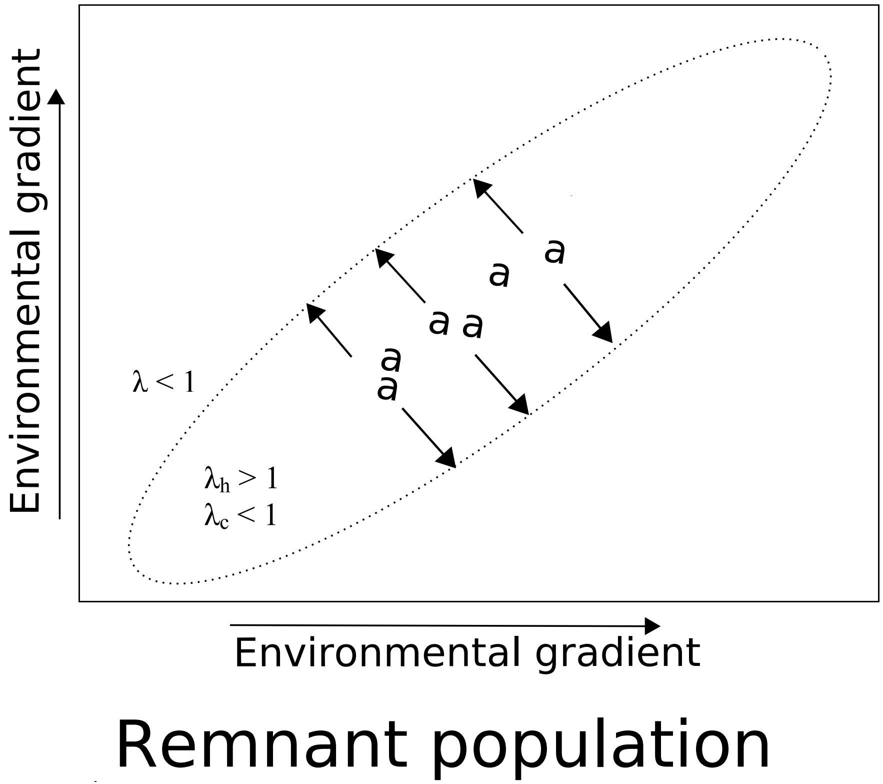


Figure 1.5. Plant populations that flourished in historically suitable habitat ($\lambda_h < 1.0$) persist for long periods in currently unsuitable habitat ($\lambda_c < 1.0$) (Eriksson 1996). Arrows represent dispersal.

CHAPTER 2

MECHANISMS DRIVING UNDERSTORY EVERGREEN HERB DISTRIBUTIONS ACROSS SLOPE ASPECTS – AS DERIVED FROM TOPOGRAPHIC POSITION

INTRODUCTION

The plant community shifts across the boundaries of nonequatorial north- and south-facing slope aspects is a striking and long-documented biotic transition. This pattern occurs worldwide (Smith 1977; Lieffers & Larkin-Lieffers 1987; Bale & Charley 1994; Sternberg & Shoshany 2001; Holst *et al.* 2005) and at every level (herbaceous, shrub and tree) of plant community composition (Cantlon 1953; Hicks & Frank 1984; Huebner *et al.* 1995; Olivero & Hix 1998; Fekedulegn *et al.* 2003; Searcy *et al.* 2003; Desta *et al.* 2004). Aspect-related plant community variation also includes species diversity (Olivero & Hix 1998; Hutchinson *et al.* 1999; Small & McCarthy 2002), phenology (Cantlon 1953; McCarthy *et al.* 2001) and productivity (Hicks & Frank 1984; Fekedulegn *et al.* 2003; Desta *et al.* 2004).

The distinct change in plant communities across north- and south-facing environments corresponds with contrasting environmental gradients driven by greater solar irradiation (18-37%) on south-facing slopes in the Northern Hemisphere (Geiger 1965; Radcliffe & Lefever 1981; Galicia *et al.* 1999; Searcy *et al.* 2003). This occurs because the surface angle of south-facing slopes orients more directly with the sun and thus the surface receives a greater duration and intensity of solar rays. Solar irradiation drives variation in temperature and moisture (Rosenberg 1983), resulting in a relatively warmer, drier south-facing slope microclimate

(Shanks & Norris 1950; Cantlon 1953; Werling & Tajchman 1984; Bolstad *et al.* 1998; Desta *et al.* 2004).

The annual cycle of the solar zenith angle (the height of the sun's path across the horizon) creates a 50-800 % annual shift in surface irradiation. This cycle, combined with the seasonal change in deciduous forest canopy cover, creates a highly variable understory light and temperature regime (Cantlon 1953; Holst *et al.* 2005), and evergreens are exposed to the full spectrum (Neufeld & Young 2003). While the impact of north- and south-facing slopes on the distribution of herbaceous plants and evergreen shrubs has been investigated (Cantlon 1953; Lipscomb & Nilsen 1990; Huebner *et al.* 1995; Valverde & Silvertown 1997; Olivero & Hix 1998; McCarthy *et al.* 2001; Ackerly *et al.* 2002), there has been scant focus on the distribution of evergreen understory plants in relation to aspect.

The overall objective of this research is to investigate the distribution and performance of understory evergreen herbaceous plants on north- and south-facing slopes. Specifically, I ask the following questions:

I. *Does increased southerly aspect orientation correlate negatively with evergreen understory plant presence, abundance and reproduction?* Elevation and slope angle are also explored.

II. *Can estimated environmental variables such as heat load and seasonal light estimate evergreen niche requirements as well as topographic position?* Topographic position has traditionally been used to explain plant community transitions between north-and south-facing aspects, and it has worked well. However, if organisms rather than environments have niches (Hutchinson 1957; Kearney 2006)—that is, the conditions at a location not the location itself determine niche space—environmental variables (seasonal light and heat load) can provide a more mechanistic estimation of evergreen understory distribution.

III. *Do both winter and summer light conditions influence evergreen understory plant distribution?* Given that the thick, tough leaves of evergreens protect them in dry, infertile habitats (Reich *et al.* 2003; Givnish *et al.* 2004), and tree canopy intercepts almost all summer light, winter rather than summer light should most limit the presence, abundance and reproduction of evergreen herbs.

METHODS

Study areas

This study was conducted in the Blue Ridge Mountains of western North Carolina at Coweeta Hydrologic Laboratory (CWT) (including some ventures into the adjacent Standing Indian Basin) in the Nantahala National Forest (35^{o}01' N latitude) in Otto-Macon County and in the Piedmont region of Georgia at Whitehall Forest (WHF) (33^{o}52' N latitude) in Athens-Clarke County. CWT is approximately 120 km north of WHF. Mean annual precipitation at WHF is 126 cm, the mean January temperature is 5.4º C and the mean July temperature is 26.4º C. Mean annual precipitation at CWT is 181 cm, the mean January temperature is 6.1º C and the mean July temperature is 24.7º C.

Study species

The understory evergreen study plants included 10 species: two ferns, *Polystichum acrostichoides* (Michx.) Schott and *Asplenium platyneuron* (L.) B.S.P.; a vine, *Mitchella repens* L.; a gramminoid, *Carex plantaginea* Lam; and six forbs, *Chimaphila maculata* (L.) Pursh, *Galax urceolata* (Poir.) Brummitt, *Goodyera pubescens* (Willd.) R. Br. ex Ait. f., *Gaultheria procumbens* L., *Heuchera villosa* Michx. and *Hexastylis arifolia* (Michx.) Small. Nomenclature follows USDA NRCS (2006). Additional understory evergreen plants were investigated but subsequently excluded from analysis because they were not found in sufficient numbers.

Data collection

Aspect transects were established across north- and south-facing slopes at CWT and WHF during July-August 2006. Using digitized U.S. Geological Survey topographical maps and GPS coordinates, east-west ridges were pre-selected at CWT and WHF based on degree of north-south aspect and potential to balance north- and south-facing plots in the study design. The location, direction and length of each transect was predetermined with no regard for plant communities or species distributions; however, all transects were located along slopes and ridges that were primarily covered in deciduous forest, and an attempt was made to avoid dense *Rhododendron*/*Kalmia* sp. stands at CWT and dense *Pinus* sp. stands at WHF once the surveys were initiated in order to standardize the plots. Along each transect 2 x 20 m plots—oriented with long axes perpendicular to slope contours—were established at 50-m intervals using GPS degrees and minutes to delineate spacing.

All herbaceous evergreen plants were surveyed within each plot. Reproductive assessment was based on the presence of reproductive structures (i.e. fruits, flowers, sporangia), but the timing of the surveys prohibited the collection of this information for *G. urceolata*, *G. procumbens*, *H. arifolia* and *Mitchella repens*. Far more plots were utilized at CWT than WHF due to the larger study area and, more importantly, the far greater relief which required more plots to characterize the entire slope aspect. At each plot, aspect (azimuth degrees), percent slope (horizontal angle) and elevation were measured with a compass, a Suunto handheld clinometer, (Vantaa, Finland) and a Garmin 12XL GPS unit (Kansas City, KA USA) with Gilsson amplified GPS antenna (Hayward, CA USA).

Data analysis

Slope aspect azimuth was first converted from the 0-360 ° compass scale to a linear (0-180) scale for regression analysis. The conversion was accomplished using the following equation: *Linear*

$\text{azimuth} = 180-\lvert \text{compass azimuth}-180\rvert$, where the upright bars indicate absolute value. This conversion gave northerly aspects a value approaching 0 and southerly aspects a value approaching 180, a useful conversion for linear or linearized models. This transformation also converted east and west azimuth degrees so that they were equally distant from north (i.e., 10 and 350 compass azimuth degrees = 10 linear azimuth degrees).

Relative solar irradiation for summer (July) and winter (December) was calculated based on slope, aspect and latitude using the tables of Frank and Lee (1966). Solar irradiation is the incident flux of radiant energy (derived from the sun) per unit area. This does not account for shading by vegetation on the ground. An approximation of a dimensionless heat load was calculated from the irradiation equation of McCune and Keon (2002): $K\downarrow = 0.339 + 0.808\cos(L)\cos(S) - 0.196\sin(L)\sin(S) - 0.482\cos(A)\sin(S)$, where L = latitude, S = slope degree, A = linear azimuth. The units of all the variables were transformed into radians. Because direct incident irradiation is symmetrical about the north-south axis, but temperatures are symmetrical about the northeast-southwest line—assuming that a slope with afternoon sun will have a higher maximum temperature than an equivalent slope with morning sun—the linear azimuth was shifted from a maximum on south slopes and minimum on north slopes to a maximum on southwest slopes and a minimum on northeast slopes. This was accomplished by changing the linear folding of aspect from a north-south line to northeast-southwest: $\text{Linear azimuth} = 180-\lvert \text{compass azimuth}-225\rvert$.

Generalized linear models

Historically, aspect research has focused upon topographic factors such as aspect, slope and elevation rather than environmental variables such as incident radiation and heat load. In order to investigate potential mechanisms for topographical distributions, the regression analysis was split into two models: topographic (aspect, slope and elevation) and environmental (heat load, summer and winter light). An additional reason for splitting the models was that the environmental covariables were generated from the topographical covariables, making their inclusion in the same models problematic due to a lack of independence.

An analysis of covariance (ANCOVA) for the dependent variables (plant presence, abundance and reproduction) treated site as a cofactor and aspect (linear azimuth degrees), elevation, slope (percent), heat load and light (summer and winter potential incident radiation) as covariables using generalized linear models (GLMs). First and second order and interaction terms were included for all covariables (Full topographic model: $Y_i = intercept + Aspect_i + Aspect_i^2 + Elevation_i + Elevation_i^2 + Slope_i + Slope_i^2 + interaction_i$; Full environmental model: $Y_i = intercept + Heat\ load_i + Heat\ load_i^2 + Summer\ light_i + Summer\ light_i^2 + Winter\ light_i + Winter\ light_i^2 + interaction_i$).

Presence and reproduction were modeled assuming binomial error distributions ($Y_i \sim Binomial\ (n_i, p_i)$) and abundance was modeled assuming a Poisson error distribution ($Y_i \sim Poisson\ (\mu_i)$). The probabilities of presence and reproduction were linked to the linear predictor variables via the logit link function ($log\ (Y_i/(1\text{-}Y_i) = \beta_0 + \beta_{Xi + \ldots}$) and the probability of abundance was linked to the linear predictor variables via the log link function ($log\ (Y_i) = \beta_0 + \beta_{Xi} \ldots$). Presence and reproduction were measures of the presence or absence of a plant and reproductive structures (flowers, fruit stalks or sporangia), respectively, per 20 m^2 plot while abundance was the total number of plants per 20 m^2 plot.

Bayesian hierarchical GLMs were used to generate 90 % credible intervals for the regression coefficients (intercept and line slopes) for both models. The Bayesian models were implemented in the WinBUGS 1.4.2 software package. The models were implemented in a hierarchical framework with normally distributed, noninformative priors (*Normal* (*0,0.001*)). Because graphical analysis suggested that the evergreens responded similarly to the environmental variables as a community (e.g. reduced presence with higher winter light), but individual species inhabited different portions of the gradient (some species only occurred in lesser light levels), random intercepts that varied per species (n=10) were included in the presence and reproduction models while random intercepts varied per landscape (n=2) in the abundance models.

The 90% credible intervals for regression coefficients were generated using Markov chain Monte Carlo (MCMC) simulations in WinBUGS. A minimum of 20,000 iterations were used to "burn-in" the models before coefficient estimates were measured and 5,000 iterations were used to generate the posterior distributions. In order to mitigate coefficient autocorrelation between iterations, the output was "thinned" by only using every 20th measure. The iterations were run with three chains and all chains converged (Gelman-Rubin statistic < 1.1).

Lastly, a generalized linear model of topographical and environmental predictor variables for the abundance of plants and reproduction plus second-order terms were projected onto a two dimensional contour model so the combined predicted slopes become contour intervals. In this framework, the contour intervals represented the expected abundance or probability of reproduction at the given combination of covariables.

RESULTS

Sites

A total of 2,408 plants (1,548 CWT; 860 WHF) were surveyed in 136 plots (93 CWT; 43 WHF). The north-south transects used for delineating the evergreen herb plots crossed topography gradients that averaged 1,163 m at CWT and 184 m at WHF; the slope of the transects averaged 45.1 % at CWT and 28.4 % at WHF. While slope and elevation were far greater at CWT than WHF, the ranges of environmental variables—summer light, winter light and heat load—were only slightly higher at WHF.

Community scale

South-facing slopes did not appear to provide suitable habitat for understory evergreen herbs in as much as the plants generally occurred and reproduced far less on south- than north-facing slopes (Table 2.1). When analyzed in conjunction with additional topographical variables, southerly aspect remained a strong negative influence upon understory herb presence, abundance and reproduction, but slope and elevation also provided strong predictive power (Figure 2.1). Plant presence, abundance and reproduction decreased with elevation, then rebounded at the highest elevations suggesting that the evergreen understory communities occur least at intermediate elevations. Conversely, presence, abundance and reproduction all peaked at intermediate slope angles. The significant aspect:elevation interaction term indicated that plant presence and abundance increased as a function of increased aspect combined with increased elevation.

Increased southerly aspect and heat load consistently correlated with decreased understory evergreen presence, abundance and reproduction (Figure 2.1). Plant presence and reproduction decreased with summer light, but growth increased. Plant presence and reproduction peaked at intermediate levels of winter light, while growth increased at the highest level of winter light. The significant heat load:winter light interaction term indicated that plant presence, abundance and reproduction increased with increased heat load combined with increased winter light. Heat load combined with summer light increased abundance but decreased reproduction.

The topographical contour graph of abundance as a function of aspect and elevation indicate that understory evergreen herbs occur most often on northerly aspects at elevations of 200-1000 m (Figure 2.2a). The reproduction graph indicates a stronger elevational impact as most reproduction is predicted to occur on northerly aspects at the lower elevations. The environmental contour graph of abundance as a function of heat load and summer light predicts that understory evergreen herbs should occur most often where summer light is highest but heat load is lowest (Figure 2.2b). The reproduction graph indicates a more intermediate affect of heat load suggesting that plant reproduction peaks at somewhat higher temperatures than plant abundance.

Species scale

Four of the study species were recorded at both CWT and WHF (*C. maculata, C. plantaginea, P. acrostichoides and G. pubescens*); while *G. urceolata, H. villosa,* and *G. procumbens* were only recorded in CWT transects, and *M. repens, A. platyneuron* and *H. arifolia* were only recorded in WHF transects (Table 2.1). *Polystichum acrostichoides* was the most widespread and abundant evergreen plant at WHF (occurring in almost 50% of the plots), while *C. maculata, M. repens* and *H. arifolia* also occurred in appreciable numbers. *Chimaphila maculata* also occurred frequently and in large numbers at CWT followed by *G. pubescens* and *P. acrostichoides*. *Galax urceolata* and *H. villosa*, both of which only occurred at CWT, appeared to have distinctly clumped distributions as they occurred in less than 20% of the plots but had the two highest CWT abundances.

The general negative trend between the evergreen herb community and south-facing slopes was reflected in the individual species (Table 2.1, Figure 2.3). Most of the species occurred far more in north- than south-facing sites. The south-avoiding pattern was particularly strong in *H. villosa*, *P. acrostichoides*, *H. arifolia* and *M. repens,* while *A. platyneuron* and *C. maculata* had similar frequencies on north- and south-facing slopes (Figure 2.2a). Elevation appeared to discriminate well among the evergreen plant species, though this pattern might be more related to geographic distribution (WHF-only plants versus CWT-only plants) than meters above sea level (Figure 2.2b).

The WHF-only plants (*M. repens, A. platyneuron* and *H. arifolia*) predictably segregated to elevations below 200 m, and the CWT-only plants (*G. urceolata, H. villosa* and *G. procumbens*) remained above 750 m. Slope discriminated among the evergreen plants similarly to elevation, likely because high elevation corresponds with increased slope angle (Figure 2.3).

There is little discrimination between evergreen speciess in response to heat load as almost all of the plants occur at lower heat load levels (Figure 2.3). Only *M. repens* and *A. platyneuron* appear indifferent to heat load. While the difference between the evergreen plants in relation to summer light was not great, *M. repens, A. platyneuron* and *H. arifolia* and *P. acrostichoides* occurred more where summer light was highest (Figure 2.3). Not surprisingly, three of these occur at WHF exclusively. Conversely, only *G. pubescens* and *G. procumbens* occurred more where light was less. A clearer community pattern emerges with winter insolation as all the evergreen plants except *C. maculata* and *A. platyneuron* occur more where winter light levels are lower (Figure 2.3).

DISCUSSION

Plant species vary across north-south slope boundaries; this is a well-established pattern that is both consistent and cosmopolitan. In general, south-facing slope environments pair relatively high temperatures with low soil moisture in the summer and relatively high light with low temperatures in the winter. Both of these combinations stress plants (Raven 1989; Pearcy *et al.* 1994; Neufeld & Young 2003), and evergreens are exposed to both extremes on south-facing slopes. Based on this knowledge and field observations, it was predicted that understory evergreen herbaceous species would occur and reproduce less on south-facing than north-facing slopes. This held true. It also was predicted that derived environmental models would explain variance in evergreen distributions as well as topographic position, and provide a more mechanistic explanation of the dynamics influencing understory evergreen distribution, which also held true. Lastly, due to the high light/low temperature environment during winter, it was predicted that winter light would best explain variance among the plants. The results of this research suggest that winter and summer light, as well as heat load, strongly influence understory evergreen distributions.

Topographic models

While some evergreen species occurred in appreciable numbers on south-facing slopes, the distribution of the evergreen community clustered on north-facing slopes (Table 2.1, Figures 2.1-2.3). Five of the species either occurred exclusively or had pronounced north-facing slope affinities with few or no outliers on southerly slopes, and community presence and abundance decreased as aspect increased in southerliness. Furthermore, reproduction decreased with southerliness.

Slope and elevation also had robust predictive power on evergreen community distribution and performance, and they discriminated well between evergreen species (Figures 2.1, 2.3). That is, individual species responded uniquely to differences in slope and elevation while they generally responded *en masse* to differences in aspect. Elevational gradients tend to vary in soil moisture and temperature, which are strong variables in sorting plant species distributions (Whittaker 1956). In a survey of evergreen and deciduous shrubs, (Ackerly et al. 2002) found elevation only second to aspect in explaining species distributions. Temperature and moisture also are two major environmental variables that change (temperature decreases, moisture increases) with elevation (Whittaker & Niering 1975; Swift Jr. *et al.* 1988; Bolstad *et al.* 1998; Bolstad *et al.* 2001), and elevation is an environmental gradient long recognized for sorting species (Whittaker 1956). The interaction effect between aspect and elevation suggested that increased elevation had a positive impact on presence with southerly aspects, possibly a mitigation of the dry, hot conditions of southerly aspects by the wet, cool conditions of upper elevations.

While aspect and elevation consistently correlated negatively with understory evergreen plants, their presence, abundance and reproduction consistently peaked at intermediate slope angles (Figure 2.1). One possible explanation for the slope response is that evergreen understory plants are poor competitors (slow growth, low rates of light harvest and diminutive height) (Lambers et al. 1998), and some species may fare better in a less competitive environment on steep slopes but fail to thrive on the steepest slopes. In addition, evergreen understory plants get buried by fallen tree leaves, and leaf accumulation is less on steep, north-facing slopes due, in part, to faster decomposition and fewer high-lignin oak leaves (Melillo *et al.* 1982; Lang & Orndorff 1983; Hicks & Frank 1984).

Environmental models

Historically, plant presence and abundance has been correlated with aspect which is associated with environmental variables, but this lacks a direct correlation between environmental variables and distribution. Topographic position has robust predictive power for the evergreen herbs, but gives little indication of the mechanism behind the distribution.

Evergreen presence, abundance and reproduction all decreased with increased heat load (Figure 2.1). Few of the evergreens had substantial abundance where exposed to the highest heat load levels, and most all of the evergreens occurred more at lower heat loads than where they were absent (Figure 2.3). Heat load likely acts as a reasonable proxy for temperature and soil moisture, both of which—particularly soil moisture—have long been linked with plant distributions (Lambers *et al.* 1998; Neufeld & Young 2003).

The seasonal shift in solar irradiation and tree canopy cover creates annual extremes in the understory environment. This seasonal dynamic creates two environmental extremes that can inhibit plants: (a) low soil moisture combined with high temperatures in summer (Raven 1989; Pearcy *et al.* 1994; Neufeld & Young 2003) and (b) high irradiance combined with low temperatures in winter (Verhoeven *et al.* 1999; Neufeld & Young 2003). Summer light is a limited resource for understory plants beneath deciduous canopy, but evergreen community presence decreased with increased summer light, though this picture was muddied at the species level as several evergreens occurred more with greater summer light and reproduction increased with summer light (Figures 2.1-2.3). Half of the evergreen species occurred more in higher summer light, with a few distributed almost exclusively in the highest light environments. Only two species occurred more in habitats with less summer light. This suggested that while presence did not hinge upon summer light, increased light in the shady understory environment benefited some species, though associated effects such as increased temperature and decreased soil moisture were detrimental.

Winter light also had a mixed impact on the evergreen community measures, though its negative effect on individual species was far more consistent (Figures 2.1, 2.3). Almost all of the evergreen plants were present more in lower winter light environments. Evergreen plants growing in shady habitats are less stressed during the winter than the same plants in sunny habitats (Logan *et al.* 1998; Adams *et al.* 2001; Adams *et al.* 2004). This suggests that evergreen plants are more sensitive to winter photoinhibition (high light, low temperature) than summer photoinhibition. The positive interaction effect of heat load and winter light on plant presence, abundance and reproduction supports this explanation. Locations with warmer winter conditions appear to ameliorate the photoinhibitory impact of winter light.

While winter light does not discriminate between species well, all of the evergreens had highest abundance at the lower range of winter incident radiation in a pattern remarkably similar to aspect (Figure 2.3). Winter insolation might act as an environmental filter limiting evergreen understory plant distribution on south-facing slopes while the effect is relatively benign or absent on north-facing slopes. The ability to adjust to cooling temperatures appears to be species specific (Tissue *et al.* 1995; Skillman *et al.* 1996; Neufeld & Young 2003), and this might explain the differences between evergreen species and winter light sensitivity.

Conclusions

The results of this survey suggest aspect provides the best predictor where evergreen understory communities will occur on the landscape while slope and elevation provide the best discrimination between species within that distribution. Furthermore, while the topographic variables suggest *where* the plants occur, heat load and seasonal light provide the best clues *why* they are there. In general, where heat load and light are highest, understory evergreen plants occur and reproduce the least (south-facing slopes)**.** This suggests that the dynamic limiting evergreen plants very well could be low soil moisture combined with high temperatures in summer and/or high irradiance combined with low temperatures in winter.

The results of this survey strongly indicate that soil moisture, temperature and light are strong candidates for further research into the distribution of evergreen understory plants. A great body of research has correlated plant communities and dichotomies in aspect with a set of assumptions about moisture, temperature, light and nutrients. In most studies, one topographic or environmental variable is paired with the change in plant communities. This traditional approach works reasonably well for pattern recognition, but lacks power in explaining the mechanism for aspect dynamics. This study takes the traditional approach one step further by measuring and estimating several covariables and using them to predict variance in plant distribution and traits. However, many explanatory variables are still left unexplored and the environmental variables used here were estimated from topographic variables rather than directly measured.

A productive next step in investigating slope aspect dynamics would involve direct field measurements of environmental variables and plant demography. In addition, experimental research, such as transplants and environmental manipulation, would further elucidate the fundamental niche requirements of evergreen herbs. Clearly, more experimentation is needed to elucidate the mechanisms behind the patterns.

This research focused on recognizing distribution patterns of understory evergreen plants across north- and south-facing slopes. The next step is an investigation of evergreen understory demography (Chapter 3). The demographic research focuses on plant population dynamics and the impact of directly measured environmental variables (such as soil moisture, light and temperature) on those patterns. The second step is a manipulative experiment investigating evergreen understory plants transplanted onto north- and south-facing slopes along with manipulations of light and soil moisture and direct measures of environmental variables (Chapter 4.). Both of these investigations should further illuminate the patterns and questions generated here.

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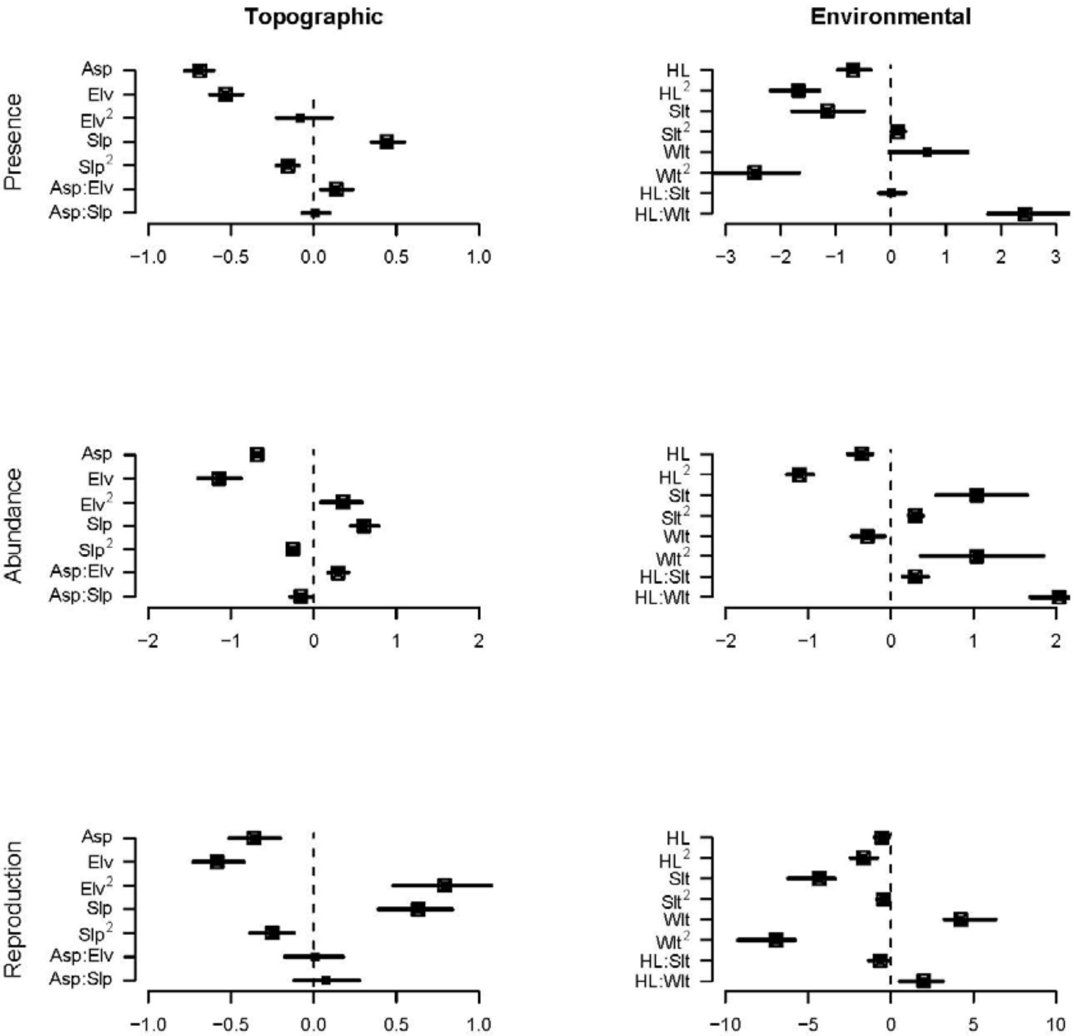
TABLES AND FIGURES

Table. 2.1. Understory evergreen herbs with frequency and abundance on from north- and south-facing plots at Whitehall Forest (WHF) in GA and Coweeta Hydrologic laboratory (CWT) in NC. Frequency is the proportion of 20m2 plots where the plant occurred and abundance is the number of plants per 100m2. For each plant, its highest frequency and abundance for each category are in

		Slope aspect				Site			
		Frequency		Abundance		Frequency		Abundance	
Species	(*n*)	North	South	North	South	WHF	CWT	WHF	CWT
Chimaphila maculata	280	0.30	**0.40**	**65.0**	45.0	**0.40**	**0.40**	32.5	**67.5**
Mitchella repens	119	**0.20**	0.10	**27.5**	2.5	**0.40**	0.00	**40.0**	0.0
Asplenium platyneuron	53	0.10	0.10	**15.0**	7.5	**0.30**	0.00	**30.0**	0.0
Hexastylis arifolia	347	**0.18**	0.06	**126.0**	27.4	**0.32**	0.00	**206.6**	0.0
Carex plantaginea	89	**0.20**	0.12	**24.0**	2.9	**0.21**	0.12	**16.5**	11.5
Polystichum acrostichoides	490	**0.45**	0.17	**181.4**	16.8	**0.47**	0.22	**170.4**	56.2
Goodyera pubescens	220	**0.29**	0.13	**46.6**	30.8	0.03	**0.32**	2.0	**60.0**
Galax urceolata	321	**0.16**	0.10	**125.0**	15.9	0.00	**0.20**	0.0	**110.8**
Heuchera villosa	436	**0.10**	0.00	**94.1**	0.0	0.00	**0.08**	0.0	**73.8**
Gaultheria procumbens	53	**0.08**	0.02	**12.3**	0.5	0.00	**0.08**	0.0	**10.0**



Topographic

Environmental

Figure 2.1—Mean values with 90% credible intervals for coefficients from the Bayesian hierarchical models of topographic (*Aspect (Asp), Elevation (Elv), Slope (Slp)*) and environmental (*Heat Load (HL), Winter Light (Wlt), Summer Light (Slt)*) covariables including second-order and interaction terms. Coefficient slopes which do not differ from 0 (dotted line) indicate a lack of significant relationship between the predictor and response variables.

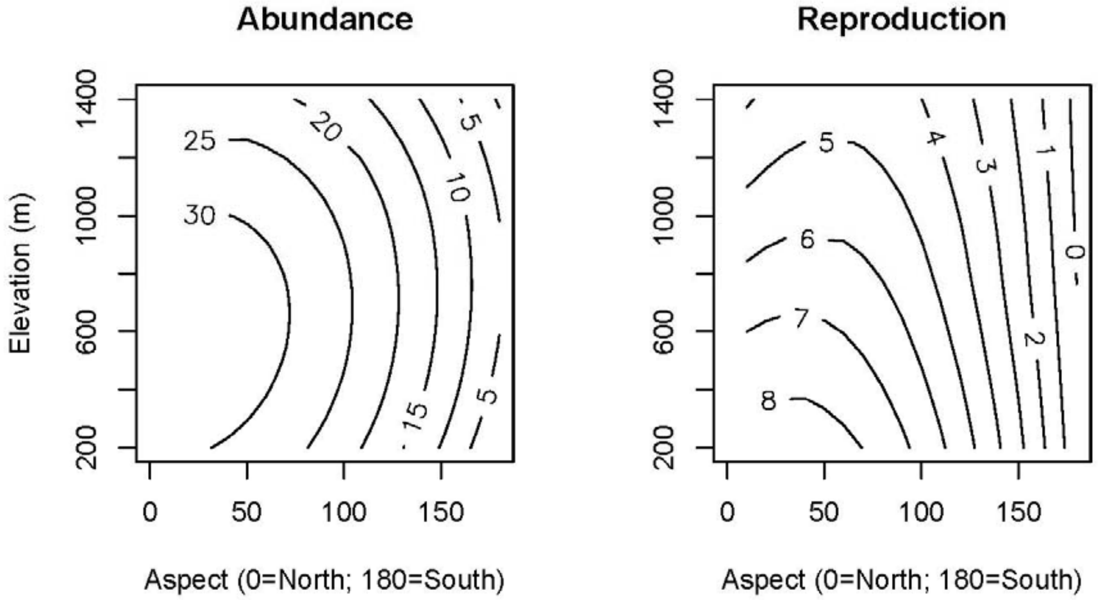


Figure 2.2a—Contour graphs for plant abundance and reproduction as functions of elevation and aspect. Contour intervals were generated by the predicted residual line for the generalized linear model $Y \sim intercept + elevation + elevation^2 + aspect + aspect^2$, where Y = either abundance or reproduction. Contour line numbers indicated expected abundance at that combination of heat load and summer light.

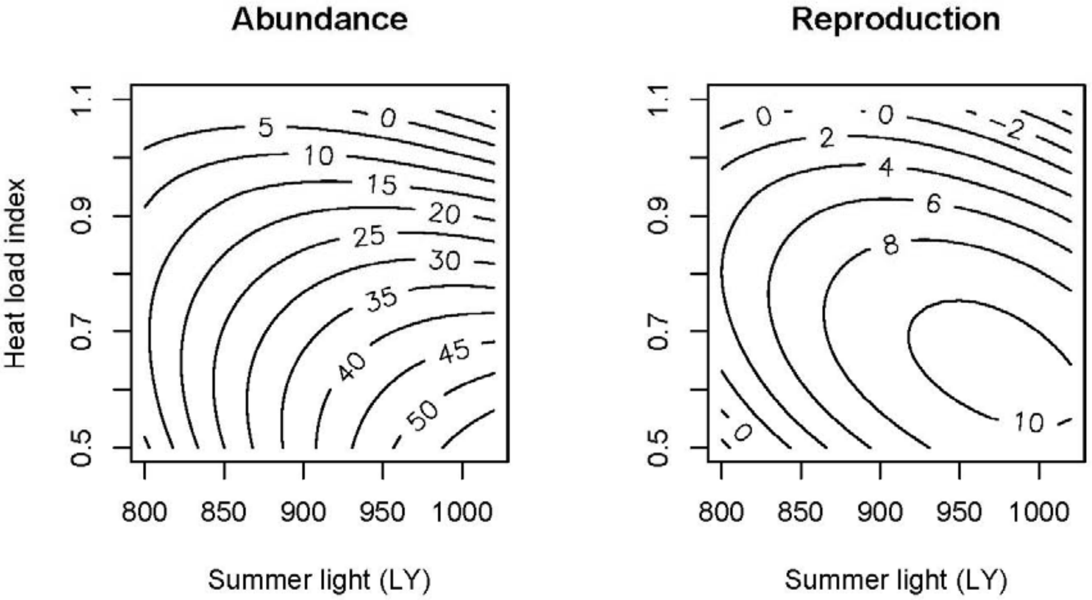
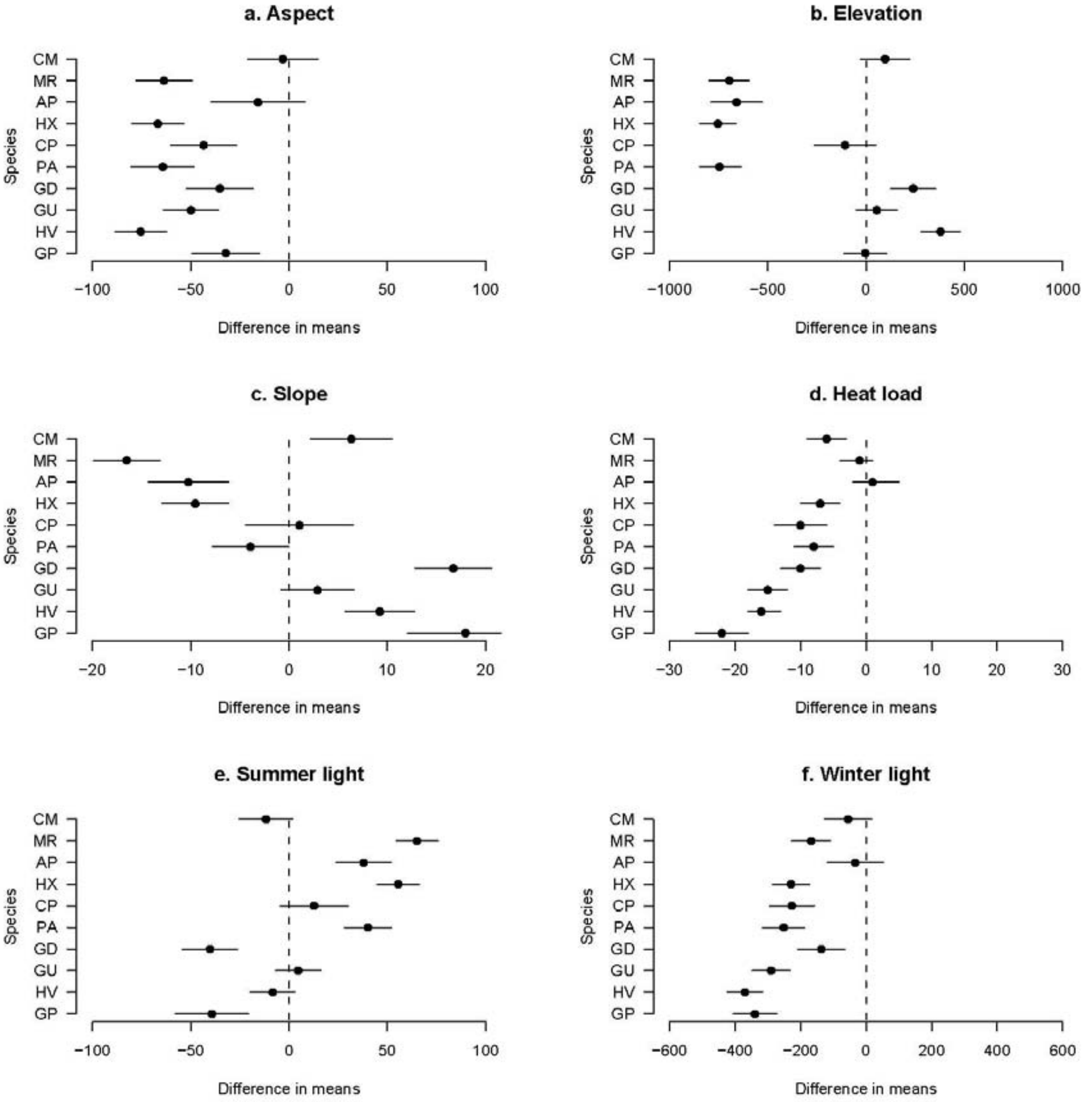


Figure 2.2b—Contour graphs for plant abundance and reproduction as functions of heat load and summer light. Contour intervals were generated by the predicted residual line for the generalized linear model *Y ~ intercept + heat load + heat load*^{2} + *winter light + winter light*^{2}, where *Y* = either abundance or reproduction. Contour line numbers indicated expected abundance at that combination of heat load and summer light.



a. Aspect

b. Elevation

c. Slope

d. Heat load

e. Summer light

f. Winter light

Figure 2.3— *t* distributions with 95% confidence intervals for the mean difference between habitat parameters where the species were present and absent (*mean value present - mean value absent = mean difference*). Positive mean differences indicate the plant was present at a larger range of the habitat parameter (i.e. aspect) than where it was absent. For example, most of the plants occurred at lower (more northerly) aspect values than where they were absent, as indicated by negative mean differences, though two of the confidence intervals contain zero (as indicated by the dotted line) and thus indicate no difference. The intervals are given for *Chimaphila maculata* (CM), *Mitchella repens* (MR), *Asplenium platyneuron* (AP), *Hexastylis arifolia* (HX), *Carex plantaginea* (CP), *Polystichum acrostichoides* (PA), *Goodyear pubescens* (GD), *Galax urceolata* (GU), *Heuchera villosa* (HV) and *Gaultheria procumbens* (GP).

CHAPTER 3

UNDERSTORY EVERGREEN HERBACEOUS NICHES AS DELINEATED BY DEMOGRAPHIC POPULATION MATRICES

INTRODUCTION

Stochastic and deterministic variation in natural processes across space and time creates environmental heterogeneity at numerous spatial and temporal scales (e.g., landscapes and years to microsites and days) (Turner 1989; Pickett & Cadenasso 1995). This environmental heterogeneity consists of patches and gradients in the distribution of resources and stressors (e.g., nutrients, light, temperature, etc.) that combine and interweave to create a mosaic of suitable and unsuitable habitat for any given species. While it is widely assumed that an organism's niche can be inferred from its presence or absence across these environmental patches and gradients (Beerling 1993; Huntley *et al.* 1995; Baker *et al.* 2000; Moody & Meentemeyer 2001; Peterson & Vieglais 2001; Welk *et al.* 2002; Ackerly 2003; Peterson 2003; Skov & Svenning 2004; Thomas *et al.* 2004; Hamann & Wang 2006), strong evidence (Pulliam 1988; Matlack 1994; Eriksson 1996; Clark *et al.* 1998; Davis *et al.* 1998; Hanski 1998; Ehrlen & Eriksson 2000; Pulliam 2000; Peterson 2003; Guisan & Thuiller 2005; Murphy & Lovett-Doust 2007) suggests that its mere presence or short-term performance cannot provide a robust delineation of the associated habitat suitability.

Instead, assuming that suitable habitat contains an organism's requisite biotic and abiotic niche requirements for indefinite existence (Pulliam 2000), measuring the change in population structure through time allows insight into underlying life history process as a function of that habitat. This demographic approach can be used to track a collection of indicators, such as growth, reproduction and survival, and determine the potential fate of a population based on its current trajectory (Menges 1990; Valverde & Silvertown 1997; Caswell 2001). Thus, rather than asking whether an organism is present or absent in a given habitat, one can ask whether the population is static, increasing or decreasing in a given habitat. More importantly, the inclusion of the per capita rate of population growth as a function of measured environmental variables furnishes a robust measure of an organism's niche (Pulliam 2000; Giladi 2004; Diez & Pulliam in press). The continued advancement of niche theory, as well as the need for predictive models in light of global climate change, depends upon a robust delineation of suitable habitat as determined by demographic parameters.

It has long been recognized that a link between an organism's niche and the environment exists in its morphological traits (Darwin 1859; Hutchinson 1959; Diamond 1975). That is, those traits necessary for the acquisition, use and conservation of resources significant for the organism's establishment, survival and fitness (Reich et al. 2003). This has traditionally been part of a predominant focus on competition and limiting similarity in niche theory (MacArthur & Levins 1967). However, there has been a growing trend in which plant functional traits have been proffered not as characteristics of the niche but as proxies for the niche (Stubbs & Wilson 2004; Thuiller *et al.* 2004; Mouillot *et al.* 2005; Schwilk & Ackerly 2005; Poorter & Bongers 2006; Shipley *et al.* 2006; Ackerly & Cornwell 2007; Poorter 2007), with some suggestion that plant functional traits might replace the difficult task of demographic data collection and analysis (McGill *et al.* 2006; Shipley *et al.* 2006).

While plant traits, just as plants, segregate along environmental gradients (Mamolos *et al.* 1995; Briones *et al.* 1996; Kobe 1999), they likely experience the same confounding dynamics as the whole plant: faux fitness (Chapter 1). That is, plant functional traits, some of which are highly plastic in response to environmental variation (Wright *et al.* 2004; Ackerly & Cornwell 2007), have been considered niche indicators without any measure of the actual niche. As such, variation in plant traits across the environment may or may not give indications about performance or suitability, and assumptions about a correspondence between specific traits and the maintenance of a population may be spurious.

The objective of this research is to use demographic population matrices combined with extensive abiotic monitoring to map the niche for two understory evergreen herbs (*Hexastylis arifolia* and *Hepatica nobilis*), as well as determine the predictability of leaf and root traits for niche characteristics. We demarcate suitable habitat for two understory evergreen herbaceous plants via demographic trends such as population growth rate and reproductive success using stage-specific matrix population models. Stage-specific rather than age-specific matrix population models are appropriate for organisms such as plants that can both advance and retreat substantially in size, when size rather than chronological age likely determines survivorship and reproductive success (Lefkovitch 1965; Caswell 2001). The projection matrix allows the measurement of the contribution of individual stages (size or life-cycle) to the overall per capital population growth rate (λ). The population growth rate provides a robust measure of fitness where $\lambda \geq 1$ indicates a population that is growing or maintaining itself over time and $\lambda < 1$ suggests a population in decline.

A species' niche is defined by the abiotic and biotic variables that accommodate its minimum needs and tolerances for birth, growth, survival, reproduction and death—collectively known as the life cycle. The movement of individual organisms through these life stages—known as vital rates—can be linked to the population as a whole via matrix population models (Menges 1990; Valverde & Silvertown 1997; Caswell 2001). The demographic dynamics of a population depend on its vital rates, which eventually depend on the characteristics of individual organisms within the population.

In many organisms, particularly plants, size or stage influences vital rates far more than age (e.g., minimum carbon storage for reproduction), and provides the best information about factors driving a population (Lefkovitch 1965; Werner & Caswell 1977; Caswell 2001).

We use stage-specific matrix population models to address the following questions:

I. *What is the projected viability of nine H. arifolia and four H. nobilis populations?* Preliminary analysis and personal observation suggest that both species are in decline. We use population matrices to determine the population growth rates and the influences of distinct life history stages (seedling, pre-reproductive and reproductive) upon those rates.

II. *What environmental variables best predict changes in λ and crucial vital rates (abundance, reproduction and growth)?* Preliminary analysis suggests that winter light inhibits *H. arifolia* presence while *H. nobili*s is far more dependent on soil moisture.

III. *Do potential differences in morphological trait characteristics correspond with differences in demographic performance and suitable habitat?* We ask how well morphological characteristics predict niche characteristics.

METHODS

Study sites

Data for this research was collected as part of a larger demographic study of six understory herbaceous plants along a 120 km geographic gradient from the Southern Appalachian mountains of North Carolina to the Georgia piedmont. The distribution of *H. arifolia* and *H. noblis* fell within a subset of these sites: both occurred at Whitehall Forest (WHF) in Athens-Clarke County, GA (33º92' N latitude, 150-240 m elevation) and *H. arifolia* occurred at the Nancytown (NT) site in Chattahoochee National Forest in Habersham County, GA (34º31' N latitude, 315-450 m elevation). Six 20 x 24m demography grids were established at WHF in 1999 and four 12 x 20m grids were established at CNF in 2001. These sites all were located in the understory shade environment of deciduous forests in mid- to mature stages of succession (60+ years of growth).

Species descriptions

Hexastylis arifolia (Michx.) Small (family: Aristolochiaceae) is a small understory evergreen with a distribution limited to the Southeastern United States: northern Florida to Virginia, North Carolina to the Mississippi River. The plant is more common in mesic than xeric habitats (Abella & Shelburne 2004), but does not appear limited by soil moisture (Gonzales 1972). It is most common in mature, deciduous forests (Gonzales 1972; Giladi 2004). It produces a single cohort of leaves each spring with a leaf life span of 12-13 months (Skillman et al. 1996). *Hexastylis arifolia* flowers in middle to late spring (Otte 1977; Giladi 2004), and it is pollinated by solitary bees and flies (Otte 1977). The cryptic, pod-like flowers occur beneath the leaf litter and are self-compatible, but not self fertile (Gonzales 1972; Otte 1977). *Hexastylis arifolia* fruits lie on the ground beneath leaf litter, and the seeds dispersed by ants (Gonzales 1972; Gaddy 1986; Giladi 2004). Only a small percentage of plants produce seeds (about 22 per fruit) and vegetative reproduction is absent or rare (Gonzales 1972; Giladi 2004).

Hepatica nobilis P. Miller (family: Ranunculaceae) is a small evergreen that occurs from northern Florida to Nova Scotia, west to Alabama and Missouri and Montana. It also is widespread in Asia and Europe, and the North American distribution is sometimes classified as *H. americana*. The plant is uncommon in dry habitats, and summer drought stress is a major cause of mortality for both mature juvenile and mature plants (Tamm 1956; Inghe & Tamm 1985, 1988). *Hepatica nobilis* is one of the earliest (late winter/early spring) flowering plants in the eastern United States (Motten 1982). The dominant pollinators of the multiple flowers are solitary bees and flies (Bernhardt 1976; Motten 1982). The flowers are self-compatible but not self fertile, and the seeds are dispersed by ants (Motten 1982). Vegetative reproduction is infrequent (Tamm 1956; Inghe & Tamm 1985, 1988).

Abiotic and biotic monitoring

The study grids were divided into 2 x 2m cells and every plant was individually flagged and monitored in annual censuses until 2004, and plants in a subset of 16 cells per grid were monitored until 2006. Each plant was visited at least twice annually to assess survival, growth, reproduction and fecundity. Survival was based on the presence or absence of a plant as identified by its flagged identification number (per grid and individual). For absent plants, mortality was distinguished from dormancy by leaving flag markers in place and recording the subsequent return of an adult plant to the same location. Growth was based on leaf size. Reproduction was based on the presence of reproductive structures, flowers or fruit, and fecundity was based on the appearance of local seedlings which could be identified by their distinctive dicotyledon morphology. As dormancy is not uncommon with these plants, flags were not removed due to the absence of a previously measured plant which allowed for the assessment of dormancy rates upon its potential return.

Within each grid, 16 “intensive” cells were utilized for abiotic monitoring. The volumetric soil moisture percentage was measured with a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific, Inc.). The probe uses a pair of 12-cm rods inserted into the soil to estimate volumetric moisture content via dielectric permittivity (how an electric field effects and is affected by a medium). Measurements were taken at each intensive cell every two weeks through 2004, and seasonally through 2006. Percent photosynthetically active radiation (PAR, wavelength: 400-700 nm) was calculated as the difference between the understory PAR readings on the grids and a fully exposed PAR reference site. The understory grid measurements were taken with a 0.5-m handheld AccuPAR ceptometer (Decagon Devices, Inc.) and the open reference measurements were taken with a Li-200 spherical PAR sensor (LiCor, Inc.) and logged with a LI-1400 datalogger (LiCor, Inc.). Measurements were taken seasonally on cloudy days between 10 a.m. and 2 p.m. By using this protocol, we assumed minimal inter-grid variation in PAR as there is little difference in the solar zenith angle during this time interval; by assessing percent PAR on cloudy days via diffuse light we avoided the tremendous variance caused by intermittent clouds and sunflecks (Messier & Puttonen 1995; Parent & Messier 1996; Gendron *et al.* 1998).

Plant functional traits

In order to measure plant functional traits, 20 individuals of each *H. arifolia* and *H. noblis* were randomly selected from the same WHF location at the same time, the sample size based on the recommendations of Cornelissen et al. (2003) for the selected traits. Above-ground tissue was separated from below-ground tissue, and leaf area (cm^2) immediately was measured using a LI-3100C leaf area meter with measurement accuracy confirmed by a $50cm^2$ disc (Licor, Inc.). Rooting depth was the maximum length (depth) of 95% of the root mass. The leaf parts were then placed in a drying oven set at 60º C for 72 hours. Specific leaf area (SLA)—the ratio of leaf area to oven-dried masswas then calculated, following the process outlined in Cornelissen et al. (2003).

Data analysis

a. Projection matrices

We constructed stage projection matrices for both *H. arifolia* and *H. nobilis* using leaf area (cm^2) to assign plants into stage categories; the categories based on those developed by Giladi (2004) and Harris (2000) for *H. arifolia* and *H. nobilis,* respectively (Table 3.1). Additional stages were created for both seedlings and dormant plants. Plants were categorized as dormant if no leaf was present during census in year t, but reappeared during census in year $t + 1$ or $t + 2$. Because vegetative reproduction is rare in both plants, and neither produces seeds that are viable long enough to form a seed bank (Tamm 1956; Gonzales 1972; Inghe & Tamm 1985, 1988; Giladi 2004), categories were not created for either of these processes. In order to complete the life cycle projection, however, seedlings were associated with fruit-bearing plants. This was calculated at the grid level by proportionally assigning seedlings in year t to fruit-bearing plants in year $t - 1$, with the probability of being assigned a seedling based on number of fruits produced. This assumes limited seed import and export between populations, which is reasonable considering both plants bear ant-dispersed seeds (Gonzales 1972; Motten 1982; Gaddy 1986; Giladi 2004) and seeds are rarely carried more than a few meters by ants (Giladi 2004).

The population projection matrix was constructed using the R statistical package (2006), and the stage categories were used to derive the dominant eigenvalue: $n_{t+1} = \lambda n_t$, where n_t describes the number of individuals in each stage category at time t, and λ is the geometric rate of increase for a population in a stable stage distribution. We calculated λ for each species, population and year, which provided a measure of population growth—positive ($\lambda > 1$) or negative ($\lambda < 1$)—independent of the current population size. Additional demographic statistics—stable stage distribution, sensitive and elasticity and damping ratio—were calculated from the projection matrix using the “popbio” package for R. Sensitivity indicates which stage transitions are most influential upon λ, while elasticity does much the same but makes the response proportional in order to reconcile the difference between transitions probabilities and fertility totals (Caswell 2001).

b. λ uncertainty

The implementation of stage projection matrices improves the estimation of population growth rates by minimizing the variation in vital rates within a stage class, but the maximum likelihood estimates of transition probabilities are deterministic. In order to generate credible estimates of population growth rates, uncertainty must be incorporated into the estimates (Menges 1990). Bayesian hierarchical models are a powerful method for estimating uncertainty in vital rates and generating stochastic population growth rates (Clark 2003; Giladi 2004; Diez & Pulliam in press). The Bayesian approach assigns distributions to the parameters rather than assuming they have a fixed value. We used WinBUGS (Winbugs 1996-2003, Imperial College and MRC, UK) a Bayesian software package that uses a Gibbs Sampler (and a Metropolis-Hastings algorithm when needed) to execute Markov Chain Monte Carlo (MCMC) simulations and generate the distributions of the λ's for each grid for each interval.

The transition probabilities for individual plants progressing through the stage classes of the projection matrix for each yea and grid was estimated assuming a multinomial distribution ($Y_{ij} \sim Multinomial(p_{ij}, n_i)$), where Y_{ij} is the number of individuals transitioning from stage i in year t, to stage j in year t+1 when there are n_i individuals of stage i in year t. The prior for the transition probabilities was modeled using the gamma approximation to a Dirichlet distribution ($Y_{ij} \sim Dirichlet(T)$). Each element (T_{ij}) of the vector T was modeled as an independent gamma distributed random variable, $T_{ij} \sim Gamma(aT_{ij}, bT_{ij})$, where the priors, aT_{ij}, bT_{ij}, where also drawn from independent gamma distributions. The multinomial proportions (p_{ij}) of individuals moving from stage i to stage j were then estimated as $p_{ij}=T_{ij}/\sum_{i=1}^{m} T_{ij}$. The hierarchical organization of priors and hyperpriors within the Bayesian structure pooled the distribution of estimated transition probabilities across years and grids, allowing larger samples to influence the calculation of smaller samples and missing data. Thus strong mean values based on robust sample sizes influence weak or missing samples. This is particularly important for years 2005 and 2006 when populations were sampled in 16 subsamples rather than in all cells per grid. While these data were not used for calculating the demographic statistics, they were useful for estimating dormancy in years 2003 and 2004.

Stage specific fertility assigns reproductive output to stage classes in year t based on censused seedlings in year t-1 assuming the relative number of seedlings produced by each stage is directly proportional to the relative number of fruits produced by each stage. This was estimated for each year and grid assuming a multinomial distribution ($Y_i \sim Multinomial(p_i, n_i)$), where n_i equals the total number of seedlings in year t and p_i equals the proportion of fruits attributed to each stage i in year t-1. This assigned seedlings to each size class using the probability that a specific stage produced seedlings based on the proportion of that size class the produced potential seedlings via fruit in the previous year.

c. Vital rate estimation at multiple scales

An analysis of covariance (ANCOVA) for the dependent variables (abundance, reproduction and growth) at the cell-level treated temperature as a cofactor and PAR (winter and summer), soil moisture, pH and nitrogen as covariables using generalized linear models (GLMs). First and second order terms were included for all covariables ($Y_i = intercept_i + PARwinter_i + PARwinter_i^2 + PARsummer_i + PARsummer_i^2 + soil\ moisture_i + soil\ moisture_i^2$. Plant abundance and growth were modeled assuming Gaussian error distributions ($Y_i \sim Normal\ (\mu_i, \sigma_i)$) and reproduction was modeled assuming a Poisson error distribution ($Y_i \sim Poisson\ (\mu_i)$). The probabilities of presence and reproduction were linked to the linear predictor variables via the log function ($log\ (Y_i = \beta_0 + \beta X_{i + \dots}$) and the probability of reproduction was linked to the linear predictor variables via the log link function ($log\ (Y_i) = \beta_0 + \beta X_i \ldots$). All variables were based on abundance in 2 x 2 cells except temperature, which was measured at the grid level.

Bayesian hierarchical GLMs were used to generate 90% credible intervals for the regression coefficients (intercept and line slopes). The Bayesian models were implemented in the Winbugs 1.4.2 software package in a hierarchical framework with normally distributed, noninformative priors (*Normal* (*0,0.001*)). The intercepts were allowed to vary randomly with grid to incorporate individual population responses. The 90% credible intervals for regression coefficients were generated using Markov chain Monte Carlo (MCMC) simulations in Winbugs. A minimum of 20,000 iterations were used to "burn-in" the models before coefficient estimates were measured and 1,000 iterations were used to generate the posterior distributions. In order to mitigate coefficient autocorrelation between iterations, the output was "thinned" by only using every 20th measure. The iterations were run with three chains and all chains converged (Gelman-Rubin statistic < 1.1).

d. λ as a function of environment

Estimating λ as a function of environmental variables essentially combines the two previous analyses by calculating λ at the cell rather than grid level and relating it to abiotic variables operating at that scale. Essentially, this asks how the probability of a plant transitioning to another stage class depends upon its abiotic environment. Rather than calculate all possible stage transitions and environmental variables, stage transitions were selected based on prior knowledge and elasticities, and the environmental parameters selected based on the vital rate ANCOVAs. Assuming that reproduction and seedling survival form the cornerstones of population viability, we modeled the transition from seedling to size class 2, as well as seedling production by the reproductive stage classes for each species (*H. arifolia*: size classes 5:6; *H. nobilis*: size classes

3:6) collapsed into one reproductive stage for each species. Ramet survival was calculated as mortality for all non-seedling or dormant stages collapsed into one stage. Light and soil moisture were used as they appeared to best predict plant vital rates, and density dependence (*N*) was calculated as the sum of all ramets (stages 2:7) in the given cell per grid and year. First and second order terms as well as a PAR:soil moisture interaction term were included for all covariables ($Y_i = intercept_i + b_1 * PAR_i + b_2 * PAR_i^2 + b_3 * soil\ moisture_i + b_4 * soil\ moisture_i^2 + b_5 * PAR{:}soil\ moisture_i + b_6 * N_{i.}$

Ramet mortality was estimated assuming a multinomial distribution ($Y_i \sim Multinomial(p_i, n_i)$), where Y_i equals the number transitioning from stages i to j in year $t + 1$ out of a total of n_i individuals in year t. Seedling mortality also was estimated assuming a multinomial distribution ($Y_i \sim Multinomial(p_i, n_i)$), where Y_i equals the number of individuals failing to survive out of a total of n_i individuals in year t. The number of seedlings produced by reproducing stages were modeled as a Poisson distribution ($Y_i \sim Poisson\ (\mu_i)$) where μ_i is the mean number of seedlings per adult. PAR and soil moisture were modeled assuming normal distributions ($Y_i \sim Normal\ (\mu_i, \sigma_i)$), where μ_i was a noninformative, normally distributed hyperprior (*Normal* (*0,0.01*)) and σ_i was a noninformative, Gamma distributed hyperprior (*Gamma* (*10,10*)). All of the models were implemented in a hierarchical framework with normally distributed, noninformative priors (*Normal* (*0,0.001*)) for intercept and slope parameters.

RESULTS

A total of 6,235 *H. arifolia* (in 9 populations) and 3,874 *H. nobilis* (in 4 populations) plants were monitored on study grids at WHF and CNF between the years 1999-2006. While no attempt was made to link size classes and age, transitions from larger to smaller size classes were observed frequently in both *H. arifolia* and *H. nobilis*, justifying size classes (Lefkovitch matrix) rather than age classes (Leslie matrix). There was a distinct break point between the most frequent size class (*H. arifolia*: size class 4; *H. nobilis*: size class 3) and those after that coincided with the transition between pre-reproductive and reproductive stages (*H. arifolia*: size classes 5-6; *H. nobilis*: size classes 4-6) (Figure 3.1). *Hexastylis arifolia* size classes progressively increased from seedling to pre-reproductive, and dropped dramatically for the reproductive size classes. The *H. nobilis* size classes dropped sharply after seedlings and between pre-reproductive to reproductive size classes. The dormant stage made up about 14% of all stage transitions for each species.

Pooled population growth rates

Pooled-population Lefkovitch matrices for the years 1999-2003 were constructed from the census data for both plants. In order to estimate dormancy—based on the return of a missing plant after a 1-2 year absence—for years 2002 and 2003, census data from 2004 and 2005 was used but not reported. Each matrix consisted of vectors for the probabilities of each stage transition (e.g., $P_{ij} = Pr(stage_i, year_j \rightarrow stage_j, year_{j+1})$), including dormancy, for each population. As noted earlier, stages could advance or retreat into larger or smaller stages, including dormancy. The matrices also included a vector for reproductive output assigned to transitions as the probability that a given transition produced a seedling in year *t* based on the presence of a fruiting body in year *t*-1. A Lefkovitch matrix provided an estimate of population growth (λ) independent of the population size distribution based on the dominant eigenvalue for all stage transitions. The pooled population trend from 1999 to 2003 fell below replacement ($\lambda < 1$) for both *H. arifolia* ($\lambda = 0.95$) and *H. nobilis* ($\lambda = 0.93$).

Sensitivity and elasticity

Because the dominant eigenvalue is a function of the stage transitions, a perturbation of a stage transition, and the resulting degree of change in λ, gives a measure of that transition's influence upon the population growth rate (Caswell 2001). Thus, transitions with large sensitivity values indicated a strong influence on the population growth rate. For *H. arifolia* and *H. nobilis*, the transitions from the most common size classes (*H. arifolia*: size class 4; *H. nobilis*: size class 3) predictably had the most influence on the population growth rate (Table 3.2). This included transitions to larger size classes, dormancy and seedling production. The survival of seedlings, as indicated by the transitions from size class 1 to size class 2 or 3, had more influence on *H. nobilis* λ than *H. arifolia*, but seedling survivorship had far less impact on λ for both species as did adult survivorship.

Because transitions probabilities can not exceed 1, while reproductive output can, elasticity analysis was developed to consider both demographic elements at the same scale as well as provide a proportional measure of λ perturbation (Caswell 2001). This gives an indication of the relative contribution of each transition to λ proportional to all other transitions. This allows for the partitioning of transition elasticities into categories such as growth (an increase in size class), stasis (a return to the same size class), retrogression (a decrease in size class) and seedling recruitment. In *H. arifolia*, stasis had the highest (31.5%) relative contribution to λ, followed by retrogression (28.3%), growth (20.8%), dormancy (17.9%) and fertility (1.5%). In *H. nobilis*, retrogression had the highest (26.3%) relative contribution to λ, followed by growth (24.6%), dormancy (21.3%), stasis (21.0%) and fertility (6.8%).

Stable stage distribution

The stable stage distribution is the proportion of plants predicted in each stage class if the population transition matrix is stable and the population growth rate (λ) is constant. The projected stable stage distribution for *H. arifolia* based on the pooled matrix placed most plants in size class 3 and above, including dormant, and included a relatively small amount of seedlings. The stable stage distribution for *H. nobilis*, included a somewhat larger seedling contingent, but an appreciably smaller size class 2, which indicated high seedling mortality. A comparison of projected versus actual size class frequencies indicated that the dominance of the most frequent size class for each species (*H. arifolia*: size class 4; *H. nobilis*: size class 3) differed substantially from that expected for stable populations (Figure 3.2). Except for *H. nobilis* seedlings, which occurred in far greater numbers than expected for a stable stage distribution, both species appeared to have distributions heavily weighted in the middle at the cost of the rest of the size classes. The damping ratio (ρ), which indicates how rapidly a population can converge toward its stable stage distribution (Caswell 2001), was far greater for *H. nobilis* than *H. arifolia*. This indicated that *H. nobilis* (ρ=5.2) can converge toward an equilibrium distribution much more rapidly than *H. arifolia* (ρ=2.3), likely due to the greater seedling production.

Individual population growth rates

Lefkovitch matrices for each year and individual population were constructed from the census data, and transition probabilities were generated 1,000 times for each year-population combination. The posterior distributions gave stochastic λ values for each population and year, and these were presented as frequency distributions (Figures 3.3-3.5). The simulated distribution of λ values for those populations with large numbers of plants (e.g., *H. arifolia* at Whitehall 12;

Figure 3.3) were predictably narrow while the distributions for those populations that were poorly represented (e.g., *H. nobilis* at Whitehall 11; Figure 5) covered a wide range of possible λ values.

If the λ distribution overlapped 1, the population was considered stable, but if the entire distribution was less than 1, the population was considered to be in decline. At WHF, λ was not significantly less than 1 for all *H. arifolia* populations in 1999, but steadily dropped with each year until 2003 in three of the four populations (Figure 3.3). The λ estimations for the population at Whitehall 15 generally remained steadily at or above 1. Higher variance in λ and fewer years of data made NT population trends less clear, but the λ estimations generally fell at 1 or less (Figure 3.4). Smaller sample sizes also were reflected in λ estimations for *H. nobilis* at WHF, but populations at Whitehall 12 and 17 showed the same steady decline as *H. arifolia* populations (Figure 3.5). Rather than a steady decline, λ estimations for the populations at Whitehall 11 and 13 were consistently well below 1, though the λ estimations for the small population at Whitehall 11 generally could not be distinguished from zero due to a high level of variance.

Vital rates

Hexastylis arifolia abundance, reproduction and growth all declined with increasing summer light, though growth increased at the highest levels of summer light as indicated by the second-order term; and high winter light also caused declines in all the *H. arifolia* vital rates (Figure 3.6). *Hexastylis arifolia* growth increased with the first-order soil moisture term and decreased with the second-order term, indicating that it grew best at intermediate levels of soil moisture while soil moisture had no effect on plant or reproductive abundance. *Hepatica nobilis* abundance, reproduction and growth consistently peaked at intermediate levels of soil moisture (Figure 3.6). Both summer and winter light had a deleterious affect upon *H. nobilis* reproduction, but growth only decreased at the highest levels of winter light and light had no effect on abundance.

In order to connect these vital rates with population dynamics, cell-level population growth rates were calculated as a function of cell-level environmental variables. Instead of examining each stage transition, the mortality of all stages except seedlings was collapsed into ramet mortality—reported as *1-mortality* (survival) for ease of interpretation. Seedling mortality also was reported in this manner (seedling survival). For the third transition, fertility, the production of seedlings by reproductive stages was calculated. Across species, *H. arifolia* λ appeared far less sensitive to environmental variables than *H. nobilis*, and seedling production and survival appeared more sensitive to environmental variables than did adult survival (Figure 3.7). *Hepatica arifolia* seedling survival correlated negatively with density dependence, and fertility increased with high levels of winter soil moisture; *H. nobilis* seedling survival increased at intermediate levels of summer soil moisture and declined at high levels of winter light while both summer and winter light negatively affected fertility. Ramet survival in *H. nobilis* increased with summer light.

Functional traits

Hexastylis arifolia and *H. nobilis* (*t*-test: p=0.07; means: 15.3, 21.6 cm^2) had a similar specific leaf area (*t*-test: p=0.21; means: 182.16, 168.54 $\text{g}^{-1}\ \text{cm}^2$), but *H. arifolia* had deeper roots than *H. nobilis* (*t*-test: p=0.00007; means: 8.94, 5.73 cm) (Figure 3.8).

DISCUSSION

The study populations of both *H. arifolia* and *H. nobilis*—two phylogenetically distinct plants—are projected to decline ($\lambda < 1$). That they share some fundamental life history characteristics—herbaceous, shade-tolerant, evergreen and ant-dispersed—suggests similar mechanisms might lie behind these declines, and they do; however, we also find unique mechanisms driving *H. arifolia* and *H. nobilis* demographic dynamics, and the environmental drivers behind those are species-specific.

Demographic inertia

The demographic differences between *H. arifolia* and *H. nobilis* can essentially be framed as a trade-off between life history strategies with *H. nobilis* producing relatively larger numbers of offspring with high mortality rates versus *H. arifolia*, which produces few offspring with high survival rates (Figure 3.1). Adult rather than seedling survivorship is far more influential upon λ for both species; and seedling survival has about three times more influence on *H. nobilis* than *H. arifolia* λ (Table 3.2). The relatively high seedling production and growth of *H. nobilis* leads to faster population adjustments and potential convergence upon a stable stage distribution, as reflected in its higher damping ratio. The projected stable stage distributions for *H. arifolia* and *H. nobilis* indicate that both species have deficiencies in the reproductive size classes, but *H. nobilis* has a surplus of seedlings while *H. arifolia* has a deficit. The surplus of seedlings apparently does not offset their high mortality as both species also show a deficit in size class 2 for a stable stage distribution (Figure 3.2).

More than 77% of *H. arifolia* λ and 68% of *H. nobilis* λ can be explained by stasis, retrogression and dormancy (Table 3.2). These factors far outweighed growth and fertility for both species, and in fact Silvertown et al. (1993) found that stasis and growth and are predictably negatively correlated. This is reflected by the clumping of individuals in the middle, pre-reproductive classes of both species (Figure 3.1), which is incongruent with their projected stable stage distributions (Figure 3.2). The far greater importance of stasis than fertility is consistent with long-lived, slow-growing species (Bierzychudek 1982; Vega & Montana 2004), which is consistent with understory, evergreen herbs (Neufeld & Young 2003). These dynamics indicate populations that are not growing, nor dying, just collapsing into static, non-reproductive stages. This inertia has the most impact on *H. nobilis*, which depends on high fertility rates to offset high seedling mortality. Because fertility is based on larger size classes, *H. nobilis* depends upon the progression of pre-reproductive plants into reproductive stages. Between 1999 and 2004, censused seedlings declined rather steadily, resulting in a 40% drop in seedlings between 1999 and 2004. This corresponded with a significant (linear regression, $p = 0.05$, $R^2 = 0.59$) drop in *H. nobilis* fertility during the same period, while seedling survival remained unchanged (linear regression, $p = 0.52$, R2 = 0.11) (Figure 3.9). At the same time, *H. arifolia* fertility remained unchanged (linear regression, $p = 0.35$, R2 = 0.03), but seedling mortality increased significantly (linear regression, $p = 0.09$, R2 = 0.44) (Figure 3.9). While retrogression does not occur, or is not measured as often as stasis, populations where stasis outweighs growth seem to have lower λs than those where the influence of growth dominates λ (Eriksson 1988; Charron & Gagnon 1991; Silvertown *et al.* 1993; Vega & Montana 2004).

These trends are crucial in the context of the life history strategy of each plant. *Hexastylis arifolia* study populations depend on their relatively fewer, but hardier offspring while *H. nobilis* populations depend upon high fruiting rates to produce large numbers of less hardy seedlings. This highlights two weak points in the life cycle of each species: *H. arifolia* seedling survival and *H. nobilis* fertility. Thus, it appears individuals in *H. arifolia* populations produce enough seedlings; they just are not surviving and progressing into the next stage class. In fact, *H. arifolia* λ is more influenced by the transition of all other stage classes into stage class 2 than seedlings (Table 3.2). Conversely, *H. nobilis* λ is more influenced by the transition of seedlings into stage class 2 than most other stages. However, individuals in *H. nobilis* study populations are not produce enough seedlings to overcome the constant high mortality rate.

Habitat suitability

When plant vital rates are examined based upon actual abundance per plot, both species showed significant declines in plants, reproductive output and growth with increased summer and winter light (Figure 3.6). This might be interpreted in a physiological context, such as photoinhibition. Photoinhibition occurs when the leaf enzymes that control the conversion of light energy into carbon are denatured by temperature extremes while the light harvesting machinery is unaffected (Raven 1989). This creates excess leaf energy which must be dissipated or the leaf suffers damage—in either case the process costs energy that might otherwise go toward vital rates. Conditions that encourage photoinhibition include low soil moisture combined with high temperatures in summer (Raven 1989; Pearcy *et al.* 1994; Neufeld & Young 2003) and high irradiance combined with low temperatures in winter (Verhoeven et al. 1999, Adams et al. 1991, Oquist and Huner 1991). While both plants exhibited similar intolerances toward increased light, the dependence of *H. nobilis* on moist soils clearly outweighed that of *H. arifolia* (Figure 3.6). *Hepatica nobilis* abundance, reproduction and growth all peaked at intermediate soil moisture levels, while only *H. arifolia* growth exhibited a similar pattern.

The relationship between vital rates and environment is less clear when examining stage transitions (Figure 3.7). *Hexastylis arifolia* stage transitions appear far less sensitive to environmental variables than *H. nobilis*. Only *H. arifolia* fertility (the production of seedlings attributable to reproductive-size adults) and seedling survival transitions show significant responses to environmental variables. This is consistent with sensitivity analyses that showed *H. arifolia* λ was very sensitive to changes in the number of reproductive age individuals (Table

3.2), and growth per plot depended upon moist soil (Figure 3.6). *Hepatica arifolia* reproduction depends on plant size, and the correlation between high winter soil moisture and adult fertility coincides with the formation of *H. arifolia* fruit in late winter/early spring. The lack of correlation between adult survival and environmental conditions may reflect the high level of stasis in adult *H. arifolia* plants, and indicates that the soil moisture threshold for *H. arifolia* persistence is much lower than the threshold for fertility. The lack of correlation between *H. arifolia* adult survival and environmental conditions reflects the dynamics of a persistent species that competes well for limiting resources, such as soil moisture, and persists in inertia.

Notably, the only environmental signal that appeared to influence *H. arifolia* seedling survival was density dependence. While the mechanism for seedling density dependence cannot be elucidated from this data, the seedling response to density follows the well-established Janzen-Connell hypothesis (Janzen 1970; Connell 1971) which predicts higher seedling mortality near parents due to pathogen or herbivore clustering. *Hexastylis arifolia* seedlings exhibit a life history pattern similar to *H. nobilis*, however, they are released in early summer rather than early spring, and they are larger (associated with more energy reserves) and have hard seed coats. Larger seeds convey greater tolerance for environmental stressors than smaller seeds and increase survival likelihood (Leishman 2001; Moles *et al.* 2003; Moles & Westoby 2004).

While *H. nobilis* abundance, reproduction and growth per plot show a clear relationship with soil moisture (Figure 3.6), seedling survival is the only *H. nobilis* stage transition to do so (Figure 3.7). This indicates that the other responses, to some degree, are vestiges of seedling survival patterns, and that the seedling stage heavily influences *H. nobilis* distributions. *Hepatica nobilis* seeds are dropped in late spring, and they are relatively small with little reserves and highly susceptible to desiccation (pers. obs.). Species that produce small seeds generate far more at less energy cost that than large-seeded species, but they lose the advantage during establishment when mortality is much higher than large-seeded species(Jakobsson & Eriksson 2000; Henery & Westoby 2001; Moles *et al.* 2003; Moles & Westoby 2004). *Hepatica nobilis* seeds immediately germinate and form roots but do not send up shoots until the following season, making their initial survival contingent upon summer conditions.

Both fertility and seedling survival transitions respond negatively to winter light, and fertility to high summer light, which is consistent when scaled up to patterns of *H. nobilis* abundance per plot. However, ramet survival increases positively with summer light (Figure 3.7), a pattern not reflected by any vital rate when scaled up to cell abundances (Figure 3.6). While the positive response of ramet survival in sunnier conditions is not reflected by increased *H. nobilis* abundance, decreased fertility and seedling survival in sunnier conditions is reflected by declines in growth and reproduction when scaled up to plot abundance. The connection between growth and fertility is consistent with size-dependent reproduction.

In general, soil moisture appears an important variable in predicting demographic dynamics—more so with *H. nobilis* than *H. arifolia*—and as such, suitable habitat for these plants. Wetter conditions likely prompt growth and thus increased fertility, as well as increased fecundity with higher seedling survival. Conversely, drier conditions seem to promote stasis and even retreat from reproductive size in plants and lower seedlings survival. Vega and Montana (2004) found that the influence of sexual reproduction and growth upon λ increased in bunch grass during years with more rainfall and stasis and retrogression was more influential upon λ during dry years. The *H. nobilis* populations in grids with the highest relative soil moisture had significantly (linear regression, $p = 0.09$, $R^2 = 0.72$) more years where $\lambda \geq 1$ while *H. arifolia* populations exhibited no such trend (linear regression, $p = 0.71$, $R^2 = 0.37$). The negative light response did not scale up, however, as the number of years where $\lambda \geq 1$ did not correspond significantly with light in individual populations of *H. arifolia* (linear regression, $p = 0.86$, $R^2 = 0.02$) or *H. nobilis* (linear regression, $p = 0.34$, $R^2 = 0.15$).

Functional traits and niche

A well-established trade-off occurs between leaf lifespan and maximum photosynthetic rates (Wright et al. 2004), and the lack of difference in leaf thickness, which corresponds with differences in potential growth rates, likely reflects the similar leaf lifespans between the evergreen species. While both plants had similar specific leaf areas, the roots of *H. arifolia* are significantly longer (and thus reach deeper in the soil) than those of *H. nobilis* (Figure 3.8). Because *H. arifolia* showed greater tolerance for soil moisture deficits than *H. nobilis*, its deeper roots do provide a link between morphology and niche requirements. Rooting depth appears to best distinguish the two species and their associated life history strategies. Because reproduction for both plants is size-specific, leaf area (as recorded in the field during demography data collection) might be considered a rough proxy for fitness, as larger leaves clearly correspond with greater reproductive potential. The caveat here, however, is that while leaf area might well reflect the underlying fitness of *H. nobilis*, in which population growth appears more dependent upon fertility than seedling survival, the opposite is true for *H. arifolia*, and leaf area gives no indication of seedling survival. Thus, the leaf traits only gave insight into the specific plant niches when paired with demographic analysis. These finding suggest that (1) the emphasis upon leaf traits in elucidating niche parameters (Stubbs & Wilson 2004; Wright *et al.* 2004; Wright *et al.* 2005; Poorter & Bongers 2006; Ackerly & Cornwell 2007)—while logistically more feasible and certainly worthwhile—might miss key morphological characters belowground and (2) suggestions that functional traits might replace demographic study for elucidating niches and suitable habitat (McGill *et al.* 2006; Shipley *et al.* 2006; Whitfield 2006) are likely premature and possibly overzealous.

Conclusions

Projected population declines for both *H. arifolia* and *H. nobilis* are driven by a shift away from reproductive-sized plants and decreases in *H. arifolia* seedling survival and *H. nobilis* fertility. The life cycle of *H. nobilis* clearly depends upon relatively higher soil moisture as reflected both in fertility and seedling survival, while *H. arifolia* is far less soil moisture sensitive. However, *H. arifolia* growth and fertility are correlated with increased soil moisture.

Eriksson (1996) defined remnant populations as systems of local populations with a declining growth rate ($\lambda < 1$) maintained by population inertia. He suggested that long-lived plants with clonal propagation or extensive seed banks buffer against extinction and can persist in declining populations to withstand periods of unfavorable environmental conditions. However, neither *H. arifolia* nor *H. nobilis* clone nor maintain seed banks. Eriksson also suggested that remnant populations may occur in habitat that has permanently shifted to unsuitable (e.g. succession or climate change). Increased light consistently poses a strong negative influence upon both species, but other than small-scale gaps or successional changes (which likely would decrease rather than increase light penetration through the tree canopy), there is no compelling evidence of an understory light trend corresponding with decreases in *H. arifolia* and *H. nobilis* population growth.

Meteorological data indicates that temperatures have increased, and precipitation has decreased, during the 50-year interval preceding this research (Pulliam in prep). Soil moisture models based on these trends indicate that soil moisture has likely decreased during this interval (Pulliam in prep), which provides a plausible explanation for the demographic inertia and reproductive decline in the understory evergreens. The differences in soil moisture sensitivity correspond well with contrasts in root functional traits between species as *H. arifolia* has deeper roots and allocates more biomass belowground than *H. nobilis*. This may explain the greater distribution of *H. arifolia*, which only occurs in the Southeastern United States, in the study grids (91%), than the far more cosmopolitan *H. nobilis* (23%), which occurs throughout Eastern North America and Asia. The greater λ and the relatively greater ability of *H. arifolia* for stasis suggest that it not only has a greater breadth of suitable habitat in northeastern Georgia, but that it can persist somewhat longer in unsuitable habitat than *H. nobilis*. If projected trends continue, the extirpation of local *H. arifolia* and *H. nobilis* populations looms on the horizon, yet this cannot lead to predictions of extirpation. Both plants demonstrate capabilities for persistence, *H. arifolia* more than *H. nobilis*, and populations could rebound if conditions change.

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TABLES AND FIGURES

Table 3.1. Site variables for experimental common garden grids on north- and south-facing aspects at Whitehall Forest in Athens, GA and Coweeta Hydrologic Laboratory in Otto, NC.

	Whitehall Forest					
	Elevation (m)	Slope°	Azimuth°		Plots	Plants
North 1	204	15	350		12	72
North 2	172	16	340		12	72
North 3	172	22	340		12	72
South 1	182	15	180		12	72
South 2	172	15	140		12	72
South 3	182	22	160		12	72
mean=	180.7	17.5		*n*=	72	432

	Coweeta Hydrologic lab					
	Elevation (m)	Slope°	Azimuth°		Plots	Plants
North 1	750	17	330		12	72
North 2	1023	15	0		12	72
North 3	783	16	10		12	72
South 1	801	16	180		12	72
South 2	755	17	180		12	72
South 3	1025	21	180		12	72
mean=	856.2	17.0		*n*=	72	432

Table 3.2. Population matrix sensitivities and elasticities for *Hexastylis arifolia* and *Hepatica nobilis*. The values indicate the sensitivity of the per-capita growth rate to changes in stage transitions, represented by rows to columns. Stages 1 and 7 are seedlings and dormants for both species, while *H. arifolia* stages 4-6 and *H. nobilis* stages 3-6 are reproductive sized plants. The highest sensitivity and elasticity for each stage transition are highlighted.

Hexastylis arifolia

Sensitivities

Stage	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	0.000	0.034	0.047	0.000	0.000	0.000	0.052
2	0.000	0.053	0.073	0.078	0.081	0.084	0.081
3	0.000	0.133	0.183	0.196	0.205	0.210	0.203
4	0.085	0.200	0.275	0.294	0.308	0.316	0.305
5	0.037	0.086	0.119	0.127	0.133	0.136	0.132
6	0.039	0.090	0.125	0.133	0.139	0.143	0.138
7	0.050	0.118	0.162	0.173	0.181	0.186	0.179

Elasticities

Stage	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	0.000	0.009	0.003	0.000	0.000	0.000	0.002
2	0.000	0.014	0.019	0.008	0.002	0.001	0.010
3	0.000	0.008	0.071	0.057	0.010	0.003	0.034
4	0.001	0.006	0.042	0.126	0.043	0.021	0.054
5	0.003	0.002	0.007	0.030	0.034	0.032	0.025
6	0.007	0.001	0.004	0.012	0.025	0.070	0.024
7	0.003	0.013	0.038	0.061	0.019	0.016	0.030

Hepatica nobilis

Sensitivities

Stage	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	0.000	0.107	0.144	0.000	0.000	0.000	0.205
2	0.000	0.012	0.016	0.023	0.025	0.027	0.023
3	0.122	0.191	0.256	0.351	0.384	0.423	0.364
4	0.041	0.065	0.087	0.120	0.131	0.144	0.124
5	0.066	0.104	0.140	0.192	0.210	0.231	0.199
6	0.035	0.000	0.074	0.101	0.111	0.122	0.105
7	0.071	0.111	0.149	0.205	0.224	0.247	0.213

Elasticities

Stage	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	0.000	0.006	0.043	0.000	0.000	0.000	0.019
2	0.000	0.001	0.006	0.001	0.001	0.000	0.003
3	0.005	0.003	0.099	0.041	0.048	0.008	0.053
4	0.006	0.000	0.016	0.018	0.039	0.012	0.028
5	0.024	0.000	0.023	0.018	0.057	0.041	0.047
6	0.027	0.000	0.009	0.009	0.020	0.035	0.022
7	0.007	0.002	0.060	0.033	0.044	0.026	0.040

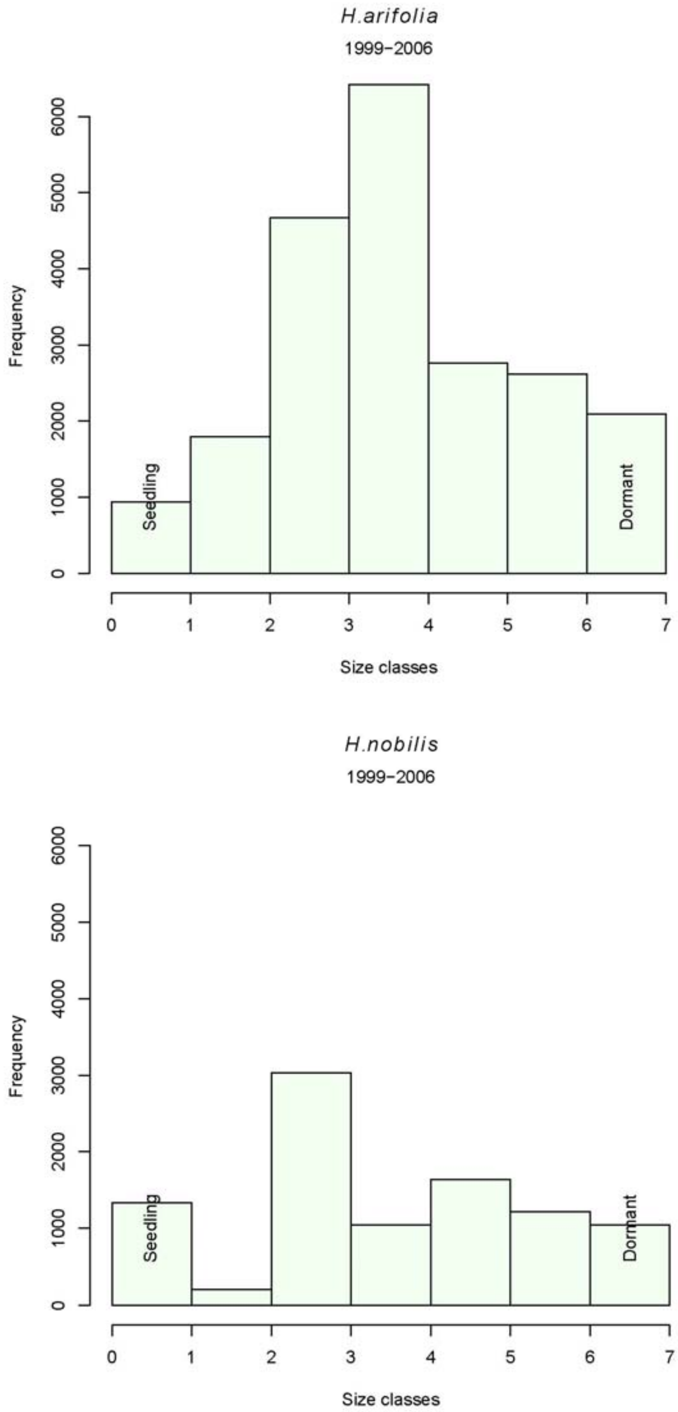
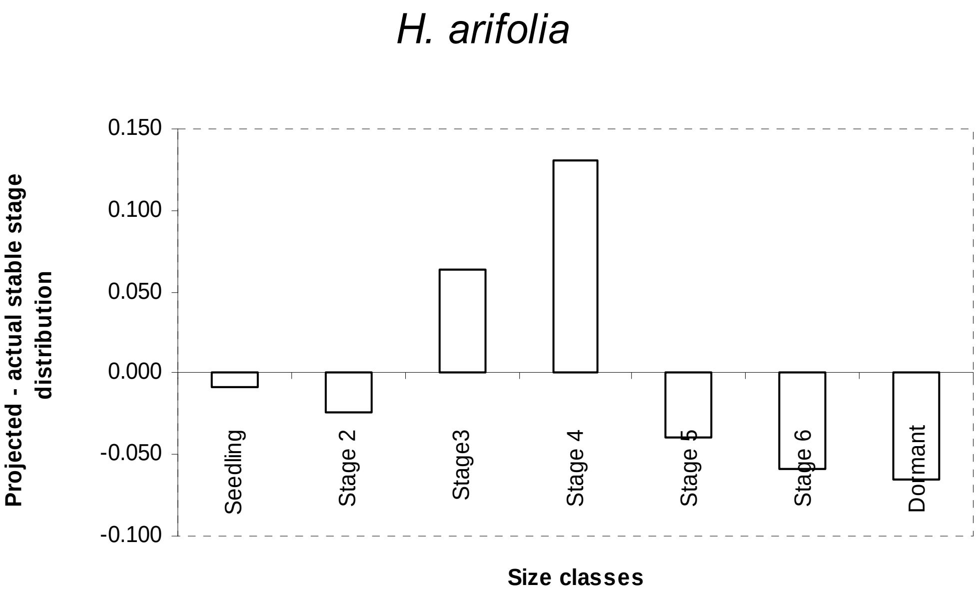


Figure 3.1. Size class frequencies for *Hexastylis arifolia* and *Hepatica nobilis* populations for the years 1999-2003 at Whitehall Forest in Athens, Georgia.



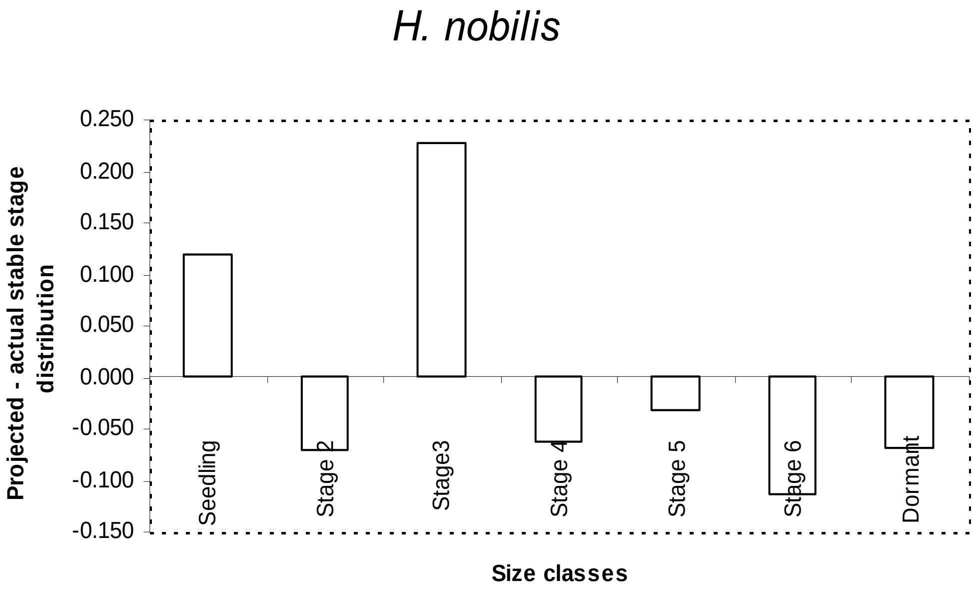


Figure 3.2. Differences between projected and actual stable stage class proportions for *Hexastylis arifolia* and *Hepatica nobilis*. Positive numbers indicate that the actual size class distribution is greater than that projected for a stable stage distribution, and negative numbers mean the actual distribution is less than the projected.

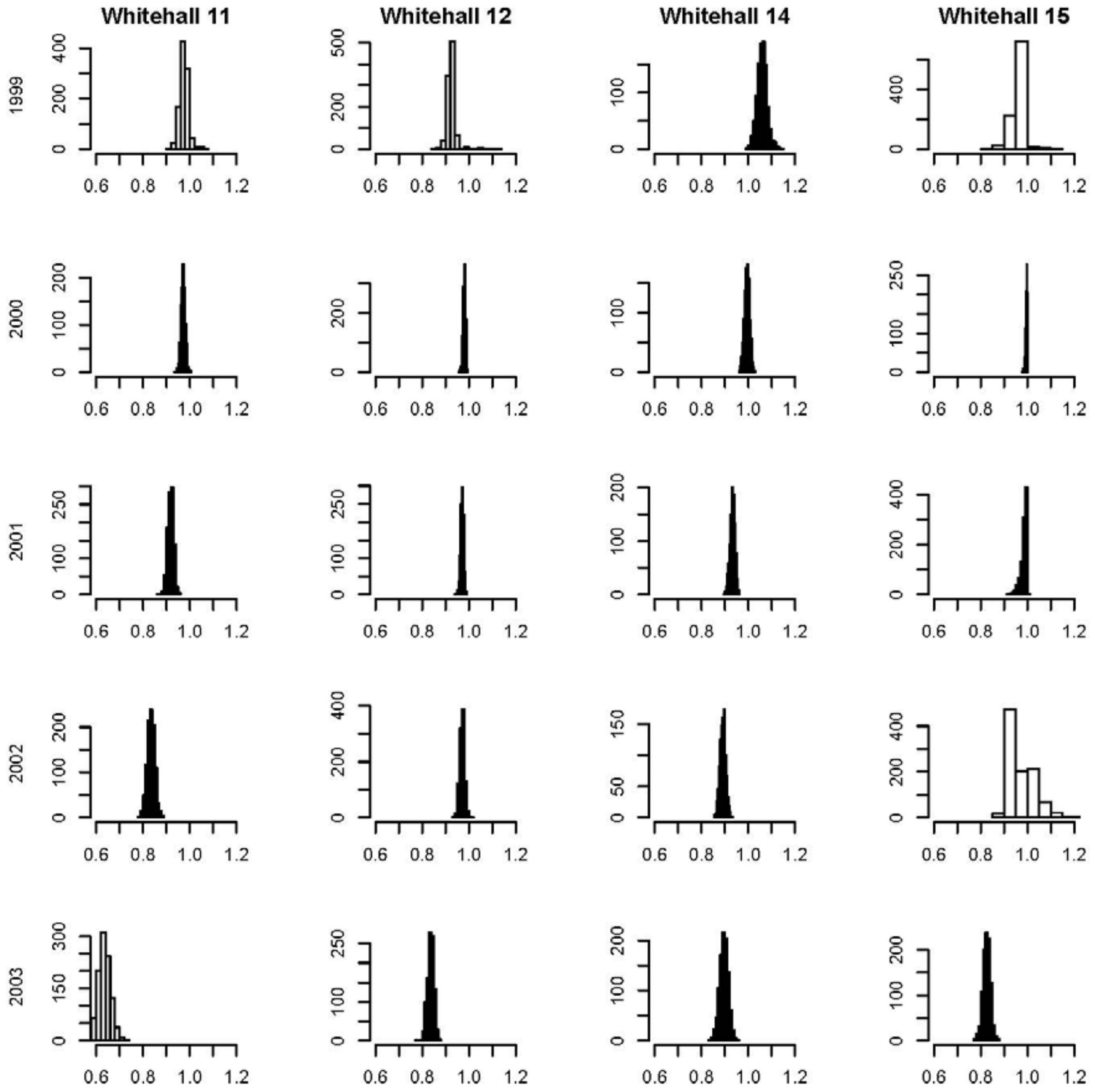


Figure 3.3. Population growth rates (λ) for *Hexastylis arifolia* populations at Whitehall Forest in Athens, Georgia. The histograms are based on data from 1,000 iterations.

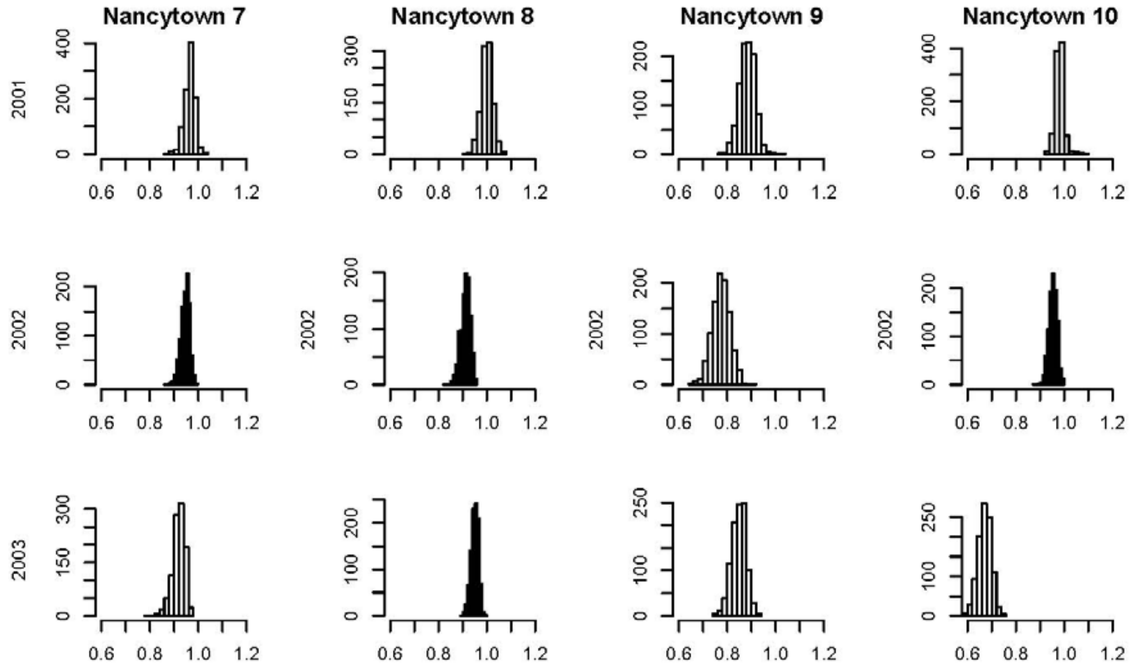


Figure 3.4. Population growth rates (λ) for *Hexastylis arifolia* Nancytown populations at Chattahoochee National Forest near Cornelia, Georgia. The histograms are based on data from 1,000 simulations.

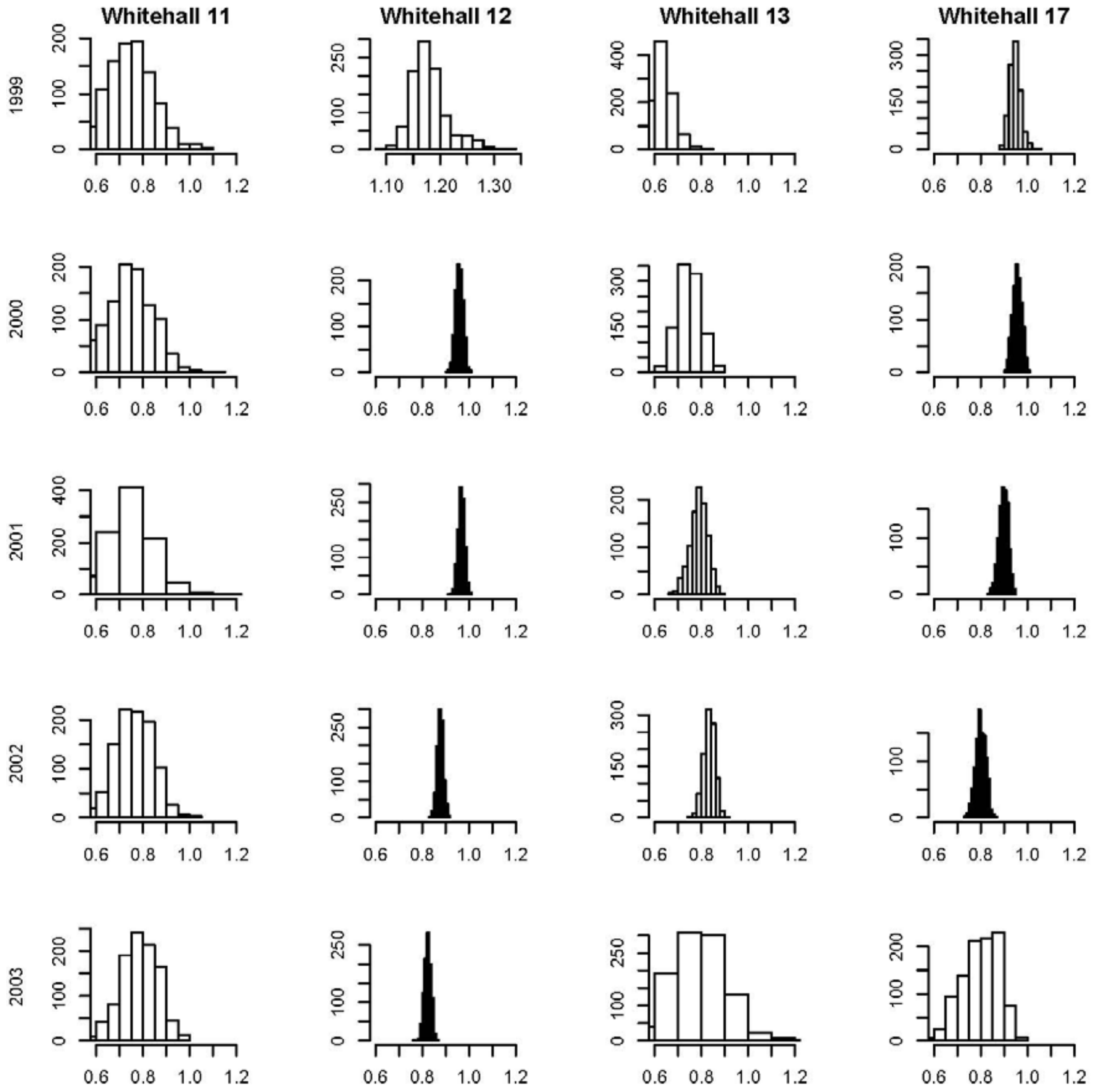


Figure 3.5. Population growth rates (λ) for *Hepatica nobilis* populations at Whitehall Forest in Athens, Georgia. The histograms are based on data from 1,000 simulations.

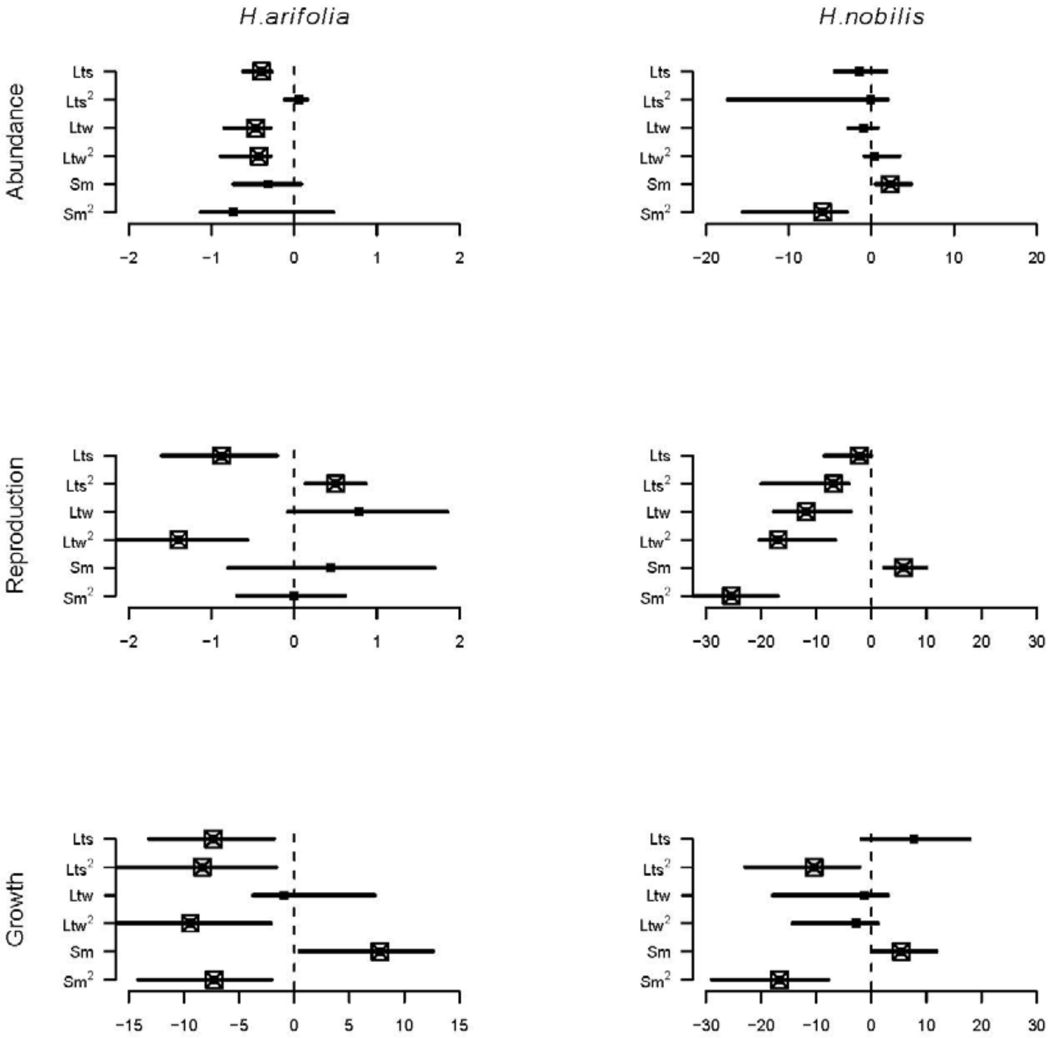


Figure 3.6. Mean values with 90% credible intervals for coefficients from the Bayesian hierarchical models of vital rates (*Abundance*, *Reproduction* and *Growth*) as a function of first- and second-order covariables (*Summer light (Lts), Winter light (Ltw)* and *Soil moisture (Sm)*. Coefficient slopes which did not differ from 0 (dotted line) indicated a lack of significant relationship between the predictor and response variables.

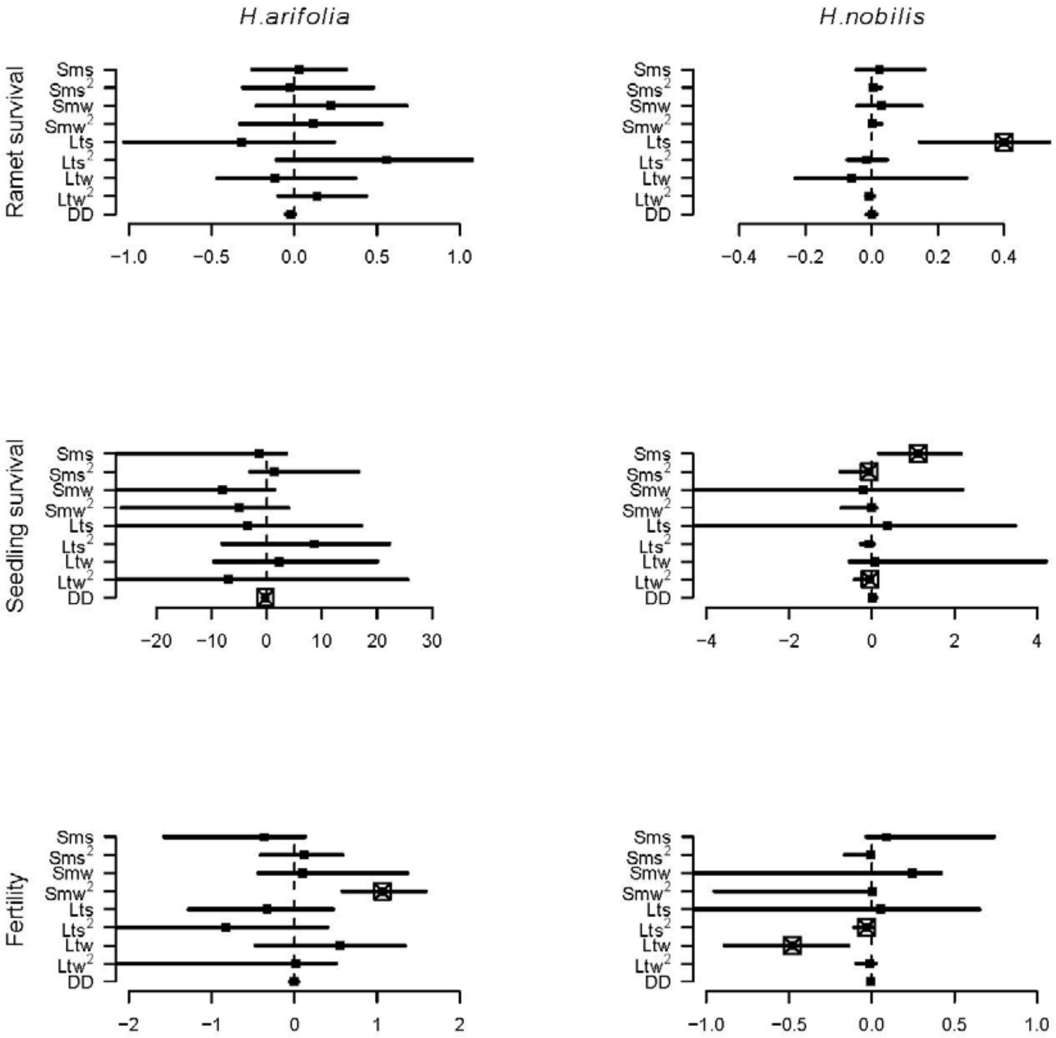


Figure 3.7. Mean values with 90% credible intervals for coefficients from the Bayesian hierarchical models of stage transitions (*Ramet survival*, *Seeding survival* and *Fertility*) as a function of first- and second-order environmental covariables (*Summer soil moisture (Sms), Winter soil moisture (Smw), Summer light (Lts), Winter light (Ltw) and Density dependence (DD)*). Coefficient slopes that did not differ from 0 (dotted line) indicated a lack of significant relationship between the predictor and response variables.

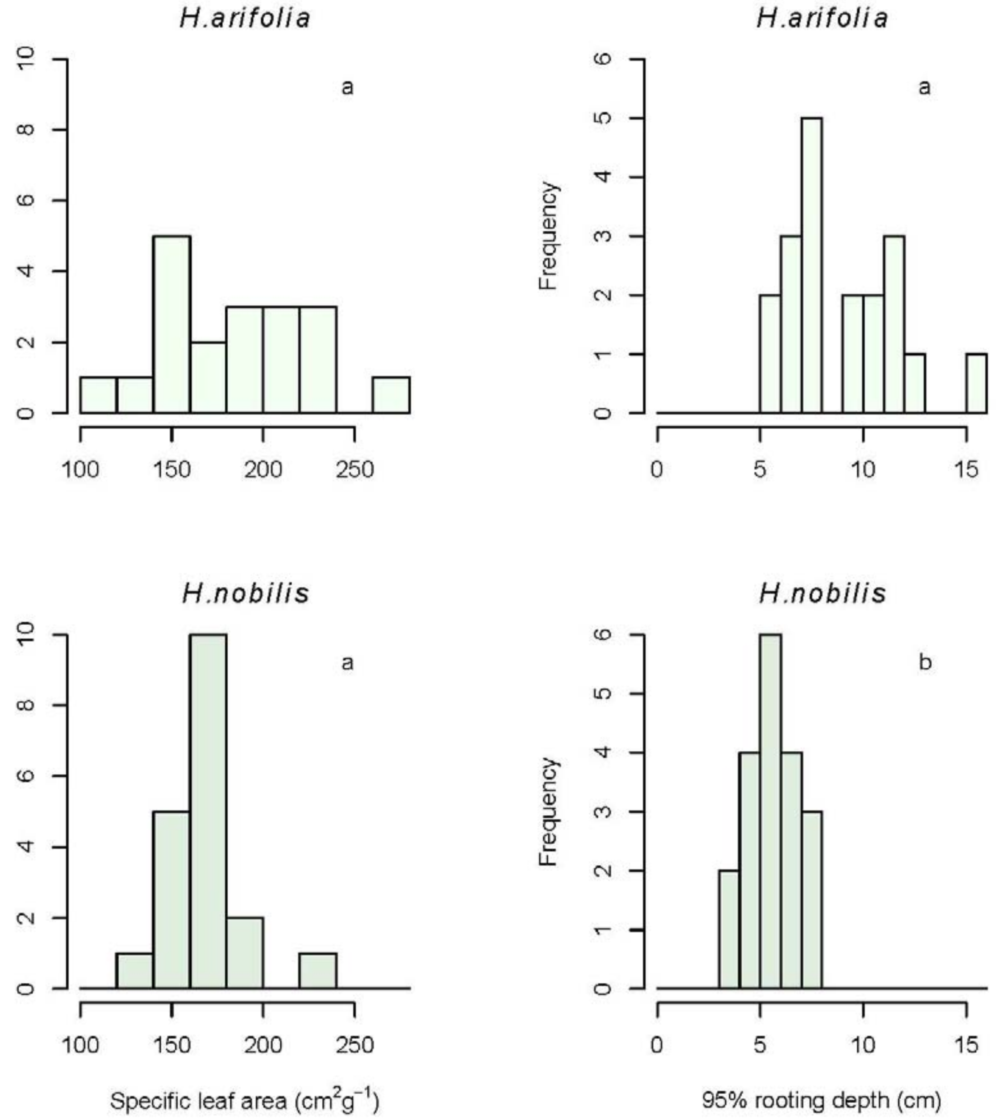


Figure 3.8. Frequency histograms of the specific leaf area and 95% rooting depth of *Hexastylis arifolia* and *Hepatica nobilis* collected from overlapping populations at Whitehall Forest in Athens, Georgia (n=20 each). Trait histograms with the same letter for both species indicate no significant difference ($p < 0.10$) in that trait between *H. arifoli*a and *H. nobilis*.

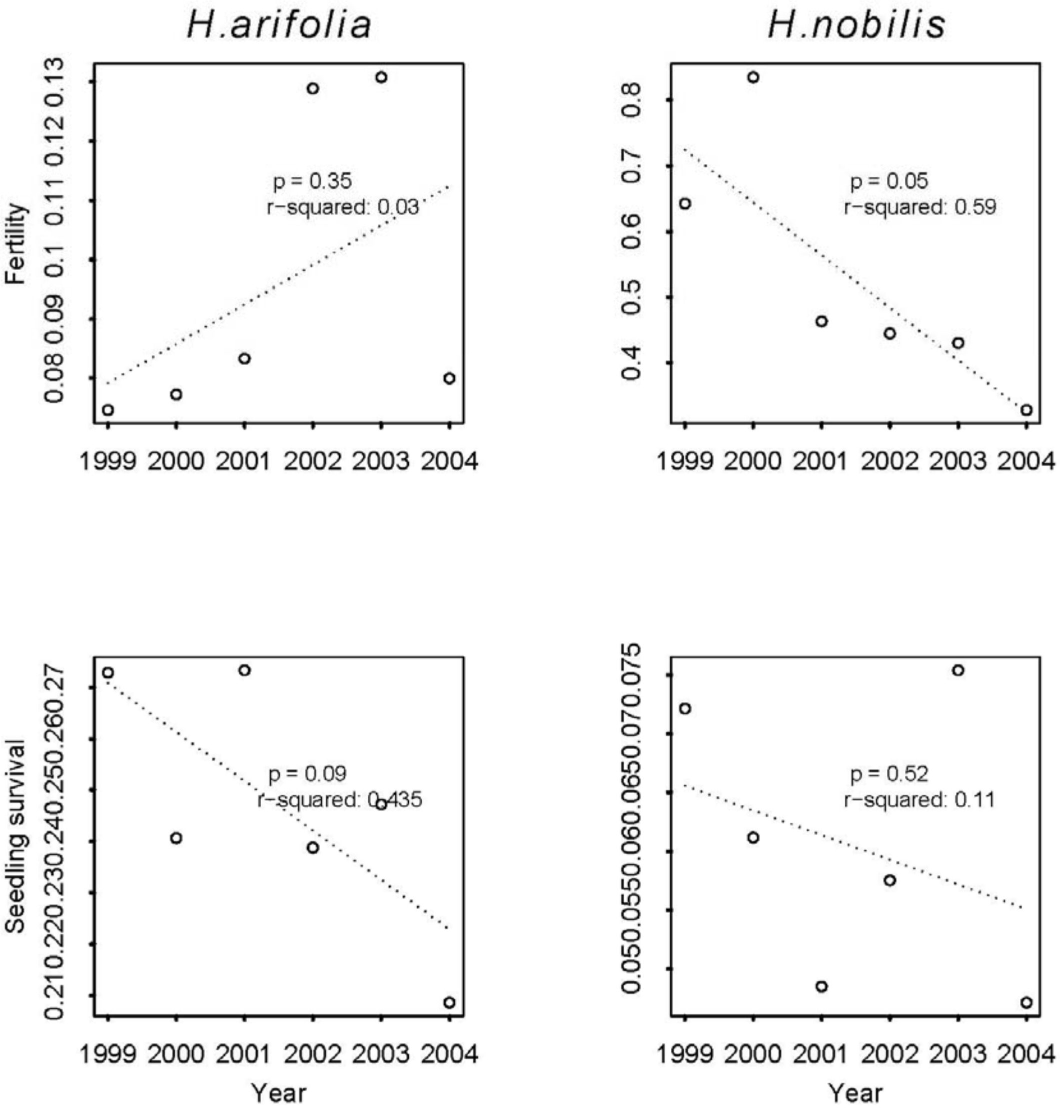


Figure 3.9. Average fertility (reproductive → seedling) and seedling survival (seedling → size class 2) transitions for all populations per year for *Hexastylis arifolia* and *Hepatica nobilis*.

CHAPTER 4

THE EFFECT OF MANIPULATED LIGHT AND WATER ON EVERGREEN UNDERSTORY HERB VITAL RATES IN NORTH- AND SOUTH-FACING COMMON GARDENS

INTRODUCTION

The understory environment within temperate forests undergoes dramatic annual shifts driven by seasonal climate combined with tree canopy senescence. In summer, temperatures are high and sunlight is scarce; in winter, sunlight is plentiful and temperatures are low. Understory herbaceous plants have developed distinct guilds that take advantage of these annual shifts (e.g., spring ephemerals, summergreens, wintergreens) (Neufeld & Young 2003), but only understory evergreen herbs face the full range of environmental extremes.

By investing in relatively thick, dense leaves, evergreen plants exhibit a level of herbivory resistance and nutrient retention that exceeds that of their deciduous counterparts; and they counterbalance the increased outlay by retaining the leaves much longer (Gray 1983; Reich *et al.* 1992). This enables year-round photosynthesis with relatively low resource requirements (e.g., nutrients and water) (Chabot & Hicks 1982; Delucia & Schlesinger 1995; Givnish 2002; Neufeld & Young 2003). A common trade-off for the tough, persistent evergreen leaves, however, is an inherent physiological ceiling on maximal photosynthetic rates and a limited ability to adjust to shifting environmental conditions (e.g., temperature), and consequently understory evergreen herbs often have low growth rates and limited competitive ability (Reich *et al.* 1992; Skillman *et* *al.* 1996). These limitations may, in turn, influence the distribution of understory evergreen herbaceous plants in deciduous forests as a function of environmental conditions (Lipscomb & Nilsen 1990; Oberhuber & Bauer 1991; Hughes *et al.* 2005).

Depending on slope aspect and angle, annual changes in the solar zenith angle create enormous shifts in annual solar irradiation, and this results in variable contrasts between north- and south-facing slopes from slight gradients during the summer to 50-800% differences in winter (Cantlon 1953; Frank & Lee 1966; Holst *et al.* 2005). In deciduous forests, this change in solar insolation combined with the opening of the canopy during winter, creates an extreme seasonal light and temperature gradient across slopes (Cantlon 1953; Holst *et al.* 2005). This seasonal shift likely has little impact on deciduous plants which are inactive during the winter portion of the seasonal extremes; however, evergreen species are exposed to the full range.

While light absorption by chlorophyll is largely insensitive to temperature and drought, the enzyme-catalyzed reactions involved in CO_2 assimilation are not (Lambers *et al.* 1998). The enzymes involved in CO_2 fixation can be denatured by high or low temperatures, or inhibited by drought-induced stomatal closure (Wise 1995; Lambers *et al.* 1998). This condition, called photoinhibition, can simply inhibit photosynthesis or, in the extreme, cause the formation of highly reactive oxidants that can damage the plant (Raven 1989; Logan *et al.* 1999). The higher potential irradiance on south-facing slopes creates two potential seasonal peaks in photoinhibition: one in summer as a result of low soil moisture combined with high temperatures (Raven 1989; Pearcy *et al.* 1994; Neufeld & Young 2003) and one in winter due to high irradiance combined with low temperatures (Verhoeven et al. 1999, Adams et al. 1991, Oquist and Huner 1991). While the photoinhibitory effect of seasonal environmental shifts on evergreen understory herbs per aspect has not been explored, Mediterranean shrubs exhibit greater levels photoinhibition on south-facing slopes (Bellot *et al.* 2004), and understory evergreen herbs respond to environmental variables in a manner consistent with seasonal photoinhibition (Chapters 2 and 3).

Understory evergreen herbs occur less on south- than north-facing slopes, and this dynamic appears related to contrasts in soil moisture, light, temperature and, more importantly, combinations of the three (Chapters 2 and 3). While correlations between plant distributions, performance and environmental conditions are suggestive, they are not conclusive. Of 225 plant-aspect studies examined for Chapter 2, only three used experimental techniques to investigate the north- and south-facing slope dynamics (Shanks & Norris 1950; Gauslaa *et al.* 2001; Sanders & McGraw 2005). This included placing bryophytes on tilted boxes in an open field with varying degrees of exposure (Gauslaa et al. 2001), transplanting a single understory herbaceous plant along aspect transects (Sanders & McGraw 2005) and planting garden tomatoes on adjacent slopes (Shanks & Norris 1950). However, none of these manipulated any explanatory variables such as light or soil moisture. The objective of this research is to investigate how evergreen understory herbs respond (survival, growth and photoinhibition) to environmental variables under standardized field conditions via common gardens that span north- and south-facing aspects and include manipulations of soil moisture and light. The following questions are addressed:

I. *What environmental variables best explain variation in understory evergreen herb vital rates?* Given that survey and demography data suggest that soil moisture correlates strongly with understory evergreen herb distributions and performance, and that seasonal environmental extremes also appear relevant (Chapters 2 and 3), I expected that increased soil moisture (treatment and ambient) would best explain variation in vital rates. Aspect and shade treatments, as well as ambient soil moisture, temperature, photosynthetically active radiation (PAR) and ultraviolet light (UV-B) also were explored. The impact of these variables, alone and in concert, are evaluated within the context of summer (tree canopy leaves on) and winter (tree canopy leaves off) intervals. I predicted that the combined low temperature-high irradiance stress of winter would better predict decreased vital rates than the high temperature-low soil moisture stress of summer.

II. *Can abiotic (environmental) variables account for the observed limited distribution of understory evergreen herbs on south-facing slopes?* Given that south-facing slopes contain unsuitable conditions for this guild (Chapter 2), and abiotic factors associated with these habitats (e.g., high light and low soil moisture) negatively influence these plants (Chapter 3), I predicted that understory evergreen transplants will survive and perform worse on south-facing than on north-facing experimental plots.

III. *Do three phylogenetically distinct understory evergreen herbs respond similarly or in a species-specific manner in response to environmental gradients?* While the strictest interpretation of Hubbell's neutral theory suggests that all members of a community guild or trophic level are functionally equivalent (Hubbell 2001), classical niche theory implies that they will occupy different microhabitats (Hutchinson 1957, 1959; MacArthur & Levins 1967). Given that demographic analysis of three understory evergreen species suggests differential sensitivities to soil moisture and light (Chapter 3, Diez and Pulliam *in pres*s); I predicted that the three evergreen species will exhibit unique vital rate responses to environmental variables.

METHODS

Study species

All three study species are small, perennial understory evergreen herbs common in the temperature deciduous forests of the eastern United States: (a) *Hexastylis arifolia* (Michx.) Small (family: Aristolochiaceae) has a distribution limited to the Southeastern United States from Florida to Virginia, North Carolina to the Mississippi River. The plant is more common in mesic than xeric habitats (Abella & Shelburne 2004), but is not limited by soil moisture (Gonzales 1972). It produces a single cohort of leaves each spring with a leaf life span of 12-13 months (Skillman et al. 1996). (b) *Hepatica nobilis* P. Miller (family: Ranunculaceae) occurs in the United States from northern Florida to Nova Scotia, west to Alabama and Missouri and Montana. It also occurs in Europe and Asia. The *Heptaica nobilis* that occurs in the United States is sometimes classified as *H. americana*. The plant is somewhat limited in dry habitats, particularly those with summer droughts (Tamm 1956; Inghe & Tamm 1985, 1988) and is more common on north slopes and near streams (Harris 2000). (c) *Goodyera pubescens* (Willd.) R. Br. ex Ait. f. (family: Orchidaceae) occurs throughout most of eastern North America west to the Mississippi River. It reproduces both sexually and asexually (McCormick et al. 2006). The species is dependent on mycorrhizal fungi for germination success, which increases in locations with higher soil moisture and soil organic matter (Diez 2007).

Transplant sites

During February 2006, 288 *H. arifolia* and 288 *H. nobilis* plants were collected from the same populations at Whitehall Forest (WHF) in Athens-Clarke County, GA (33^{o}92’ N latitude, 150-240 m elevation) and 288 *G. pubescens* plants were collected from a single population at Coweeta Hydrologic Laboratory (CWT) in the Nantahala National Forest (35^{o}01' N latitude) in

Otto-Macon County, NC. The plants were extracted with roots intact and transported in closed containers. They were transplanted into 12 cm^2 circular holes on north- and south-facing slopes at CWT and WHF (see Table 4.1 for site characteristics) before the next year's flush of leaves emerged. Two of each species were placed at random in 12, 1 x 1 m plots within 5 x 7 m grids (with 1 x 1 m spaces between plots). At each site (CWT and WHF), six grids were split among three north- and three south-facing slopes, resulting in 12 grids of 144 plots containing 864 plants (Table 4.1). All of the grids were located in deciduous forest sites with similar elevations and slope angles coupled between north- and south-facing grids at each site. Less than 10% of plants died within the first two weeks of transplanting and were promptly replaced. In addition, seeds from *H. arifolia* (WHF) and *G. pubescens* (CWT) were collected and planted in six plots within each grid during the spring (*H. arifolia*) and fall (*G. pubescens*) of 2006.

Treatments

In order to attenuate solar irradiation, custom made polyvinyl chloride (PVC) frames (1 x 1 x 0.5 m) were randomly assigned to half the plots in each grid. Black knitted 60% neutral shade cloth (International Greenhouse Co.) was placed over the top and partially down the sides of each frame. In order to augment soil moisture, water was delivered from two approximately 190-liter reservoirs via drip irrigation (Dripworks, Inc.) to the lower (slope position) two rows of each grid. The barrels were refilled weekly (May-August 2006, and thus each watered plot received approximately 63 liters of water per week during late spring and summer.

Physical monitoring

Volumetric soil moisture percentage was measured with a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific, Inc.) in July 2006 and in January 2007. Percent photosynthetically active radiation (PAR, wavelength: 400-700 nm) was calculated from hemispherical photographs (Nikon SLR; Nikon fisheye lens; self-leveling gimbal) using Gap Light Analyzer 2.0 software (Frazer et al. 1999). In order to reduce contrast between reflection and true sky and control temporal variation between grids, all photographs were taken at each plot on cloudy days between 10 a.m. and 2 p.m. in July 2006 and January 2007. Diffuse ultraviolet-B light was measured using an erythemal-weighted (280-400 nm) UV detector (Solar Light PMA1101, Solar Light Co.; LI-1400 data logger, LI-COR, Inc.). Measurements were made in shaded spots above each plot on clear days between 10 a.m. and 2 p.m. in July 2006 and January 2007 and percent diffuse UV-B was calculated based on hourly reference measurements beneath open sky with the same sensor (Grant 1997; Grant & Heisler 2001; Foyo-Moreno *et al.* 2003; Webb 2003). HOBO Pendent 64k data loggers (Onset Computer Co.) were placed above ground at each grid to record hourly surface temperatures throughout the duration of the experiment (February 2006-February 2007). In addition, four of the temperature data loggers were placed beneath shade cloth plots at both sites and on each aspect in order to assess whether the light treatment was confounded with temperature.

Biotic monitoring

All 864 plants were surveyed in July 2006 and January 2007, and presence, leaf number and longest leaf were recorded. Plant vital rates (survival, growth and chlorophyll fluorescence) were assessed in summer (July 2006) and winter (January 2007). Survival was calculated as the proportion of each species per cell that survived from transplanting in February 2006 to July 2006 (summer) and separately the proportion per cell surviving from July 2006 to January 2007 (winter). Growth similarly was calculated per summer and winter, and was based on leaf size and number. Because leaf length in *H. arifolia* and *H. nobilis* is closely correlated with leaf width

(Harris 2000; Giladi 2004), leaf growth was derived from leaf size: $Growth = leaf\ length_t - leaf\ length_{t-1}$, where *t* equals time of measure.

The photoinhibition of photosynthesis (i.e. temporary or permanent damage to photosynthetic apparatus) is a clear indicator of plant stress (Maxwell & Johnson 2000), and chlorophyll fluorescence can be used to detect photoinhibition. The use of chlorophyll fluorescence to detect photoinhibition stems from the underlying theory that light energy absorbed by chlorophyll can undergo three fates: electron transport, dissipation as heat or fluoresced as light (Maxwell & Johnson 2000). By controlling the first two factors, the yield of chlorophyll fluorescence can be measured and information about the status of photochemistry can be assessed. Chlorophyll fluorescence measurements were taken using the Fv/Fm setting on a Mini-PAM (Heinz Walz GmbH) modulated fluorometer (which allows measurement regardless of background light) on a subsample of 144 plants per species, equally representing slope, light and soil moisture treatments. The measurements were taken on leaves dark-adapted (20 minutes) with 2030-B leaf clips (Heinz Walz GmbH). Dark-adapted values of Fv/Fm reflect the potential quantum efficiency of photosystem II (PSII) and indicate plant photosynthetic performance. The mean value of Fv/Fm (PSII efficiency) in non-stressed C3 plants is 0.84 (Bjorkman & Demmig 1987). PSII efficiency values below 0.84 are measured when the plant has been exposed to stress, and this reveals damage to PSII (photoinhibition) or the onset of protective mechanisms against excess light energy (photoprotection) (Demmig & Bjorkman 1987; Maxwell & Johnson 2000).

In order to determine germination success, *Hexastylis arifolia* seeds were extracted from dehiscing fruits at WHF in May 2006 and *G. pubescens* seed capsules were harvested at CWT in October 2006. For both species, seeds were collected from the same adult populations, placed in seed packets and stored in airtight containers at 5° C until planted three days later. Five *H.*

arifolia and an indeterminate number of *G. pubescens* (due to the minute size) seeds were placed in each seed packet. The seeds were placed within folded 3 x 6 cm pieces of 36 micron nylon mesh held in place with 5 x 5 cm slide mounts. Seed packets for each species were inserted in 8 plots at each grid (n = 96/species) and flagged for retrieval in April (*H. arifolia*) and June (*G. pubescens*) 2007. Germination success was determined by the proportion of seed packets with emerged seedling roots in *H. arifolia* and the presence of protocorms in *G. pubescens*. In addition, 5 *H. arifolia* seeds were planted in the soil near the respective seed packet, and surviving *H. arifolia* seedlings were censused in June 2007.

Data analysis

Variance in vital rates as a function of site and treatments was assessed using an analysis of variance model, where the dependent variables were survival, growth and PSII efficiency and the cofactors were site (CWT or WHF), aspect (north or south), water (added or not added) and shade (shadecloth or no shade). In addition, interaction terms for all the cofactors were included in the model. The generalized linear model structure was used to transform the dependent variables to linearity assuming a binomial error distribution ($Y_i \sim Binomial\ (n_i, p_i)$) with the logit link function for survival and the normal error distribution ($Y_i \sim normal\ (\mu, \sigma^2)$) with the identity link function for growth and PSII efficiency. Tukey's 'Honest Significant Difference' (HSD) method was used for *post hoc* analyses of significant differences in means. Tukey's HSD creates a set of confidence intervals of the differences in cofactor means. The ANOVAs and *post hoc* analyses were implemented using the "R" statistical package (R_Development_Core_Team 2006).

Variance in vital rates as a function of ambient environmental variables was assessed using separate analysis of covariance models for summer and winter, where the dependent variables were summer and winter survival, growth and PSII efficiency (using the same error distributions as outline above) and summer and winter soil moisture and light were covariables and summer and winter temperature was a cofactor. Colinearity prevented the combination of treatment and ambient variables as the ambient soil moisture and light measurements include the influence of water and shade treatments. Furthermore, a correlation between UV-B and PAR ($p = 0.04$) prompted the exclusion of UV-B from the models. *Hexastylis arifolia* and *G. pubescens* seed germination, and *H. arifolia* seedling survival, also were analyzed using ANCOVAs with seasonal soil moisture and light as covariables and site, aspect and temperature as cofactors. The modeled error distributions were assumed to be normal for *H. arifolia* germination, binomial for *G. pubescens* germination and Poisson ($Y_i \sim Poisson\ (\mu_i)$) for *H. arifolia* seedling survival.

Bayesian hierarchical GLMs were used to generate 90% credible intervals for the regression coefficients (line slopes) of all ANCOVAs. The Bayesian models were implemented in the WinBUGS 1.4.2 software package. The models were implemented in a hierarchical framework with normally distributed, noninformative priors ($Normal\ (0,0.001)$). The 90% credible intervals for regression coefficients were generated using Markov chain Monte Carlo (MCMC) simulations in WinBUGS. A minimum of 20,000 iterations were used to “burn-in” the simulations before coefficient estimates were measured and 5,000 iterations were used to generate the posterior distributions. In order to mitigate coefficient autocorrelation between iterations, the output was “thinned” by only using every 20th measure. The iterations were run with three chains and all chains converged (Gelman-Rubin statistic < 1.1).

RESULTS

Sites and treatments

The mean ambient temperature remained about 3º C warmer, and the average soil moisture about 3% lower, at WHF than CWT during both summer and winter. Light penetration (UV-B and PAR) at both sites was about the same with ~2% reaching the understory in summer and ~33% in winter. Temperature differed little between north- and south-facing aspects during the summer; however, the temperature was about 2.5º C warmer on south-facing aspects during winter. Soil moisture was about 1% higher on north- than south-facing aspects while UVB and PAR differed little. Watering increased soil moisture by an average of 6%; and shadecloth reduced PAR by an average of 66%. Temperature was about 1º C lower in plots with shade cloth than those without. While this difference appeared small, the shade cloth muted extreme high temperatures during the winter, and thus may indeed have posed a confounding effect in shaded plots.

While survival differed little between sites, *G. pubescens* had the highest proportion of plants survive (> 90%) followed by *H. nobilis* (80-81%) and *H. arifolia* (71-75%) (Table 4.2). Both *G. pubescens* and *H. nobilis* had more leaf growth at CWT than WHF, and both had greater leaf growth than *H. arifolia*. PSII efficiency was lower during the winter for all three species; *H. arifolia* and *H. nobilis* had similar PSII efficiencies while *G. pubescens* appeared lower.

Vital rates as a function of treatments

Water augmentation had the greatest treatment effect as it significantly increased survival and growth for all three study species (TukeyHSD, $p < 0.10$; Figure 4.1). *Hexastylis arifolia* and *H. nobilis* survival, and *H. arifolia* growth, also increased more on north- than south-facing slopes (TukeyHSD, $p < 0.10$). Aspect appeared to have little impact on *G. pubescens*

(TukeyHSD, $p > 0.10$), though PSII efficiency was significantly greater on north- than south-facing slopes (TukeyHSD, $p < 0.10$). Shading had no significant impact on growth and survival for any plants (TukeyHSD, $p > 0.10$), but it increased PSII efficiency for both *H. arifolia* and *G. pubescens* (TukeyHSD, $p < 0.10$). The location of the experimental common garden sites (CWT vs. WHF) had no impact on *G. pubescens* vital rates (TukeyHSD, $p > 0.10$), but PSII efficiency was significantly greater at WHF for *H. arifolia* and *H. nobilis*; and *H. nobilis* growth was lower at CWT while *H. arifolia* survival was higher at CWT (TukeyHSD, $p < 0.10$).

Interaction terms for the treatment ANOVAs (not included in Figure 4.1) indicated that *H. arifolia* survival increased on south-facing slopes with water or shade augmentation (Asp:Wtr, Asp:Shd), while *G. pubescens* survival on south-facing slopes increased at CWT (Land:Asp) (ANOVA, $p < 0.10$). *Hepatica arifolia* and *H. nobilis* growth also was greater on south-facing slopes at CWT (Land:Asp), while watering at CWT (Land:Wtr) and when combined with shading (Wtr:Shd) also significantly increased *H. nobilis* and *G. pubescens* growth (ANOVA, $p < 0.10$).

Vital rates as a function of environmental variables

Increased summer soil moisture correlated positively with growth in all three species, though *H. nobilis* and *G. pubescens* peaked at intermediate soil moisture levels (Figure 4.2). Increased summer soil moisture also correlated positively with *H. nobilis* survival. Summer light had mixed impacts on *H. arifolia* and *H. nobilis*. Growth declined with light for both species, and *H. arifolia* survival decreased with increased light, but survival increased at the highest light levels for both. However, the significant interaction term indicated that *H. nobilis* growth responded positively to light when paired with higher soil moisture. PSII efficiency also correlated negatively with summer light in both *H. arifolia* and *H. nobilis*. Higher summer temperatures correlated with decreased survival in *H. arifolia* and *G. pubescens* and increased growth in *H. nobilis* and *G. pubescens*.

Winter light only affected *H. arifolia*, and the affect was negative as both *H. arifolia* survival and growth correlated negatively with winter light (Figure 4.3). High levels of winter soil moisture generally had a negative impact, as *H. arifolia* and *G. pubescens* PSII efficiency and *H. arifolia* growth, declined significantly at high soil moisture levels. While increased temperature had mixed results during summer, the trend was unambiguous during winter as it correlated positively with *H. arifolia* and *H. nobilis* PSII efficiency, *H. arifolia* growth, and at the higher winter temperatures, survival for all three species.

In general, *H. arifolia* was most sensitive to light while *H. nobilis* and *G. pubescens* responded more to soil moisture (Figures 4.2 and 4.3). Both *H. arifolia* and *H. nobilis* underwent seasonal photoinhibitory responses as PSII efficiency decreased with light in summer (and decreased with summer temperatures in *H. arifolia*) and increased with temperature in winter.

Soil moisture was the only environmental variable that impacted germination in either *H. arifolia* or *G. pubescens* (Figure 4.4). The germination of *H. arifolia* seeds correlated negatively with high levels of winter soil moisture, while *G. pubescens* seed germination correlated positively with both summer and winter soil moisture. While *H. arifolia* seed germination was insensitive to most environmental variables and decreased with high winter soil moisture, *H. arifolia* seedlings were sensitive to most environmental variables and increased at intermediate winter soil moisture levels (Figure 4.4). *Hexastylis arifolia* seedling survival rates were highest at WHF and on north-facing slopes. Seedling survival increased with summer light but decreased at high levels of winter light and decreased at higher temperatures.

DISCUSSION

The understory evergreen herbs responded to the environmental variables (both treatments and ambient) in a manner consistent with a guild that has limited distribution on south-facing slopes. While there were species-level differences, increased summer temperature and light exposure, and lower soil moisture, negatively correlate with vital rates. Environment had less influence in winter, but decreased temperature and increased light also correlate negatively with vital rates. All three plants fare worse in the drier, hotter environment of south-facing slopes, and watering and shading demonstratively ameliorate these stressors.

Environmental variables and vital rates

The negative response of evergreen understory herbs to conditions on south-facing common gardens, and to the environmental variables associated with south-facing aspects (higher temperatures and light, and lower soil moisture), confirms that their limited distribution in these habitats across the landscape (Chapter 2) is attributable, at least in part, to physiological niche limitations (Figures 4.1-4.4). While additional factors such as competition, disease and dispersal limitation may play into this distribution pattern, there appear to be core environmental barriers against evergreen understory herbs occupying south-facing aspects in abundance. The strongest of these appears to be soil moisture (Figures 4.1-4.4). Water augmentation has far more impact upon the plants than location, aspect or shading (Figure 4.1), and watering and shading appears to offset the negative impact of south-facing slopes upon plant vital rates.

Attempting to gain insight into the understory evergreen herbaceous niche requires consideration beyond the traditional spring/summer growing season due to the persistence of biologically active leaves into the fall and winter. The physiological make-up of evergreen leaves, particularly those belonging to shade tolerant species, leave them susceptible to photodamage, both in winter and summer, due to high temperatures and light combined with low soil moisture in summer and high light and low temperatures in winter (Pearcy *et al.* 1994; Lambers *et al.* 1998; Neufeld & Young 2003). Because of the relatively extreme conditions in winter compared to summer (in this experiment: > 15 times the light and UVB exposure, a mean 3° C cooler), I expected that winter conditions would act as the bottleneck limiting the herb survival and growth, and indeed winter conditions pose a negative influence upon the plants, particularly *H. arifolia* (Figure 4.2). Nevertheless, the plants appear more sensitive to summer conditions, based on vital rates, even though the below-canopy ambient light during summer is far less than that in winter (Figure 4.3).

In summer, the higher temperatures and light levels, and lower soil moisture on south-facing aspects, provides the best explanation for reduced survival and growth in all three species (Figures 4.1 and 4.2), though *G. pubescens* survival and growth appears the least influenced by aspect and environmental variables. *Hexastylis arifolia* did most poorly on south-facing slopes based on survival and growth, and consistently responded negatively to high summer temperatures and light; *H. nobilis* survival and growth also responded negatively to summer light, but appeared far more dependent on soil moisture than the other species. The negative performances of *H. arifolia* and *H. nobilis* in summer might be explained, in part, by summer photoinhibition as evidenced by decreased PSII efficiency correlating with higher light.

Evergreen leaves are not as active during winter due to a progressive decline in photosystems with age and an inability to adjust to changing temperatures (Skillman *et al.* 1996; Neufeld & Young 2003). While the effects of the winter environment are not as pervasive as summer, one clear pattern emerges: all plants better survive winter in warmer environments (Figure 4.3). Furthermore, photoinhibition again plays a part in *H. arifolia* and *H. nobilis* performance, and temperature is the key component. PSII efficiency increased in both species with increased temperature. Interestingly, both *H. arifolia* and *G. pubescens* PSII efficiency decreases at high levels of soil moisture, and this is the only environmental factor that significantly influenced *G. pubescens* PSII efficiency in any season.

Germination success and seedling survival

Adult vital rates go a long way in accounting for actual natural distributions, particularly at the microsite scale, but *G. pubescens* and *H. arifolia* transplants grew and survived equally well at both CWT and WHF, while natural populations of *G. pubescens* are far more abundant at CWT than WHF, and *H. arifolia* does not occur at CWT (Chapter 2). This large-scale pattern is somewhat reconciled when analyzed at the seedling stage (*H. nobilis* seeds died in storage) (Figure 4.4). While *H. arifolia* seed germination appear largely impervious to environmental conditions, only showing a negative correlation at the highest levels of winter soil moisture, *H. arifolia* seedlings are quite susceptible to light, soil moisture and temperature. Most notably, *H. arifolia* seedling survival is much lower at CWT than WHF. The seedlings survive better on south-facing slopes, at intermediate winter soil moisture levels, with increased summer and decreased winter light and at lower temperatures. That some of these results, particularly increased *H. arifolia* seeding survival on south-facing slopes, contradict adult performance suggests that both seedling and adult stages are integral in determining *H. arifolia* distributions. *Goodyera pubescens* germination success does not correspond with common garden location; it should be noted, however, that *G. pubescens* germination only occurred at WHF in plots that received shade or water augmentation. *Goodyera pubescens* germination did correlate with increased summer and winter soil moisture, conditions more common at CWT than WHF.

Furthermore, *G. pubescens* germination depends upon colonization by mycorrhizal fungi (Diez 2007), the distribution of which may be determined by landscape factors not measured here.

Niche differentiation

Performance indicators in natural populations of *H. nobilis* and *G. pubescens* (*H. arifolia* less so) demonstrate intermediate responses to environmental variables, particularly growth (Chapter 3, Diez and Pulliam in press). Keddy (1989) interprets this type of pattern as an indication of competition. He proposes that all species have physiological optima at the upper end of a resource gradient but differ in competitive abilities, which results in a unimodal response. However, when competition and other biotic interactions were standardized by transplanting both species into experimental common gardens, the transplants retain the unimodal response to summer soil moisture for 2/3 species (*H. nobilis and G. pubescens*), and in seedling survival for *H. arifolia* (Figure 4.2). Within the limits of the current study design, and with species *n*=3, this suggests that the study species might segregate at both large and small scales based on environmental filtering rather than competition. However, *H. nobilis* and *G. pubescens* plants in natural populations also exhibited unimodal vital rate responses that are not retained in the transplants, which suggest competition also may play an important role in distribution.

Weiher and Keddy (1999) propose that environmental filtering acts upon species and structures communities at the larger scale, while limiting similarity (Gause 1934; Hutchinson 1957, 1959; MacArthur & Levins 1967) is more important at smaller scales. At the scale of aspect transitions, the three species respond similarly, though *G. pubescens* is consistently less sensitive to aspect shifts than the other two species (Figure 4.1, also see Chapter 2). In addition, all three species exhibit a robust and similar positive vital rate response to winter temperature, though, again, *G. pubescens* less so than the other two (Figure 4.3). At the microsite scale, *H.*

nobilis is unambiguously the most sensitive to soil moisture and least drought-tolerant of the three species (Figures 4.1-4.3); while *H. arifolia* appears most sensitive to increased winter light and decreased temperatures (Figure 4.2). Both *H. arifolia* and *H. nobilis* appeared stressed (less PSII efficiency) by increased light in summer and decreased temperature in winter, while *G. pubescens* PSII efficiency—the lowest of the three species (Figure 4.3)—was highly variable and did correlate well with environmental variables. These data suggest *H. arifolia* and *H. nobilis* indeed have specific physiological niches while *G. pubescens* adults appear more intermediate—though this is not true for *G. pubescens* seedlings which are very soil moisture dependent and better explain the species distribution than adults (Figure 4.4). These data correspond with assumptions of niche differentiation—optimal performance at different points along at least one environmental gradient, i.e. fundamental niche differentiation (Whittaker 1975, Curtis 1959, Gleason 1926).

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TABLES AND FIGURES

Table 4.1. Site variables for experimental common garden grids on north- and south-facing aspects at Whitehall Forest in Athens, GA and Coweeta

	Whitehall Forest					
	Elevation (m)	Slope°	Azimuth°		Plots	Plants
North 1	204	15	350		12	72
North 2	172	16	340		12	72
North 3	172	22	340		12	72
South 1	182	15	180		12	72
South 2	172	15	140		12	72
South 3	182	22	160		12	72
mean=	180.7	17.5		*n*=	72	432

	Coweeta Hydrologic lab					
	Elevation (m)	Slope°	Azimuth°		Plots	Plants
North 1	750	17	330		12	72
North 2	1023	15	0		12	72
North 3	783	16	10		12	72
South 1	801	16	180		12	72
South 2	755	17	180		12	72
South 3	1025	21	180		12	72
mean=	856.2	17.0		*n*=	72	432

Table 4.2. Summary of *Hexastylis arifolia* (Hx), *Hepatica nobilis* (Hp) and *Goodyera pubescens* (Gd) mean vital rates at Coweeta Hydrologic Laboratory (Otto, NC) and Whitehall Forest (Athens, GA).

	Survival		Leaf growth (cm^2)		PSII efficiency			
	Whitehall	Coweeta	Whitehall	Coweeta	Whitehall		Coweeta	
					summer	winter	summer	winter
Hx	71.5%	75.0%	544	558	0.811	0.677	0.800	0.693
Hp	80.6%	81.9%	6012	2846	0.822	0.720	0.810	0.719
Gd	90.3%	92.4%	14535	9815	0.781	0.577	0.775	0.561

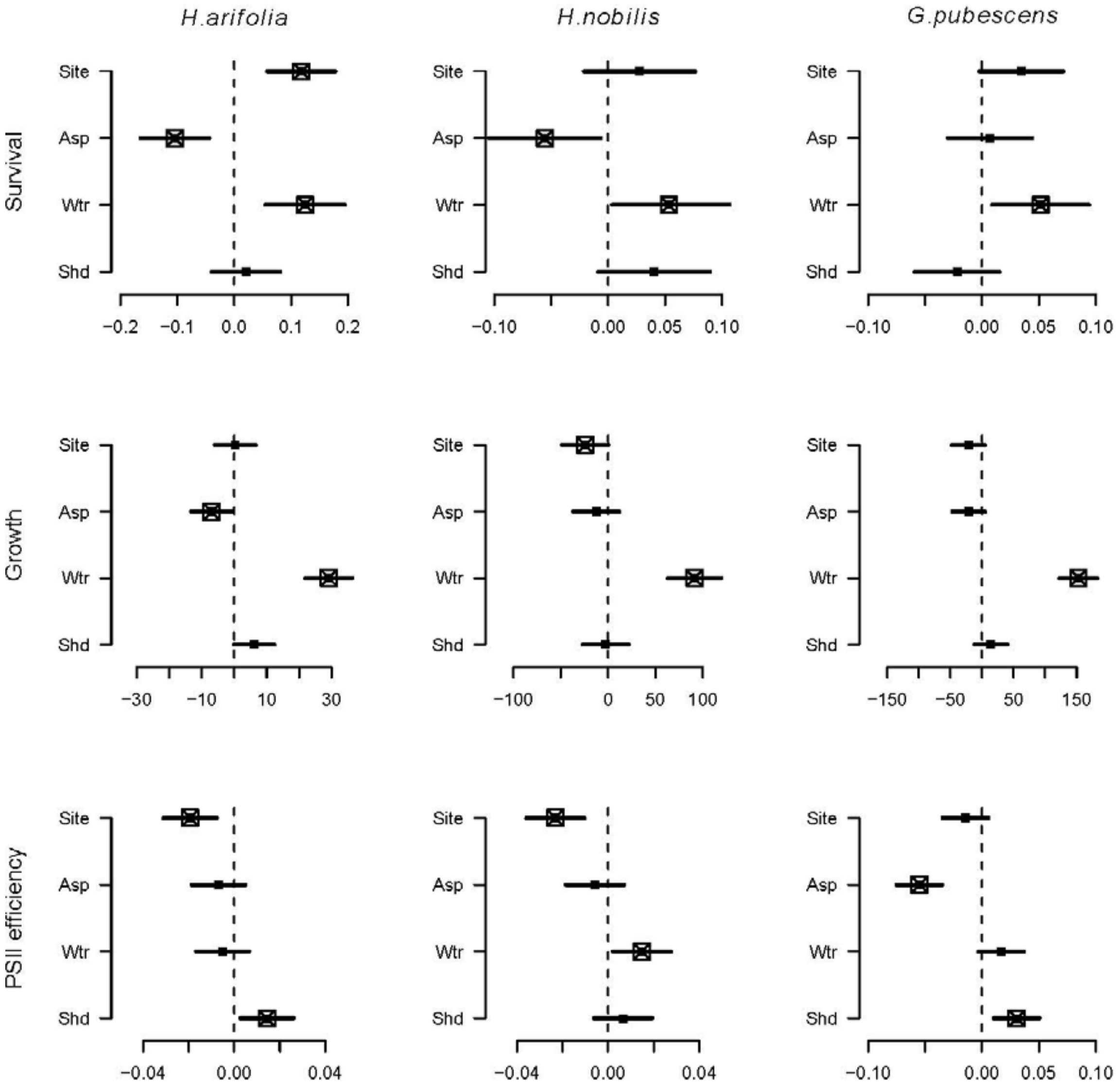

Figure 4.1. Mean treatment differences with 90% confidence intervals for cofactors using Tukey's 'Honest Significant Difference' method as a *post hoc* test of ANOVA models of vital rates (*Survival, growth* and *PSII efficiency*) as functions of landscape and treatment cofactors (*Site, Aspect* (*Asp*), *Water* (*Wtr*) and *Shade* (*Shd*). Dummy variables were used to code each treatment such that: Site (Whitehall Forest = 0, Coweeta Hydrological lab = 1), Aspect (North = 0, South = 1), Water (not added = 0, added = 1) and Shade (no shadecloth = 0, shadecloth = 1). Intervals that cross zero indicate that the vital rate did not differ significantly with the cofactor. Significant point values are highlighted with a box.

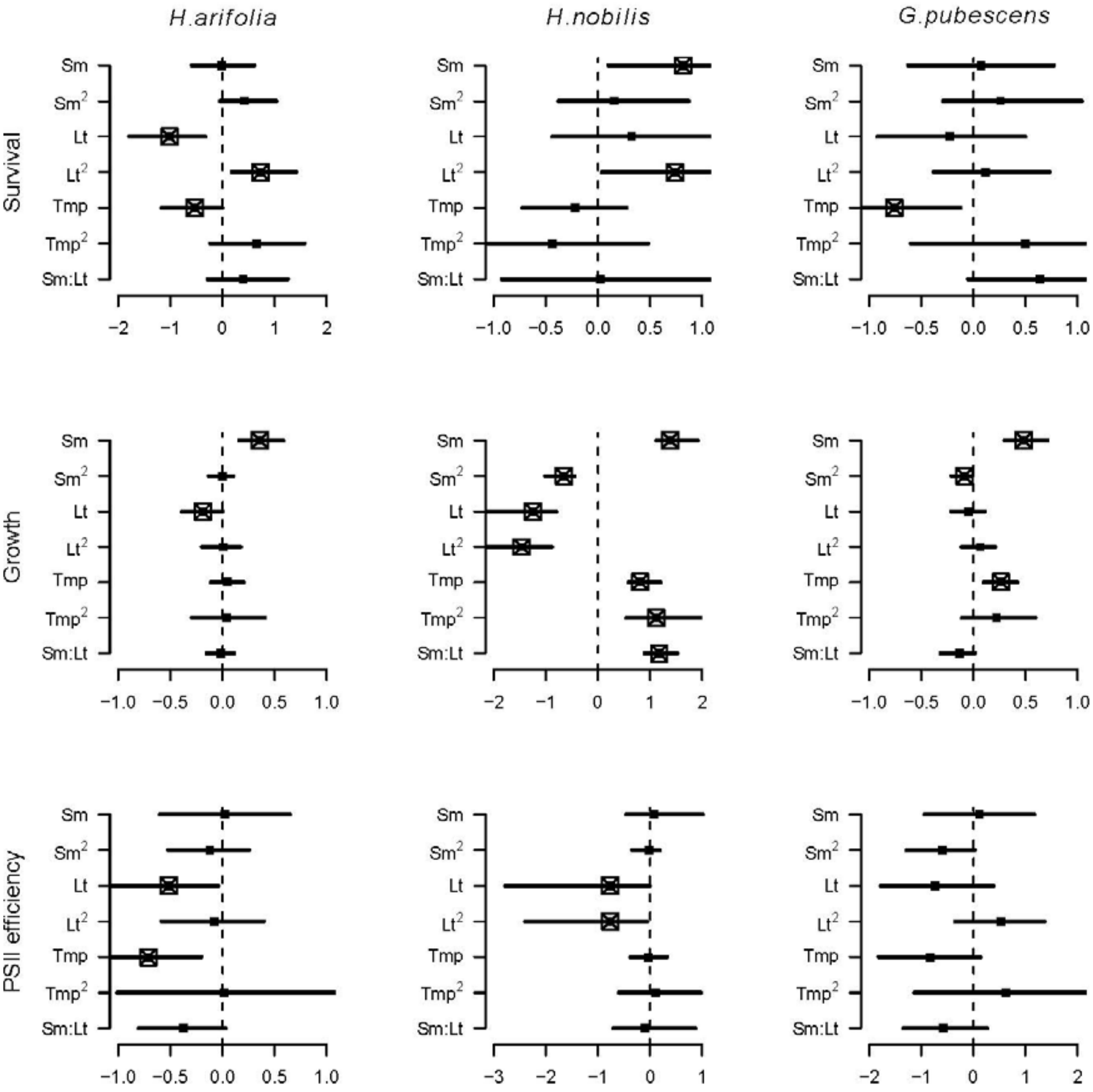

Figure 4.2. Mean summer values with 95% credible intervals for coefficients from the Bayesian hierarchical models of vital rates (*Survival, Growth* and *PSII efficiency*) as a function of first- and second-order summer covariables (*Soil moisture* (*Sm*)*, Light* (*Lt*) and *Temperature* (*Tmp)*, as well as an interaction term for soil moisture: light. Coefficient slopes differ from 0 (dotted line) indicated a significant slope values and thus a correlation between the predictor and response variables.

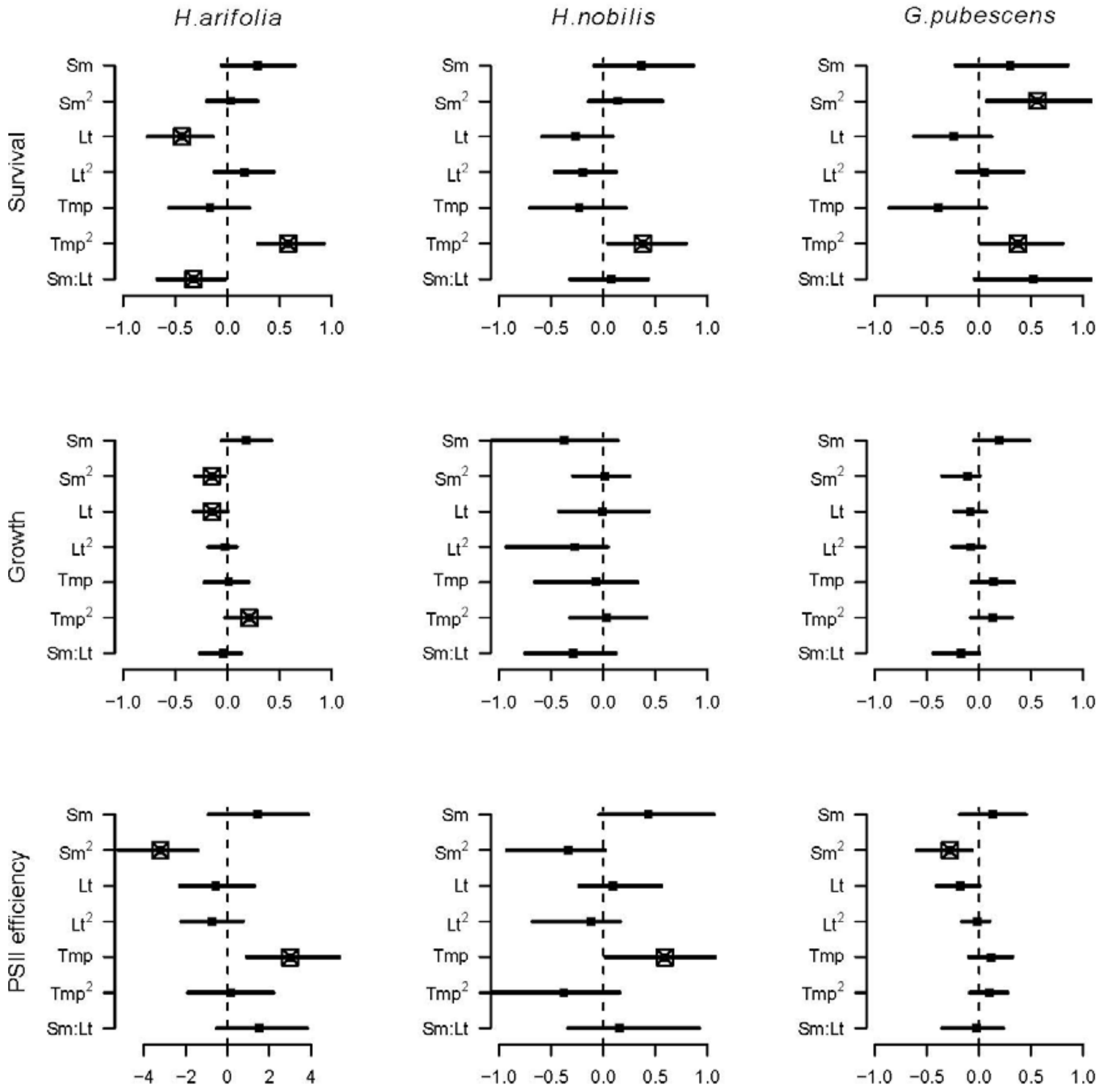

Figure 4.3. Mean winter values with 95% credible intervals for coefficients from the Bayesian hierarchical models of vital rates (*Survival, Growth* and *PSII efficiency*) as a function of first- and second-order winter covariables (*Soil moisture* (*Sm*)*, Light* (*Lt*) and *Temperature* (*Tmp)*, as well as an interaction term for soil moisture: light. Coefficient slopes differ from 0 (dotted line) indicated a significant slope values and thus a correlation between the predictor and response variables.

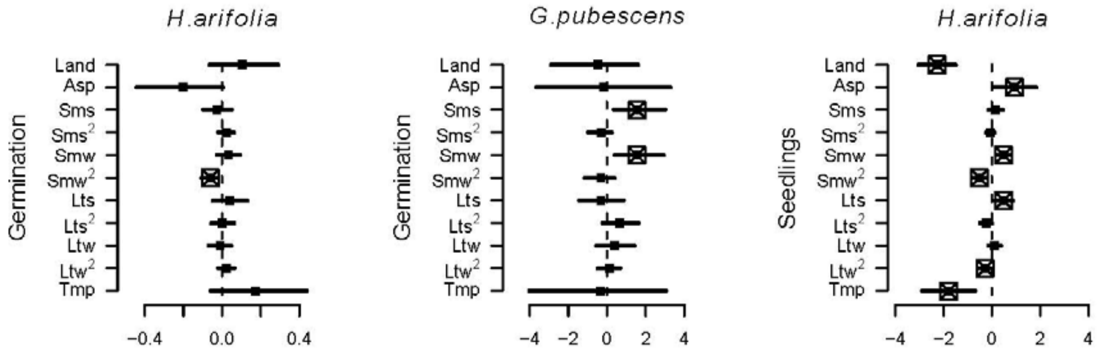

Figure 4. Mean germination and seedlings values with 95% credible intervals for coefficients from the Bayesian hierarchical models of germination and seedlings survival as a function of first- and second-order cofactors (*Landscape* (*Land*) and *Aspect* (*Asp*) and covariables (*Soil moisture* (*Sm*), *Light* (*Lt*) and *Temperature* (*Tmp)* in summer (s) and winter (w). Coefficient slopes differ from 0 (dotted line) indicated a significant slope values and thus a correlation between the predictor and response variables.

CONCLUSIONS

I outlined the problems with assuming a 1:1 correspondence between current species' distributions and "suitable habitat" in Chapter 1. There are four relatively common and well-documented ecological dynamics where species distribution unmistakably does not equal suitable habitat: (1) metapopulation, (2) dispersal limitation, (3) remnant population and (4) source/sink. I summarized these as *faux fitness*. Faux fitness implies that species distributions are not consistent correlates of suitable habitat. Given the likelihood that global climate change will prompt amplified changes in species distributions, faux fitness makes the use of current species distributions problematic for predicting future distributions without a rigorous assessment of demographic fitness.

As predicted in Chapter 2, evergreen understory herbs occurred less and performed worse on south-facing than north-facing slopes, though variance in these patterns generally was better predicted via topographic position. Contrary to expectations, heat load proved to be a far more robust predictor of evergreen herb occurrence and performance than winter light, though both winter and summer light remained significant. Nevertheless, while the topographic variables predicted where the plants occur, environmental variables provided the mechanisms behind the distribution. Evergreen plants likely are limited on south-facing slopes by low soil moisture combined with high temperatures in summer and high irradiance combined with low temperatures in winter.

In Chapter 3, I showed that populations of the understory evergreen herbs, *Hexastylis arifolia* and *Hepatica nobilis* are in decline, indicating the plants reside in unsuitable habitat. These declines are driven by a population shift away from reproductive-size plants, a decline in

H. arifolia fertility and a decline in *H. arifolia* seedling survival**.** The life cycle of *H. nobilis* clearly depends upon relatively higher soil moisture as reflected both in fertility and seedling survival, while *H. arifolia* is less soil moisture sensitive, particularly for persistence over progression. Both plant populations appear to be in a holding pattern that may require increased soil moisture for release. I also found that leaf traits have potential in predicting niche characteristics only when paired with demographic analysis, and that differences in suitable habitat between *H. arifolia* and *H. nobilis* correspond much better with below-ground than above-ground traits.

In chapter 4, I reported results of experimental common garden experiments that showed that *H., H. nobilis* and *Goodyear pubescens*, three understory evergreen herbs, responded to the environmental variables in a manner consistent with a guild that has limited natural distributions on south-facing slopes. Increased temperatures and light exposure and lower soil moisture generally led to decreased vital rates, and the responses varied among the three species with each falling at different portions of the environmental continuums. Furthermore, germination and seedling survival data suggested that regeneration performance rather than adult vital rates might provide the best explanation of natural distributions.

In conclusion, understory evergreen herbs often occur in unsuitable habitat, both at landscape and microsite scales (Chapters 2 and 3), and performance and physiological responses to environmental variables provide better estimations of the species' niche than presence. This suggests that the potential distribution of plants might be better predicted, or at least augmented, by measuring their response to environmental conditions rather than their mere presence or absence.