

An experimental test of well-described vegetation patterns across slope aspects using woodland herb transplants and manipulated abiotic drivers

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Summary

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• The ubiquitous transition of plant communities across slope aspects is a well-described, but rarely tested, ecological dynamic. Aspect position is often used as a proxy for microclimate changes in moisture, light and temperature, but these abiotic drivers are seldom decoupled and very rarely manipulated across slope aspects.

• To investigate the mechanisms and demographic stages driving the observed distribution patterns of two woodland herbs in the southeastern USA, seeds and adults were transplanted across north- and south-facing slopes, and moisture and light were experimentally manipulated.

• Stage- and species-specific abiotic responses resulted in similar landscape-level patterning for *Hexastylis arifolia* and *Hepatica nobilis*, but the underlying abiotic drivers were unique. Adult rather than seed survival best explained the natural distributions across slope aspects, and *Hexastylis arifolia* was limited by higher temperature, whereas *Hepatica nobilis* was limited by lower soil moisture.

• The stage- and species-specific responses indicated that the use of slope aspect to explain plant distributions not only obfuscates explanatory mechanisms, but probably undermines the portability of results. As abiotic drivers, not topographical proxies, are projected to shift with global climate change, distribution research requires direct abiotic data in association with key demographic stages rather than topographical proxies.

Introduction

The ubiquitous association between vegetation shifts and microclimate transitions across slope aspects is one of the most extensively described dynamics in plant community ecology (Turesson, 1914; Cottle, 1932; Boyko, 1947; Oosting & Billings, 1951; Cantlon, 1953; Pook & Moore, 1966; Smith, 1977; Hicks & Frank, 1984; Lieffers & Larkin-Lieffers, 1987; Bale & Charley, 1994; Olivero & Hix, 1998; Sternberg & Shoshany, 2001; Holst *et al.*, 2005; Boerner, 2006; Chmura, 2008; Albrecht & McCarthy, 2009). Equatorial slopes (south-facing in the northern hemisphere) receive far more solar irradiation than nonequatorial slopes, and this creates striking gradients in irradiation, temperature and moisture availability (Radcliffe & Lefever, 1981; Parker, 1991; Galicia *et al.*, 1999; Geiger *et al.*, 2003; Searcy *et al.*, 2003). This results in a relatively warmer, drier microclimate on equatorial-facing slopes

(Kirkpatrick & Nunez, 1980; Rosenberg *et al.*, 1983; Xu *et al.*, 1997), and the transition across slope aspects has long been coupled with shifts in plant communities (e.g. Warren, 2008). This venerable correlation is intuitive, but fails to recognize that soil edaphic factors can also differ by aspect (Mowbray & Oosting, 1968), and that solar irradiation, temperature and soil moisture are highly confounded (Thornthwaite, 1948; Frank & Lee, 1966).

Whittaker (1956) delineated tree distributions and communities in the Great Smoky Mountains by topography, but the biological processes that determine species' distributions rely on abiotic variables, such as temperature, precipitation and evapotranspiration, rather than geomorphology. Defining niche by topography lumps critical environmental drivers into topographical proxies. Not surprisingly, parameters based on topographical space often do not accurately reflect parameters in environmental space (Hijmans & Graham, 2006). For example, understory evergreen herbs

occur more often on north- than south-facing slopes in the southeastern USA (Warren, 2008), but this topographical distribution reflects temperature and soil moisture requirements rather than an affinity for north-facing landscapes (Giladi, 2004; Diez & Pulliam, 2007; Warren, 2007). The occurrence of woodland herbs at higher elevations on south- than north-facing slopes in the southern Appalachian Mountains (Warren, 2008) indicates that neither slope nor elevation drives the distribution, but rather an unmeasured variable (i.e. temperature) that occurs at the intersection of the topographical gradients (e.g. temperature increases with southerly aspect in the northern hemisphere and decreases with elevation).

In contrast with the large body of work pairing plant communities with aspect transitions, there is a dearth of experimental verification of the mechanisms behind these patterns. Verification requires direct abiotic measurements and experimental manipulation, both uncommon practices in slope aspect research. A thorough investigation of vegetation-aspect research revealed only five studies that translocated study species across aspect gradients (Shanks & Norris, 1950; Rorison *et al.*, 1986a; Gauslaa *et al.*, 2001; Sanders & McGraw, 2005; Albrecht & McCarthy, 2009), and these included a bryophyte and domestic cultivar, and none manipulated abiotic variables in the field. Warren (2008) found that evergreen woodland herbs occur less on south- than north-facing slopes in the deciduous forests of the southeastern USA, and this pattern corresponded with increased solar irradiation. This suggested that higher potential irradiance on south-facing slopes can create seasonal periods of heightened stress for woodland evergreens, in summer as a result of low soil moisture and high temperatures (Raven, 1989; Pearcy *et al.*, 1994; Neufeld & Young, 2003), and in winter because of high irradiance and low temperatures (Adams *et al.* 2004; Oquist & Huner 1991; Verhoeven *et al.* 1999). In this article, experimental transplants were used and soil moisture and diffuse light were manipulated to investigate these mechanisms. As the observed distribution of species across topographical gradients reflects the plant's full life history, and niche requirements can shift through demographic stages (Clark *et al.*, 1998; Pulliam, 2000), both the adult and seed stages of two woodland herbs were transplanted across north- and south-facing slopes. Two understory woodland herbs, *Hexastylis arifolia* and *Hepatica nobilis*, were chosen because they are both dispersal limited, nonclonal and do not form seed banks, and these qualities limit the possibility of seedling transplant contamination. Further, as evergreens, they experience the full range of annual climate shifts across slope aspects.

This experimental approach minimized the influence of land use history and biotic interactions, particularly propagule dispersal, whilst decoupling the influence of soil moisture and diffuse light, in testing two hypotheses. (1)

Seedling recruitment rather than adult abundance can be a critical bottleneck in plant population growth (Grubb, 1977; Albrecht & McCarthy, 2009; Moore, 2009), and the separation of life history by adults and recruitment stages will provide evidence as to whether the slope aspect distributions reflect limitations in recruitment, adult survival or both. (2) Given that evergreen woodland herbs generally decrease in performance and abundance with decreased soil moisture (Neufeld & Young, 2003; Giladi, 2004; Diez, 2007; Diez & Pulliam, 2007; Warren, 2007), watering should increase transplant survival and growth in otherwise unsuitable habitats on south-facing slopes. Increased diffuse light, particularly in winter, is also detrimental to evergreen herbs (Egerton *et al.*, 2000; Neufeld & Young, 2003; Adams *et al.*, 2004; Hughes *et al.*, 2005; Warren, 2008) and, if light exposure is a driving variable, shade treatment will increase survival and growth on south-facing slopes.

Materials and Methods

Study species

The transplant species are small (10–15 cm tall), perennial, understory evergreen herbs that occur in the temperate deciduous forests of the eastern USA. *Hexastylis arifolia* (Michx.) Small (Aristolochiaceae) is limited to the southeastern USA from Florida to Virginia, North Carolina to the Mississippi River. It is more common in mesic than xeric habitats (Abella & Shelburne, 2004) and on north- than south-facing slopes (Warren, 2008), but is not limited by soil moisture (Gonzales, 1972; Warren, 2007). *Hepatica nobilis* Schreb. var. *obtusata* (Pursh) Steyererm. (Ranunculaceae) occurs in the USA from northern Florida to Nova Scotia, west to Alabama and Missouri and Montana, and also occurs in Europe and Asia. It is limited in dry habitats (Inghe & Tamm, 1985) and is more common near streams (Harris, 2000). Both plants are limited on south-facing slopes, depend on ants for propagule dispersal and produce no clonal offspring (Harris, 2000; Warren, 2007).

Experimental plots and treatments

In January 2006, *Hx. arifolia* and *Hp. nobilis* individuals were collected at Whitehall Forest (WHF) in Georgia, USA (33°53'N, 83°21'W). Because plant size is typically a better indication than plant age (Lefkovitch, 1965; Caswell, 2001) of viability (particularly reproductive potential), individuals were selected by size class to minimize the influence of life history stage. Specifically, only reproductive-sized individuals were translocated. The baseline leaf area for reproductive-sized individuals was derived from established research connecting leaf area and demographic stage analysis. For *Hx. arifolia*, the minimum largest leaf was $\geq 25 \text{ cm}^2$ (Giladi, 2004; Warren, 2007). For *Hp. nobilis*, the minimum

largest leaf was $\geq 30 \text{ cm}^2$ (Harris, 2000; Warren, 2007). *Hexastylis arifolia* is relatively widespread at WHF, whereas *Hp. nobilis* is restricted to smaller populations. The plants were extracted with roots intact (maximum rooting depth, 12 cm; digging depth, *c.* 20 cm) and transported in closed containers to experimental grids located on north- and south-facing slopes. Across each slope aspect, three 35 m^2 experimental grids were established at similar elevations (172–204 m) and slope angles (10–21°). Two individuals of each species were placed at random in 1 m^2 cells within these grids, leaving 1 m^2 spaces between each cell. This created 12 cells per grid, with each grid containing 24 individuals of each species. The transplants were placed in 12 cm^2 circular holes during the month of collection, which was before new leaf emergence. Overall, there were 12 experimental grids [six at WHF and six at Coweeta Hydrologic Laboratory (CWT), NC, USA], containing 144 cells with transplants, and therefore 576 experimental individuals (Fig. S1, see Supporting Information). At both sites, < 10% of transplants died within the first 14 d and were promptly replaced. Grids at both locations were located in mature (*c.* 60–80 yr old trees) deciduous forest habitats dominated by oak, hickory and tulip poplar. The locations were qualitatively chosen for similarities in canopy coverage, and this was quantitatively accounted for by direct measurement of transmitted light, soil moisture and temperature.

Seeds were collected from natural populations of *Hx. arifolia* (June 2006) and *Hp. nobilis* (March 2006) and immediately planted at a depth of 2 cm ($n = 5$ seeds per hole) in a subset of eight cells in each experimental grid ($n = 12$) for a total of 480 seeds per species. However, because the seeds were planted in clusters of five, there were essentially 96 units, and recruitment success was analyzed as surviving seedlings per unit. This experimental design was replicated at CWT (35°03'N, 83°25'W) across north- and south-facing slopes at similar elevations (750–1025 m) and slope angles (15–21°). Both study species also occur at CWT, which is 100 km north of WHF in the southern Appalachian Mountains where the topographical relief and precipitation are far greater (CWT: 750–1025 m elevation, 1826 mm annual precipitation; WHF: 150–240 m elevation, 1219 mm annual precipitation). The rationale for adding CWT was to increase the degree of environmental heterogeneity (and thus treatment effect) across slope aspects, as well as to increase the generalizability of the results.

Environmental manipulations

Soil moisture and diffuse light were experimentally manipulated to ameliorate conditions on south-facing slopes. Soil moisture was augmented by delivering water from two 200 l reservoirs via drip irrigation (Dripworks, Inc., Willits, CA, USA) to the lower (slope position) two rows of each

grid (Fig. S1, see Supporting Information). The maximum distance between a watered and unwatered row was 4 m, and all rows shared the same slope angle. Approximately 70 l of water was delivered weekly per plot during May–August 2006, which is the time period in the year when moisture is expected to limit performance of the study species in the southeastern USA. As both theoretical and empirical data suggest that high light levels increase mortality in understory evergreen herbs, and this is exacerbated during the leafless period of late fall and winter (Neufeld & Young, 2003; Adams *et al.*, 2004; Hughes *et al.*, 2005; Warren, 2008), the second treatment was a limitation of solar irradiation. To attenuate solar irradiation, custom-made polyvinyl chloride frames ($1 \times 1 \times 0.5 \text{ m}$) were randomly assigned to half the plots in each grid. Black knitted 60% neutral shade cloth (International Greenhouse Co., Georgetown, IL, USA) was attached to the top of each frame (Fig. S1, see Supporting Information). The efficacy of these treatments (slope aspect, moisture augmentation and light attenuation) is reported in the results.

Transplant surveys and physical monitoring

Transplants were surveyed in January 2007. Survival was calculated from those plants that survived between February 2006 and January 2007. Plant growth was calculated as $\text{Growth}_t = (\text{LN}_t \times \text{LA}_t) - (\text{LN}_{t-1} \times \text{LA}_{t-1})$, where LN is leaf number, LA is leaf area and t is time. Growth values were rounded to the nearest integer. Soil moisture augmentation was discontinued in February 2007 and shade treatments were removed in June 2007. However, to assess longer term aspect effects, the transplants were again sampled in 2009, and survival and growth were calculated for the 2007–09 interval.

Across the six survey grids, volumetric soil moisture percentage was measured in each cell with a hand-held Hydro-sense Soil Water Content Measurement System (Campbell Scientific, Inc., Logan, UT, USA). Incident photosynthetically active radiation (diffuse light; wavelength, 400–700 nm) was calculated as the percentage of photosynthetic photon flux density at a fully exposed reference site and the percentage of photosynthetic photon flux density transmitted through the forest canopy at each cell. The understory grid measurements were taken with a hand-held AccuPAR ceptometer (Decagon Devices, Inc., Pullman, WA, USA) and the open reference measurements were taken simultaneously with an LI-200 spherical photosynthetically active radiation (PAR) sensor and logged with an LI-1400 datalogger (LiCor, Inc., Lincoln, NE, USA). Measurements were taken on cloudy days between 10:00 h and 14:00 h to minimize the relative error in diffuse light (Messier & Puttonen, 1995; Parent & Messier, 1996; Gendron *et al.*, 1998; Diez & Pulliam, 2007). The AccuPAR ceptometer integrates PAR measurements over a 1 m probe, which

accounts for fine-scale light heterogeneity in understorey environments. Because the percentage transmitted, not absolute percentage, of PAR was used for analysis, and this method was consistent across sites and grids, any difference between instruments was minimized and unlikely to confound the results. A HOBO Pendant 64k data logger (Onset Computer Co., Bourne, ME, USA) was placed on the soil surface at the center point of each grid ($n = 12$) to record hourly surface temperatures throughout the duration of the experiment (February 2006–February 2007). In addition, temperature data loggers were placed on the soil surface beneath shade cloth treatments at both sites and each aspect ($n = 4$) in order to assess whether the treatments confounded temperature. Soil moisture was sampled at five averaged points within each cell ($n = 144$) in June and July 2007, January 2008 and April 2009; diffuse light was sampled in each cell ($n = 144$) in July and January 2007 and 2008.

Data analysis

The fixed effects of slope aspect (north or south), water augmentation (\pm) and light amelioration (\pm) on the survival and growth of adult transplants and on the recruitment success (germination and initial seedling survival) of seed introductions were evaluated by fitting generalized linear mixed models using the Laplace approximation in the 'lme4' package for the 'R' statistical program (R, 2005). Transplant site and grid locations were included in the models as random effects to account for potential spatial autocorrelation and unobserved error in the experimental design. The inclusion or exclusion of the fixed effects and their interactions, as well as the random effects, in the 'best fit' or minimum adequate models was based on Akaike information criterion (AIC) values and average AIC weights for similar models ($\Delta\text{AIC} < 5$). The significance of retained parameters was also reported. The variance inflation factors for the fixed effects in all models were less than three, indicating that they independently predicted variance, and overdispersion was < 1.1 in all models, which meets the assumptions of the binomial and Poisson distributions.

The conditional relationships between the landscape variables (site and aspect) and ambient environmental conditions (covariables: soil moisture, diffuse light; cofactor: temperature) were explored using classification and regression tree (CART) models. The CART model approach was chosen as a result of the hierarchical experimental design and high degree of potential interaction between ambient covariables. CART models provide a robust alternative to multiple regression and analysis of variance, and do not require data transformation or normalization, can handle continuous and discrete variables and are more straightforward in the interpretation of interactions and complex patterns (Breiman *et al.*, 1984; De'ath & Fabricius, 2000).

The CART models partition data in a hierarchical fashion based on the explanatory power of the response variables, resulting in a 'tree' that can be represented graphically, where each branch split (node) indicates the partitioning of variance based on a single explanatory variable. This variance splitting continues, with each subsequent branch representing variables that explain less response variance than the previous branches, as well as exhibiting dependence on the previous splits. Here, the CART models were used to analyze 2007 adult transplant survival and growth, and recruitment success. The CART model algorithm goes through comprehensive iterations to select covariates that best explain partitions in deviance in the dependent variable.

The CART models were constructed using the RPART package in the R statistical program (R, 2005). To prevent overfitting (too many tree branches), trees were 'pruned' using 10-fold cross-validation in the RPART package with the 1 – standard error (SE) rule established by Breiman *et al.* (1984), so that the final CART model was the smallest within one SE of the minimum model. The control parameters for model fitting were five minimum observations in a node before attempting a split, and a minimum of two observations in a terminal node. Output from the RPART summary information was used to evaluate surrogate splits and root node error. Surrogate splits are those that provide similar reductions in deviance as the variables chosen by the model fitting for a given node. Surrogate splits that were $> 75\%$ in agreement with the fitted tree splits were reported.

In order to assess the consistency in adult survival and recruitment success responses across years (2007–09), the difference in mean survival between site and aspect positions, and the difference in environmental parameters at sites at which the plants survived and died, were analyzed using *t*-distributions with 95% confidence intervals.

Results

Species and site characteristics

Mean annual diffuse light did not differ between sites ($t = -1.42$, d.f. = 531.1, $P = 0.16$) or slope aspects ($t = -2.02$, d.f. = 567.5, $P = 0.84$) (see Table S1 for mean values; see Supporting Information). The mean annual temperature was significantly higher and the percentage soil moisture was significantly lower at WHF than at CWT (temperature: $t = 51.99$, d.f. = 502.7, $P < 0.001$; soil moisture: $t = -6.22$, d.f. = 542.1, $P < 0.001$) and on south- than north-facing slopes (temperature: $t = 51.99$, d.f. = 502.7, $P < 0.001$; soil moisture: $t = 2.04$, d.f. = 565.2, $P < 0.04$). Water augmentation increased soil moisture significantly ($t = -15.1$, d.f. = 211.1, $P < 0.001$), but had no effect on temperature ($t = 0.09$, d.f. = 242.1, $P < 0.92$) or diffuse

light ($t = -1.64$, d.f. = 225.3, $P < 0.11$); shade cloth decreased diffuse light significantly ($t = 21.2$, d.f. = 424.5, $P < 0.001$), but had no effect on soil moisture ($t = 1.01$, d.f. = 571.5, $P = 0.32$) or temperature ($t = 0.19$, d.f. = 6, $P < 0.43$) (Table S1, see Supporting Information). Although the mean values were the same between shade treatments, the shade cloth muted extreme temperatures (maximum temperature with shade cloth, $15.2 \pm 4.8^\circ\text{C}$, $n = 100$; maximum temperature without shade cloth, $24.1 \pm 10.6^\circ\text{C}$, $n = 100$), and may have confounded temperatures. The senescence of the overstorey canopy corresponded with a marked increase ($1.8 \pm 0.1\%$ – $33.3 \pm 16.6\%$) in diffuse light reaching the experimental plots. However, summer diffuse light better explained the variation in the survival and growth of adult transplants than did winter diffuse light or the annual mean (Δ deviance explained across models = 1–2%) and was used as the explanatory parameter.

Treatment effects on survival and growth

Adult *Hx. arifolia* plants showed lower overall survival rates than *Hp. nobilis* in 2007 (*Hx. arifolia*, $73.2 \pm 44.4\%$; *Hp. nobilis*, $81.3 \pm 39.1\%$) and 2009 (*Hx. arifolia*, $38.9 \pm 48.9\%$; *Hp. nobilis*, $61.6 \pm 48.8\%$). *Hexastylis arifolia* plants showed similar growth to *Hp. nobilis* in 2007 (*Hx. arifolia*, $1.52 \pm 1.60\text{ cm}^2$; *Hp. nobilis*, $1.54 \pm 1.78\text{ cm}^2$) and somewhat less in 2009 (*Hx. arifolia*, $1.47 \pm 2.14\text{ cm}^2$; *Hp. nobilis*, $2.11 \pm 3.84\text{ cm}^2$). *Hepatica nobilis* plants showed higher recruitment success than *Hx. arifolia* in 2007 (*Hx. arifolia*, $51.0 \pm 50.3\%$; *Hp. nobilis*, $17.3 \pm 38.1\%$), whereas subsequent seedling survival to 2009 was higher in *Hp. nobilis* (*Hx. arifolia*, $67.3 \pm 47.4\%$; *Hp. nobilis*, $76.5 \pm 43.7\%$).

The effects of aspect, watering and shading and their interactions on the survival, growth and recruitment of *Hx. arifolia* and *Hp. nobilis* were evaluated in generalized linear mixed models using AIC to select the best predictors from the full model: (response variable \sim aspect + water + shade + aspect \times water + aspect \times shade + site + grid). The inclusion of the site location as a random effect improved all models somewhat (Δ AIC ~ 2), whereas the inclusion of grid identity as a random effect improved survival and recruitment models greatly (Δ AIC ~ 30 – 300), but had little impact on growth models (Δ AIC ~ 0 – 2). Both site and grid were therefore included in all models (except *Hp. nobilis* growth) as random effects. The difference in the impact of random site and grid effects may be attributable to the difference in effect levels (site = 2; grid = 12) (Bolker *et al.*, 2009), but suggests that transplant site location did not have a strong impact. The robust improvement in the survival models (adult and recruitment) with the inclusion of grid suggests that these responses were influenced by omitted variables, one of which is probably temperature (see ambient results). Aspect had strong negative effects on the survival and growth of both species

Table 1 Fixed effects from generalized linear mixed models for *Hexastylis arifolia* and *Hepatica nobilis*

Model	Fixed effects	Estimate	SE	z-value
(a) Adult survival				
<i>Hexastylis arifolia</i>	Intercept	2.25	0.52	0.00***
	Aspect	−2.07	0.67	−3.09**
	Aspect:shade	0.88	0.37	2.38*
<i>Hepatica nobilis</i>	Intercept	1.74	0.26	6.79***
	Aspect	−0.75	0.32	−2.39**
	Water	0.74	0.41	1.79†
(b) Adult growth				
<i>Hexastylis arifolia</i>	Intercept	0.20	0.10	2.07*
	Aspect	−0.43	0.18	−2.37*
	Aspect:water	0.72	0.23	3.14**
<i>Hepatica nobilis</i>	Intercept	0.67	0.09	7.73***
	Aspect	−0.16	0.09	−1.65†
	Shade	0.07	0.10	0.64 ^{ns}
(c) Recruitment				
<i>Hexastylis arifolia</i>	Intercept	−1.35	0.78	−1.72†
	Aspect	−0.04	0.83	−0.04 ^{ns}
	Shade	−0.13	0.24	−0.53 ^{ns}
	Aspect:water	−0.48	0.40	−1.20 ^{ns}
<i>Hepatica nobilis</i>	Intercept	−3.47	0.49	−7.04***
	Water	−0.87	0.54	−1.62†
	Shade	0.91	0.42	2.15*

All models included aspect (north–south slope aspect), water (watering treatment) and shade (shade cloth treatment), together with their interaction terms, as fixed effects, and transplant site and grid locations as random effects. (a) 2007 survival of experimental transplants assuming a binomial; (b) 2007 growth of experimental transplants assuming a Poisson distribution; (c) experimental recruitment success (germination and initial seedling survival) assuming a binomial error distribution.

***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; †, $P < 0.1$; ns, not significant.

(Table 1). For *Hx. arifolia*, the negative effect of aspect on survival was muted by shading, and the negative effect on growth was muted by watering (Fig. 1). *Hepatica nobilis* survival increased with watering, regardless of aspect. Watering appeared to have a deleterious effect on the recruitment success of both species, although the effect on *Hx. arifolia* was only on north-facing aspects and not statistically significant. Shading increased *Hp. nobilis* recruitment success significantly.

Ambient conditions and survival

The CART models illustrate the hierarchical interactions between the ambient landscape (site and aspect) and environmental variables (soil moisture, diffuse light and temperature), rank the importance of the retained variables (the highest explain the most variance) and indicate at what threshold values the response data segregate between survival and mortality (Figs 2,4) and relatively high and low growth (Fig. 3). Temperature, diffuse light and soil moisture were the most important variables explaining survival

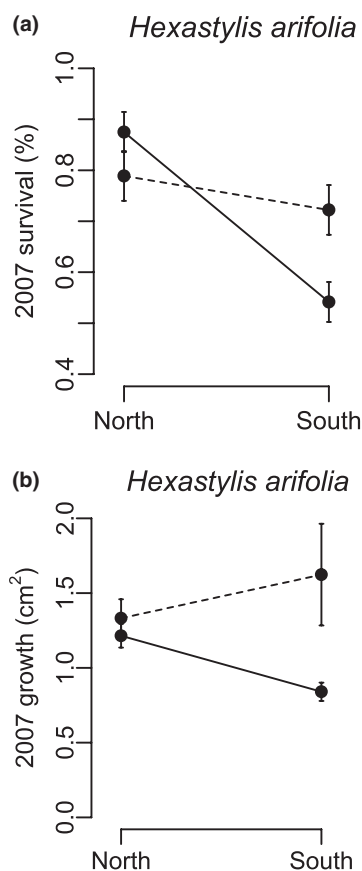


Fig. 1 Interaction plots of the effects of slope aspect and 2007 experimental treatments (water augmentation, light amelioration). (a) Effect of aspect (north, south) and presence of shade cloth (broken line, shaded; full line, unshaded) on *Hexastylis arifolia* adult survival. (b) Effect of aspect and watering (broken line, watered; full line, unwatered) on *Hx. arifolia* adult growth.

and adult transplants for *Hx. arifolia* and *Hp. nobilis* (Fig. 2). For *Hx. arifolia*, temperature best explained survival, and this was highest (94%) at the coolest sites (Fig. 2a). At the warmer sites, diffuse light became important, and survival was *c.* 79% higher where the light was > 0.5%. Two surrogate splits at the first node showed a high degree of concordance with temperature, indicating that soil moisture (76.3% agreement with the optimal split) and aspect (75.3% agreement) were somewhat interchangeable with temperature. For *Hp. nobilis*, soil moisture best explained survival, and it was relatively low (58%) where soil moisture was < 8.5% (Fig. 2b). When soil moisture was > 8.5%, light became important, and *Hp. nobilis* survival was 64% higher where diffuse light was > 0.7%. Diffuse light also showed a high degree of concordance with soil moisture at the first node (88.2% agreement).

Hexastylis arifolia growth appeared to be most dependent on soil moisture; however, temperature was a surrogate for the split at the first node with 100% agreement, indicating that they are interchangeable (Fig. 3a). When soil moisture

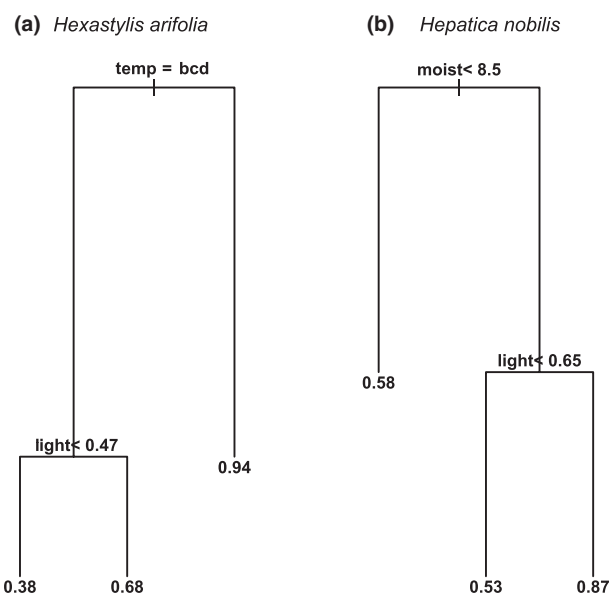


Fig. 2 Classification tree model between 2007 survival of *Hexastylis arifolia* (a) and *Hepatica nobilis* (b) and ambient abiotic variables (moist, percentage soil moisture; light, percentage diffuse light; temp, temperature). Soil moisture (range, 3–51%) and diffuse light (range, 0.3–4.9%) were covariables, while temperature is a cofactor with dummy variables for grids ranked into categories from coolest to warmest (a–d, where a = $13.2 \pm 0.4^\circ\text{C}$, b = $14.9 \pm 0.3^\circ\text{C}$, c = $16.9 \pm 0.2^\circ\text{C}$, d = $17.9 \pm 0.5^\circ\text{C}$). Split notes are identified by the value of the abiotic variable that best split the deviance in survival ('<', lower values split to the left). Survival values are given at each terminal node.

was < 21.5% (warmer sites), aspect became important, with 45% less growth on south- than north-facing slopes; growth was highest (1.9 cm²) where soil moisture was > 25.5%. For *Hp. nobilis*, growth was lowest (1.5 cm²) where temperatures were extreme, and soil moisture became important at intermediate temperatures (Fig. 3b). By examining nodes 1–4, growth was shown to peak (5 cm²) where temperatures were intermediate, soil moisture was between 18.5 and 26.5%, and diffuse light was < 1.4%.

Hexastylis arifolia recruitment success was also dependent on the temperature, and was highest at the warmer sites where soil moisture was > 11.5% (Fig. 4a). Survival decreased by 54%, however, at the warmer sites, where soil moisture was < 11.5%. At the cooler sites, recruitment success was highest where soil moisture was < 14.5% and was dependent on diffuse light where soil moisture was lower. Transplant site was interchangeable with temperature as they showed 100% agreement at the first node (the cooler sites were at CWT, the warmer sites at WHF). For *Hp. nobilis*, diffuse light explained the most variance in recruitment success, and it was relatively low (10%) where light was > 1.3% (Fig. 4b). *Hepatica nobilis* recruitment success was highest where diffuse light was between 1.1 and 1.3%, and, where light was lower, soil moisture of > 15.5% appeared to ameliorate the low light effect.

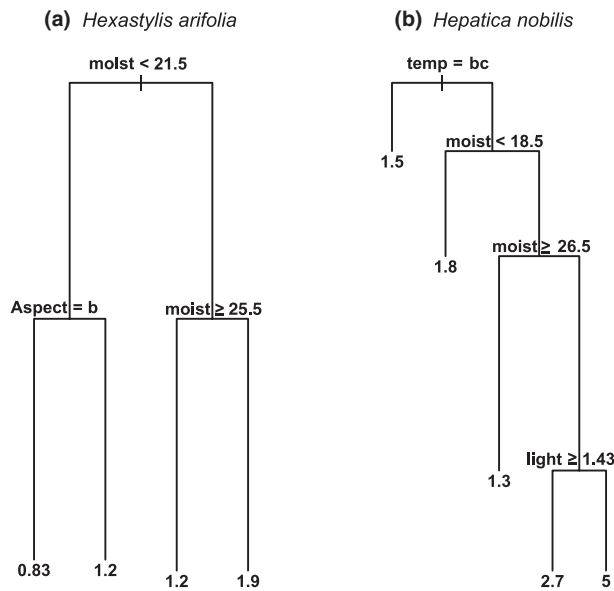


Fig. 3 Regression tree model between 2007 growth of *Hexastylis arifolia* (a) and *Hepatica nobilis* (b) and ambient abiotic variables (moist, percentage soil moisture; light, percentage diffuse light; temp, temperature). Temperature is ranked into categories from coolest to warmest (a–d, where a = $13.2 \pm 0.4^\circ\text{C}$, b = $14.9 \pm 0.3^\circ\text{C}$, c = $16.9 \pm 0.2^\circ\text{C}$, d = $17.9 \pm 0.5^\circ\text{C}$). Split notes are identified by the value of the abiotic variable that best split the deviance in survival ('<', lower values split to the left; '>', higher values split to the left). Survival values are given at each terminal node.

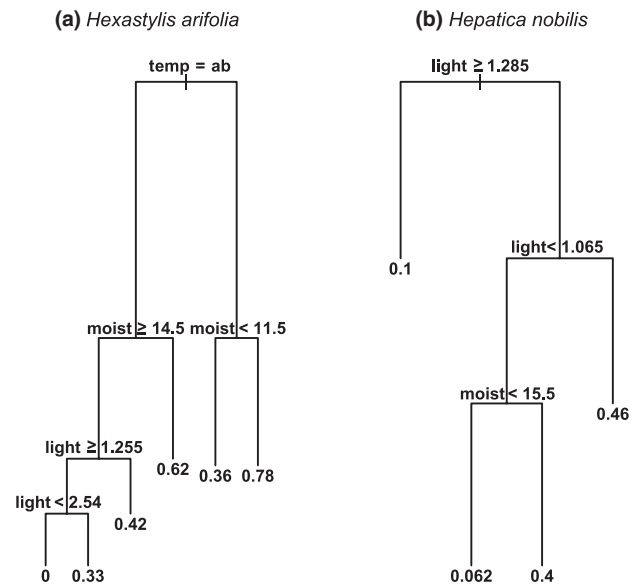


Fig. 4 Classification tree model between 2007 recruitment success of *Hexastylis arifolia* (a) and *Hepatica nobilis* (b) and ambient abiotic variables (moist, percentage soil moisture; light, percentage diffuse light; temp, temperature). Temperature is ranked into categories from coolest to warmest (a–d, where a = $13.2 \pm 0.4^\circ\text{C}$, b = $14.9 \pm 0.3^\circ\text{C}$, c = $16.9 \pm 0.2^\circ\text{C}$, d = $17.9 \pm 0.5^\circ\text{C}$). Split notes are identified by the value of the abiotic variable that best split the deviance in survival ('<', lower values split to the left; '>', higher values split to the left). Survival values are given at each terminal node.

Consistency of landscape and ambient effects

The survival of adult transplants did not differ significantly across sites, except that *Hx. arifolia* survival was higher at CWT in 2009 (Fig. 5a). Adult transplants of both species consistently showed significantly higher survival on north-facing slopes and at high levels of soil moisture in both 2007 and 2009 (Fig. 5b,c). *Hepatica nobilis* survival was greater where diffuse light was highest in 2007 and 2009, but *Hx. arifolia* survival did not differ with light (Fig. 5d). Conversely, *Hx. arifolia* survival was greater where temperature was lowest in 2007 and 2009, whereas *Hp. nobilis* survival did not differ with temperature (Fig. 5e). *Hexastylis arifolia* recruitment success was higher at WHF than at CWT in 2007, and higher at WHF than at CWT in 2009; *Hp. nobilis* recruitment success was also higher at WHF than CWT in 2007, but higher at CWT than WHF in 2009 (Fig. 5a). Although aspect and soil moisture were significant predictors of adult survival for both species in both years, neither had significant impact on recruitment success for either species in either year (Fig. 5b,c). Recruitment success did not differ across diffuse light or temperature for either species in 2007 or 2009, except that the success of *Hp. nobilis* was significantly higher in 2009 where diffuse light and temperature were low (Fig. 5d,e).

Discussion

Variation in landscape topography drives heterogeneity in regional climate and weather (Barry, 1992; Dubayah & Rich, 1995; Bolstad *et al.*, 1998; Geiger *et al.*, 2003), and few topographical features contain as strong a microclimate shift as slope aspect (Galicia *et al.*, 1999; Geiger *et al.*, 2003). The associated shifts in plant communities across slope aspects have long been studied and described (e.g. Cantlon, 1953), but rarely tested (Rorison *et al.*, 1986a; Albrecht & McCarthy, 2009). Here, experimental manipulations of plants and environmental drivers were used to test mechanisms behind slope aspect-driven vegetation patterns. The survival and growth of evergreen woodland herbs indicate that they generally respond to environmental variables (both treatment and ambient) in a manner consistent with a guild that has limited distribution on the relatively warmer, drier south-facing slopes in deciduous forests of the southeastern USA. This supports a long-held supposition about plant distributions across slope aspects: higher temperatures and lower soil moisture select out certain plant types on south-facing slopes (e.g. Schulze *et al.*, 2005). What appears to be a simple pattern apparently has complex mechanisms, however. The plant responses are stage and species specific. Adult transplant survival and growth correspond better than seedling recruitment with natural slope aspect distributions.

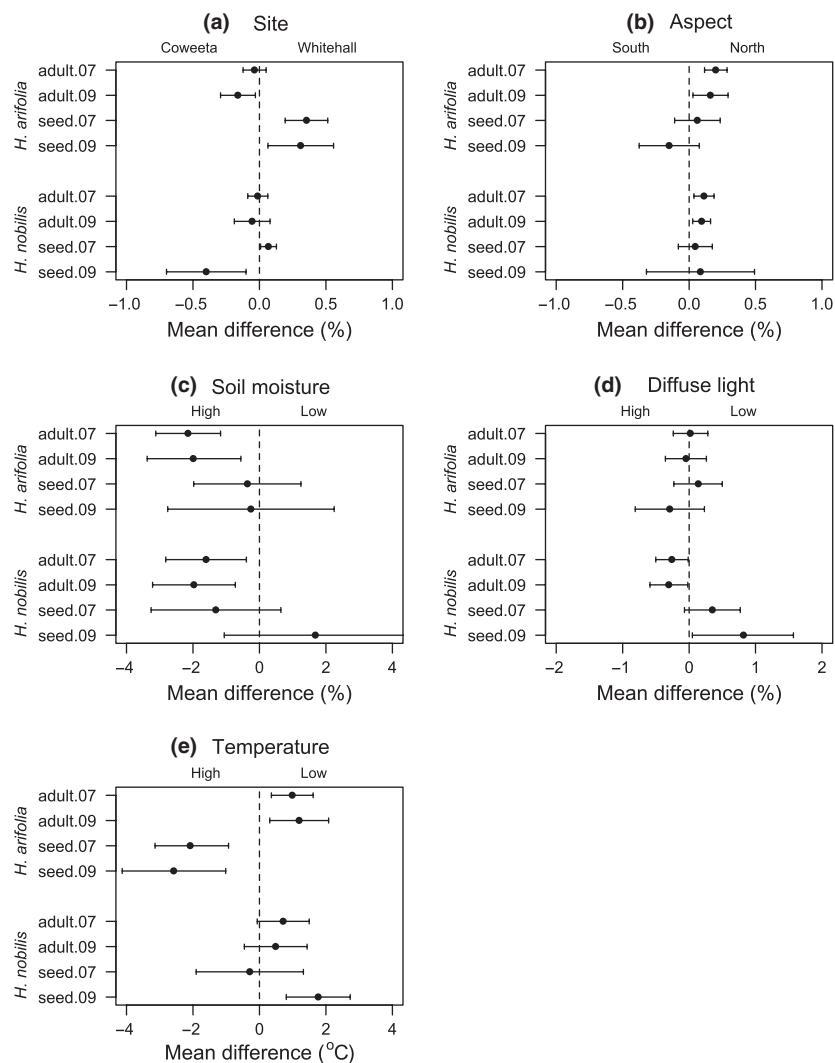


Fig. 5 *t*-distributions with 95% confidence intervals for the mean difference in survival of *Hexastylis arifolia* and *Hepatica nobilis* across the landscape variables site (a) and aspect (b), and for the mean difference in abiotic variables soil moisture (c), diffuse light (d) and temperature (e) between sites at which plants survived and died. The intervals are given for adult and seedling survival for the years 2007 and 2009 (broken lines, confidence intervals that contain zero, indicating no difference between mean values.)

This suggests that the limited presence of plant populations on south-facing slopes is not determined by seed recruitment, but instead by survival through the subsequent life history stages. Moreover, although both species exhibit the same landscape pattern, the experimental manipulations and environmental responses indicate that *Hx. arifolia* and *Hp. nobilis* exhibit unique response and tolerances for the abiotic drivers behind slope aspect patterns: soil moisture, diffuse light and temperature. Finally, although the slope aspect patterns observed in natural populations (Warren, 2008) may be influenced by dispersal dynamics, the significantly higher mortality of adult transplants in south-facing plots is more consistent with physiological limitations.

Species-specific abiotic responses

The experimental plots span large-scale (geographical) and small-scale (aspect) ecological boundaries and include direct augmentation (soil moisture) and amelioration (diffuse light) of abiotic variables. This exposes the transplants to

considerable gradients of light, soil moisture and temperature. Moreover, the manual transplanting of the woodland herbs excludes or diminishes biotic interactions, such as dispersal services and competition, resulting in resource responses that reflect physiological limits. The adaptations that allow shade tolerance in woodland herbs appear to be a trade-off with drought tolerance (Smith & Huston, 1989; Neufeld & Young, 2003). For this reason, it was expected that water augmentation would benefit the survival and growth of both species, particularly in the drier plots at WHF and on south-facing slopes. Water augmentation benefits *Hp. nobilis* survival at all plots across sites and slope aspects (Table 1a), and, as expected, *Hx. arifolia* growth on south-facing slopes (Fig. 1). These results provide important evidence that water limitation is a plausible mechanism for the natural distributions of these plants, but because the experimental treatment does not benefit *Hx. arifolia* survival, nor is it site or aspect specific, the premise is weakened. Although weekly summer watering increased soil moisture by *c.* 50% (Table S1), this may fall short of

biological significance for *Hx. arifolia*. Furthermore, the initiation of watering in the spring and cessation in the fall does not cover the full leaf lifespan of the woodland evergreens, and thus may fall temporally short. For these reasons, ambient soil moisture levels were also monitored and analyzed, and these data provide further insight. *Hexastylis arifolia* survival is 33% higher on north- than south-facing slopes, and temperature (see temperature discussion below) provides the best explanation for adult survival and recruitment success (Figs 2a,4a); however, higher soil moisture (corresponding to a north-facing aspect) has > 75% concordance with temperature, and *Hx. arifolia* growth peaks where soil moisture is highest (Fig. 3a). *Hepatica nobilis* survival is 15% higher on north-facing slopes, and soil moisture is strongly associated with higher adult survival and growth (Table 1a, Figs 2b,3b). Unlike the adult transplants, water augmentation has a deleterious effect on *Hp. nobilis* recruitment (Table 1c), and ambient soil moisture is not a primary driver in recruitment success (Fig. 4b).

High irradiation combined with low temperatures causes photodamage in overwintering evergreen plants (Adams *et al.*, 1991; Oquist & Huner, 1991; Verhoeven *et al.*, 1999), but winter light explains less variation in transplant survival and growth than summer light in this study and is not used for analysis. Furthermore, summer diffuse light does not differ by slope aspect here (Table S1), and thus provides a poor explanation for slope aspect distributions. Light amelioration reduces ambient PAR by 64%, but this treatment has little effect on plant survival or growth (Table 1), except that shade treatment increases *Hx. arifolia* survival on south-facing slopes and *Hp. nobilis* recruitment success (Fig. 1). Although shade treatment did not influence mean temperatures, it did mute extreme temperatures, and this may better explain this pattern, particularly on south-facing slopes (see temperature discussion below). Ambient diffuse light did not provide the best explanation for the survival or growth of both species, and did not correspond to slope aspect differences.

The similarity in transmitted summer light on both north- and south-facing slopes measured here is typical for the growing season when tree canopies are fully intact and the solar zenith angle is highest, and the greatest discrepancy between slope aspects usually occurs during the winter season when tree canopies have senesced and the solar zenith angle is lowest (Cantlon, 1953; Frank & Lee, 1966; Rorison *et al.*, 1986b; Holst *et al.*, 2005). However, the angle and proximity of the sun during the summer season can make temperature rather than light the larger effect of solar irradiation across slope aspects (Cantlon, 1953). Temperature links soil moisture and diffuse light (Thornthwaite, 1948), but is not a variable easily amenable to field manipulation. As shown, temperature varies across site and slope aspect, and the corresponding variation in soil moisture makes topographical position a poor proxy. For these reasons, ambient

temperatures were also monitored and analyzed. Cooler temperatures best explain *Hx. arifolia* adult (0.75% concordance with soil moisture) and recruitment success, and is interchangeable with soil moisture in explaining *Hx. arifolia* growth (Figs 2–4). The consistent overlap between temperature and soil moisture suggests that their influence on *Hx. arifolia* cannot be fully decoupled. Conversely, *Hp. nobilis* survival and growth clearly depend on higher soil moisture, but show a smaller temperature response. *Hepatica nobilis* growth peaks at intermediate temperatures (Fig. 3b), but temperature has no discernible effect on adult or recruitment success. This may explain *Hp. nobilis*' relatively greater tolerance than *Hx. arifolia* for south-facing slopes.

Demographic stage and spatial distribution

Dispersal is a core component in determining large- and small-scale species' distributions (Clark *et al.*, 1998; Pulliam, 2000; Flinn & Vellend, 2005). For both plants, dispersal is mediated by ants, which means that population spread is very slow (Cain *et al.*, 1998; Giladi, 2004) and suitable habitat may remain unoccupied (Pulliam, 2000). The decreased abundance of these two species on south-facing slopes may reflect associated dispersal barriers that could include land use history effects or natural barriers to ant-mediated facilitation. If so, transplanted seeds and adults should exhibit similar survival rates across north- and south-facing slopes, which they do not, suggesting that the natural distributions reflect physiological limitations, although this is not a rigorous test of dispersal limitation. The physiological limitations appear to be stage specific, as adult transplants show significantly higher mortality on south- than north-facing slopes, but recruitment success does not differ. Conversely, adult transplants fare equally well at both CWT and WHF in 2007, but recruitment success is higher at WHF than CWT (Fig. 5). As the natural distributions of both species include both CWT and WHF, but they occur far less on south- than north-facing slopes, the survival of adult transplants has the highest concordance with actual distributions. The aspect pattern is consistent in both measured survival intervals (2006–07 and 2007–09) (Fig. 5), indicating that decreased adult survival on south-facing slopes is more than just first-year transplant shock.

The discrepancy between adult survival and recruitment success goes beyond landscape patterns. Water augmentation and higher diffuse light environments increase adult *Hp. nobilis* survival, but both decrease recruitment success. Adult *Hx. arifolia* plants show higher survival rates in low temperatures, whereas the seedlings do better where temperatures are relatively higher. The use of multiple demographic stages in transplant research is important, as real populations are not static and life history stages do not contribute equally to persistence and observed distributions (Grubb, 1977; Caswell, 2001). Because the highest life-stage

mortality typically occurs in the transition from seed to juvenile (Harper, 1977; Fenner, 1987; Lambers *et al.*, 1998; Fenner & Kitajima, 1999), recruitment success or the 'regeneration niche' is often considered a bottleneck in plant demography which structures the spatial distribution of plants (Grubb, 1977; Albrecht & McCarthy, 2009; Moore, 2009). Although recruitment success is higher on north- than south-facing slopes, these differences are not statistically significant and pale in comparison with the discrepancy in survival across slope aspects in adults. These results suggest that the spatial structuring across slope aspects occurs in the latter demographic stages rather than during recruitment.

A critical demographic parameter has been omitted from this analysis, however. Comparative investigation of *Hx. arifolia* and *Hp. nobilis* reproduction was not possible because of a lack of seed production in *Hx. arifolia* transplants. However, *Hp. nobilis* flowered significantly more ($t = 3.16$, d.f. = 128.9, $P < 0.002$) on north-facing (4.64 ± 0.2 flowers per plant) than south-facing (3.49 ± 0.3 flowers per plant) slopes, reproduction in natural populations of both plants was size specific (Warren, 2007), and both exhibited significantly less growth on south- than north-facing slopes, suggesting that natural populations of *Hx. arifolia* also suffer from decreased reproductive output on south-facing slopes. Albrecht & McCarthy (2009) manipulated seedling recruitment in shade-tolerant woodland across slope aspects, and determined that recruitment success was consistent with natural distributions. Those species that were found most frequently on north-facing slopes also showed the highest recruitment failure when planted on south-facing slopes. Although these results are not consistent with the patterns observed here, Albrecht & McCarthy (2009) did not transplant adults, and so a relative comparison between recruitment and adult stages is not possible. Rorison *et al.* (1986a) found that translocated adult plants generally showed higher growth on north- than south-facing slopes, which is consistent with the patterns observed here; however, they used grassland species in open habitat.

Conclusions

Stage- and species-specific abiotic responses culminate in similar landscape-level distributions for two woodland herbs. Adult survival and growth outstrip the predictive power of dispersal and recruitment in explaining coarse patterning, and the demographic stages, as well as the individual species themselves, respond vigorously to different abiotic variables associated with the slope aspect dichotomies. Overall, drought and temperature stress appear to be the mechanisms behind decreased abundance of these understorey evergreen herbs on south-facing slopes. Low soil moisture and large fluctuations in temperature occur more on south- than north-facing slopes (Werling & Tajchman, 1984; Bolstad *et al.*, 1998; Geiger *et al.*, 2003;

Desta *et al.*, 2004), and these appear to be critical for the survival and growth of these plants, particularly *Hx. arifolia*. Even with experimental manipulation, it is difficult to decouple environmental effects on plant demography under field conditions, and the measurement of temperature at the grid rather than cell scale here exacerbated this problem. Although mean rather than extreme temperature values provide a better fit for the models used in this study, infrequent, extreme events can be more determinant of species' distributions than mean environmental conditions (Pykala *et al.*, 2005; Bennie *et al.*, 2006), and certainly justify further investigation. Further research into the mechanisms behind species' distributions across slope aspects may consider differences in extreme events, such as summer drought and understorey sunflecks, and include more fine-scale analysis of temperature effects.

Although both species showed lower adult survival and growth on south-facing slopes, each exhibited species-specific responses to the experimental treatments and ambient conditions, suggesting that the natural distribution patterns reflect different environmental tolerances for the two species. This suggests that simply using slope aspect as a proxy for distribution misses both explanatory mechanisms and portability of results (Austin, 2002). Associating plant communities with topographical features (e.g. Stoutjesdijk & Barkman, 1992; Badano *et al.*, 2004) assumes long-term climate stability at temporal scales aligned with geographical transformations, and treats these communities as inevitable extensions of relatively invariant climates (Clements, 1936). Climate has changed, and is expected to change, at rates exceeding that of geomorphological evolution; as a result, abiotic drivers, not topographical proxies, are projected to shift. That is, temperature and precipitation are expected to vary significantly in the next century, but elevations and latitudes are not. The results here suggest that, rather than refining or expanding the use of topographical proxies (Gallardo-Cruz *et al.*, 2009), plant research will be better served by direct abiotic data collected in association with key demographic stages (Pulliam, 2000).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Experimental grid containing *Hexastylis arifolia* and *Hepatica nobilis* transplants and seed plantings.

Table S1 Mean temperature, percentage soil moisture and percentage light for plots at Whitehall Forest (WHF) and Coweeta Hydrologic Laboratory (CWT).

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