Mechanisms driving understory evergreen herb distributions across slope aspects: as derived from landscape position

Robert J. Warren II

Abstract In the Northern Hemisphere, the surface of south-facing slopes orients toward the sun and thus receives a greater duration and intensity of solar irradiation, resulting in a relatively warmer, drier microclimate and seasonal environmental extremes. This creates potentially detrimental conditions for evergreen plants which must endure the full gamut of conditions. I hypothesize that (1) increased southerly aspect will correlate negatively with evergreen understory plant distributions; (2) derived environmental variables (summer and winter light and heat load) will predict variance in evergreen distributions as well as topographic position (aspect, slope, and elevation) and (3) winter light will best predict evergreen understory plant distributions. In order to test these hypotheses, survey data were collected characterizing 10 evergreen understory herb distributions (presence, abundance, and reproduction) as well as the corresponding topographical information across north- and south-facing slopes in the North Carolina mountains and Georgia piedmont. The best predictive models were selected using AIC, and Bayesian hierarchical generalized linear models were used to estimate the strength of the retained coefficients. As predicted, evergreen understory herbs occurred and reproduced less on south-facing than north-facing slopes, though slope and elevation also had robust predictive power, and both discriminated well between evergreen species. While the landscape variables explained *where* the plants occurred, winter light and heat load provided the best explanation *why* they were there. Evergreen plants likely are limited on south-facing slopes by low soil moisture combined with high temperatures in summer and high irradiance combined with lower temperatures in winter. The robust negative response of the understory evergreen herbs to increased winter light also suggested that the winter rather than the summer (or growing season) environment provided the best predictive power for understory evergreen distributions, which has substantive implications for predicting responses to global climate change.

Keywords Community ecology · Southern Appalachian mountains · Piedmont · Climate · AIC · Bayesian

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Introduction

The remarkable shift in plant communities 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 and Larkin-Lieffers 1987; Bale and Charley 1994; Sternberg and Shoshany 2001; Holst

et al. 2005) and at every level (herbaceous, shrub and tree) of plant community composition (Cantlon 1953; Hicks and Frank 1984; Huebner et al. 1995; Olivero and Hix 1998; Fekedulegn et al. 2003; Searcy et al. 2003; Desta et al. 2004). Aspect-related plant community variation also includes species diversity (Olivero and Hix 1998; Hutchinson et al. 1999; Small and McCarthy 2002), phenology (Cantlon 1953; McCarthy et al. 2001), and productivity (Hicks and 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 and 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 et al. 1983), resulting in a relatively warmer, drier south-facing slope microclimate (Shanks and Norris 1950; Cantlon 1953; Werling and 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% seasonal 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 and 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 and Nilsen 1990; Huebner et al. 1995; Valverde and Silvertown 1997; Olivero and 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 of understory evergreen herbaceous plants across north- and south-facing slopes. Specifically, I ask the following questions:

I. *Does increased southerly aspect orientation predict evergreen understory plant distribution as characterized by presence, abundance and reproduction?* Given that there is a cosmopolitan pattern of plant community shifts across slope aspects, and understory evergreen herbs are exposed to greater extremes in those shifts than deciduous species, it is expected that increased southerly aspect will correlate negatively with understory evergreen distributions. Elevation and slope angle are explored as alternate explanations.

II. *Can estimated environmental variables such as heat load and seasonal light predict evergreen niche requirements as well as landscape position?* Landscape 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, 1959; Kearney 2006)—that is, the conditions at a location not the location itself determine niche space—environmental variables (seasonal light and heat load) should 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. Heat load is explored as an alternate explanation.

Methods

Study areas

This study was conducted in the Blue Ridge Mountains of western North Carolina at Coweeta Hydrologic Laboratory (CWT) (some transects crossed into the adjacent Standing Indian Basin) in the Nantahala National Forest (35°01′ N latitude) in Otto-Macon County and in the Piedmont region of Georgia at Whitehall Forest (WHF) (33°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 5.4°C and the mean July temperature is 26.4°C. Mean annual precipitation at CWT is 181 cm; the mean January temperature is 6.1°C and the mean July temperature is 24.7°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 graminoid, *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 (2008). 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 to balance north- and south-facing plots in an attempt to balance environmental variables (e.g., elevation, slope angle, latitude, and precipitation). The location, direction and length of each transect were 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 in order to standardize the plots. Along each transect, 2 × 20 m plots—oriented with long axes perpendicular to slope contours—were established at 50-m intervals based on GPS coordinates. 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). All herbaceous evergreen plants were surveyed within each plot. The assessment of reproduction was based upon 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 *M. 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 topographic gradient.

Data analysis

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 azimuth = 180− |compass azimuth − 180|, 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 per day, and its estimation by Frank and Lee (1966) was based upon the empirical relationships between seasonal solar zenith angles and the geometry of land surface orientation and topography. The Frank and Lee (1966) estimates were converted from Langleys to the SI unit, W m^{-2}.

An approximation of a dimensionless heat load was calculated using 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. (All variables were transformed into radians.) This equation is based upon the same solar/surface interactions as Frank and Lee (1966); however, it integrates irradiation over an entire season and can be readily modified to estimate heat load. 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 solar exposure will have a higher maximum temperature than an equivalent slope with morning exposure; 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 a northeast–southwest line: Linear azimuth $= 180 - |\text{compass azimuth} - 225|$.

Because the solar irradiation models are based on topography and geography, they do not account for overstory shading. Shading for all plots was calculated using data collected at both sites as part of a larger demographic project that included percent forest light transmission. Percent shade was added to the environmental models as both an explanatory term and an ameliorate of heat and light terms but failed to add predictive value or change parameter relationships in any model and was thus removed.

Generalized linear models

Historically, aspect research has focused on landscape 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: landscape (aspect, slope, and elevation) and environmental (heat load, summer and winter light). An additional, and critical, reason for splitting the models was that the environmental covariables were generated from the landscape covariables, making their inclusion into one model problematic due to a lack of independence (collinearity).

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 landscape model: $Y_i = \text{intercept} + \text{Aspect}_i + \text{Aspect}_i^2 + \text{Elevation}_i + \text{Elevation}_i^2 + \text{Slope}_i + \text{Slope}_i^2 + \text{interaction}_i$; Full environmental model: $Y_i =$

intercept $+ \text{Heat load}_i + \text{Heat load}_i^2 + \text{Summer light}_i + \text{Summer light}_i^2 + \text{Winter light}_i + \text{Winter light}_i^2 + \text{inter-action}_i$). The covariables were standardized to a mean of 0 and unit standard deviation ($(x_i - \mu)/\sigma$).

Stepwise model selection (step-up and step-down) was used to select reduced models (those with the best predictive ability and fewest parameters) from the full models (all possible parameters) as well as select the statistical distribution (binomial, Poisson, normal) that best-explained model variance. Models were ranked using Akaike's information criterion (AIC) using the "R" statistical package (2005). The AIC method rewards models that include parameters with higher predictive ability while penalizing the models for superfluous parameters. As a measure of the goodness of model fit, the "pseudo-coefficient of determination" (Swartzman et al. 1992) was calculated. The pseudo R^2 estimates the fraction of the total deviance explained by the model: $(1 - \text{residual deviance/null deviance})$, where null deviance is the total deviance in the model, i.e., total sum of squares, and residual deviance is the discrepancy between the data and model, i.e., residual sum of squares (which is used to estimate standard deviation about the regression line in linear regression).

Generalized linear models were used to transform the data to linearity assuming a binomial error distribution ($Y_i \sim \text{Binomial } (n_i, p_i)$) with the logit link function ($\log (Y_i \beta/(1 - Y_i)) = \beta_0 + \beta_{X_i} + \cdots$) for presence and a Poisson error distribution ($Y_i \sim \text{Poisson } (\mu_i)$) with the log link function ($\log (Y_i) = \beta_0 + \beta_{X_i} + \cdots$) for abundance and reproduction. Presence was calculated as the presence (1) or absence (0) of understory evergreen plants per plot, abundance was the number of plants per plot, and reproduction was the proportion of plants with reproductive structures.

Bayesian hierarchical GLMs were used to generate 95% credible intervals for the regression coefficients for both models. Second-order coefficients were dropped if they had the same slope direction as the first-order term. The Bayesian models were implemented in the WinBUGS 1.4.3 software package (Lunn et al. 2000). 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 model while random intercepts that varied per landscape ($n = 2$) were included in the abundance and reproduction models.

The 95% 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).

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 $1,163 \pm 284$ m (mean $\pm$ SE) at CWT and 184 ± 9 m at WHF; the slope of the transects averaged $45 \pm 18\%$ at CWT and $28 \pm 10\%$ at WHF. Heat load (CWT: 0.88 ± 0.16; WHF: 0.93 ± 0.09), summer light (CWT: 450.8 ± 29.9 W m^{-2}; WHF: 473.7 ± 17.1 W m^{-2}), and winter light (CWT: 181.6 ± 158.2 W m^{-2}; WHF: 187.2 ± 117.3 W m^{-2}) were slightly higher at WHF than CWT, but the differences were minor.

Evergreen distribution

The presence models with the lowest AICs retained all of the parameters except that the aspect:slope interaction term was dropped from the landscape model and the second-order winter light term was dropped from the environmental model (Table 1). However, while most parameters were retained, only the coefficients for aspect, elevation, and slope were significantly different than zero in the landscape model while all of the parameters differed

significantly from zero in the environmental model (Fig. 1).

Both the abundance and reproduction landscape models with the lowest AICs retained aspect, elevation, slope, and slope^2, though the reproduction model also retained the aspect:elevation interaction term (Table 1). Similarly, both the abundance and reproduction environmental models with the lowest AICs retained site, heat load, winter light, and the heat load:winter light interaction term (Table 1). However, only the coefficients for heat load and winter light in the abundance model and winter light in the reproduction model differed significantly from zero (Fig. 1).

The landscape models suggested that increased southerly aspect and elevation corresponded with decreased evergreen presence, abundance, and reproduction (Fig. 1). All three variables increased with slope steepness, and the significant second-order term indicated that both abundance and reproduction decreased on the steepest slopes; thus, the plants performed best on intermediate slopes. The significant aspect:elevation interaction term in the reproduction model suggested that the negative effects of each parameter were offset in high elevation, south-facing habitats as reproduction increased as a function of increased aspect combined with increased elevation.

The environmental models suggested that only increased winter light had a negative impact on all three variables, while increased heat load corresponded with decreased presence and abundance (Fig. 1). Increased summer light only had a negative impact upon evergreen plant presence. The significant negative heat load:summer light and heat load:winter light interaction terms indicated that the plants occurred less where increased temperature was paired with either increased summer or increased winter light.

In all cases—presence, abundance, and reproduction—the environmental models explained variation in the plant distribution variables better than the landscape models. While the improved fit was small ($\sim$2–5%), and a great deal of deviance was left unexplained by both model types (80–85%), this suggested that the environmental models provided somewhat better explanatory power than the landscape models. The unexplained variance likely stemmed from error created by the coarse scale of

Table 1 Understory evergreen herb distribution models

Model	Error distribution: binomial; deviance explained: 12.7%	AIC
Landscape model: Presence		
Full	Presence: Site + Asp + Elv + Slp + Asp^2 + Elv^2 + SIp^2 + Asp:Ely + Asp:Slp	3896.8
Reduced	Presence: $-$Site $-$ Asp + Elv + Slp $-$ Asp^2 + Elv^2 + Slp^2 + Asp:Ely	3896.0

Model	Error distribution: Poisson; deviance explained: 15.1%	AIC
Landscape model: Abundance		
Full	Abundance: Site + Asp + Elv + Slp + Asp^2 + Elv^2 + Slp^2 + Asp:Ely + Asp:Slp	1312.2
Reduced	Abundance: $-$Asp $-$ Elv + Slp $-$ Slp^2	1305.0

Model	Error distribution: Poisson; deviance explained: 12.9%	AIC
Landscape model: Reproduction		
Full	Reproduction: Site + Asp + Elv + Slp + Asp^2 + Elv^2 + Slp^2 + Asp:Ely + Asp:Slp	1007.8
Reduced	Reproduction: $-$Asp $-$ Elv + Slp $-$ Slp^2 + Asp:Elv	1002.0

Model	Error distribution: binomial; deviance explained: 14.7%	AIC
Environmental model: Presence		
Full	Presence: Site + Htl + Slt + Wlt + Htl^2 + Slt^2 + Wlt^2 + Htl:Slt + Htl:Wlt	3805.6
Reduced	Presence: $-$Site $-$ Htl + Slt $-$ Wlt $-$ Htl^2 + Slt^2 + Htl:Slt + Htl:Wlt	3804.0

Model	Error distribution: Poisson; deviance explained: 20.2%	AIC
Environmental model: Abundance		
Full	Abundance: Site + Htl + Slt + Wlt + Htl^2 + Slt^2 + Wlt^2 + Htl:Slt + Htl:Wlt	1305.9
Reduced	Abundance: $-$Site $-$ Htl $-$ Wlt $-$ Htl^2 + Htl:Wlt	1298.0

Model	Error distribution: Poisson; deviance explained: 13.1%	AIC
Environmental model: Reproduction		
Full	Reproduction: Site + Htl + Slt + Wlt + Htl^2 + Slt^2 + Wlt^2 + Htl:Slt + Htl:Wlt	1006.2
Reduced	Reproduction: $-$Site $-$ Htl $-$ Wlt $-$ Htl^2 + Htl:Wlt	1001.0

Reduced models (which contained parameters with the highest likelihoods) that best predicted presence, abundance, and reproduction were selected from the full models (all parameters) via stepwise (step-up, step-down) selection using AIC in the R Statistical package AIC. The direction of regression slope for each parameter is indicated by sign (+/−). The goodness of fit (pseudo-coefficient of determination) of the reduced models is given as "deviance explained". The landscape models include site, aspect (Asp), elevation (Elv), and slope (Slp) along with second-order and interaction terms. The environmental models include site, heat load (Htl), summer light (Slt), and winter light (Wlt) along with second-order and interaction terms

measurement as well as unmeasured explanatory variables.

Individual species

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 at CWT, and *M. repens*, *A. platyneuron*, and *H. arifolia* were only recorded at WHF. *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.

Fig. 1 Mean values with 95% credible intervals for coefficients from the Bayesian hierarchical models of landscape [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
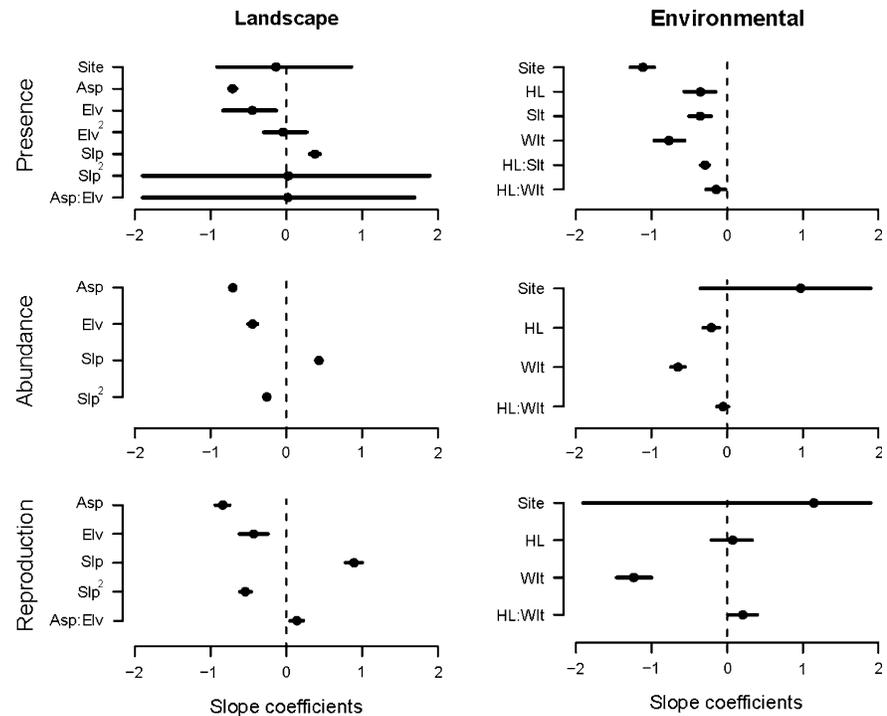
Most of the species occurred far more in north- than south-facing sites (Fig. 2). The south-avoiding pattern was particularly strong in *H. villosa*, *P. acrostichoides*, *H. arifolia*, and *M. repens*, while *A. platyneuron* and *C. maculata* had similar frequencies on north- and south-facing slopes. 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. 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.

There is little discrimination between evergreen species in response to heat load as almost all of the plants occurred more at lower heat load levels (Fig. 2). 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*, *H. arifolia*, and *P. acrostichoides* occurred more where summer light was highest (Fig. 2). Not surprisingly, three of these occurred at WHF exclusively. Conversely, only *G. pubescens* and *G. procumbens* occurred more where light was less. A clearer pattern emerges with winter insolation as all the evergreen plants except *C. maculata* and *A. platyneuron* occurred more where winter light levels were lower (Fig. 2).

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 lower temperatures in the winter. Both of these combinations are known plant stressors (Raven 1989; Pearcy et al. 1994; Neufeld and 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. Both community- and species-level data
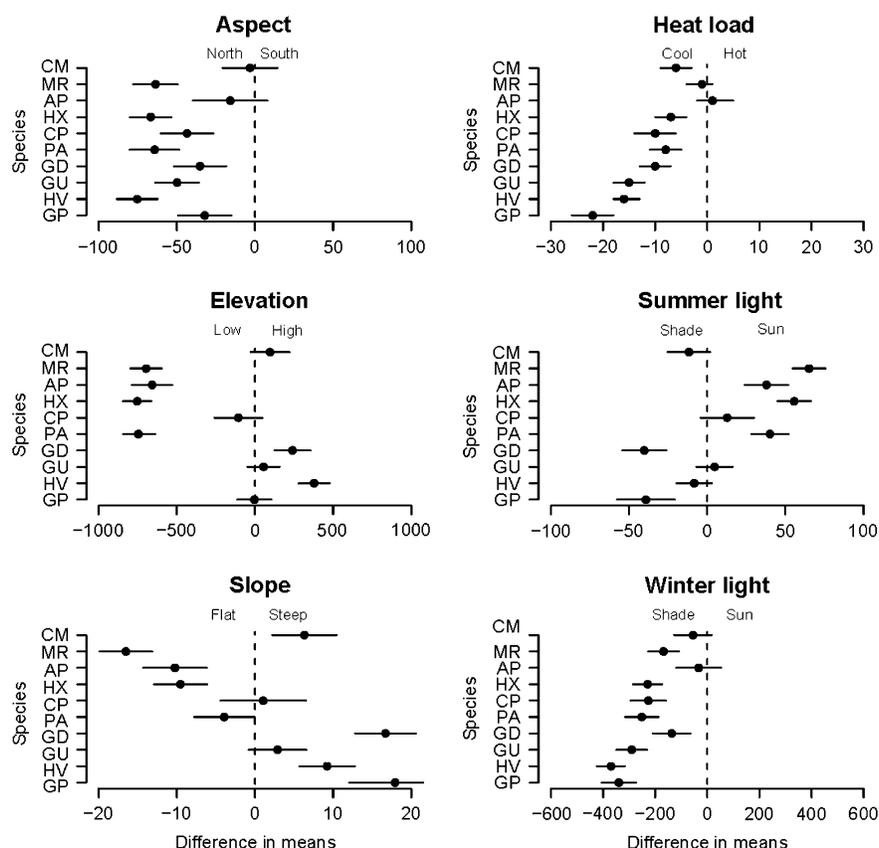
Fig. 2 *t* Distributions with 95% confidence intervals for the mean difference between habitat parameters where the species were present and absent (mean difference = mean value present − mean value absent). Thus, positive mean differences indicate the plant occurred at higher values of the habitat parameter (e.g., light) than where it was absent. For example, most of the plants occurred at lower winter light levels than where they were absent, as indicated by negative mean differences. Confidence intervals that contain zero (as indicated by the dotted line) indicate no difference between means. The intervals are given for *Chimaphila maculata* (CM), *Mitchella repens* (MR), *Asplenium platyneuron* (AP), *Hexastylis arifolia* (HX), *Carex plantaginea* (CP), *Polystichum acrostichoides* (PA), *Goodyera pubescens* (GD), *Galax urceolata* (GU), *Heuchera villosa* (HV), and *Gaultheria procumbens* (GP)

support this prediction, though elevation and slope remain important predictors of evergreen plant distributions. Derived environmental variables did indeed predict evergreen herb distributions somewhat better than landscape position. As it is the mechanistic explanatory power of environmental values that make the environmental models extremely useful, they would remain superior to landscape position even if they were equal or somewhat inferior in predicting distributions. Due to the harsh high light/low temperature environment during winter, it was predicted that winter light would best explain variance among the plants. Both community- and species-level data strongly support this prediction,

though heat load also explains a great deal of evergreen plant presence and abundance.

Species-level responses

The data suggest that, as a community, the understory evergreen herbs respond similarly to aspect, heat load, and winter light, but individual species respond differently to elevation, slope, and summer light. The three species that were only surveyed at WHF are predictably found more in flat, low elevation locations while those found only at CWT are predictably found somewhat more in steeper, high elevation locations. However, WHF is far warmer and

somewhat sunnier than CWT, and there is little difference between individual species in aspect, heat load, and winter light, suggesting that the species-level differences are not a product of site effects alone. Furthermore, the differences in occurrence per site reflect differences in species' environmental requirements, and taken within the context of the species models, provide insight into understory evergreen herb distributions.

Landscape 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 1, Figs. 1 and 2). 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 have robust predictive power on evergreen community distributions, and they discriminate well between species (Figs. 1 and 2). That is, individual species respond uniquely to differences in slope and elevation, while they generally respond *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 and Niering 1975; Swift et al. 1988; Bolstad et al. 1998, 2001), and elevation is an landscape gradient long recognized for sorting species (Whittaker 1956). The interaction effect between aspect and elevation suggests that increased elevation has a positive impact on reproduction 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 correlate negatively with understory evergreen plants, their distributions peaked at intermediate slope angles (Fig. 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 and Orndorff 1983; Hicks and Frank 1984).

Environmental models

Historically, plant presence and abundance have been correlated with aspect, which is associated with environmental variables, but this lacks a direct correlation between environmental variables and distribution. Landscape position has robust predictive power for the evergreen herbs but gives little indication of the mechanism behind the distribution. In this research, I used derived environmental variables in order to infer characteristics of the understory evergreen niche based on distributions.

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 and Young 2003) and (b) high irradiance combined with low temperatures in winter (Verhoeven et al. 1999; Neufeld and Young 2003). Summer light is a limited resource for understory plants beneath deciduous canopy, but it appears to have little impact upon evergreen community distributions. This relationship is somewhat mixed, however, as several species occur more in higher summer light while the overall community responds negatively (Figs. 1 and 2).

The impact of winter light is much clearer; increased winter light exposure results in decreased understory evergreen distributions (Figs. 1 and 2). Almost all of the evergreen plants are found more in lower winter light environments, and as a community they occur and reproduce less where winter light is highest. This is consistent with previous research which found that evergreen plants growing in shady habitats are less light stressed during the winter than

those in sunny habitats (Logan et al. 1998; Adams et al. 2001, 2004). These data suggest that evergreen plants are more sensitive to winter photoinhibition (high light, low temperature) than summer photoinhibition. The likely explanation is that while the light-harvesting machinery of plants remains relatively unaffected by low temperatures (even freezing), the enzymes that use light energy to fix carbon are denatured at suboptimal temperatures and thus fail to utilize light (Raven 1989; Lambers et al. 1998; Neufeld and Young 2003). The excess light is costly in terms of photodamage or photoprotection. 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 shadier north-facing slopes.

Though not as strong or consistent as winter light, heat load also provides robust predictive power for evergreen presence and abundance, which decreases with increased heat load (Fig. 1). Few of the evergreens have substantial abundance where exposed to the highest heat load levels, and most all of the evergreens occur more at lower heat loads than where they are absent (Fig. 2). 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 and Young 2003). The negative interaction effects between heat load and summer light and heat load and winter light in the presence model suggests that the detrimental effect of heat load is furthered when paired with increased light in either season.

Conclusions

Aspect provides the best predictor where evergreen understory communities will occur while slope and elevation best discriminate between species within that distribution. Furthermore, while the landscape variables suggest *where* the plants occur, winter light, and heat load provide the best mechanism as to *why* they are there. In general, where winter light and heat load 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 lower temperatures in winter.

The results of this survey strongly indicate that soil moisture, temperature, and seasonal light are strong candidates for further research into the distribution of evergreen understory plants. A great body of research has correlated plant communities and aspect dichotomies with a set of assumptions about dichotomies in moisture, temperature, light, and nutrients. In most studies, one landscape 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. The derived environmental variables provide a somewhat better fit to the data, and, more importantly, (if one considers a niche the requirements of an organism and not a space in the environment) they provide mechanistic explanations for the plant distributions. However, the better fit of the environmental variables still left a great deal of variance in the data unexplained. This is not surprising when using estimated and derived variables taken at a coarse scale and suggests that 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 niche requirements of evergreen herbs.

An important implication of these results relates to global climate change. If the shift in climate from north- to south-facing slopes at all mimics the predicted shift in climate toward warmer, potentially drier conditions (or at minimum increased drought intervals) (Weltzin et al. 2003; Wentz et al. 2007; Zhang et al. 2007), then these results suggest most of the understory evergreen herbs surveyed in this research will fare poorly (*C. maculata* and *A. platyneuron* being the exceptions). Furthermore, most models used to predict species and community responses to climate change focus upon summer or growing season conditions, while these results suggest that warmer conditions may have the most impact upon understory evergreen herbs. Given that winter temperatures are expected to increase more

than summer temperatures (National Assessment Synthesis Team 2000), this trajectory deserves further investigation.

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