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Author(s) :Carolyn Pucko, Brian Beckage, Timothy Perkins, and William S. Keeton

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Species shifts in response to climate change: Individual or shared responses?^{1,2}

Carolyn Pucko³ and Brian Beckage

Department of Plant Biology, University of Vermont, Burlington, VT 05405

Timothy Perkins

Proctor Maple Research Center, University of Vermont, Underhill Center, VT 05490

William S. Keeton

Rubenstein School of Natural Resources, University of Vermont, Burlington, VT 05405

PUCKO, C., B. BECKAGE (Department of Plant Biology, University of Vermont, Burlington, VT 05405), T. PERKINS (Proctor Maple Research Center, University of Vermont, Underhill, VT 05490), AND W. S. KEETON (Rubenstein School of Natural Resources, University of Vermont, Burlington, VT 05405). Species shifts in response to climate change: Individual or shared responses? *J. Torrey Bot. Soc.* 138: 156–176. 2011.— Individual species are expected to shift their distributions in response to global climate change. Species within existing communities may respond to climate change individually, resulting in the formation of novel communities, or may instead shift as intact communities. We examined whether montane plant communities in the northeastern United States have shifted their elevational range as intact assemblages or individually in response to recent regional climatic and environmental change. We used non-metric multidimensional scaling (NMDS) to examine changes in plant community composition and species distributions using vegetation surveys repeated five times between 1964 and 2006 across an elevational gradient (549–1158 m) on Camels Hump Mountain, Vermont, USA, in conjunction with an analysis of local climate change. We found evidence that species elevational distributions and community compositions have shifted in response to a 0.49 °C per decade warming. These species responses were complex and largely individualistic at some elevations, while at other elevations species in a given community tended to respond similarly. The magnitude of community compositional change was largely dependent on location with respect to the ecotone between northern hardwood and boreal forests. While climate change likely contributed to the large shifts in species within NMDS space, these shifts may also be a response to invasive earthworms at low elevations and to prolonged exposure to acid deposition at high elevations. Though we found evidence of shared species responses within communities, future species responses may become increasingly divergent as the magnitude of climate change increases causing species-specific environmental thresholds to be reached and as the synergistic effects of multiple anthropogenic perturbations rise.

Key words: Acid Deposition, Climate Change, Community Shift, Elevation Shift, Non-metric Multidimensional Scaling (NMDS).

Understanding how species will respond to ongoing climate change is increasingly important as the rate of anthropogenic climate change increases (Walther 2003, IPCC 2007, Walther 2010). The effects of recent warming have already been observed in an array of terrestrial, aquatic and marine habitats (Scavia et al. 2002, Naidoo 2004, Winder and Schindler 2004) and are evidenced by the shifting

ranges of many species either poleward or upward in elevation (Root et al. 2003, Krajick 2004, Beckage et al. 2008b, Kelly and Goulden 2008). While the literature on species responses to recent climate change is extensive (cf. Parmesan and Yohe 2003), less attention has been given to the examination of community responses. Investigations of community responses to climate change have recently become more common (Genner et al. 2004, Suttle et al. 2007, Grime et al. 2008, Willis et al. 2008, Kelly and Goulden 2008), but studies of community response that also comprehensively examine species responses to climate change have remained much more limited (Walther 2003).

We examine species assemblages across an elevational gradient in order to distinguish between two historically competing hypotheses of community assembly (Clements 1916,

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³ Author for correspondence: E-mail: cpucko@uvm.edu

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Gleason 1939, Callaway and Walker 1997, Brooker et al. 2008). The Individualistic Response Hypothesis (IRH) asserts that co-occurring species will respond independently to changes in the environment (Gleason 1939, Jackson and Overpeck 2000, Williams and Jackson 2007), forming novel species assemblages with climate change (Walther 2003, le Roux and McGeoch 2008). There is substantial evidence in support of this hypothesis, provided, for example, by tree pollen extracted from lake sediment cores from around the world (Overpeck et al. 1992, Umbanhower et al. 2006). However, similar data for understory forest herbs are extremely limited (Cain et al. 1998). The Shared Response Hypothesis (SRH) predicts that co-occurring species will respond similarly to changes in their environment due to common climatic tolerances (Walther et al. 2002) or interspecific facilitative relationships that promote co-occurrence (Bruno et al. 2003, Freestone 2006). This hypothesis suggests that communities will shift as intact assemblages, preserving species associations, in response to climate change.

Recent evaluations of this dichotomy acknowledge that neither hypothesis satisfies the complexities observed in natural communities (Bruno et al. 2003, Lortie et al. 2004). Instead, it is preferable to view the responses of co-occurring species to climatic or environmental change in terms of a continuum (Brooker et al. 2008). Though not a novel viewpoint (Goodall 1963, Callaway and Walker 1997), Lortie et al. (2004) called this concept the Integrated Community (IC), and theorized that the level of shared response was based on the relative influence of species interactions, abiotic factors, and stochastic processes. This view of species assemblages postulates that harsh environments lead to increased levels of facilitation among species (Callaway and Walker 1997, Brooker and Callaghan 1998), which can result in intact community shifts while simultaneously allowing for species to exhibit divergent responses to more subtle environmental change (Lortie et al. 2004, Brooker et al. 2008).

In this study, we examined plant communities in order to determine the degree to which species have shifted independently in response to recent climate change. We examined changes in community composition across an elevational gradient in the northeastern United States using permanent vegetation plots that

spanned four decades. Our vegetation plots were established on Camels Hump in the Green Mountains, Vermont, in 1965 (Siccama 1968) and were resurveyed in 1979, 1983, 1986 and 2006. Montane environments provide ideal locations to study climate-related species shifts because their steep slopes result in spatially compressed climate gradients (Kupper and Cairns 1996, Kelly and Goulden 2008) where even relatively small changes in climate can result in observable shifts in species elevational distributions (Beckage et al. 2008b, Lenoir et al. 2008). We focused on understory communities because of their higher species richness relative to the overstory in our study system. This allowed us to investigate the effects of climate change in terms of both individual species shifts as well as changes to community composition, and thus, to examine the relative support for the individualistic versus shared response hypotheses. In addition, understory species may be capable of responding more quickly to changes in climate, sometimes exhibiting more rapid altitudinal shifts than long-lived canopy species due to shorter generation times (Lenoir et al. 2008). We concurrently examined the response of canopy tree species to determine whether overstory shifts might be driving any observed understory changes.

The specific objectives of our study were to i) determine if montane understory communities shifted their elevational range in response to recent climatic and environmental change, and ii) determine to what degree observed responses were consistent with either the individual or shared response hypothesis. If species have shared responses to environmental change, we would expect current communities to be analogous to those observed in 1965 with correspondingly few communities defined by novel species assemblages. However, if species are responding individually, we expect to see divergence in both the magnitude and direction of species shifts within a community, resulting in new species assemblages.

Methods. STUDY SITE. We conducted our study on Camels Hump ($44^{\circ} 19'N$, $72^{\circ} 53' W$), which, at 1244 m a.s.l., is the third highest peak in Vermont, USA. The geology of Camels Hump is representative of the Green Mountains, a northern extension of the Appalachians, and is dominated by schist

(graphitic, quartz-albite-muscovite) and gneiss (Siccama 1974) bedrock.

Soils are predominantly spodosols, consisting of acidic stony loams (NRCS 2006, NRCS 2008). The climate in this region is characterized by large daily and annual temperature ranges, with an average January temperature of -7.8°C and an average July temperature of 21.4°C . Precipitation is evenly distributed throughout the year, averaging 91.6 cm annually (Burlington International Airport Station, NOAA 2002). However, at high elevations, cloud water deposition can increase precipitation by a conservative estimate of 50–65% (Vogelmann et al. 1968, Lovett et al. 1982).

Two general forest types, stratified by elevation, occupy the majority of the area on Camels Hump and other montane regions of New England. Northern hardwood forest is found at elevations below approximately 750 m and is dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britt.). Boreal forest occurs at higher elevations, above approximately 900 m, and is dominated by red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) P. Mill.), and mountain paper birch (*Betula papyrifera* var. *cordifolia* (Regel) Fern.) (Siccama 1974, Cogbill and White 1991). This boreal forest extends upward until it reaches the small alpine summit of Camels Hump at approximately 1200 m. Between the northern hardwood and boreal forests, from approximately 700–900 m, lies a spatially compact transition zone referred to as the Boreal to Deciduous Ecotone (BDE) (Siccama 1974, Beckage et al. 2008b).

The vegetation survey plots used in this study were located in the Camels Hump Forest Ecology Research Area, which has a well-documented land use and disturbance history (Siccama 1968, Whitney 1988). In order to minimize the influence of successional changes in our sites, plots were established in locations free from major disturbance or recent human activity (Foster et al. 1998, Hall et al. 2002). While the majority of the upper slopes of Camels Hump have not been logged, there has been some limited removal of trees at lower elevations. However, with the exception of the removal of individual yellow birch and red spruce at elevations extending up to 700 m in the mid 1930s and 1950s (Whitney 1988), no other potentially disruptive logging activity

has been located in the research area (Siccama 1968, Whitney 1988). In 1964, during the initial canopy survey, the forest composition was classified as late successional (Siccama 1968), containing the same overstory species as today. Hence succession has probably not contributed to any stand-scale changes in species composition in the subsequent forty years. However, the forest is likely to have developed structurally (Franklin et al. 2002) and ongoing gap phase processes may influence species composition at small scales within our study sites (e.g., Perkins et al. 1992, Battles and Fahey 2000, Beckage et al. 2008a). These internal dynamics alone should not result in distributional changes of species but could, however, influence the rate at which species are able to respond to shifting climate (e.g., Beckage et al. 2008b).

FIELD METHODS. Vegetation was sampled using a nested plot design established in 1964 (Siccama 1968) to capture both over- and understory vegetation characteristics. Overstory plots were distributed up the western slope of Camels Hump in 1964 at intervals of 61 vertical meters (200 feet) between 549 and 1158 m for a total of 11 sample elevations, e.g., 549, 610, 671, 732, 792, 853, 914, 975, 1036, 1097, and 1158 m. At each elevation, 5 to 10 overstory plots (3×30 m) were placed perpendicular to the contour and separated by 6 m. Rebar marks the top and bottom of each plot's centerline. The six lower elevation sites had 10 such plots, while the upper five elevations had only five plots in order to better maintain a westerly aspect. In 1964 and 2004, the species and diameter at breast height (dbh) for each tree with a basal diameter > 2 cm within each overstory plot was recorded. Nested in each of these plots were six 1×1 m understory quadrats evenly distributed along the center line for a total of 510 understory quadrats. To sample understory vegetation within each quadrat we performed a stem count and visually estimated percent cover (Dethier et al. 1993) of each vascular species present including club mosses (*Huperzia* spp. Bernh.), in accordance with the original understory survey conducted in 1965 (Siccama 1968). All taxonomy and nomenclature were updated and are consistent with Magee and Ahles (1999). Woody shrub species incapable of reaching the canopy, with a dbh less than 2 cm, were included as part of the

understory (i.e. *Viburnum lantanoides* Michx., *Cornus alternifolia* L.). We excluded canopy tree species from the understory analyses. As in the initial survey, percent cover of mosses was recorded while lichens, liverworts and fungi were excluded.

COMMUNITY COMPOSITION. A species assemblage was defined as the suite of species found within a plot. Overstory assemblages were defined by the basal area of canopy species present rather than stem counts. This was done in order to more accurately represent the community structure of canopy stems and to avoid overrepresentation of smaller, sub-canopy individuals (Hedman et al. 2000). Understory assemblages were defined by the average percent cover of species found within plots (Collins et al. 2006). Average percent cover represented the mean cover of species present within the six 1 m² understory quadrats nested within each overstory plot.

Each plant in an understory quadrat was sampled once in each survey year. Though most individuals were identified and recorded at the species level, some were aggregated by genus or family for three reasons. As a result of surveying each plot only once per growing season, some plants sampled could not be identified to species since flowers or other diagnostic field characteristics were not always present at the time of data collection (e.g., *Trillium* spp. and *Viola* spp.) (Smith et al. 2008). Some species were aggregated at the genus or family level to maintain consistency across sampling years (*Rubus* spp. and *Galium* spp.) (Siccama 1968). Other species were aggregated to accommodate changes in taxonomy (e.g., *Streptopus* spp.). In addition, mosses were aggregated into either the genus *Sphagnum* or with all other genera of mosses combined into a single group.

Our analyses of understory communities only considered species that were present in at least three of the five sampled years (Table 1). This was done to preclude any disproportionate influence that rare species might have on community characterization (Hedman et al. 2000) and also to decrease the impact of survey timing by reducing the number of spring ephemerals included in the analyses. Tree species found in our plots were analyzed separately from the understory due to differences in physiognomy and life history characteristics.

CLIMATE. We examined trends in regional climate over the period of our vegetation censuses. Regional climate change was examined through the use of annual climate variables, derived from data collected at the Burlington International Airport, Burlington, Vermont, located less than 30 km from our study site. These data are archived and maintained by the US Historical Climatology Network (Williams et al. 2006). Seasonal temperatures and precipitation were also calculated for winter (December, January and February) and summer (June, July and August) months in order to highlight seasonal differences in long-term trends. Additional climatic and biologically significant variables such as the number of frost-free days (FFD) and growing degree days (GDD) were also derived. FFD was defined as the number of days annually in which the minimum temperature was above 0 °C, while GDD was defined as the cumulative number of degree-days above a base of 10 °C. Linear regressions were then performed using R statistical software (R Development Core Team 2006) to estimate the long-term trends between 1965 and 2006.

VEGETATION ANALYSIS. We analyzed individual species and community responses to observed climate change through the use of non-metric multidimensional scaling (NMDS). NMDS was used because of its ability to highlight patterns within multidimensional data without making distributional assumptions, and is widely used in community change analyses (Hedman et al. 2000, McCune and Grace 2002, Smith et al. 2008, Greenstein and Pandolfi 2008). The objective of the non-parametric NMDS is to reduce the dimensionality of multivariate data and group more similar observations closer together by preserving rank-order distances between observations. NMDS therefore allows for the visualization of the ranked dissimilarities between multivariate data points in a reduced number of dimensions (Kruskal and Wish 1978). NMDS was selected over other ordination techniques (DCA, PCA, PCoA, CA) because of its ability to accurately identify gradients beneath overlapping and non-normal data distributions. This type of data is common in studies of plant community composition and has led to the wide acceptance and use of NMDS as a tool in community change

Table 1. The species used in our over- and understory analyses. The community analyses were limited to understory species that were observed in at least 3 of the 5 survey years and the species analysis were further limited to species found in 1965 and 2006, the end points of our vegetation censuses. This resulted in more species used for the community analysis than the species analysis. The taxa not included in the species analyses are identified with an (*). All nomenclature is consistent with Magee and Ahles (1999).

Understory Species	Overstory Species
* <i>Actaea pachypoda</i> Ell.	<i>Abies balsamea</i> (L.) P. Mill.
<i>Aralia</i> spp. L.	<i>Acer saccharum</i> Marsh.
<i>Arisaema triphyllum</i> L.	<i>Betula alleghaniensis</i> Britt.
<i>Aster</i> spp. L.	<i>Betula papyrifera</i> var. <i>cordifolia</i> (Regel) Fern.
* <i>Athyrium</i> spp. Roth	<i>Fagus grandifolia</i> Ehrh.
* <i>Botrychium virginianum</i> (L.) Sw.	<i>Fraxinus americana</i> L.
<i>Cardamine diphylla</i> (Michx.)	<i>Picea rubens</i> Sarg.
<i>Caulophyllum thalictroides</i> (L.) Michx.	
<i>Clintonia borealis</i> (Ait.) Raf.	
<i>Coptis trifolia</i> (L.) Salisb.	
<i>Cornus alternifolia</i> L.	
<i>Cornus canadensis</i> L.	
Cyperaceae	
<i>Demstaedia punctilobula</i> (Michx.) Moore	
<i>Dryopteris</i> spp. Adans.	
<i>Galium</i> spp. L.	
<i>Huperzia</i> spp. Bernh.	
<i>Hydrophyllum virginianum</i> L.	
<i>Impatiens capensis</i> Meerb.	
<i>Laportea canadensis</i> (L.) Wedd.	
* <i>Lonicera canadensis</i> Bartr.	
<i>Maianthemum canadense</i> Desf.	
<i>Maianthemum racemosum</i> (L.) Link	
* <i>Medeola virginiana</i> L.	
<i>Mitchella repens</i> L.	
<i>Monotropa uniflora</i> L.	
Moss (except <i>Sphagnum</i> spp.)	
* <i>Osmorhiza claytonii</i> (Michx.) C.B. Clarke	
<i>Oxalis</i> spp. L.	
<i>Phegopteris connectilis</i> (Michx.) Watt.	
Poaceae	
<i>Polystichum acrostichoides</i> (Michx.) Schott	
<i>Prenanthes altissima</i> L.	
<i>Ribes</i> spp. Wildl.	
<i>Rubus</i> spp. L.	
* <i>Sambucus</i> spp. L.	
* <i>Solidago</i> spp. L.	
* <i>Sphagnum</i> spp. L.	
<i>Streptopus</i> spp. Michx.	
* <i>Thalictrum pubescens</i> Pursh	
* <i>Thelypteris noveboracensis</i> (L.) Nieuwl.	
<i>Tiarella cordifolia</i> L.	
<i>Trientalis borealis</i> Raf.	
<i>Trillium</i> spp. L.	
<i>Uvularia sessilifolia</i> L.	
<i>Veratrum viride</i> Ait.	
<i>Viburnum lantanoides</i> Michx.	
<i>Viola</i> spp. L.	

analyses (Wentworth and Ulrey 2000). In addition, NMDS is able to dimensionally reduce data containing outliers, which occur frequently and are important in identifying range shifts, but can be problematic for other ordination techniques that rely on distributional assumptions such as detrended corre-

spondence analysis (DCA) (Ruokolainen and Salo 2006).

The NMDS ordinations of our species and assemblage data were based on Bray-Curtis dissimilarities of non-transformed percent cover (understory analyses) or basal area (overstory analyses) data (Bray and Curtis

1957). Dissimilarities of zero, resulting from the existence of identical compositional or distributional data, were maintained in the analyses by assigning them a small dissimilarity that would not affect the overall rank-order of points. We did not have to address zero dissimilarities resulting from joint absences, because there were no empty vegetation plots and only species that were observed in a given year were used in the computation of the Bray-Curtis dissimilarity matrices. For both community and species analyses, the data were summarized by plot. Community NMDS analyses therefore, resulted in either 5 or 10 individual data points per elevation per year. Species NMDS analyses sought to characterize changes in distribution over time by using the percent cover data for each species from all 85 plots surveyed, in each of the five survey years. This resulted in a single data point representing each species in each year it was observed. Ordinations were based solely on metrics of species abundance, i.e., percent cover for understory analyses and basal area for overstory analyses. Analyses did not include any elevational information; therefore, any grouping of communities or species through NMDS by elevation is strictly a product of similarities in the abundance of species. All NMDS analyses were performed in the R statistical software package using the metaMDS function (vegan library; Oksanen et al. 2009).

The efficacy of the dimension reduction is measured by the stress value. Stress is a measure of mismatch between the rank-ordered multivariate distance between points and their relative distances in two-dimensional ordination space; e.g., a measure of goodness of fit of the ordination. Lower stress values indicate smaller mismatch between calculated and ordination distances and thus a better ordination. Stresses reported from a majority of our NMDS analyses are < 0.2 , and are therefore reliable for interpretation based on the rule-of-thumb presented in Clarke (1993). One of the two-dimensional analyses resulted in a stress greater than 0.2, but was still below the 0.3 threshold value considered to represent a poor ordination (Clarke 1993, Zuur et al. 2007).

Each of the four NMDS analyses presented in this paper (understory communities, understory species, overstory communities and overstory species) represents a single two-

dimensional ordination. The two-dimensional ordinations were used for their ease of interpretation though we also examined three-dimensional ordinations that resulted in very similar point configurations but lower stress values. The resemblance of two-dimensional and three-dimensional ordinations (which all had stress values below 0.2) supports the reliability of the two-dimensional analyses presented.

Elevation isolines and vectors were added to community change ordinations in order to more clearly illustrate how compositions have changed over time. The isolines in each panel were calculated using the “ordisurf” function (vegan library; Oksanen et al. 2009) in R and were derived from the ordination position of each community recorded in the initial survey year (1964 or 1965) using generalized additive models (GAMs). The locations of communities in subsequent years with respect to the isolines indicate their relative similarity to these initial communities. Points representing communities that are located outside the bounds of the isolines indicate the presence of species assemblages not found on Camels Hump in 1965. Similar contours could not be added to NMDS plots representing species distributions because the data used in these analyses were vectors of species abundance across elevations. Change vectors were added to community ordinations to represent shifts over time of study plots within NMDS space. The terminus of each vector represents the average position within NMDS space of communities in the most recent vegetation survey (2004 or 2006), while the start of each vector represents the average position of those same communities in the initial survey year (i.e., 1964 or 1965).

Results. Average annual temperatures increased by $0.49\text{ }^{\circ}\text{C}$ per decade between 1965 and 2006. During this time period, winter temperatures (DJF) warmed more rapidly than summer temperatures (JJA) at the rate of $0.78\text{ }^{\circ}\text{C}$ versus $0.32\text{ }^{\circ}\text{C}$ per decade (Fig. 1). The number of growing degree days and frost-free days also increased with temperature at a rate of 55 GDD and 4.7 FFD per decade, indicating that climate has warmed significantly. Winter precipitation has decreased slightly since 1965, despite an overall increase in annual precipitation of over 2 cm per decade realized during other seasons. Result-

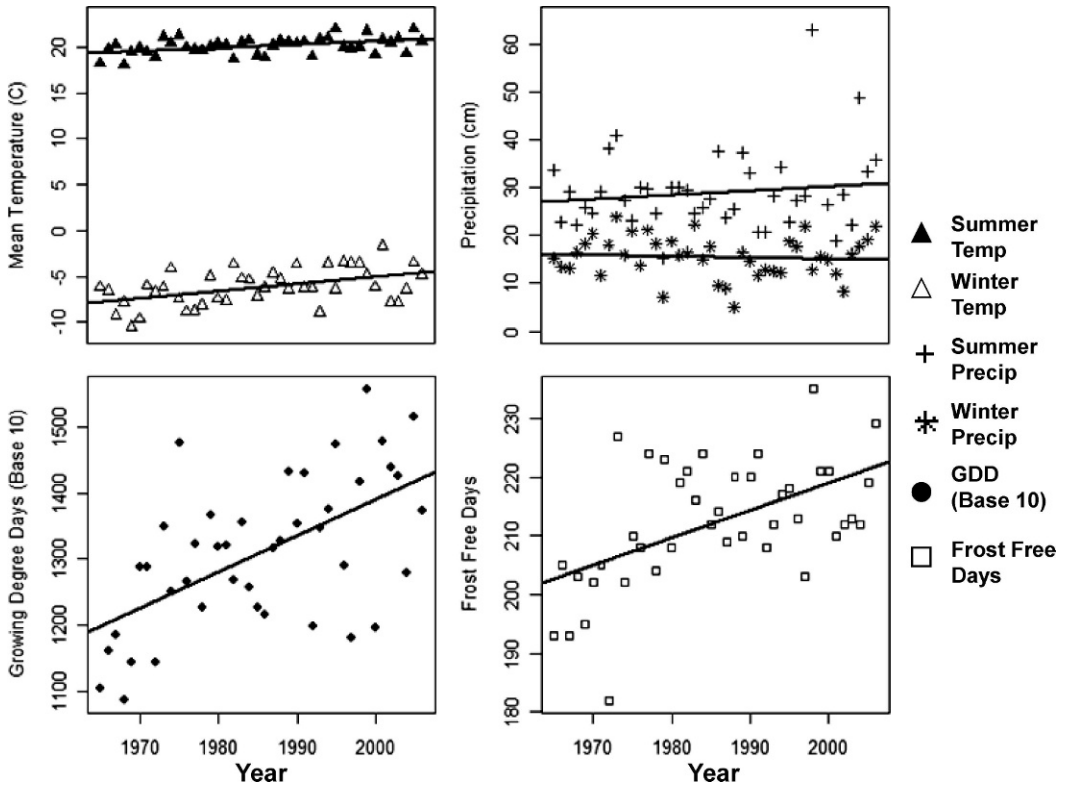


FIG. 1. Trends in A) mean winter and summer temperatures, B) winter and summer precipitation, C) annual number of growing degree days with a base of 10 °C, and D) number of frost free days between 1965 and 2006, based on records from Burlington International Airport (BTV).

ing changes to the snow pack could influence understory species compositions and alter seedling establishment rates (Frey 1983).

The results of the NMDS ordination of understory communities revealed that the largest observed changes to species assemblages occurred at elevations near the upper end of the ecotone (Fig. 2 G, H; elevation panels 914 and 975 m) as determined by the length of the change vector in each panel. The least amount of understory community change occurred at the lowest elevations (Fig. 2 A–C; elevation panels 549 to 671 m), while intermediate amounts of change were seen surrounding the upper ecotone (Fig. 2 E, F, I, J; elevation panels 792, 853, 1036 and 1097). In addition to variations in the amount of compositional change that took place across elevations, the nature of the change also differed. In a majority of the elevations examined, current species assemblages were analogous to those found at lower elevations in the past, evidenced by change vectors terminating near

lower elevation contours within NMDS space. However, in the upper ecotone, at elevations 914 m and 975 m, the vectors do not point to lower elevations within the bounds of the isolines, but instead point to NMDS space unoccupied by communities measured in 1965. This indicates that the current species assemblages at these elevations are unlike any observed in 1965 at any elevation.

Overstory communities showed relatively little change in community composition over our study period, particularly in comparison to the changes observed in the understory (Fig. 3). These differences could be due to the long generation times of trees and the resulting demographic inertia. Balsam fir and paper birch for instance can live up to 200 years, while red spruce and sugar maple may live up to 400 years (Burns et al. 1990). The apparent decoupling of understory and overstory community dynamics suggests that climate and other abiotic factors can affect ground-level vegetation independently of the overstory.

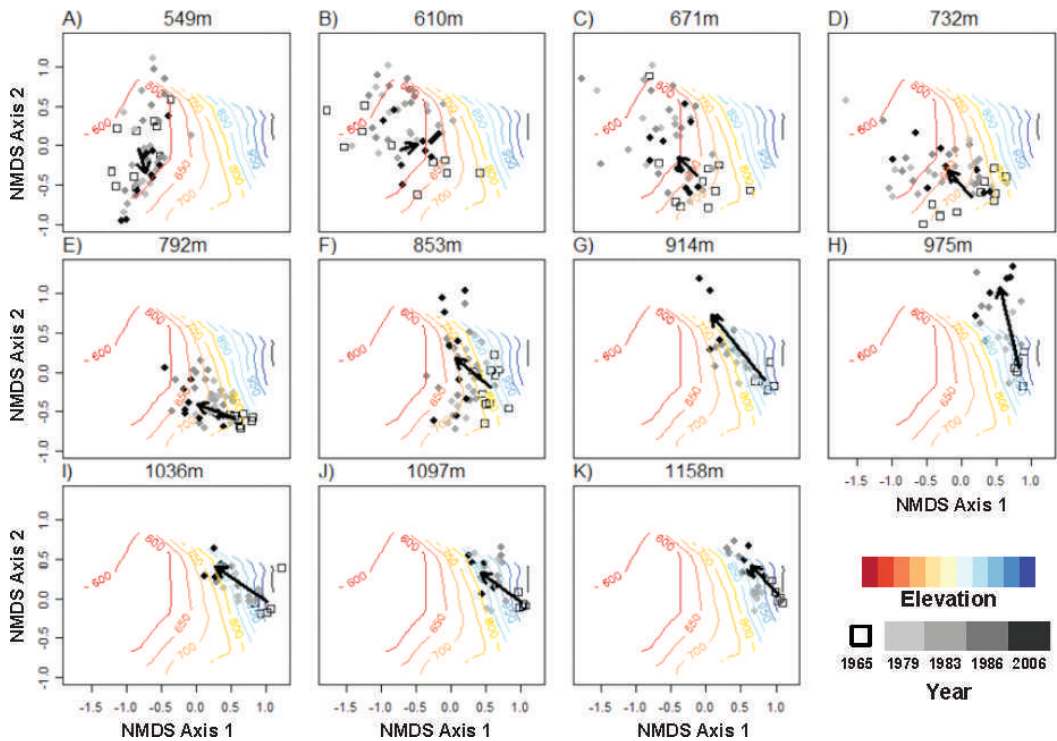


FIG. 2. Changes in understory community composition within NMDS ordination space by elevation. Each point represents an understory community as defined by the average percent cover of each species present in a plot. All point locations are the result of a single ordination. Vectors represent the average magnitude and direction of community shift between 1965 and 2006 within the NMDS ordination space at each of the 11 sampled elevations. Panels A through D represent the northern hardwood forest elevations, panels I through K represent boreal forest elevations, and panels E through H represent ecotonal elevations between the two forest types. Isolines were calculated based on the elevational position of understory communities in 1965. Vectors that indicate a shift from high to low elevation, based on the isolines, represent communities that currently contain species assemblages previously found at lower elevations. For example, a data point representing a community sampled in 2006 at 792 meters (panel E) located close to the 650 m isoline indicates that the species assemblage found at this location is most similar to assemblages found at 650 meters in 1965. Stress: 0.19.

While individual understory species abundances and distributions changed in a variety of ways between 1965 and 2006, most species experienced declining populations (Table 2). Though it would be easy to attribute these changes to differences in cover estimation between researchers, most species exhibiting an overall decline in abundance did so gradually, showing declines between each of the five survey years (Appendix). Despite general reductions in cover, *Aralia* spp., *Cardamine diphylla* Michx., *Mitchella repens* L., *Polystichum acrostichoides* (Michx.) Schott and *Rubus* spp. increased in abundance at the upper limit of their range. Also, most species found exclusively in upper elevations, *Coptis trifolia* (L.) Salisb., *Cornus canadensis* L. and *Monotropa uniflora* L., increased in abundance

within the core of their range and declined at the tails. *Sphagnum* spp. was the only high elevation taxa with more widespread increases. Among the 48 species used in our analyses, only *Arisaema triphyllum* L. increased in abundance across its entire range.

Shifts in NMDS space of individual understory species are also broadly similar, particularly for species at similar elevations (Fig. 4). Species at lower elevations had the largest shifts over the period of this study and these shifts were mostly in a similar direction within NMDS space. The higher elevation species generally had smaller shifts in NMDS space, with slightly less concordance in the direction and magnitude of these shifts across species. The distributions of a few species, however, had markedly different responses (i.e. *Aris-*

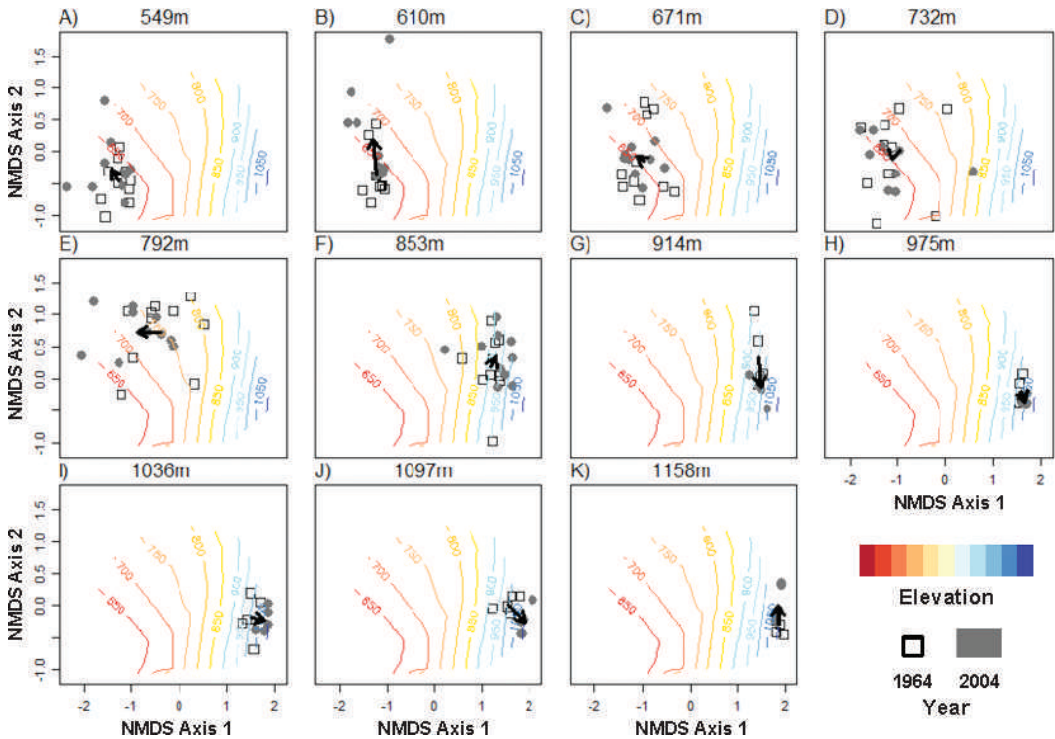


FIG. 3. Change in overstory community composition within NMDS ordination space by elevation. As in Figure 2, all point locations are the result of a single ordination and vectors indicate the canopy compositional change within NMDS ordination space between 1964 and 2004 at each of the 11 sampled elevations. Isolines were again calculated based on the elevational position of communities in 1964. Stress: 0.12.

aema triphyllum and *Cardamine diphylla*). Changes in canopy species distributions do not exhibit any coherent pattern (Fig. 5), again suggesting the decoupling of understory and overstory species.

Discussion. COMMUNITY SHIFTS. We identified changes in understory communities that are consistent with observed regional climate warming and other anthropogenic disturbances over the period of 1965 to 2006. Communities near a climatic threshold along an elevational ecotone are expected to exhibit the most compositional shift in response to climate change, while communities that are further away from these thresholds may exhibit relatively little change (Fig. 6) (Kupfer and Cairns 1996). We found greater compositional change in the uppermost elevations than might be expected with global warming alone (Fig. 7A), but that is consistent with the combined effects of climate change and acid deposition (Fig. 7B). The observed

understory compositional change generally followed a unimodal distribution centered on the upper bound of the ecotone between forest types (Fig. 7C). Previous studies on acid deposition in the northeast confirm that acidification has caused changes to forest ecosystems since the 1960s primarily by decreasing soil pH and leaching away essential nutrients such as calcium (Yanai et al. 1999, Oimet et al. 2006). These effects generally increase with elevation due to higher inputs through precipitation and exposure to acidic cloud moisture (NEG/ECP 2005, Vogelmann et al. 1968, DeHayes et al. 1999, Richardson et al. 2004). While canopy communities were exposed to the same environmental changes in climate and acid deposition as the understory, they did not display the same pattern of compositional change, suggesting that understory species may be more responsive indicators of environmental change and may respond largely independent of the overstory.

Table 2. Trends in percent cover between 1965 and 2006 are shown by elevation for each understory species used in the understory community analysis. "0" indicates no change and "NA" indicates that the species was not found at the given elevation.

	Elevation (m)										
	549	610	671	732	792	853	914	975	1036	1097	1158
<i>Actaea pachypoda</i> ¹	0	—	—	NA	NA	NA	NA	NA	NA	NA	NA
<i>Aralia</i> spp. ²	+	+	+	—	—	—	—	NA	NA	NA	—
<i>Arisaema triphyllum</i> ³	+	+	+	+	NA	+	NA	NA	NA	NA	NA
<i>Aster</i> spp. ⁴	—	—	—	—	—	—	—	—	—	—	+
<i>Athyrium</i> spp. ⁵	—	—	—	—	—	0	NA	NA	NA	NA	NA
<i>Botrychium virginianum</i> ⁶	NA	—	0	—	NA	NA	NA	NA	NA	NA	NA
<i>Cardamine diphylla</i> ⁷	—	NA	+	NA	NA	NA	NA	NA	NA	NA	NA
<i>Caulophyllum thalictroides</i> ⁸	—	—	—	+	NA	0	NA	NA	NA	NA	NA
<i>Clintonia borealis</i> ⁹	+	—	—	—	—	—	—	—	—	—	—
<i>Coptis trifolia</i> ¹⁰	NA	NA	NA	NA	NA	—	+	+	+	—	—
<i>Cornus alternifolia</i> ¹¹	+	—	+	—	NA	NA	NA	NA	NA	NA	NA
<i>Cornus canadensis</i> ¹²	NA	NA	NA	NA	NA	NA	—	+	—	—	—
<i>Cyperaceae</i> ¹³	—	—	—	—	—	—	—	0	+	—	—
<i>Dennstaedtia punctilobula</i> ¹⁴	—	+	—	—	+	—	—	—	0	NA	NA
<i>Dryopteris</i> spp. ¹⁵	+	—	—	—	—	—	—	—	—	—	—
<i>Galium</i> spp. ¹⁶	—	+	—	0	—	NA	NA	NA	NA	NA	NA
<i>Huperzia</i> spp. ¹⁷	+	—	—	—	—	—	—	—	—	+	—
<i>Hydrophyllum virginianum</i> ¹⁸	—	—	—	—	NA	NA	NA	NA	NA	NA	NA
<i>Impatiens capensis</i> ¹⁹	—	—	—	—	—	NA	NA	NA	NA	NA	NA
<i>Laportea canadensis</i> ²⁰	—	—	—	—	NA	NA	NA	NA	NA	NA	NA
<i>Lonicera canadensis</i> ²¹	0	0	0	0	—	NA	NA	NA	NA	NA	NA
<i>Maianthemum canadense</i> ²²	—	—	—	—	—	—	+	0	NA	—	+
<i>Maianthemum racemosum</i> ²³	—	—	—	—	0	NA	NA	NA	NA	NA	NA
<i>Medeola virginiana</i> ²⁴	—	NA	0	NA	NA	NA	NA	NA	0	NA	NA
<i>Mitchella repens</i> ²⁵	+	NA	+	—	NA	+	NA	NA	NA	NA	NA
<i>Monotropa uniflora</i> ²⁶	NA	NA	0	NA	0	—	+	+	0	0	NA
Moss ²⁷	+	+	—	—	—	—	—	+	+	—	—
<i>Osmorhiza claytonia</i> ²⁸	—	—	—	—	NA	NA	—	NA	NA	NA	NA
<i>Oxalis</i> spp. ²⁹	—	—	—	—	—	—	—	—	—	—	—
<i>Poaceae</i> ³⁰	—	—	—	—	—	—	NA	0	+	NA	NA
<i>Polystichum acrostichoides</i> ³¹	—	—	—	+	NA	NA	NA	NA	NA	NA	NA
<i>Prenanthes altissima</i> ³²	—	—	—	+	—	NA	NA	NA	NA	NA	NA
<i>Ribes</i> spp. ³³	NA	—	—	—	+	—	—	—	—	—	—
<i>Rubus</i> spp. ³⁴	—	+	—	—	—	+	NA	NA	NA	NA	NA
<i>Sambucus</i> spp. ³⁵	—	—	—	—	—	NA	0	NA	NA	NA	NA
<i>Solidago</i> spp. ³⁶	0	—	—	—	—	—	NA	NA	NA	—	—
<i>Sphagnum</i> spp. ³⁷	NA	NA	NA	NA	NA	+	+	+	+	—	+
<i>Streptopus</i> spp. ³⁸	—	—	—	—	—	+	0	0	NA	NA	NA
<i>Phegopteris connectilis</i> ³⁹	+	0	—	0	+	—	—	—	—	—	NA
<i>Thalictrum pubescens</i> ⁴⁰	+	+	+	0	NA	NA	NA	NA	NA	NA	NA
<i>Thelypteris noveboracensis</i> ⁴¹	—	0	—	—	—	0	0	NA	NA	NA	NA
<i>Tiarella cordifolia</i> ⁴²	—	—	—	—	—	NA	NA	NA	NA	NA	NA
<i>Trientalis borealis</i> ⁴³	+	NA	—	0	NA	NA	NA	+	0	—	—
<i>Trillium</i> spp. ⁴⁴	—	—	—	—	—	—	NA	NA	NA	NA	NA
<i>Uvularia sessilifolia</i> ⁴⁵	—	—	0	0	0	NA	NA	NA	NA	NA	NA
<i>Veratrum viride</i> ⁴⁶	NA	—	+	+	—	NA	NA	NA	NA	NA	NA
<i>Viburnum lantanoides</i> ⁴⁷	+	+	—	—	—	—	—	0	0	NA	NA
<i>Viola</i> spp. ⁴⁸	—	—	—	—	—	—	NA	NA	NA	NA	NA

The direction and magnitude of compositional change across elevations can help determine whether species are shifting as intact communities or as individuals. As expected given our conceptual model (e.g., Figs. 6 and 7), understory communities in the lowest of our studied elevations changed relatively little over the study period. Understory communi-

ties in both the lower ecotone and in our highest elevation sites changed more substantially than at low elevations, as illustrated by the change vectors in Fig. 2. The change vectors of these communities point more consistently toward lower elevation isolines, and stay within the bounds of the isolines, supporting the shared response hypothesis

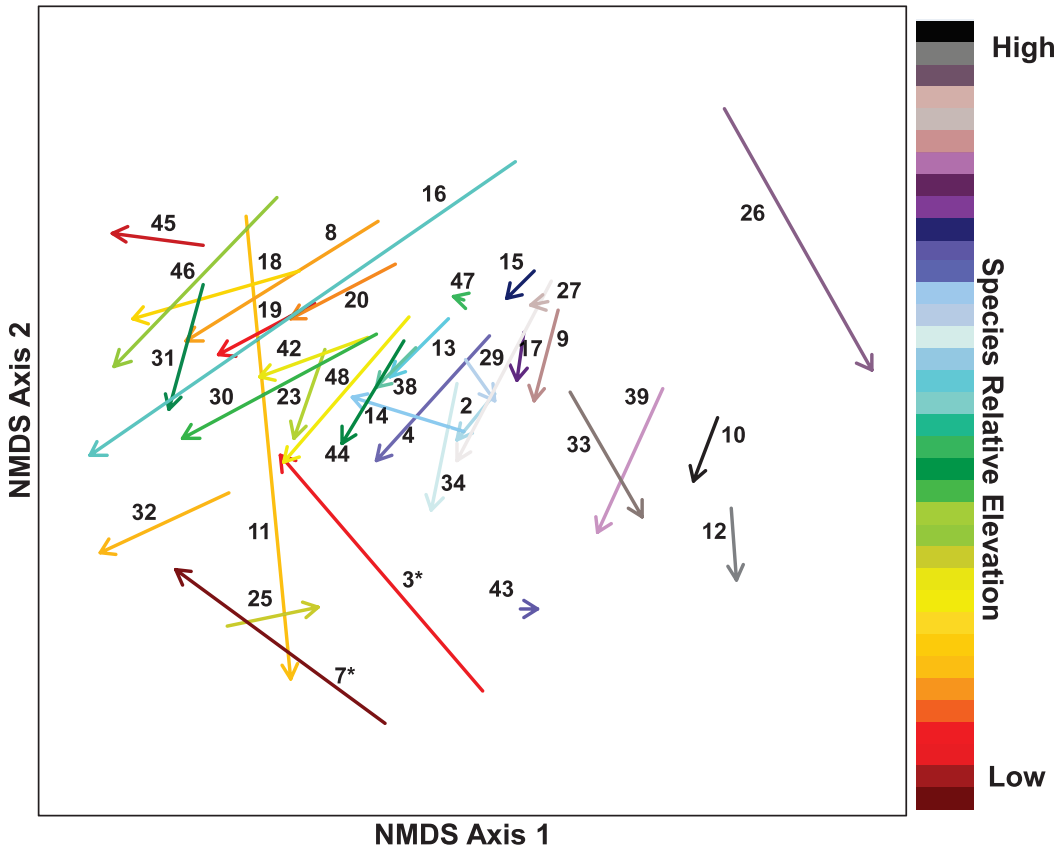


FIG. 4. Changes in the elevational distribution of understory species within NMDS ordination space from 1965 to 2006. Each vector connects the location of species in their initial survey year to their location in the most recent survey, indicating overall change. The color of the points in this case does not correspond to a specific elevation, but instead conveys the rank-order of species from low (red) to high elevations (black) based on their average elevation. The numbers identifying each vector correspond to the superscripts assigned to each species in Table 2. The asterisks (*) in the figure denote the understory species *Arisaema triphyllum* and *Cardamine diphylla* that exhibit a shift that contrasts with other low elevation species. Stress: 0.25.

(SRH). In contrast, species assemblages currently found in the upper ecotone sites (i.e., 914 and 975 m) likely represent communities that have no prior analog in our 1965 vegetation surveys and seem to be the result of the gradual loss of *Dennstaedtia punctilobula* (Michx.) Moore and *Ribes* spp. along with the addition of *Aralia* spp., *Trientalis borealis* Raf., *Maianthemum canadense* and *Viburnum lantanoides* Michx. among others. The emergence of these novel communities in the upper ecotone indicates the independent shift of some species at these elevations, in contrast to the dominant trend across elevations of similar species responses to recent climatic and environmental change. This places these montane forests much closer to

the SRH end of the shared/individualistic response continuum.

SPECIES SHIFTS. Understory species shifts across all elevations were relatively similar within NMDS space (Fig. 4). This corroborates evidence from the community analyses and provides further support for a largely shared response of species to climate change. The degree of coherence of species shifts, however, appeared to vary with elevation. Lower elevation species had similar directional shifts but exhibited a wide range of magnitudes. Mid-elevation species had less directional coherence as they likely responded to both climate change and acid deposition. With the exception of *Monotropa uniflora* L., most

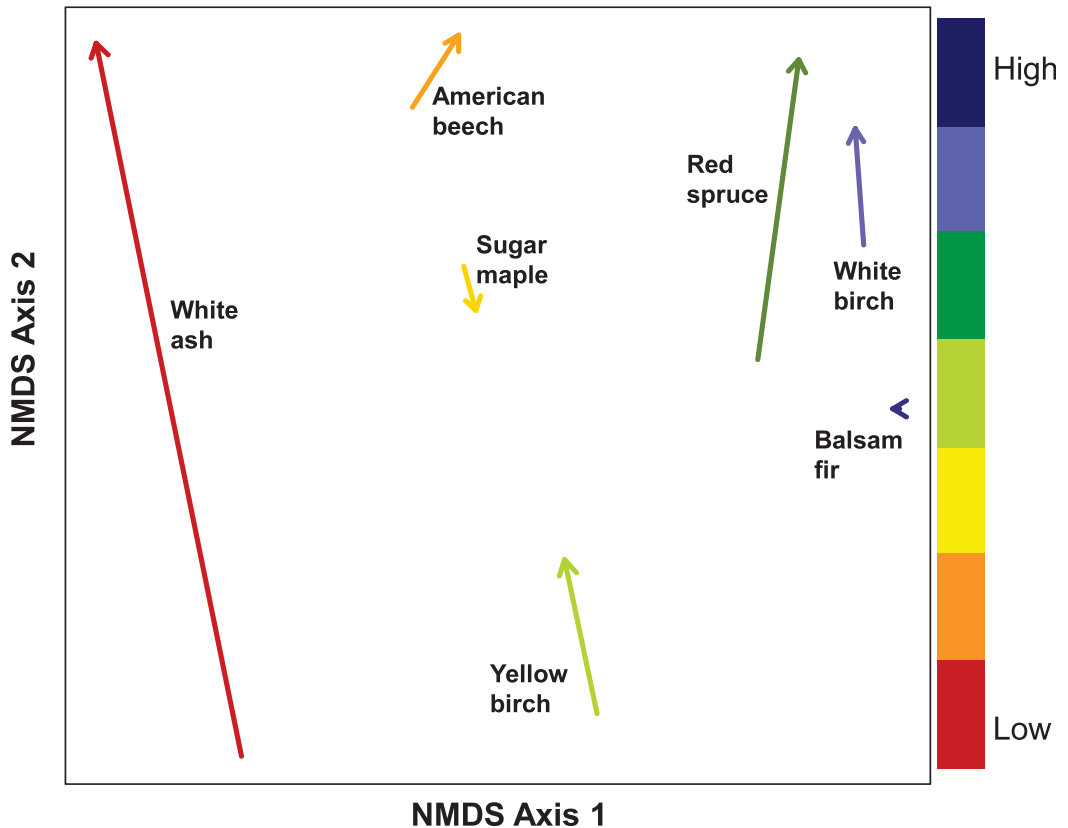


FIG. 5. Changes in the elevational distribution of overstory species from 1964 to 2004. Vectors indicate change as in Figure 4 and colors represent elevation from low (red) to high (blue). Stress: 0.07.

of the co-occurring species at high elevations had comparatively small shifts. *Monotropa uniflora* is a non-photosynthetic plant which tends to be short lived, weather-dependent, and easily missed in surveys done at different times during the growing season. This could lead to its unique response within NMDS space (Fig. 4). In general, the resulting shift of many understory species in NMDS space is the result of complex responses that included, for example, changes in frequency internal to their elevational range, as well as shifts both upward and downward in elevation, suggesting the importance of other biotic or abiotic controls (Table 2).

We also see evidence suggesting that both climatic and non-climatic factors have impacted species distributions. For instance, *Aralia* spp., *Cardamine diphylla*, *Mitchella repens*, *Polystichum acrostichoides* and *Rubus* spp. increased in abundance at the upper limit of their ranges, while some boreal species such as *Coptis trifolia* and *Cornus canadensis*, declined

at their lower elevational limits which is consistent with expectations under increasing temperatures (Table 2). Two understory species that have likely responded to non-climatic controls are *Arisaema triphyllum* (Jack-in-the-Pulpit) and *Cardamine diphylla* (Toothwort). Both of these species exhibit unusual patterns of change in NMDS space (Fig. 4). Studies in northern forests have shown that both *A. triphyllum* and *C. diphylla* are abundant in sites with high densities of non-native earthworms (Corio et al. 2009). *Arisaema triphyllum* has been shown to increase in abundance in response to earthworm invasions, although similar studies have not been done for *C. diphylla* (Bohlen et al. 2004, Hale et al. 2006). The responses of these two species in our study is consistent with our observations of non-native earthworms at low to medium densities ($\sim 50\text{--}100$ worms m^{-3}) in sites up to at least 700 m in elevation. Earthworm invasion has been shown to cause changes in forest herb communities by facilitating the mixing of soil

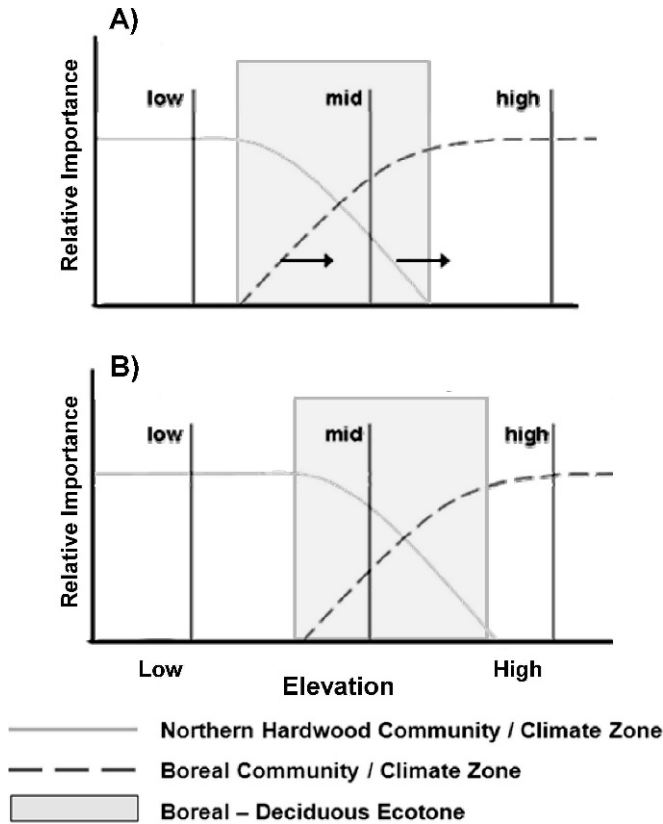


FIG. 6. A conceptual representation of community change in response to warming temperatures between northern hardwood and boreal species at three elevations (low, mid, and high). A) The relative importance of community types and climate zones before any warming has occurred. The height of the curves represents the relative importance or performance of each community type at a given elevation. B) The abundance of community types and the location of climate zones following warming at the same three elevations. Note that the relative competitive advantage of the northern hardwood species has surpassed that of the boreal species at the mid elevation, suggesting that the greatest change in species composition should occur within the ecotone compared to higher or lower elevations.

layers, altering nutrient cycling rates and disrupting belowground microbial communities (Bohlen et al. 2004, Hale et al. 2006).

While support for both the shared and the individual response hypotheses is found in the literature (Bruno et al. 2003, Williams and Jackson 2007), the degree of coherence likely depends on both the environmental driver (e.g., climate change, acid deposition, biological invasion, or a combination of these) and the magnitude of the change in the driver. We might not, for example, expect a coherent response across species within a community to a perturbation such as acid deposition in the absence of a strong alkalinity gradient, whereas we might *a priori* expect a more coherent response to climate change in the presence of a strong temperature gradient (i.e., elevation).

We also suggest that the degree of coherence in species shifts in response to climate, for example, should vary with the magnitude of climate change. The responses of most species to climate change are likely to be nonlinear (reflecting climatic thresholds) over broad temperature and precipitation ranges, but their shifts might appear linear in response to small climatic perturbations. This could result in a high coherence across species in response to moderate changes in climate, but an increasing divergence of species across larger changes in climate, particularly as multiple climatic components (i.e. temperature, precipitation, frost free period) may change independently in a complex manner (e.g., precipitation may increase or decrease with temperature and plant available water further depends on the

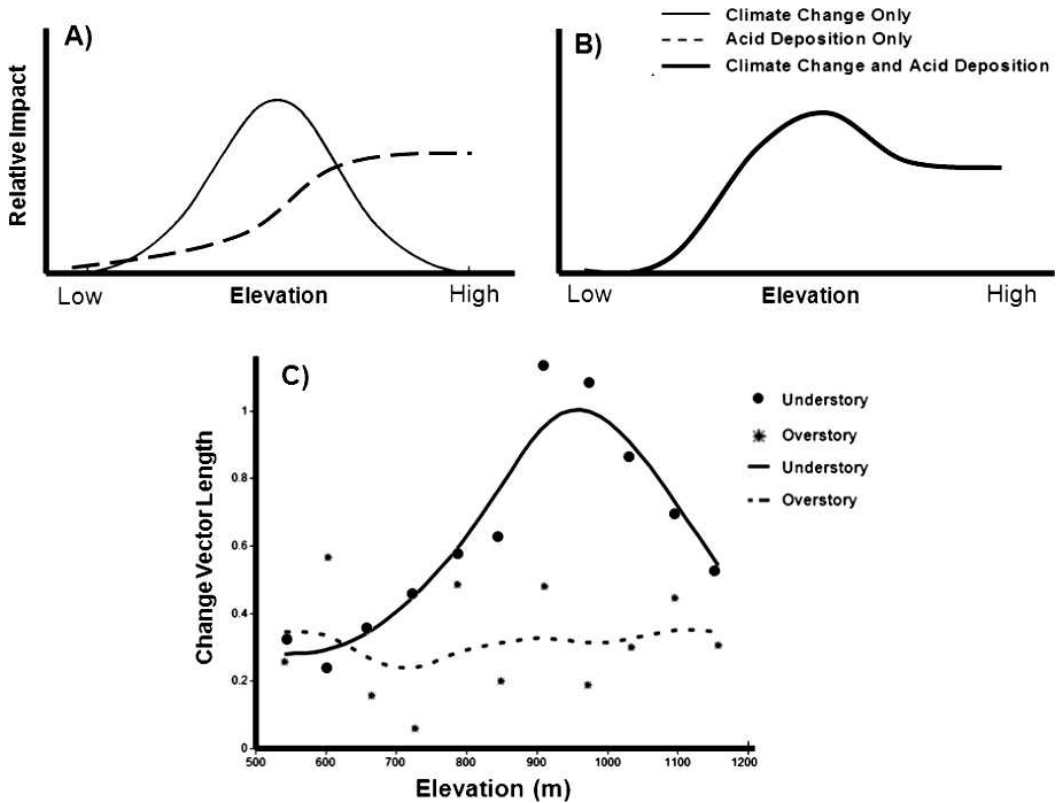


FIG. 7. The expected impacts of climate change and acid deposition on community composition. A) The expected relative contributions of climate change and acid deposition on plant community compositional change across our elevational gradient. B) The combined impact of climate change and acid deposition on plant community compositional change across our elevational gradient. C) Arrow lengths for over- and understory communities indicating the average change in community composition at each sample elevation. Trends in arrow lengths across elevations were smoothed with a cubic spline. $\lambda = 0.05$.

rate of these changes). As the magnitude of climate change increases, we might expect that species would diverge in their responses to climate change, reflecting species-specific threshold responses to different components of climate change with the potential for novel ecological community formation. The question of individualistic versus shared responses of species within communities might thus depend on the magnitude of climate change, accommodating evidence of novel communities associated with large climate shifts (e.g., Williams and Jackson 2007) while being consistent with shifts of intact communities with more modest climate change. The divergence of species' responses to climate change are also likely to be increased by the concurrent occurrence of other anthropogenic perturbations such as acid deposition and biological invasions, as these disturbances are likely

to introduce additional species-specific thresholds.

We expect the rate of species shifts to remain constant or accelerate over the next century. The changes we observed in the overstory and understory vegetation resulted from an increase in annual mean temperature of less than 2 °C, while regional climate models predict that the northeastern US can expect an additional 2.9 to 5.3 °C increase in average annual temperature by 2100 with associated increases of 6.4 to 11.4% in precipitation (Hayhoe et al. 2007, Tang and Beckage 2010). This amount of climate change is likely to have a large impact on future species distributions, resulting in increasingly divergent responses among co-occurring species with the potential for the formation of novel communities. Responses of vegetation to recent climate change may therefore not be

indicative of future responses as climate thresholds for individual species are reached. Interactions between climatic changes and other anthropogenic stressors, such as airborne pollution, land use changes, and the spread of exotic organisms, are likely to exacerbate rates of change and the potential for localized extirpations, rendering future projections of vegetation change uncertain (Aber 2001), and increasing the potential for ecological surprises or state shifts (e.g., Paine et al. 1998, Platt et al. 2002, Beckage and Ellingwood 2008).

Conclusion. We examined understory species shifts across an elevational gradient in response to 40 years of regional climatic and environmental change. The pattern of observed responses indicates that species are responding to multiple anthropogenic perturbations in a complex manner with relatively similar species responses at some elevations, while at others, species respond more individually. We suggest, however, that due to nonlinear responses to species-specific climatic thresholds, communities will become increasingly divergent as the magnitude of climate change increases. Anthropogenic acid deposition and invasive earthworms, in conjunction with climate change, may have contributed to individual species responses and community shifts at affected elevations. The increasing magnitude of climate change together with interactions with other anthropogenic perturbations such as acid deposition and the spread of invasive organisms may cause rapid changes in species distributions and the formation of novel plant assemblages as the responses of species within communities diverge.

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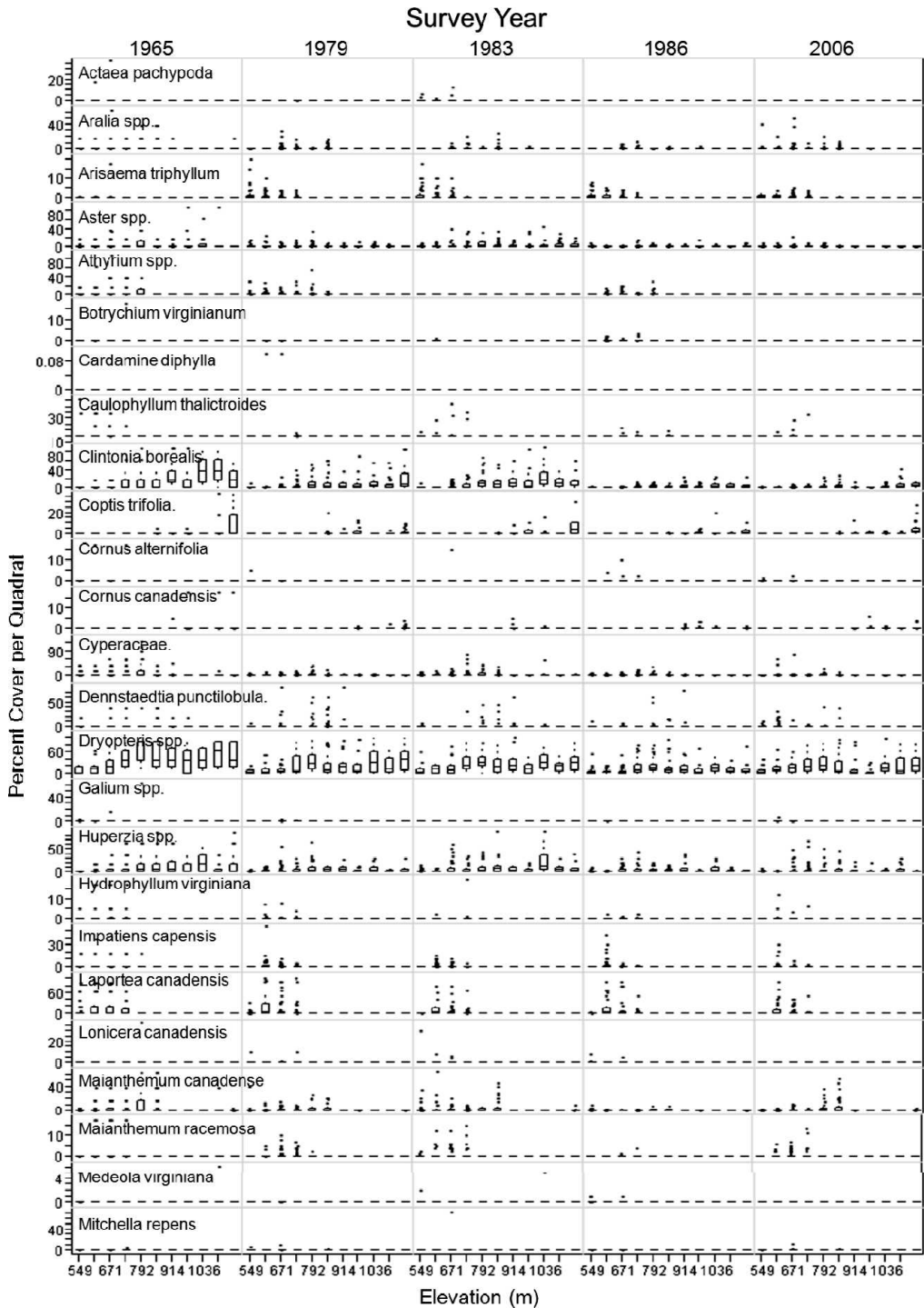
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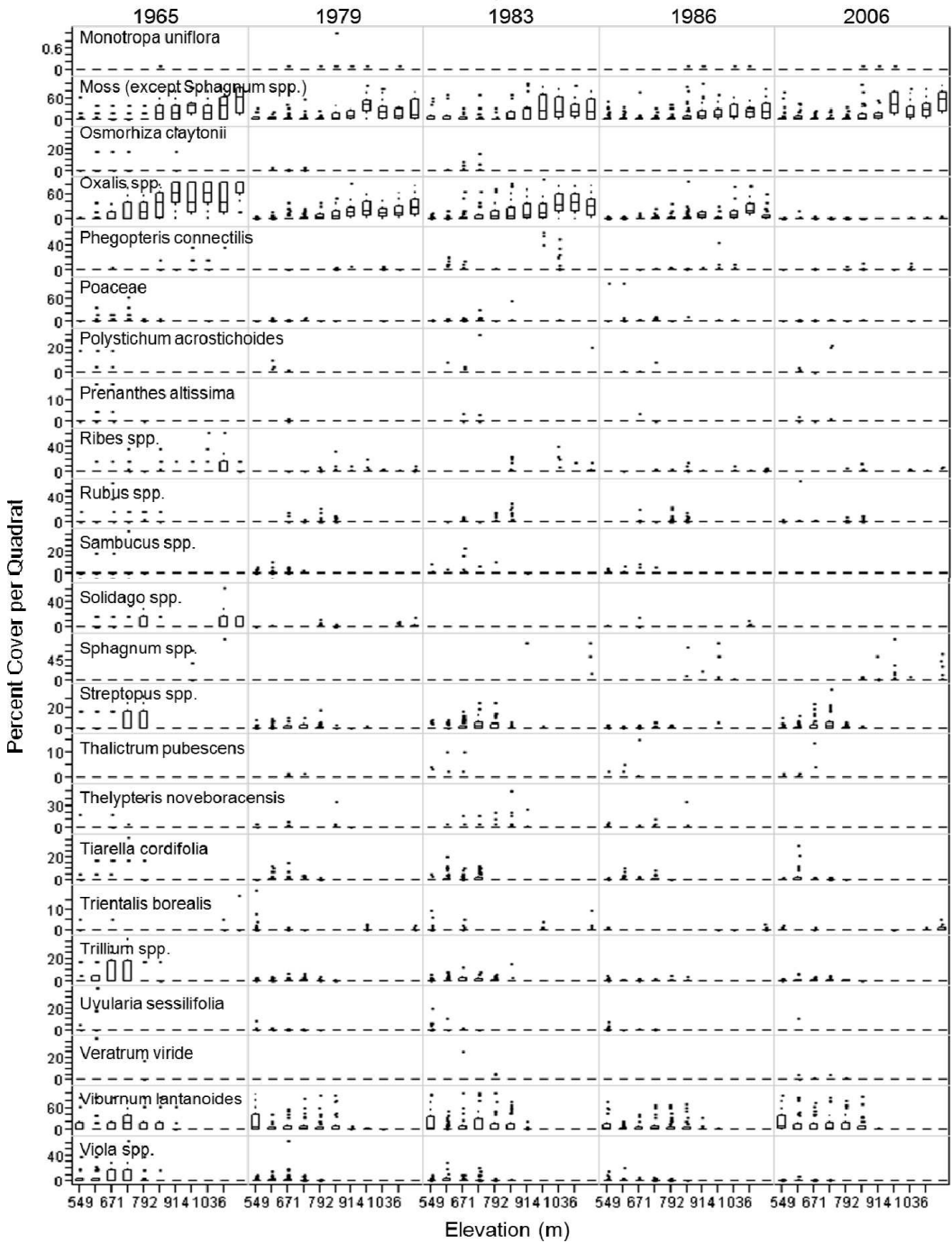
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Appendix 1:

Boxplots of the percent cover of each species in each of the five survey years across the entire elevational range. While this figure does show changes over time in the relative abundances of species, it is important to note that the scaling of the y-axis varies across species.



Survey Year



Appendix 2:

Arrow lengths as seen in the NMDS community analyses (Figures 2 and 3). These arrow lengths represent the magnitude of total compositional change in communities between 1965 and 2006 at each elevation.

Elevation (m)	Understory Arrow Length	Canopy Arrow Length
549	0.3295	0.2584
610	0.2374	0.5644
671	0.3565	0.1578
732	0.4598	0.0623
792	0.5734	0.4829
853	0.6204	0.202
914	1.1255	0.4785
975	1.0705	0.1904
1036	0.8517	0.2993
1097	0.7026	0.4437
1158	0.5243	0.3055

Appendix 3:

Changes in the elevational distribution of understory species within NMDS ordination space from 1965 to 2006. Each vector connects the location of species in their initial survey year to their location in the most recent survey, indicating overall change. Other points represent species in 1978, 1983 and 1986. The color of the points and vectors in this case does not correspond to a specific elevation, but instead conveys the rank-order of species from low (red) to high elevations (black) based on their average elevation. The numbers identifying each vector correspond to the superscripts assigned to each species in Table 2. The asterisks in the figure denote the understory species *Arisaema triphyllum* and *Cardamine diphylla* that exhibit a shift that contrasts with other low elevation species and may be indicative of establishment of invasive earthworms.

