



EDITOR'S
CHOICE

Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming

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Many species show evidence of climate-driven distribution shifts towards higher elevations, but given the tremendous variation among species and regions, we lack an understanding of the community-level consequences of such shifts. Here we test for signatures of climate warming impacts using a repeat survey of semi-permanent vegetation plots in 1970 and 2012 in a montane protected area in southern Québec, Canada, where daily maximum and minimum temperatures have increased by $\sim 1.6^{\circ}\text{C}$ and $\sim 2.5^{\circ}\text{C}$ over the same time period. As predicted, the abundance-weighted mean elevations of species distributions increased significantly over time (9 m/decade). A community temperature index (CTI) was calculated as the abundance-weighted mean of the median temperature across occurrences within each species geographic range in eastern North America. CTI did not vary significantly over time, although the raw magnitude of change ($+0.2^{\circ}\text{C}$) matched the expectation based on the upward shift in distributions of 9 m/decade. Species composition of high elevation sites converged over time toward that observed at low elevation, although compositional changes at low elevation sites were more modest. As a consequence, the results of a multivariate analysis showed a decline in among-plot compositional variability (i.e. beta diversity) over time, thus providing some of the first empirical evidence linking climate warming with biotic homogenization. Finally, plot-scale species richness showed a marked increase of $\sim 25\%$ on average. Overall, elevational distribution shifts, biodiversity change, and biotic homogenization over the past four decades have been consistent with predictions based on climate warming, although the rate of change has been relatively slow, suggesting substantial time lags in biotic responses to climate change.

Climate warming over the past century appears to have prompted poleward and upward-elevational distribution shifts in many species (Parmesan and Yohe 2003, Chen et al. 2011). However, the magnitude and even the direction of such shifts vary tremendously among species and regions (Cannone et al. 2007, Chen et al. 2011, Crimmins et al. 2011, Feeley et al. 2011, Freeman and Class Freeman 2014, Rehm 2014), and the geographic representation of existing studies is quite sparse (Feeley et al. 2011). For example, the global meta-analysis of Chen et al. (2011) included just one study in all of eastern North America for elevational distribution shifts in plants (Beckage et al. 2008). In addition, great uncertainty remains concerning the presence and magnitude of time lags in biotic responses to climate change (Beckage et al. 2008, Bertrand et al. 2011, Corlett and Westcott 2013, Vellend et al. 2013b), and the associated consequences for patterns of biodiversity (Pauli et al. 2012, Vellend et al. 2013a). Opportunities for assessing long-term community change provided by georeferenced historical biodiversity surveys are relatively rare and must be exploited in order to test hypotheses concerning the long-term consequences of environmental change (Dornelas et al. 2013, Vellend et al. 2013b).

Time lags in biotic responses to environmental change are typically inferred by comparing the magnitude of observed

changes (e.g. meters of elevational distribution shift) with expectations based on the magnitude of environmental change itself over the same time period (e.g. meters of elevational shift in isotherms) (Bertrand et al. 2011, Devictor et al. 2012, Feeley et al. 2013). Many studies have reported both substantial lags in response to climate warming, for example with observed changes $< 50\%$ of those expected (Davis 1986, Bertrand et al. 2011, Devictor et al. 2012), as well as a fairly close match between observed and expected ecological changes. For example, Beckage et al. (2008) suggested that the deciduous-boreal ecotone in mountains of northeastern North America had shifted upward in elevations more or less in concert with regional climate warming. It is unclear whether this apparent rapid ecological tracking of climate change applies more broadly to the full suite of plants in these systems.

Studies in which long-term vegetation change has been attributed to climate warming have found both increases and decreases in local plant species richness (Damschen et al. 2010, Danby et al. 2011, Vellend et al. 2013a). With high elevations typically characterized by relatively low richness, increased richness is expected, although a priori expectations for lower elevations are more difficult to derive. Although many studies have explored changes in alpha diversity in

response to climate, we know of no studies to date that have directly addressed the consequences of climate warming for beta diversity. However, previous studies suggest that the ecological consequences of climate warming might be most pronounced at high elevation (Bertrand et al. 2011), due to factors such as colonisations at high elevation outpacing extinctions at low elevation, or differences across elevation in species persistence via short distance dispersal to suitable topographic microclimates (Jump et al. 2009, Scherrer and Körner 2010, Bertrand et al. 2011). Regardless of underlying mechanisms, the pattern of greater community change at high elevation leads to a clear prediction of a decline in beta diversity over time (i.e. biotic homogenization). That is, if high elevation sites shift towards a community composition typical of low elevations faster than corresponding changes at low elevations, the ecological gradient should effectively 'shrink'. Here we present one of the first explicit tests of this prediction.

In this paper, we report vegetation changes observed over ~40 yr in Parc national du Mont Mégantic in southern Québec, Canada, where vegetation ranges from northern hardwood forests dominated by sugar maple *Acer saccharum* at low elevation (~450 m a.s.l.) to spruce-fir boreal forest at high elevation (up to ~1100 m) (Marcotte and Grandtner 1974). Temperature has increased ~2°C in this region over the past 40 yr (Fig. 1), and our primary objective was to test for the predicted ecological impacts of such warming: 1) upward elevational shifts in species distributions; 2) local shifts in community composition favouring warm-adapted species; 3) a decrease in beta diversity due to an asymmetric 'shrinking' of the elevational gradient. We also tested for temporal changes in local species richness and assessed time lags in vegetation responses by quantifying expected changes based on observed climate warming.

Material and methods

Study site

Parc national du Mont-Mégantic is a 54.9 km² protected area in southern Québec, Canada with a mix of northern hardwood and boreal forest stands. Between 1970 and 2012, the mean daily maximum temperature in the surrounding region increased 1.6°C, the mean daily minimum increased 2.5°C, while there has been no temporal trend in precipitation (Fig. 1). Historical disturbances in the park include spruce budworm outbreaks (1974–1984), ice storm damage (1998) and logging in some areas prior to 1970 (Parc National du Mont-Mégantic 2007).

The vegetation of Mont-Mégantic was surveyed in 1970 in 94 plots of 400 m² (coniferous forests) or 800 m² (deciduous forests) distributed over the entirety of the current park (48 plots, 24 deciduous + 24 coniferous) as well as surrounding areas up to several km outside the current park boundary (46 plots) (Marcotte and Grandtner 1974). Marcotte and Grandtner (1974) followed traditional phytosociological methods aimed at classifying naturally occurring vegetation types; as such, we assume they focused their surveys on mature forests, avoiding major recent disturbances such as logging (C. Anseau, Univ. de Sherbrooke pers. comm.). We include here one test for a possible signature of successional dynamics.

Data collection in contemporary surveys

The historical plots were not permanently marked, but their locations are shown quite precisely on a 1:50 000 map (Supplementary material Appendix 1, Fig. A1), and as such are considered 'semi-permanent' (Persson 1980).

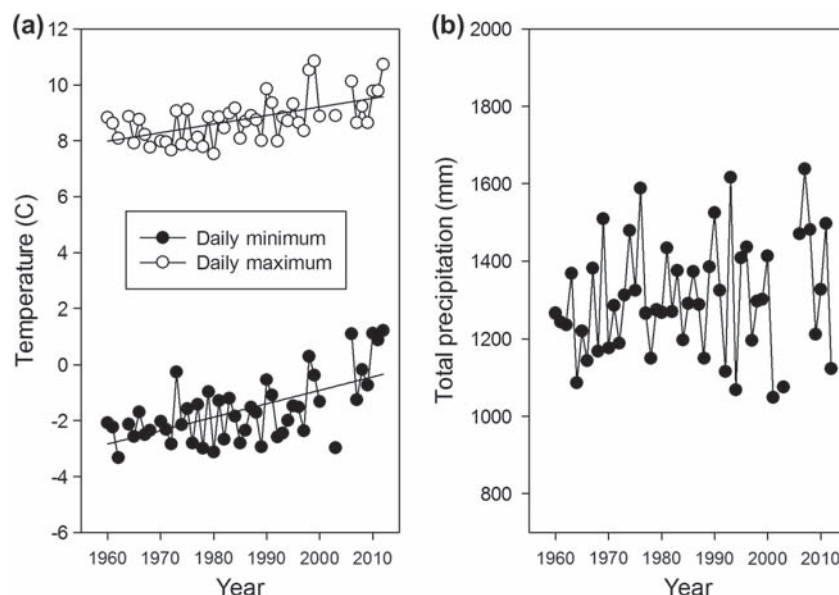


Figure 1. Trends in (a) mean maximum and minimum temperatures (across all days of the year), and (b) total annual precipitation measured at a government weather station in Milan, Québec, located 15 km north of Mont-Mégantic. Straight lines show least-squared linear regressions: maximum temperature = $0.04 \times \text{year} - 73.4$, $p < 0.001$, $r^2 = 0.33$; minimum temperature = $0.06 \times \text{year} - 116.9$, $p < 0.001$, $r^2 = 0.37$; precipitation = $0.3 \times \text{year} + 1893$, $p = 0.68$, $r^2 = 0.003$. Data used with permission: © Gouvernement du Québec, ministère du Développement durable de l'Environnement de la Faune et des Parcs, 2013.

Resurveying semi-permanent plots is a widespread and well-established method for quantifying temporal community change (Damschen et al. 2010, Harrison et al. 2010, De Frenne et al. 2013, Johnson et al. 2013, McCune and Vellend 2013, Vellend et al. 2013b): when the same protocol used for sampling initial plots is followed as closely as possible, and if fine-scale plot maps allow minimization of relocation errors, such studies can reliably characterize temporal vegetation changes (Chytrý et al. 2014). We established tentative plot locations by first georeferencing the plot-location map using ArcGIS ver. 10.1. Plot coordinates were then used with site descriptions (slope, aspect, dominant trees) to determine the placement of our plots, likely within 30 m of the original locations. Given that the plots are semi-permanent, we make inferences based on tendencies across the full set of plots (which cover the exact same range of all environmental conditions in the two time periods), rather than changes in individual plots. While imperfect accuracy in plot relocation can represent a source of variance in the data (thereby reducing power to detect temporal change), there was no systematic bias in plot relocation that would favour finding any particular direction of vegetation change.

We re-surveyed the vegetation in the 48 plots inside the park between May and August 2012; the abundances of vascular plant species in the herbaceous, shrub and tree strata were recorded using Braun-Blanquet cover classes. These plots are distributed across the entire elevational gradient, from ~450–1100 m elevation, and on a variety of aspects. The surrounding landscape consists of the Appalachian Mountains to the south and east, and rolling hills varying between ~400–500 m elevation to the north and west (Marcotte and Grandtner 1974). We standardized plant nomenclature across past and contemporary data sets using the Taxonomic Name Resolution Service (TNRS, <<http://tnrs.iplantcollaborative.org>>), and combined taxa at the level of genus when the accuracy of species identifications was in doubt in either time period (e.g. *Carex* spp. did not include any of the *Carex* species identified to the species level). Some species such as spring ephemerals and *Botrychium matricariifolium* were excluded from analyses because of likely detection issues in either 1970 or 2012. Tree seedlings were excluded from all analyses due to massive yearly fluctuations in abundance. The final data set included 145 taxa (Supplementary material Appendix 1, Table A1).

Species and community indices for temperature, light and moisture

In order to test the hypothesis of climate-warming impacts, for each species we calculated a species temperature index (STI) as the median annual temperature across the species range, by combining climate and occurrence data (Devictor et al. 2012, Feeley et al. 2013). Specifically, we overlaid interpolated climate data (mean annual temperature averages from 1950–2000 at a spatial resolution of 1 km²) (Hijmans et al. 2005), and occurrence data in eastern North America (Global Biodiversity Information Facility (GBIF) Data Portal 2009, <<http://data.gbif.org>>) for all species found on Mont-Mégantic in either the past or contemporary surveys. We retained only species with at least 100 occurrence records for analysis

(4 species excluded). The temperature for each occurrence was extracted, and the median of these temperature values, the STI, was taken as an index of a species' association with temperature. We also calculated the 10th and 90th percentiles of the temperature distributions, and found that they were highly inter-correlated ($r > 0.95$); therefore the results should be robust to different possible choices at this stage. Community temperature indices (CTI) were then calculated for each plot as the mean of the STI values weighted by the abundances of the species present in that plot. The analysis of CTI is complementary to the analysis of elevational distribution shifts in that it incorporates some of the same data (plot-level species abundances) but also independent data on broad-scale geographic distributions. The CTI analysis is also directly comparable to the analyses of species-level associations with other environmental variables, as described in the next paragraph.

We compiled data on other species characteristics to test whether vegetation changes had occurred as predicted if post-disturbance succession or moisture stress (via warming) were important drivers of temporal community change. As indices of species light (SLI) and species moisture (SMI) affinities, we obtained two traits – light regime and water preference – from the TOPIC (Traits of Plants in Canada) database (Aubin et al. 2007). SLI values were 0 for shade tolerant, 1 for mid-tolerant and 2 for shade intolerant species; SMI values ranged from 0 for species associated with dry habitats up to 5 for species associated with moist habitats (Supplementary material Appendix 1). For CTI, CLI and CMI calculations, we used taxa that included multiple species (due to identification uncertainty) only if the individual species values covered < 20 % of the range of values across species. For example, *Ribes glandulosum* and *Ribes triste* were grouped together for STI since their values differed by only 0.2°C, compared to a range of 4–12°C across all species. The number of taxa for which we made these calculations was 123 for STI, 132 for SLI and 129 for SMI. CLI (community light index) and CMI (community moisture index) were calculated as for CTI.

Statistical analyses

All analyses were conducted separately for understory species (herbs and shrubs), for canopy trees, and for all species pooled together. Given their shorter life cycles, one might expect more rapid temporal change for understory species, although many understory species can be quite long lived. All cover values for the 1970 and 2012 data were transformed to the percent cover midpoints of the Braun-Blanquet cover scale; for tree species, we used the maximum of the cover between the upper and lower canopy layers, which were estimated separately in the raw data.

We tested for an increase in the mean elevation of species distributions by calculating the abundance-weighted mean elevation across occurrences of each species in 1970 and in 2012, and then a paired t-test for a difference across time. Only species that were present in at least 4 plots in both time periods were used in this analysis (58 species). We tested for an increase over time in plot-level CTI using linear mixed-effects models including effects of elevation, year and the

year \times elevation interaction (total of 5 models). The approximate normality of residuals was verified, plot identity was used as a random factor to account for the paired nature of the plots over time, and model selection was based on AIC. The same analyses were conducted for CLI and CMI.

We tested for temporal change in species richness (the number of species per plot), plot species composition and homogeneity in multivariate space. A change in species richness over time was assessed using a mixed-effects model including effects of elevation, year and the year \times elevation interaction. Plot size was included in all candidate models to account for the difference between coniferous and deciduous forests and plot identity was used as a random factor to account for the paired nature of the plots over time. To test for a significant shift in species composition over time, we used permutational MANOVA, or PERMANOVA (Anderson et al. 2008) with year of survey as a fixed variable and plot identity as a random variable. Finally, to test for possible biotic homogenization (or differentiation), we tested for a change in beta diversity across all plots between the two years. Here we used a distance-based test for homogeneity of multivariate dispersions (PERMDISP; Anderson et al. 2008). To visualize any shifts in composition or changes in dispersion, we used nonmetric multidimensional scaling (NMDS) ordination. We used the Bray–Curtis dissimilarity metric for multivariate analyses (Legendre and Legendre 2012).

PERMANOVA and PERMDISP were carried out using PRIMER ver. 6 with PERMANOVA+ (Anderson et al. 2008). All other analyses were carried out in R ver. 2.4.1.5, using the ‘extract’ function of the ‘dismo’ package for STI calculations, the ‘metaMDS’ function of the ‘vegan’ package for NMDS, the ‘functcomp’ function of the ‘FD’ package for CTI calculations, and the ‘lme4’ package for linear mixed models (R Core Development Team).

Results

Distributional shifts

The mean abundance-weighted elevation of species’ distributions increased significantly between 1970 and 2012 (Fig. 2). Mean upward elevations shifts were 37.2 ± 8.4 m for understory species ($n = 45$, $t = 4.4$, $p < 0.001$), 27.4 ± 10.2 m for canopy trees ($n = 13$, $t = 2.7$, $p = 0.02$) and 35.7 ± 6.9 m overall ($n = 58$, $t = 5.3$, $p < 0.001$). The increase in elevation was evident for species across the entire elevational gradient (Fig. 2). Only one species, *Oxalis montana*, showed a downward shift of > 50 m in elevation (the rightmost point in Fig. 2). Variation in elevational shifts among species was not predicted either by the initial proportion of plots where a species was present (linear regression, $t = -0.301$, $p = 0.764$), nor the logarithm of initial average abundance ($t = -0.644$, $p = 0.522$).

Changes in the community indices for temperature, light and moisture

Overall, the community indices for temperature (CTI), light (CLI) and moisture (CMI) showed clear trends with

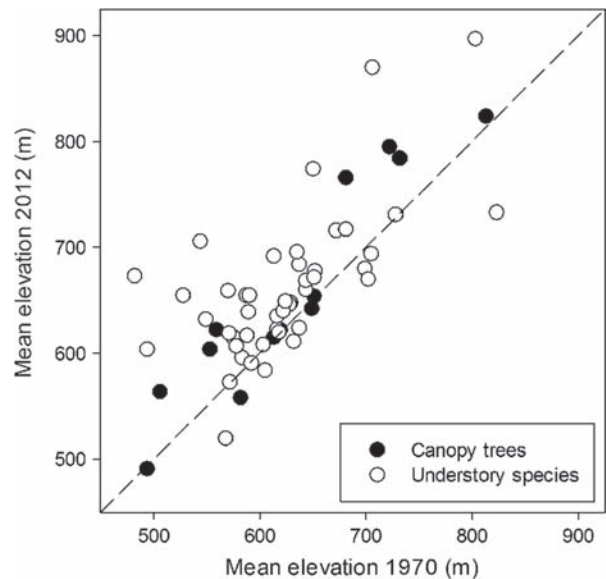


Figure 2. Mean abundance-weighted elevation of species distributions in 1970 and 2012. Each point represents a single species ($n = 45$ understory species, $n = 13$ canopy trees). Distributions of species above the diagonal 1:1 line increased in mean elevation, and vice versa.

elevation, but only weak or inconsistent tendencies to change across time. CTI showed a clear decline with increasing elevation, as expected, but there was only a small and non-significant increase over time (Fig. 3a–c, Table 1–2). In predicting variation in CTI, model selection indicated support for models including or not including an effect of year, with each having between 27 and 47% probability of being the best model, depending on the stratum considered (Table 1). Therefore, we used model averaging to estimate model coefficients and their significance based on whether 95% confidence intervals excluded zero. There was some support for a model including an interaction between year and elevation in predicting CTI, but only for understory species considered separately, and the estimate for this interaction was not significant (Table 2). The raw CTI difference between 2012 and 1970 of $\sim 0.2^\circ\text{C}$ was similar for each stratum considered (Table 2), but not significantly different from zero.

The community light index (CLI) showed a decline with elevation as well, indicating a decline in light-demanding species at high elevation (Fig. 3d–f, Table 2). However, the best predictors of variation in CLI varied among strata (understory or canopy). For understory species, a model including main effects of year and elevation had the most support, but for canopy species support was slightly higher for a model including only elevation (Table 1). When all species were pooled together, the two models were equivalent. Indeed, model averaged estimates of year were significant only for understory species (Table 2). For the community moisture index (CMI), the two best models included both year and elevation, but the importance of the year \times elevation interaction term depended on the stratum considered (Table 2). This interaction term was not significant in the case of canopy species, for which there was a clear effect of year (negative; Table 2). For understory species however,

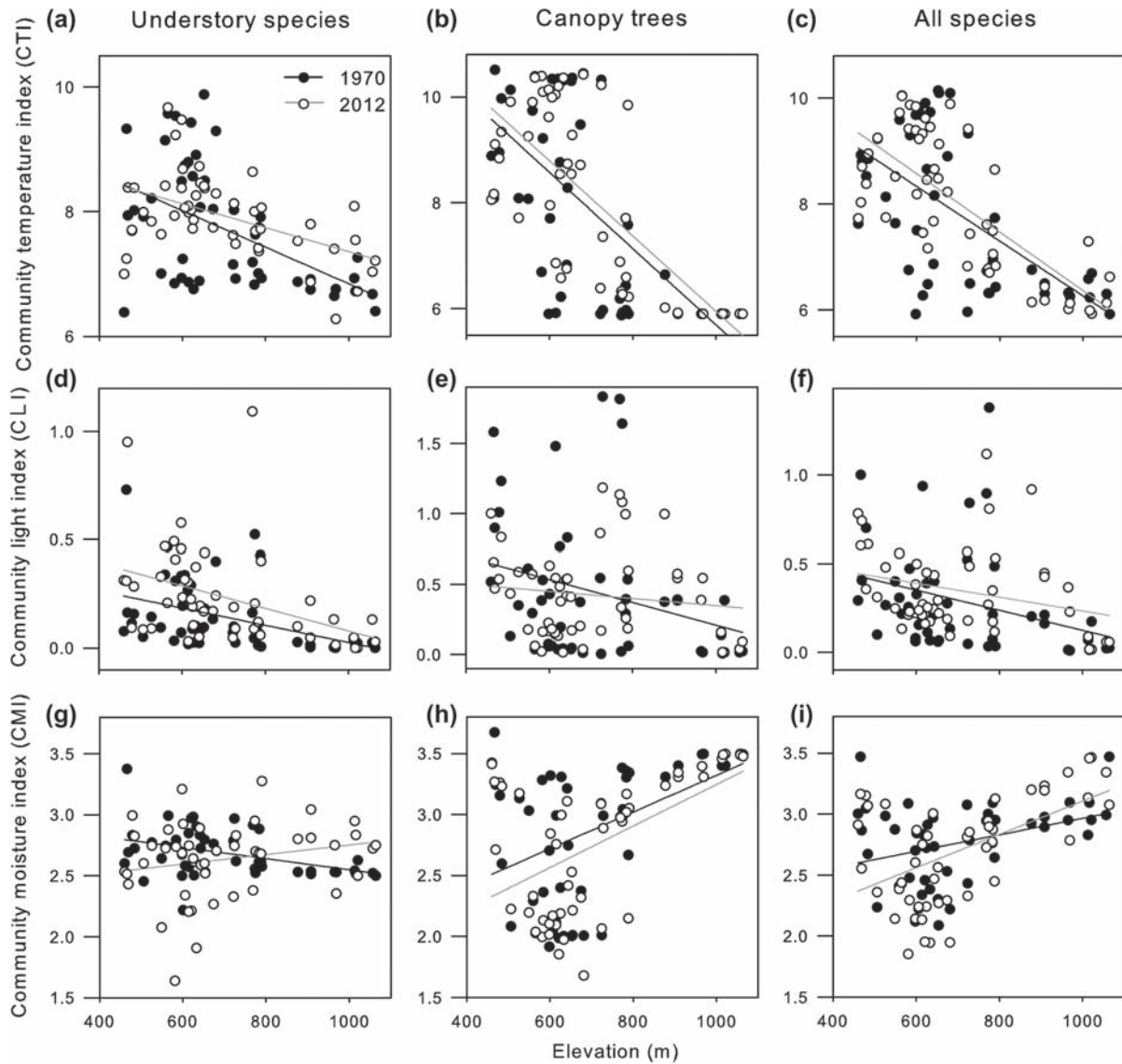


Figure 3. Relationships of the community indices for temperature (CTI), light (CLI), and moisture (CMI) with elevation, for understory, canopy and all species. Each point represents a single plot, with filled circles/black line for 1970 and open circles/grey line for 2012. Lines are from least-squares linear regressions.

the effect of year was masked by the significant interaction. Overall, when all species were pooled together, only the interaction term was significant.

Because CLI and CMI were correlated with CTI (Table 3), the variable of primary interest in these analyses, we tested whether the two cases in which we detected significant effects of year (CLI for understory species, CMI for canopy species) remained significant after controlling for CTI. In each case, we conducted an ANOVA comparison between a model including elevation and CTI, and a second model including elevation, CTI and year. The effect of year remained significant in the CLI model (log-Likelihood ratio = 4.62, $p = 0.03$), as well as in the CMI model (log-Likelihood ratio = 4.38, $p = 0.04$).

Species richness

In 1970, a total of 122 vascular plant species representing 47 families was recorded. In 2012, we observed 133 vascular

plant species representing 50 families. Twenty three species not recorded in 1970 were present in 2012, and twelve species recorded in 1970 were not observed in 2012, although the presence of these species in the park outside of our study plots (Hall 1998) and the fact that these species typically had few occurrences indicates that these changes do not represent regional colonization or extinction. At the plot level, model selection revealed one best model for species richness. This model included main effects of elevation and year, but no interaction. As expected, species richness declined with elevation. Species richness showed a marked increase between 1970 and 2012 of 6.5 ± 1.4 species per plot, which represents a 21–28% gain on average (Fig. 4). This increase was significant both for understory and canopy species (Table 2).

Species composition

The PERMANOVA showed a significant directional shift over time in species composition for all strata grouped

Table 1. Competing models of community change over the period 1970–2012. ‘Null’ includes site as a random factor (also included in all other models). ‘Elevation’ and ‘Year’ include only these variables as fixed effects; ‘Year + Elevation’ includes both, and ‘Year × Elevation’ includes the interaction as well. Shown are the number of parameters (K), log-Likelihood, and model selection results for models predicting CTI, CLI, CMI and species richness of understory (U), canopy (C) and all species (A). Parameters and their significance, based on model averaging, are shown in Table 2.

Model	K	Log-Likelihood			AICc ^a			ΔAICc ^b			AICcWt ^c		
		U	C	A	U	C	A	U	C	A	U	C	A
Community temperature index (CTI)													
Null	3	-113.9	-162.4	-141.6	234.1	331.1	289.5	17.64	32.33	30.45	0.00	0.00	0.00
Year	4	-112.4	-161.2	-140.2	233.3	330.8	288.9	16.86	32.05	29.85	0.00	0.00	0.00
Elevation	4	-104.4	-145.3	-125.6	217.2	299.0	259.6	0.74	0.24	0.55	0.27	0.40	0.36
Year + Elevation	5	-102.9	-144.0	-124.2	216.4	298.7	259.0	0.00	0.00	0.00	0.39	0.45	0.47
Year × Elevation	6	-101.9	-144.0	-124.1	216.7	301.0	261.1	0.27	2.27	2.04	0.34	0.15	0.17
Community light index (CLI)													
Null	3	20.2	-43.5	-4.3	-34.2	93.9	14.9	16.86	0.57	3.7	0.00	0.26	0.05
Year	4	23.5	-43.7	-3.2	-38.6	95.9	14.8	12.48	2.53	3.8	0.00	0.10	0.06
Elevation	4	27.6	-42.5	-1.3	-46.8	93.3	11.0	4.33	0.00	0.00	0.08	0.34	0.37
Year + Elevation	5	30.9	-42.3	-0.2	-51.1	95.4	11.1	0.00	2.01	0.01	0.66	0.13	0.36
Year × Elevation	6	31.1	-40.8	0.1	-49.2	94.6	12.7	1.89	1.29	1.66	0.26	0.18	0.16
Community moisture index (CMI)													
Null	3	-5.7	-54.8	-33.8	17.7	115.8	73.8	2.14	17.70	14.82	0.20	0.00	0.00
Year	4	-5.3	-50.7	-32.9	19.0	109.9	74.3	3.43	11.78	15.30	0.11	0.00	0.00
Elevation	4	-5.7	-47.8	-27.0	19.9	104.0	62.4	4.28	5.87	3.38	0.07	0.04	0.14
Year + Elevation	5	-5.3	-43.3	-26.1	21.2	98.1	62.9	5.61	0.00	3.90	0.04	0.68	0.11
Year × Elevation	6	-1.3	-43.5	-23.0	15.6	99.9	59.0	0.00	1.72	0.00	0.59	0.29	0.75
Species richness (alpha-diversity)													
Null	4	-361.3	-206.3	-361.3	731.1	421.1	731.1	55.11	58.34	55.11	0.00	0.00	0.00
Year	5	-352.8	-202.0	-352.8	716.3	414.6	716.3	40.31	51.87	40.31	0.00	0.00	0.00
Elevation	5	-340.0	-179.6	-340.0	690.8	369.8	690.8	14.75	7.10	14.75	0.00	0.02	0.00
Year + Elevation	6	-331.5	-174.9	-331.5	676.0	362.8	676.0	0.00	0.00	0.00	0.76	0.72	0.76
Year × Elevation	7	-331.5	-174.8	-331.5	678.3	364.8	678.3	2.31	2.09	2.31	0.24	0.25	0.24

^aAkaike information criterion, corrected for small sample sizes (when $n/K < 40$). ^bΔAICc are differences from the model with the lowest AICc; ΔAICc < 2 generally indicates good support for a model, and ΔAICc above 7 indicate no support. ^cAICc weights represent the probability of that particular model being the best one given the data.

together ($p = 0.0001$) and for understory ($p = 0.0001$) and canopy species ($p = 0.0009$) separately. The centroid in multivariate space has shifted toward communities resembling those at lower elevations (Fig. 5). There was a significant homogenization of plots over time for herbs (PERMDISP,

$p = 0.009$) and all strata grouped together ($p = 0.007$), while the effect was marginal for trees ($p = 0.06$). Plots at the high end of NMDS axis 1 (high elevation plots) tended to shift toward the centroid, while plots at the low end of this axis showed no directional trend.

Table 2. Parameters (\pm SE) estimated using model averaging to predict community indices for temperature, light and moisture, as well as species richness. See Table 1 for details of model selection.

	Intercept	Elevation	Year	Elevation × Year
Community temperature index (CTI)				
Understory	9.6 \pm 0.4*	-0.0024 \pm 0.0004*	0.21 \pm 0.12	0.0010 \pm 0.0007
Canopy	12.9 \pm 0.7*	-0.0071 \pm 0.0014*	0.23 \pm 0.14	0.0001 \pm 0.0001
All species	11.6 \pm 0.6*	-0.0053 \pm 0.0008*	0.21 \pm 0.12	-0.0004 \pm 0.0007
Community light index (CLI)				
Understory	0.5 \pm 0.1*	-0.0005 \pm 0.0001*	0.09 \pm 0.03*	-0.0001 \pm 0.0002
Canopy	0.7 \pm 0.3*	-0.0005 \pm 0.0003	-0.03 \pm 0.06	0.0006 \pm 0.0003
All species	0.6 \pm 0.2*	-0.0005 \pm 0.0002*	0.06 \pm 0.03	0.0002 \pm 0.0002
Community moisture index (CMI)				
Understory	2.9 \pm 0.2*	-0.0000 \pm 0.0002	-0.05 \pm 0.05	0.0009 \pm 0.0003*
Canopy	1.8 \pm 0.3*	0.0016 \pm 0.0004*	-0.13 \pm 0.05*	0.0002 \pm 0.0003
All species	2.2 \pm 0.2*	0.0010 \pm 0.0003*	-0.06 \pm 0.05	0.0007 \pm 0.0003*
Species richness (alpha-diversity)				
Understory	46.2 \pm 4.8*	-0.0391 \pm 0.0055*	5.3 \pm 1.5*	-0.0000 \pm 0.0089
Canopy	12.5 \pm 0.9*	-0.0098 \pm 0.0010*	1.0 \pm 0.3*	0.0009 \pm 0.0018
All species	54.9 \pm 4.7*	-0.0455 \pm 0.0055*	6.5 \pm 1.4*	-0.0011 \pm 0.0085

* 95% confidence interval of the estimated parameter does not include zero, based on AIC model averaging.

Table 3. Correlations between community indices for temperature (CTI), light (CLI) and moisture (CMI) across 48 plots in Parc national du Mont-Mégantic, for both 1970 and 2012. * $p < 0.05$.

		a) Understory species		b) Canopy species		c) All species	
		CTI	CMI	CTI	CMI	CTI	CMI
1970	CLI	0.64*	0.43	-0.17	0.23	-0.08	0.24
	CMI	0.60*	-	-0.82*	-	-0.77*	-
2012	CLI	0.46*	-0.24	-0.34*	0.41	-0.13	0.20
	CMI	0.16	-	-0.88*	-	-0.83*	-

Discussion

We observed temporal changes over the past four decades in the plant communities of Mont-Mégantic that were consistent with expectations based on climate warming. Averaged across all species, elevational distributions shifted upward ~ 9 m per decade, a rate quite close to the global average of 11 m per decade reported in the Chen et al. (2011) meta-analysis of terrestrial species (see also Felde et al. 2012, Jump et al. 2012, Bodin et al. 2013). The community temperature index (CTI) changed in the predicted direction, and by roughly the same amount for different strata ($+0.05^\circ\text{C}$ per decade). Although the change in CTI was not statistically significant, the magnitude of change corresponds closely to that expected based on a 9 m upward shift per decade in species' distributions, given an adiabatic lapse rate of $\sim 0.55^\circ\text{C}$ decrease in temperature per 100 m increase in elevation ($0.55^\circ\text{C}/100\text{ m} \times 9\text{ m/decade} = 0.05^\circ\text{C/decade}$; www.noaa.gov). For temperate forests across 29 regions of Europe and North America (including preliminary data for 17 plots on Mont-Mégantic), De Frenne et al. (2013) found significant thermophilization (i.e. increased CTI) overall, although differences were not always significant for individual sites. It thus seems likely that thermophilization has occurred in our study area, but was difficult to detect given substantial variability among plots. Finally, the decrease in the community moisture index (CMI) for canopy species is also consistent with climate-warming effects although the strong correlation between CTI and CMI (for canopy trees) makes it difficult to distinguish direct effects of temperature increase or indirect effects via decreased moisture availability.

The significant shift we observed in species composition of both understory and canopy plants toward communities resembling those at lower elevations provides further evidence that the main driver of vegetation change in our study area might be climate warming (see also Damschen et al. 2010, Lenoir et al. 2010, Bertrand et al. 2011). Interestingly, compositional change occurred mainly at higher elevations (see also Lenoir et al. 2008, Bertrand et al. 2011), indicating a 'shrinking' of the environmental gradient across elevation. While we cannot discern the underlying mechanisms, the asymmetric changes suggest the possibility that plants at high elevations are limited to a greater degree by minimum temperatures ($\sim 2.5^\circ\text{C}$ increase over 40 yr) than by maximum temperatures (weaker increase of $\sim 1.6^\circ\text{C}$), and vice versa for plants at low elevation. Evidence of biotic homogenization has been found globally and for many taxa, with

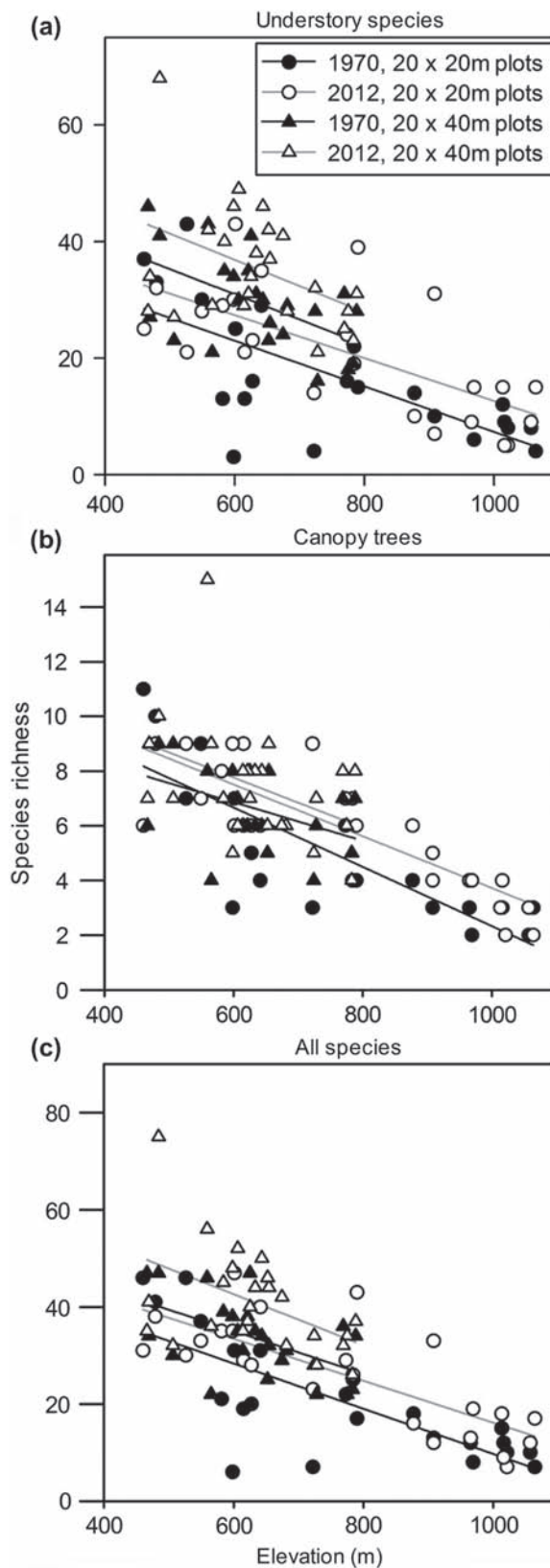


Figure 4. Relationship of species richness with elevation. Each point represents a single plot, with filled symbols/black lines for 1970 and open symbols/grey lines for 2012. Circles show plots in coniferous stands (20×20 m) and triangles show deciduous stands (20×40 m). Lines are from least-squares linear regressions.

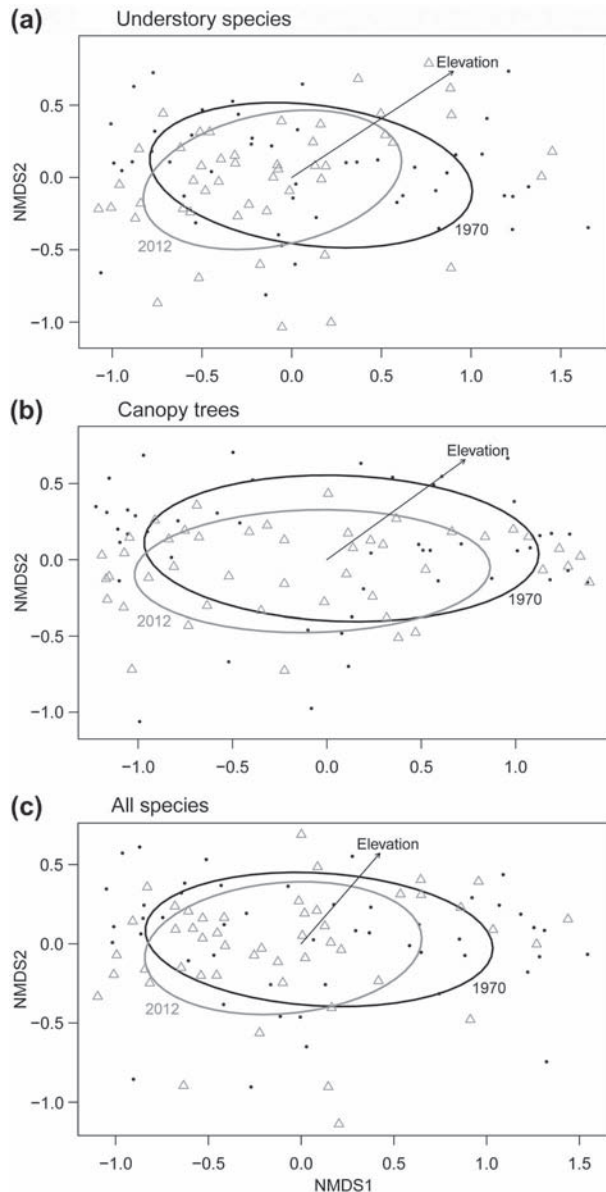


Figure 5. Non-metric multidimensional scaling (NMDS) ordination in two dimensions of all plots in 1970 and 2012 for each stratum. Each data point is a plot in a given time period (1970: black dots; 2012: grey triangles), with 95% confidence ellipses shown for each period. The Bray–Curtis dissimilarity measure was used.

an emphasis on species colonizations and extinctions (Baiser et al. 2012) or effects of land use (Vellend et al. 2007). Buisson and Grenouillet (2009) predicted homogenization of fish assemblages in France using simulations of future distribution shifts. Here we provide one of the first empirical examples suggesting a link between climate warming and biotic homogenization.

Species richness (the number of species per plot) decreased with elevation, as expected from many previous studies (McCain and Grytnes 2010). We also observed a significant increase in species richness over the past 40 yr of ~25% on average (Fig. 4). In sites subject to climate warming or other drivers of ecological change, temporal changes in richness

over time can be quite idiosyncratic, with increases just as likely as decreases (Damschen et al. 2010, Danby et al. 2011, Vellend et al. 2013a, Dornelas et al. 2014). The increase we observed over time cannot be explained by intensification of sampling effort. New species found in particular plots were typically new occurrences of species already common in 1970, rather than rarities that may have been previously missed. Consultations about methodology with a close colleague of M. Grandtner (C. Anseau, Univ. de Sherbrooke pers. comm.) ensured comparability of survey methods across time. While the increase in richness might be due to climate-driven species range expansions being greater than range contractions (Walther et al. 2002, Anderson et al. 2009), we cannot exclude the possibility that very slow post-disturbance recovery (much of the site was subject to partial logging early in the 20th century) can partly account for the increased number of species since 1970 (Flinn and Vellend 2005). While increases in species richness have often been found to be a consequence of non-native species arrivals (Sax and Gaines 2003), our results are consistent with several recent studies in which richness increases over time are due in large part to native species increases (Johnson et al. 2013, McCune and Vellend 2013) although the causes of such increases are not always clear.

We found some evidence for a possible role of non-climatic drivers in causing vegetation change. Specifically, for understory species, community light indices (CLI) significantly increased between 1970 and 2012, indicating higher relative abundance of light-demanding species. This result runs counter to what one would predict if protracted post-logging succession were important, and may be due to canopy-opening disturbances caused by two spruce budworm outbreaks and a major ice storm during the past 30 yr (Filion et al. 2006). It is possible that canopy opening at high elevation (spruce budworm attacks both spruce and fir, the dominant high-elevation trees) played some role in accelerating upslope distribution shifts of low elevation species. However, for understory species, there was a positive correlation between CTI and CLI ($r = 0.64$ in 1970, $r = 0.46$ in 2012; Table 3). This makes it difficult to disentangle possible effects of light regime and temperature on these indices of vegetation change. For canopy species, there was essentially no correlation (or a negative correlation) between CTI and CLI as well as STI and SLI. Therefore, the slight tendency for positive change over time in canopy CTI is very unlikely to result from successional changes or other changes in the light regime.

Comparing the magnitude of elevational distribution shifts observed over time with actual climate warming in the region suggests a considerable time lag between warming and plant responses. Given a temperature lapse rate of $\sim 0.55^\circ\text{C}/100\text{ m}$, isotherms should have shifted almost 300 m upslope. Compared to the much smaller upward shift of plant species of $\sim 36\text{ m}$, clearly some factors are preventing or slowing vegetation change. For example, limited dispersal could result in greatly protracted range shifts (Walther 2003), the long life spans of most forest plants could delay local extinctions (Vellend et al. 2006), or unfavorable non-climatic conditions (e.g. soil pH or biotic interactions) could prevent germination or recruitment at higher elevations, even if the climate is suitable (Walther 2003, Lafleur

et al. 2010, Corlett and Westcott 2013). We have some experimental evidence for our field site that the regeneration of sugar maple beyond its upper elevational range edge is limited by both seed predators and unfavourable soil conditions (Brown and Vellend 2014). Testing the generality of such constraints across species is an important priority for future research.

Our results also contrast directly with those of Beckage et al. (2008) from a very similar site ~200 km southwest of Mont-Mégantic, who reported a rapid shift (relative to observed temperature increase) in the deciduous-boreal forest ecotone since the 1960s. However, this inference was based largely on comparing disparate data sources (satellite images vs aerial photos), and involved just six dominant tree species. At our site, the same six species (sugar maple, American beech, yellow birch, paper birch, red spruce, balsam fir) showed a mean elevational shift as low or lower (+ 22.3 m) than the average for the full set of 13 canopy tree species (+ 27.4 m). For the broader set of plant species in eastern North American forests, extended time lags in climate change responses seem likely.

Overall, we found compelling evidence that climate change was likely an important driver in vegetation change over the last 42 yr in Parc national du Mont-Mégantic, but the biota does not appear to have tracked the degree of warming that has occurred in the region. Whether the discrepancy between temperature change and the magnitude of the biotic response is due to slow dispersal and establishment or to non-climatic barriers to range shifts is an important avenue of future research (Lafleur et al. 2010). Long-term monitoring and experimental studies are needed to assess the biotic consequences of climate change in the coming decades.

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Supplementary material (Appendix ECOG-01131 at <www.ecography.org/readers/appendix>). Appendix 1.