Title: Using Long-term Ecological Data to Identify Altitudinal Shifts of Species and Communities in Response to Recent Climate Change

Abstract:

Aim: To determine whether montane understory plant communities have shifted as intact units or whether species are responding individualistically to documented changes in climate over the past 40 years.

Location: Camels Hump in the Green Mountains of Vermont, USA

Methods: Using data collected from a repeated vegetation survey done between 1964 and 2006, changes to overstory and understory plant communities were examined through the use of non-metric multidimensional scaling (NMDS) and simple Bayesian models.

Results: Understory communities across an elevational gradient (549m to 1158m) on Camels Hump, VT have been changing in terms of species composition and have become more homogenous since the mid-1960's. The magnitude of change observed was not equal across elevations however, with the highest survey sites exhibiting the most amount of change despite experiencing the least amount of warming. The lowest elevations in turn exhibited the least amount of community compositional change. Shifts in the optimal elevations of individual species examined through the use of Bayesian models showed a wide range of migration patterns in terms of both magnitude and direction, with some species moving upslope, some remaining fairly stationary and still others shifting their optimal elevation down slope. This pattern was found to be independent of overstory elevational shift due to an average increase in the elevational optimum of understory species almost twice that of overstory species over the same time period (1964-2006) at 28.36m and 15.62m, respectively.

Main Conclusions: Spatial and temporal trends in understory communities indicate climate and acid deposition are major drivers of change to species compositions in the Green Mountains since 1964. However, differences in both the magnitude and direction of elevational change of individual species suggest that past communities are not moving as intact units in response to climate change.

Key Words: Bayesian models, climate change, community shift, elevational shift, non-metric multidimensional scaling (NMDS), understory communities

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(A) Introduction:

Determining the mechanisms by which species move and shift in response to changes in their environment is one of the fundamental objectives of ecology, and one that is gaining significance as the rate of anthropogenic climate change increases (IPCC 2007). The effects of recent warming have already been seen globally across terrestrial, aquatic and marine habitats (Walther et al 2002) and can be clearly observed by the shifting ranges of many species either poleward or upward (Krajick 2004; Parmesan & Yohe 2003, Root et al. 2003). However, despite the extensive documentation of this pattern in the literature, two dominant hypotheses persist that each attempt to describe how this shift impacts current biological communities. The first assumes that changes in climate will affect species differently causing species within a single community to shift individualistically (Jackson & Overpeck 2000; Williams et al 2004), thus dissolving current species associations and creating novel communities (le Roux & McGeoch 2008; Walther 2004; Delcourt & Delcourt 1988). The second dominant hypothesis, whose basic structure was set forth by Darwin (1859) and the one that is often used to estimate large scale future vegetation cover (All BIOME and LPJ models) predicts that species within a community coexist due to common climatic tolerances and will likely respond similarly to changes in climate. This would result in species shifting as intact units, preserving current species associations. Evidence of each of these patterns has been observed over geologic time-scales and is present in the literature (McLauchlan et al. 2005); however, studies of the response of modern communities to recent climate change are by in large absent and are of great necessity (Walther 2004; Williams et al 2004; Root & Schneider 2006).

71   The aim of this study is to differentiate between the species and community shift

72   hypotheses by examining the understory plant community of a montane forest in the

73   northeastern United States. If this community is shifting as an intact unit, we expect to

74   observe each species moving in the same direction at approximately the same rate.

75   However, if species instead are moving as individuals, we expect to see divergence in

76   both the rate and direction of shift between species. In addition, we want to determine

77   whether any shift observed in the understory is independent or linked to shifts already

78   documented in the overstory (Beckage et al 2008). If responding independently from the

79   overstory, this would further support the hypothesis that understory species are

80   responding individually to complex changes in climate.

81   Just as we have seen in the past, we expect that in the future, novel climatic

82   conditions will arise due to the complex, multidimensional nature of climate (Williams &

83   Jackson 2007). This is possible since each component which defines a climate can change

84   independently of the others, producing combinations of climatic characteristics which

85   have no current analog. The formation of these novel climates may fundamentally shift

86   competitive balances between species and favor species associations that do not currently

87   exist, ultimately leading to shifts in geographic range limits. As we predict rates of

88   climate change over the next century to exceed those experienced at any time since at

89   least the last ice age (Root & Schneider 2006), it is important that we consider the

90   potential impact that novel communities may have on future climate.

91   As we continue to develop and base conservation strategies on dynamic global

92   vegetation models (DGVM's), which incorporate climate-vegetation feedbacks (Bonan

93   2003; Krinner et al. 2005; Bachelet et al. 2001) and are used to forecast climate and biotic

94   distributions, it is increasingly important to correctly model how communities respond to

95   climate and vise versa. However, despite the fact that competitive relationships between

96   species in novel communities are by definition unknown, understanding whether species

97   move as individuals or in intact communities could provide valuable accuracy to models

98   in the future. Using the incorrect framework within DGVM's to model future climate and

99   vegetation could cause predictions of future species distribution to be dramatically

100 incorrect. A more thorough understanding of how communities have responded to recent

101 climate change through direct observation could help to identify the correct framework

102 for use in these models.

103   Because of their steep slopes which form naturally compact climate gradients,

104 montane environments provide ideal locations to study climate related species shift

105 (Stevens & Fox 1991; Kupfer & Cairns 1996). In many of these communities even

106 relatively small changes in climate are able to produce observable shifts in species

107 elevation (Guisan & Theurillat, 2000). Long-term monitoring of such locations can

108 provide insight into how climate change has impacted species distributions on shorter

109 time scales than may be expected.

110   In this study historic climate and plant distribution records dating back to 1965 as

111 well as multiple vegetation resurveys through 2006, provide the opportunity to examine

112 climate related species shift during over 40 years of documented climate change

113 (Beckage et al 2008; Siccama 1978, Perkins 1988). Temperature at our study site in the

114 Green Mountain region of Vermont has warmed by between 0.67 and 1.5°C since 1963

115 (Figure 1) depending on elevation (Beckage et al 2008), resulting in observed shifts in the

116 overstory tree community by as much as 119m in elevation (Beckage et al. 2008). The

117   understory community found here provides an ideal suite of species on which to base this

118   study. With a much greater diversity than the overstory, the understory community allows

119   us to not only look at individual species shift, but to examine how life history traits such

120   as dispersal, influence how quickly a species responds to climate change. In addition, it is

121   expected that many of the understory species are capable of showing similar if not greater

122   amounts of altitudinal shift than the canopy species due to their shorter generation times

123   (Lenoir 2008) and are therefore able to respond more quickly to changes in climate than

124   long-lived tree species. These may also be communities in which the anticipated impact

125   due to climate change has been greatly underestimated (Trivedi et al. 2008).

126   In order to differentiate between the individualistic and the community shift

127   hypotheses within the understory community of Camels Hump, the results of the repeated

128   vegetation survey were be analyzed through the use of non-metric multidimensional

129   scaling (NMDS) techniques and simple Bayesian models. NMDS was used over other

130   multivariate scaling techniques because of its ability to highlight similarities visually as

131   well as for its ability to incorporate non-normal and categorical data into analyses (REF).

132   **(A) Study Site:**

133   As the second highest peak in Vermont, Camels Hump (44° 19' N, 72° 53' W), at

134   1244 m a.s.l., has been used for many types of biological and ecosystem studies and is an

135   ideal site for the study vegetation change over time due in part to a system of permanent

136   and semi-permanent plots used to monitor plant communities as well as soil, climate and

137   forest health since the early 1960's. The geology of Camels Hump is typical to that of the

138   Green Mountains and is dominated by schist (graphitic, quartz-albite-muscovite) and

139   quartzite (USGS 1948) bedrock. Soils are predominantly entisols and spodosols

140   consisting of strongly acidic stony loams (NRCS 2003; NRCS 2006; NRCS 2008). The

141   climate in this region is characterized by a large daily and annual temperature ranges,

142   particularly in the mountains, with an average January temperature of -7.8^{o}C and an

143   average July temperature of 21.4^{o}C. Precipitation is fairly evenly distributed throughout

144   the year averaging 91.6cm annually (Burlington International Airport Station, NOAA

145   2002).

146   There are two general forest types that occupy the majority of the area on Camels

147   Hump and other montane regions of New England and are stratified by elevation. The

148   forest below approximately 760m is primarily a sugar maple (*Acer saccharum*),

149   American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*) northern

150   hardwood forest. Between 760 and 880 m lies a narrow ecotone (Siccama et al. 1982)

151   principally controlled by climate (Kupfer & Cairns 1996; Beckage 2008), which

152   transitions from the lower deciduous forest into the high elevation boreal forest, which is

153   dominated by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*) and high elevation

154   paper birch (*Betula cordifolia*) (Siccama 1974; Siccama et al. 1982). This boreal forest

155   extends upward until it reaches the small alpine summit.

156   The vegetation survey plots used in this analysis are located in the Camels Hump

157   Forest Ecology Research Area which has a well-documented land use and disturbance

158   history (Siccama 1968; Whitney 1988), allowing us to identify major disturbances that

159   may influence the stand dynamics of our sites (Pearson et al. 2004) and avoid areas of

160   recent human interference. While the majority of the upper slopes of Camels Hump have

161   not been logged, some salvage and selective logging has taken place at lower elevations.

162   However, with the exception of some selectively cut yellow birch and red spruce

163   extending up to 700m, all other potentially disruptive logging activity has been located

164   outside of the research area (Siccama 1968; Whitney 1988).

165   **(A) Methods:**

166   (B) *Field Methods*

167   Vegetation was sampled using a nested plot design established in 1965 (Siccama

168   1968; Voglemann 1985) and based on previous studies done by Cain (1935), Cantlon

169   (1953) and Oosting and Billings (1951), in order to capture both overstory and understory

170   characteristics on Camels Hump. In 1965, the understory quadrats were destructively

171   sampled, requiring that at the time they were made permanent in 1979, they be shifted

172   slightly (Perkins 1988). Overstory plots were distributed up the western slope of Camels

173   Hump at intervals of 60 vertical meters between 549 and 1158 m for a total of 11 sample

174   elevations. At each elevation, 3m x 30m overstory plots were laid down perpendicular to

175   the contour and separated by 6m. Rebar was used to permanently mark the top and

176   bottom of each plot's centerline. The six lower elevation sites were each assigned 10

177   plots, while the upper five were only assigned five in order to maintain a westerly aspect.

178   Within each of these overstory plots, the species and dbh for each tree with a diameter >

179   2cm was recorded. Nested in each of these plots were six- meter square quadrats evenly

180   distributed along the center line for a total of 510 understory quadrats. To sample

181   understory vegetation within each quadrat, a collapsible PVC frame was laid out at the

182   pre-defined locations at which point the stem count and estimated percent cover of each

183   species present was recorded. All woody species with a dbh less than 2cm were measured

184   as part of the understory. In all, more than 118 species were identified, 15 of which were

185   trees.

186   (B) *Species Data*

187   While attempting to differentiate between community and species shift, it became

188   necessary to define a community in a way that would be meaningful and could capture

189   subtle changes in species composition over time. With this in mind, we defined

190   communities as multivariate entities described by the average percent cover of each

191   species within a plot. The average percent cover was calculated from the percent covers

192   of each species recorded from within the six meter-squared understory quadrats nested

193   within each plot.

194   In order to reduce the impact of field misidentifications and to account for other

195   uncertainties such as taxonomic changes, it was often necessary to aggregate data from

196   some species present in the understory. After 1965 when destructive sampling no longer

197   took place, field identifications of some individuals to the species level were impossible

198   due to the fact that flowers were not always observed at the time of data collection. These

199   aggregations typically took place at the genus level, though grasses (Poaceae) and sedges

200   (Cyperaceae) were grouped by family. Additionally, information on moss cover was

201   collected which combined all species of moss with the exception of the genus *Sphagnum.*

202   (B) *Statistical Analysis*

203   *(C) Non-metric Multidimensional Scaling (NMDS)*

204   Whether or not understory communities have shifted on Camels Hump or in what

205   direction they have shifted was examined through the use of NMDS analyses. NMDS

206   was used in this study in order to illustrate how species and communities are changing

207   over time. Similar to a principle component analysis (PCA), the goal of NMDS is to use

208   multivariate data to group similar observations together. However, where NMDS differs

209   from PCA is that instead of preserving the spatial relationships between observations

210   within a multidimensional space, similarities and dissimilarities are exaggerated by

211   adjusting the location of points slightly in order to group more similar points more

212   tightly. This property of NMDS was advantageous to this analysis since the changes to

213   many of the understory communities we observed have not been drastic but instead have

214   been subtle changes over the past 40 years, which can be difficult to identify with other

215   methods. All NMDS analyses were performed in the R statistical software package

216   (REF?) using the isoMDS (MASS) function. Results were generated from a two

217   dimensional (k=2) analysis and were based on an initial Euclidean distance matrix. The

218   data used in these analyses were summarized by plot (community analyses) or elevation

219   (species analyses). Additionally, to avoid the artificial grouping of species or

220   communities by elevation, this information was not included when calculating similarity.

221   Instead, only frequency or percent cover for each species was utilized in order to produce

222   the graphic representations of the data. This also ensured that from year to year, the

223   similarity of communities was independent of elevation.

224   *(C)Bayesian Modeling*

225   Bayesian models were developed to estimate the elevational shift of individual

226   species over the 40 year duration of this study. Model fits for understory species were

227   generated using species frequency data summarized by elevation. Overstory tree data was

228   also summarized by elevation but instead of frequency, parameter estimates were based

229   on average basal area per plot. Quadratic model fits were used to predict the optimum

230   elevation or the elevation where a species is most likely to be found. Changes in optimum

231   elevations indicate range shift in a given direction. Many studies of range shift focus

232   solely on the fringes of a species' range (Beckage et al. 2008? – plenty of others too),

233   however, by also identifying and tracking how the core of a species range is responding

234   to climate change, we gain valuable information on how species are affected by changes

235   in climate (Lenoir et al. 2008). Parameter estimates fit to the data were generated using

236   the WinBugs computer program utilizing a Markov Chain Monte Carlo (MCMC)

237   sampler using the following models.

238   Understory Model:

239                         $P[Quadrats\ Occupied] \sim Binomial\ (\ y : \beta_0,\ \beta_1,\ \beta_2,\ N_{plots})$

240                         $Logit\ (p[i])\ <\text{-}\ \beta_0 + \beta_1 * Elevation + \beta_2 * Elevation^2$

241                         $\beta\ Priors \sim Normal(0.0,0.1)$

242   Overstory Model:

243                         $E[Basal\ Area] \sim Normal(y : \mu, \tau)$

244                         $\mu[i] <\text{-}\ \beta_0 + \beta_1 * Elevation + \beta_2 * Elevation^2$

245                         $\tau \sim Gamma\ (0.001,0.001)$

246   The parameter estimates ($\beta_0,\ \beta_1,\ \beta_2$) were then used to plot the modeled distributions in R

247   in order to estimate shifts in optimum elevations over time.

248   In order to improve the reliability of our results, the data used in both statistical

249   analyses were cropped to include only understory species present in greater than 50% of

250   the years sampled, or 3 of the 5 years. In terms of NMDS, this was done to avoid the

251   characterization of communities by the presence or absence of a rare plant and allowed us

252   instead to examine how general community compositions had changed over time. Tree

253   species were also excluded from the understory analyses even when they met the

254   understory criteria of having a dbh of < 2cm in order to prevent the influence of mast

255   years. For the Bayesian model fitting, the same suite of 48 species was used in order to

256   reduce the frequency of incorrect estimations of shift based on years when a species was

257   not observed. This method of exclusion did not distinguish between species that were not

258   observed due to limited sampling capabilities and those that were not observed because

259   their range had shifted outside of the elevational scope of this study.

260   **(A) Results and Discussion**

261   **(B) *Community Shift***

262   Understanding if and how communities in the Green Mountains are shifting in

263   response to recent climate change was one of the primary goals of this study and one that

264   was well captured in our analyses. Through the use of NMDS it becomes clear that

265   between the first vegetation survey done in 1965 and the last in 2006, current understory

266   communities at a given elevation are more similar to communities found at higher

267   elevations in the past (Figure 2). This is evidenced by the migration of the NMDS points

268   toward the left side of the parameter space as time goes forward, converging toward the

269   position occupied by the lowest elevation points. This illustrates a situation where high

270   elevation points are moving closer and closer to lower elevation points, suggesting a

271   homogenization in species composition across elevations and that communities are in

272   general following an upward migratory trend as expected when climate warms (Parmesan

273   & Yohe 2003).

274   Given that there are differences in the rate of warming experienced at high and

275   low altitudes (Figure 1), we would not, correspondingly, expect that the rate of

276   community shift would be equal across elevations. Instead, given the climate data, we

277   would expect low elevations to be shifting more rapidly since they are experiencing a

278   greater amount of change in terms of temperature. However, this is contradictory to what

279   was observed (Figure 3). The lowest elevations appear to shift very little if at all in the

280   NMDS parameter space between years and it is not until 732m that we see significant

281   amounts of shift over the course of the study. Additionally, the magnitude of this shift

282   continues to increase with elevation.

283   While part of this seemingly inconsistent result is likely explained by the location

284   of the boreal/deciduous ecotone (BDE), the amount of change observed at the highest

285   elevations is perhaps the result of interacting anthropogenic disturbances. Between 732

286   and 853m, northern hardwood and high elevation boreal forest form the BDE and

287   understory community change observed here may be the result of the advancement

288   upslope of species normally found under the hardwood canopy. Less change would be

289   expected at the low elevations despite a greater amount of warming since the forests

290   found at elevations extending some distance below our study range are also composed of

291   northern hardwoods with understory vegetation communities fairly similar to those

292   observed at our lowest study sites. Consequently, this pattern may also be expected to

293   hold true for the uppermost elevations of our study since the communities below them are

294   also similar in overstory composition. However, other anthropogenic forces may be at

295   work in these locations acting synergistically to alter understory communities. Most

296   notably among them is acid deposition.

297   With thin, rocky soils and increased exposure to acid deposition through cloud

298   moisture (Voglemann et al. 1968, Siccama et al. 1982), high elevation montane forests in

299   the northeast are disproportionately prone to acidification (Wargo & Auclair 2000;).

300   This decrease in soil pH, in conjunction with increased temperatures may have caused the

301   rapid change we observed at high elevations in the NMDS analysis (Figure 3) by creating

302   soil conditions unsuitable for some species typically found in these high elevation

303   communities (REF). Acid deposition may also have influenced understory communities

304   by causing alterations in the light environment through increases in canopy gap formation

305   (Anderson et al. 1969; Anderson & Leopold 2002). Acid deposition is indirectly capable

306   of causing gaps by reducing soil calcium levels, which can contribute to overstory loss in

307   species such as red spruce where calcium levels are linked to cold tolerance and frost

308   injury (Battles & Fahey 2000; DeHayes 1992; Schaberg et al. 2000). Since the 1960's red

309   spruce decline at mid to high elevations has been documented on Camels Hump with a

310   near 50% reduction in basal area between 1964 and 1979 (Siccama 1982). Despite these

311   differences observed in the magnitude of compositional change over the elevational

312   gradient of this study, communities did exhibit a unified direction of shift suggesting a

313   common driver such as climate (Figure 3).

314   *(B) Species Shift*

315   Despite the evidence for community shift, it is impossible to ascertain from the

316   NMDS analysis whether the changes observed in Figures 2 and 3 are being driven by a

317   consistent pattern of movement by every species within a community or whether those

318   changes are being driven instead by a small subset of species. In order to explore whether

319   these communities are remaining intact, or whether most species are shifting

320   independently and in different directions, it becomes necessary to look at each species

321   individually.

322   Through the use of simple Bayesian models, we were able to identify an optimum

323   elevation for each species in each year, indicating the elevation at which that species is

324 most likely to be found. Changes in that optimum elevation indicate both the direction

325 and magnitude of shift. Only species which were observed in both 1965 and 2006, and

326 those whose optimum elevation for each of those time periods fell within our studied

327 elevational range were considered for this analysis. Evidence from the estimated

328 optimum elevations suggests that species are not moving in a consistent fashion and are

329 instead exhibiting independent directional shift (Figure 4). While many species are

330 moving upslope (Figure 4a,c,e,f,g), others are shifting very little if at all (Figure 4d,j) and

331 some are even exhibiting a downward migration pattern (Figure 4b,h,i,l). When all

332 species are considered collectively however, the average direction of elevational shift is

333 still positive (Figure 5) as we would expect given the warming climate (Figure 1).

334 In addition to identifying the magnitude and direction in which understory species

335 are shifting, it is important to determine whether the observed shift is a reaction to

336 climate or whether understory species are simply tracking the shifts observed in the

337 overstory (Beckage et al. 2008). There are inherent links between the two including the

338 effects of canopy cover on soil chemistry (Finzi et al. 1998) and light availability

339 (Anderson et al. 1969; Reader et al. 1992). However, in this case, the average elevational

340 shift of the understory species almost doubles that of the canopy species (Figure 6, Table

341 1), indicating a sensitivity to climate that overwhelms the influences of soil and light.

342 **(A)Conclusions:**

343 Despite the consistent and unidirectional shift of communities at every elevation

344 sampled on Camels Hump, the examination of individual species leads us to believe that

345 communities are not shifting as intact units. Instead, species are shifting independently in

346 both elevational direction and magnitude, causing past community associations to

347   dissolve and novel communities to be created (Williams & Jackson 2007). This

348   reshuffling of species is likely to have far reaching effects in terms of competitive

349   interactions and ecosystem function (Millennium Ecosystem Assessment 2005). While

350   some species are likely to benefit from these changing community dynamics (Walther et

351   al. 2003), others may be negatively affected, causing declines in abundance and

352   increasing extinction probabilities (Root & Schneider 2006; Thomas et al. 2004). This

353   will likely impact conservation efforts, particularly those aimed at a single species. In

354   addition, while acknowledging the practical necessity of modeling future vegetation in

355   terms of communities at large scales, it is clear that efforts to move towards modeling

356   individual species are justified and would be more biologically accurate.

357

358   **(A) Literature Cited:**

359

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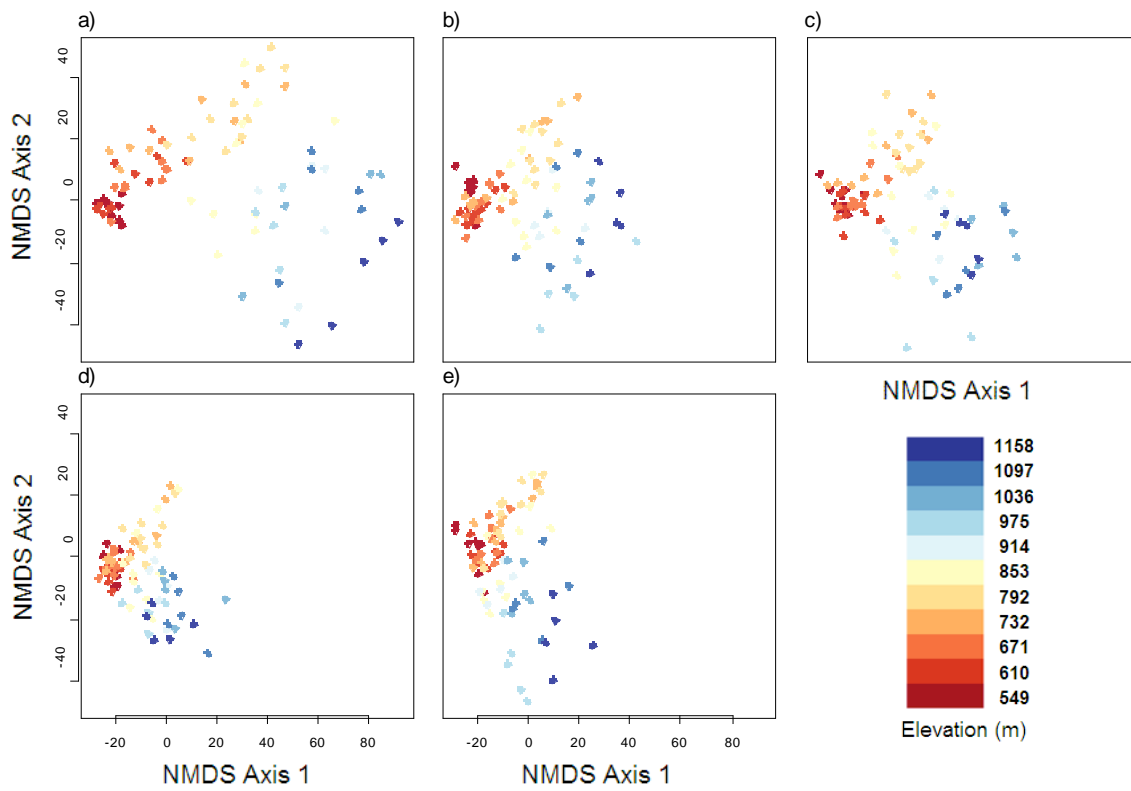469
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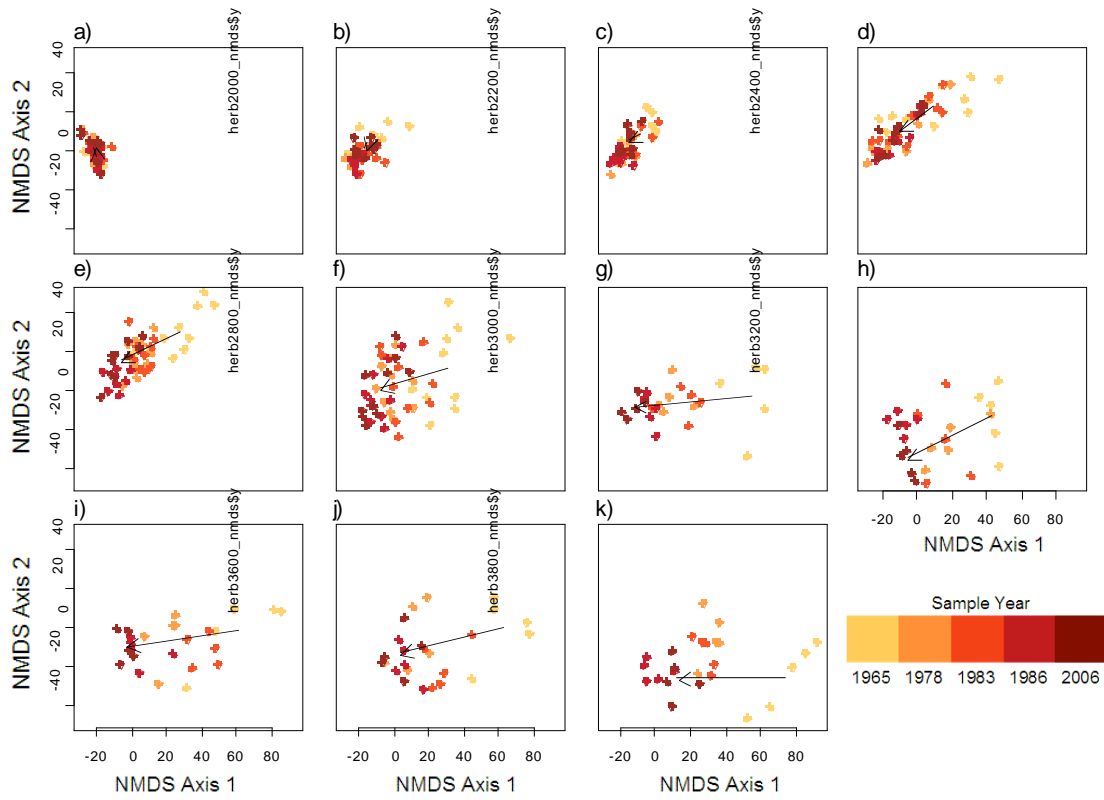526
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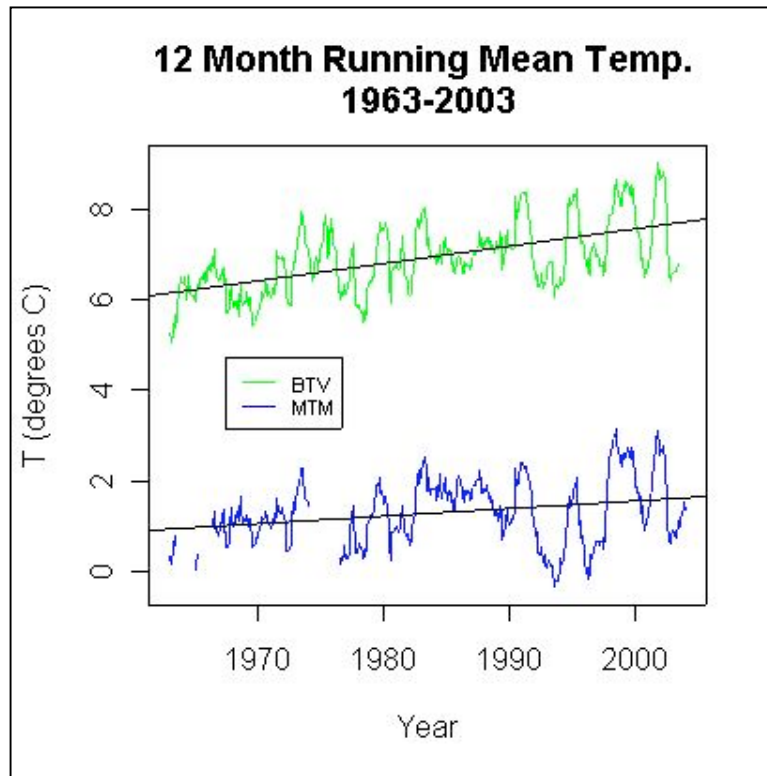
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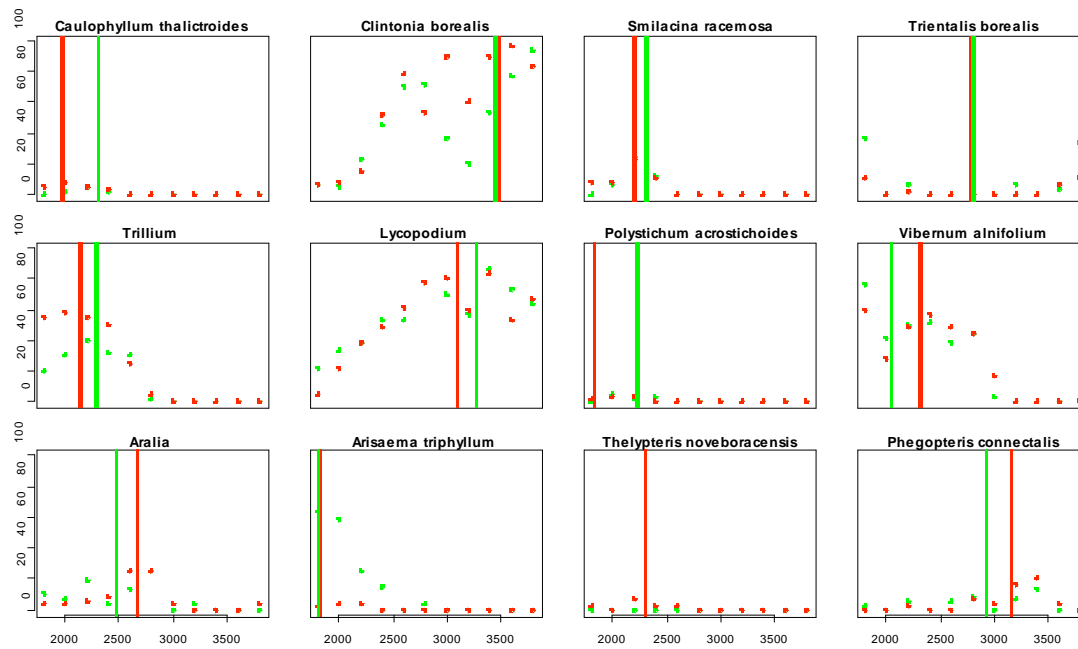545
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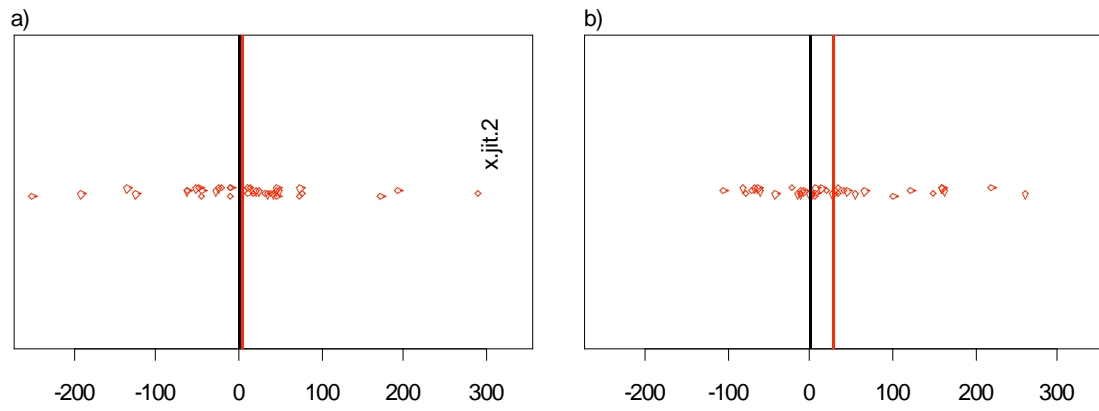579

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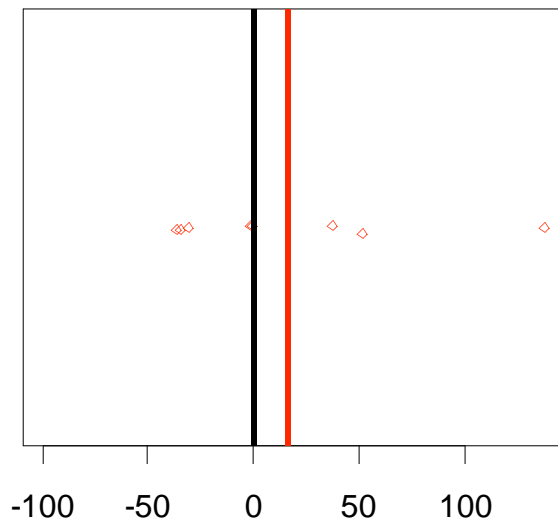581
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583   Figure 4:

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594   Figure 6: Overstory Shift
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612 Table 1:

Understory shift between 1965 to 1979	Understory shift between 1965 to 1983	Understory shift between 1965 to 1986	Understory shift between 1965 to 2006	Overstory shift between 1964 to 2004
4.64m	23.94m	45.30m	28.36m	15.62m

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657   **Figure 1: Average annual temperature at the high elevation Mount Mansfield Station (MTM) and**
658   **the low elevation Burlington Airport Station (BTV). (From Beckage et al. 2008)**
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660   **Figure 2: Changes to understory communities over time sampled across 11 elevations (549m to**
661   **1158m) as part of a repeated vegetation survey. Communities here are plotted in NMDS parameter**
662   **space for a) 1965, c) 1979, d) 1983, e) 1986 and f) 2006 with points closer together representing**
663   **communities with more similar composition.**
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665   **Figure 3: Changes to understory communities sampled 5 times between 1965 and 2006 as part of a**
666   **repeated vegetation survey and plotted in NMDS parameter space. Arrows indicate the average**
667   **magnitude and direction of community change by elevation between 1965 and 2006. a) 549m b) 610m**
668   **c) 671m d) 732m e) 792m f) 853m g) 914m h) 975m i) 1036m j) 1097m k) 1158m.**

669   **Figure 4: A subset of species exhibiting the range of directional shifts observed among components of**
670   **the understory communities on Camels Hump. Points indicate the observed frequency of each species**
671   **at a given elevation in 1965 (red) and 2006 (green) with lines indicating their corresponding modeled**
672   **optimum elevations found using Bayesian parameter estimation techniques. Species here represent a**
673   **wide range of functional forms, dispersal strategies and abundance as: a)** *Caulophyllum thalictroides*
674   **b)** *Clintonia borealis* **c)** *Smilacina racemosa* **d)** *Trientalis borealis* **e)** *Trillium sp.* **f)** *Huperzia lucidula* **g)**
675   *Polystichum acrostichoides* **h)** *Vibernum lantanoides* **i)** *Aralia* **sp. j)** *Arisaema triphyllum* **k)** *Thelypteris*
676   *noveboracensis* **l)** *Phegopteris connectalis.*
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678   **Figure 5: Optimal elevation shift of understory species between 1965 and a) 1979 and b) 2006. Points**
679   **each represent the amount of shift in meters estimated for a single species whose optimum elevation**
680   **lies within the elevational scope of this study. The black, vertical line indicates zero change and the**
681   **red line shows the average estimated change for all species in each year.**
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683   **Figure 6: Optimal elevation shift of overstory tree species between 1964 and 2004. As in figure 5,**
684   **points indicate the elevational shift in meters of each tree species whose optimum elevation lies**
685   **between 549 and 1159m. The black line indicates zero change while the red line indicates the average**
686   **amount of estimated change over all species.**
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689   **Table 1: The average amount of elevational shift over the given length of the study for all species**
690   **whose optimal elevation is within the studied elevational range.**
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