

Tree regeneration dynamics and drivers across the temperate-boreal transition zone

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Abstract

The upper Great Lakes region in central North America contains a forest transition zone where temperate and boreal tree species reach their northern and southern range limits, respectively. It is only within this narrow latitudinal band (~3 degrees), that relatively warm-adapted temperate and cold-adapted boreal tree species are found growing together in upland mesic sites. If climate is a main driver of forest dynamics within this region, recent and predicted climate change should result in major forest shifts, including the expansion of temperate species and range contraction of boreal species. Such changes should first be manifest in growth and abundance trends of tree species in the understory regeneration layers. In addition to climate, numerous other factors such as overstory composition, understory abiotic environment, competition with shrub and herbaceous layers, and browse pressure drive tree regeneration trends. Interrelationships and interactions among these drivers will ultimately determine the direction and rate of forest change. We explored these research topics through field studies of naturally established seedlings and saplings at 124 upland mesic forest sites across a three state (Minnesota, Wisconsin, and Michigan U.S.A) 170,000 km² area of the temperate-boreal transition zone.

Chapter 1 examined relative abundance shifts of temperate and boreal tree regeneration at two spatial scales: local ecotonal boundaries between temperate and boreal dominated stands and across the regional temperate-boreal transition zone. Because we compared understory performance across locally changing overstory composition, we calculated species regeneration success as the difference in relative

abundance between the understory and overstory layers. At the local scale, both shade-tolerant temperate and boreal species exhibited positive tree regeneration success across ecotonal boundaries. However, across the region, regeneration performance varied with mean summer temperature and to a lesser extent mean annual precipitation. Changes in regeneration success were generally greatest at the warm end of the transition zone, with temperate broadleaf *Acer saccharum*, *Fraxinus nigra*, and *Ostrya virginiana* responding positively and boreal *Abies balsamea* showing significantly reduced performance. For the most frequent temperate species, *Acer rubrum*, regeneration success was greatest in boreal neighborhoods and at cool and dry sites. Other species did not exhibit detectable shifts in regeneration success, potentially due to traits such as shade-tolerance, palatability, and mode of reproduction. Overall we found that numerous tree species growing across the temperate-boreal transition zone are likely sensitive to climate at early stages of development, with observed shifts in regeneration success concomitant with the direction predicted in response to climate change.

Chapter 2 assessed the relative importance of and interrelationships among explanatory variable sets in explaining the composition of the tree regeneration layer. We used redundancy analysis (RDA) and variation partitioning to quantify the unique, shared, and total explanatory power of four sets of drivers: climate, understory abiotic environment, overstory composition, and understory biota. The results showed that all four driver sets individually explained a significant portion of tree regeneration compositional variation and additionally that there were strong relationships among explanatory variables. Overstory composition, which directly influences seed

availability and also was found to be closely associated with understory environmental conditions and biota, had approximately twice the explanatory power of any of the other three driver sets. Some of the strongest individual drivers were overstory *Acer saccharum* and *Populus tremuloides*, soil pH, mean summer temperature, and mean annual precipitation. Suites of associated drivers included cool, moist, sandy, and acidic conditions; overstory boreal broadleaf species, light availability, shrub abundance, and forb cover; and warm temperatures and graminoid cover. Due to the strong interrelationships among drivers, the direction and rate of forest change will likely depend on how the importance of drivers shifts with climate and, for the biotic drivers, on the rate and magnitude of their own responses to climate change.

Chapter 3 investigated sapling height and radial growth rates of five temperate and boreal species. This study included over 1700 stems of naturally established, competing saplings growing at 14 sites across the temperate-boreal transition zone. Top performing linear mixed-effects models typically included two-way interactions among mean summer temperature, browse pressure, understory light levels, and initial sapling size. As hypothesized, temperate sapling growth increased and boreal growth decreased with increasing temperatures. However, the relative performance of competing species shifted depending on the level of browse pressure. Positive temperate growth responses to temperature were eliminated by heavy browse pressure, tilting growth rates in favor of less palatable boreal conifers at all but the warmest sites. Spatial variations in browse pressure levels across the region suggest that temperate expansion may proceed most rapidly in areas where browsing is least intense. Growth responses to temperature also

varied with sapling size and, for the least shade-tolerant species in the study, *Quercus rubra*, light availability. Enhanced growth by temperate species in response to warmer temperatures was most detectable under favorable conditions including low browse pressure and high understory light availability, suggesting that any efforts to facilitate forest compositional changes will need to take into account these trends.

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CHAPTER 1

**Tree regeneration patterns vary with size class, spatial scale and climate across
ecotonal temperate-boreal forests**

Summary

Temperate and boreal forests are forecast to change in composition and shift spatially in response to climate change. This phenomenon is most likely observable near species range limits in temperate-boreal ecotonal forests. We examined the performance of temperate and boreal tree species in two size classes, seedlings and saplings, and across two spatial scales, local ecotones and the regional transition zone in central North America, to explore indications of climate-mediated shifts in regeneration success. We hypothesized that temperate species should exhibit more positive regeneration success than boreal species across local ecotones due to warming in recent decades and that success would be mediated by regional climate gradients across the transition zone. Because we are comparing understory performance across locally changing overstory composition, we calculated regeneration success as the difference in relative abundance between the understory and overstory layers. At the local scale across ecotones, several temperate species exhibited positive regeneration success and the ability to establish within boreal neighborhoods. In opposition to our hypotheses, boreal *Abies balsamea* also had positive regeneration success across local ecotones and *Picea glauca* was not inhibited from establishing in temperate neighborhoods. At the regional scale, changes in regeneration success were greatest at the warm edge of the transition zone where the performance of boreal *A. balsamea* dropped sharply and temperate *Acer saccharum*, *Fraxinus nigra* and *Ostrya virginiana* responded positively. *Acer rubrum* was the only temperate species showing increased regeneration success at cool sites. Responses to precipitation were generally weak, likely due to recent above average rainfall. Overall,

regeneration performance in ecotonal temperate-boreal forests varied by species, size class, climate regime and spatial scale. Temperate species dominated the seedling layer whereas boreal conifers were most abundant in the sapling layer. Expansions of both temperate and boreal species across local ecotones were mediated by climate at the regional scale with changes in regeneration success strongest at the warm end of the transition zone. Based on this evidence, temperate species will likely be able to replace boreal species across the region with the projected magnitude of 21st Century warming.

Introduction

Understanding and detecting compositional and spatial shifts in ecological communities has become a pressing task given recent and predicted rates of anthropogenic climate change. Numerous studies around the world have detected species-level responses, especially for mobile species with short generation times such as insects and birds (Walther et al. 2002; Parmesan & Yohe 2003). Tree species have much longer generation times and thus evidence of present-day tree-range shifts are only beginning to appear (Lenoir et al. 2009; Beckage et al 2008; Woodall et al. 2009; Feeley et al. 2011). Many tree species are foundation species influencing terrestrial ecosystem functions and services (Ellison et al. 2005; Begon, Townsend & Harper 2006), and a major unknown is whether tree range shifts will be able to keep pace with rapid temperature and precipitation changes. Several modeling efforts predict considerable climate-driven forest shifts by the end of the 21st century (Iverson &

Prasad 1998; Scheller & Mladenoff 2005; Morin, Viner & Chuine 2008). Field based research aimed at early detection of species level responses is needed to assess the direction of forest change and the ability of species to shift their ranges.

Due to the long lifespans of trees and a scarcity of multi-decadal regional forest data, evidence of recent forest shifts remains sparse. Ecologists have had to either look at the few sources of local-scale long-term data (Beckage et al. 2008), or utilize comparisons of understory and overstory species abundances from regional datasets (Lenoir et al. 2009; Woodall et al. 2009; Kharuk, Ranson & Dvinskaya 2007; McEwan, Dyer & Pederson 2011). Given the paucity of long-term data, comprehensive studies of understory performance are needed to document how forests vary in relation to historical climate gradients, whether they are already responding to recent climate change, and to reveal how they will respond to future changes.

Tree seedling establishment and growth into the sapling layer are vital first steps towards capturing future canopy space. Because species have differing functional traits and advance regeneration strategies (Messier et al. 1999; Kneeshaw et al. 2006), understory abundances will vary by species and size class. Traits such as shade-tolerance, palatability, mode of regeneration, and seedbed requirements may impact both size class abundances and sensitivity and detectability of responses to climate. Most previous understory-overstory comparisons only used a single understory size class and thus may not fully capture size class shifts (Lenoir et al. 2009, Woodall et al. 2009, McEwan, Dyer & Pederson 2011; Kharuk, Ranson & Dvinskaya 2007). This research attempts to look at understory-overstory comparisons using two understory

size classes, seedlings (≤ 1 m height) and saplings (> 1 m height & < 10 cm diameter), for more than a dozen co-occurring tree species with differing regeneration strategies.

Vegetation boundaries have been proposed as one of the best places to detect early signs of climate-mediated community shifts (di Castri, Hansen & Holland 1988; Parmesan et al. 2005). Spatial transitions from one ecological community type to another can be divided into two categories, local sharp transitions or ecotones and broad regional shifts or transition zones (di Castri, Hansen & Holland 1988, Goldblum & Rigg 2010). The upper Great Lakes region in North America contains the western portion of the regional temperate-boreal forest transition zone (Pastor & Mladenoff 1992). Within this zone, temperate and boreal tree species reach their northern and southern range limits, respectively, and can be found growing together over a relatively small temperature gradient. In addition, the Great Lakes region is at the western, moisture driven range limit of both forest types, thus facilitating examinations of tree performance response to both temperature and precipitation variables. The broad transition zone is a mosaic of temperate and boreal dominated stands with local ecotones separating these more 'pure' overstory types (Goldblum & Rigg 2010). This mosaic patterning of stands allows for the investigation of tree species performance across two spatial scales, local ecotones and the regional transition zone.

The goal of the present study was to quantify the understory performance of temperate and boreal species across local and regional scales and assess potential responses to recent and future climate change (Fig. 1.1a,b). In order to examine species-level regeneration performance, we evaluated relative abundance trends and compared

differences in relative abundance between the understory seedling and sapling layers and the overstory tree layer. Given the regional warming trend of 1 °C mean annual temperature over the past four decades (Karl, Melillo & Peterson 2009; Kucharik et al. 2010), we hypothesized that temperate tree species will exhibit more positive understory success across local ecotones than boreal species (Fig. 1.1c). Shade-tolerant temperate species would thus be able to establish beneath all overstory types while boreal regeneration should be limited to the boreal end of ecotones. Across the regional transition zone and hence across regional climate gradients, we hypothesized that species regeneration success will display a similar pattern, with boreal species more adversely affected by warm and dry conditions than temperate species.

Materials and methods

STUDY SITES AND EXPERIMENTAL DESIGN

The locations of the 124 ecotone study sites, each with nested plots, span 3 degrees of latitude and 7 degrees of longitude and are spread across a 170,000 km² area of northern Minnesota, Wisconsin and the western end of Michigan's Upper Peninsula, USA (Fig.1). The climate of the region varies from dry continental in the west to lake moderated cool and wet in northeastern Minnesota and northern Michigan. Climate data (1978-2007 averages) for each study site were extracted from PRISM 4 km² resolution climate surfaces (Daly et al. 2008). Annual precipitation (65.5 – 98.6 cm) generally increases from west to east and mean annual temperature (2.5 - 5.6 °C) from north to south. Mean summer temperature, June through August (15.8 - 19.4 °C), has a more

complex pattern with increasing temperatures from north to south in Wisconsin and Michigan and increasing temperatures from northeast to southwest in Minnesota. Recent climate change has not been uniform across the region. Although mean annual temperature has increased roughly 1 °C across the entire region (1968-2007), summer temperatures have warmed significantly more at the warm southern edge (1 °C) than the cool northern edge (0.6 °C) of the transition zone (rates and differences based on linear regression, $P < 0.01$). Annual precipitation over the past 40 years has also only increased significantly at the dry end of the transition zone (62.6 mm) while wet sites have shown no change in precipitation. These trends indicate that the summer temperature gradient has increased while annual precipitation differences have shrunk across the region in recent decades.

Each site contained a gradient in overstory composition (ecotone) from temperate to boreal dominated. In order for a site to be accepted into the study it had to possess four characteristics: 1) contain both temperate and boreal species in the overstory, 2) have an overstory of mature stature and thus have reached the understory reinitiation stage (Oliver 1981), 3) be free from signs of recent human disturbance, especially logging, that might have an unknown or biased effect on the composition and density of tree species in the overstory and understory layers and 4) be situated on an upland site. In order to facilitate overstory to understory comparisons within plot, large overstory gaps were avoided and plots contained a minimum of five overstory trees.

Sites were sampled during the growing season (June-August) 2008-2010. An average of four plots per site were established across each ecotone to capture the full

range of overstory composition, although the number of plots varied between two and seven based on the width of the ecotone and variation in overstory composition. The initial plot was randomly located at one end of the ecotone and subsequent plots placed at 50 m intervals. Overstory, sapling and seedling data were collected within nested circular plots. Tree species density and basal area within the overstory neighborhood were determined from all live stems ≥ 10 cm diameter 1.3 m above ground level (dbh) within the entire 10 m radius plot. Overstory neighborhood patch size within a similar forest type was previously determined to be roughly 10 m in radius (Frelich et al. 1993). Sapling stems, ≥ 1 m in height and < 10 cm dbh, were identified to species and tallied in a 5 m radius subplot centered within the 10 m radius tree plot. We sampled species densities of tree seedlings, > 1 year old (not germinants) and < 1 m in height, in four 1 m radius microplots located within the 5 m radius sapling subplot. Browse damage, mainly by white-tailed deer (*Odocoileus virginianus*) but also including moose (*Alces alces*) and snowshoe hare (*Lepus americanus*), was assessed for each tree species on a four point scale based on the proportion of twigs browsed on understory stems 0.25- 2.0 m in height (Frelich & Lorimer 1985).

Common tree species found across the transition zone are shown in Table 1.1. For analyses, the species *Populus tremuloides* and *Picea glauca* each included closely related species with similar traits such as shade-tolerance and regeneration strategy (see Gleason & Cronquist 1991 for naming authorities). *Populus grandidentata* and *Populus balsamifera* were included with *P. tremuloides* and *Picea mariana* was included with *P. glauca*, although these additional species were infrequent and typically at low density.

We designated each tree species as ‘temperate’ or ‘boreal’ based on northern and southern range limits mapped by Little (1971) and to match designations used in other studies (Pastor & Mladenoff 1992). Species varied widely in observed browse damage, with the boreal conifers having the lowest levels of browse and temperate species generally exhibiting higher damage. The two most heavily browsed species, *Quercus rubra* and *Fraxinus nigra*, on average had browse damage on more than two-thirds of their branches. Although most of the study species are capable of some form of vegetative reproduction, only four species were regularly observed as basal sprouts or root suckers.

For analyses, we assigned plots to one of three overstory community types, temperate, mixed or boreal, based on the relative abundance of temperate and boreal tree species in the overstory. Temperate overstories had > 67% temperate species, boreal overstories had > 67% boreal species and mixed plots had less than two-thirds of either species group. Data from plots within each site with the same overstory type were averaged together, resulting in 243 plots at 125 sites. Not all sites had all overstory types owing to either very sharp ecotones or an incomplete shift in overstory composition.

STATISTICAL ANALYSES

The species included in analyses were each present in at least 10 plots per overstory type (Table 1.1). The most common species, present in more than 60% of plots, included two boreal broadleaf species, *Populus tremuloides* and *Betula papyrifera*, two boreal conifers, *Picea glauca* and *Abies balsamea*, and two temperate

broadleaf species, *Acer saccharum* and *Acer rubrum*. The performance of each tree species was based on its relative abundance in each of the three size classes. Species' seedling and sapling relative abundances were calculated as the relative density of stems in each size class within a plot. For overstory trees we used the importance value, calculated as the average of relative density and relative basal area, as it moderates the differences between abundant small diameter trees that dominate the relative density metric and individual large diameter trees that dominate plot basal area. Because plots were placed across ecotonal boundaries as defined by overstory composition, a measure of regeneration success for seedlings and saplings was calculated for each species which simultaneously takes into account both understory and overstory relative abundance (Fig. 1.1). Regeneration success is defined as the difference in relative abundance between each individual understory layer and the overstory tree layer. Thus seedling and sapling regeneration success varied between -1 and +1 and was calculated only from plots where the species was present in at least one size class. Regeneration success defined in this fashion has two advantages over using understory density values: 1) it facilitates the direct comparison of species level success across ecotones by incorporating overstory relative abundance shifts within the measurement; and 2) unlike stem density which has a large number of zeros and skewed distribution, regeneration success has a reasonably normal distribution which permits the use of parametric statistical tests. Other analyses (Chapter 2) found overstory composition to be the strongest driver of tree regeneration within ecotonal stands and thus by controlling for overstory abundance within our regeneration success measure we can more adequately

compare understory performance across plots and sites with differing overstory abundances.

Local ecotone hypotheses of relative abundance and regeneration success differences across overstory types and size classes were examined with mixed model ANOVAs. All ANOVA tests included site or plot nested within site as random effects to account for the hierarchical sampling structure and analyses were carried out using the ‘nlme’ package (v. 3.1) (Pinheiro et al. 2009) in R (v. 2.12) (R Development Core Team 2008).

Finally, we contrasted site level regeneration success at the edges of the transition zone to examine indications of climate-mediated shifts in performance near range limits. For each species, we compared the coldest and warmest and wettest and driest 20% of sites and also included the middle 20% to study whether trends varied continuously across the region or if there were indications of nonlinear thresholds. Using a multivariate analysis of tree regeneration drivers, we found mean summer temperature (June-August) and mean annual precipitation to be the two most significant climate variables driving tree regeneration (Chapter 2), thus these two factors were used for categorizing sites. Utilizing the outer and middle 20% of sites was a best compromise between capturing trends at the extremes of the climate gradients and having sufficient sample sizes for analyses. Furthermore, using a similar ANOVA framework and number of category levels at local and regional scales permits a more straightforward comparison of trends at differing spatial scales.

Results

RELATIVE ABUNDANCES

Tree, sapling and seedling relative abundance trends across local ecotones are shown in Fig. 1.2. Understory relative abundances varied significantly by overstory type for three species and by size class for nine out of the twelve species (Table S1.1). There was no significant interaction between size class and overstory type for any species. The three species showing understory shifts across local ecotones were *Abies balsamea* ($F_{2,100} = 4.70$, $P = 0.01$), *Acer rubrum* ($F_{2,98} = 5.64$, $P = 0.005$) and *Acer saccharum* ($F_{2,89} = 14.54$, $P < 0.0001$). *Acer saccharum* understory relative abundance increased from the boreal to temperate end of ecotones while the other two species had greatest relative abundance beneath boreal overstories. *Abies balsamea* and *A. saccharum* understory relative abundances paralleled tree layer values across ecotones while *A. rubrum* showed opposing relative abundance trends between the understory and overstory layers.

Size class differences in relative abundance were found for species from both biomes and with both leaf types (Fig. 1.2, Table S1.1). The boreal conifers *A. balsamea* and *P. glauca* and temperate broadleaf *O. virginiana* had significantly higher sapling than seedling relative abundances ($F_{1,218} = 86.26$, $P < 0.0001$; $F_{1,155} = 30.00$, $P < 0.0001$; and $F_{1,78} = 38.62$, $P < 0.0001$; respectively). Species relatively more abundant in the seedling than sapling layer included the three most abundant temperate species, *A. rubrum*, *A. saccharum* and *F. nigra* ($F_{1,215} = 195.86$, $P < 0.0001$; $F_{1,183} = 24.66$, $P < 0.0001$; and $F_{1,88} = 30.83$, $P < 0.0001$; respectively).

LOCAL ECOTONE REGENERATION SUCCESS

Species regeneration success values varied significantly by overstory type for six species and by size class for five species (Fig. 1.3), but there was no interaction, indicating that the direction of trends was similar across ecotones though often at strongly differing size class values (Table S1.2).

Regeneration success for both of the early-successional boreal broadleaf species was increasingly poor as neighborhoods became more boreal (*B. papyrifera*, $F_{2,53} = 12.57$, $P < 0.0001$ and *P. tremuloides*, $F_{2,59} = 12.57$, $P < 0.0001$), but trends did not differ by size class for either species (Fig. 1.3a,b). Not surprisingly for these shade-intolerant species, regeneration success was neutral or negative in all contexts. The strongly negative success for these two species in mixed and boreal dominated plots emphasizes their regeneration failure and the positive regeneration success opportunities for more shade-tolerant species in boreal neighborhoods.

The two boreal conifers differed markedly in response (Fig. 1.3c,d). *Abies balsamea* regeneration success did not differ across local ecotones ($F_{2,100} = 0.80$, $P = 0.45$) although success varied strongly by size class ($F_{1,206} = 128.53$, $P < 0.0001$), with neutral success in the seedling layer and strongly positive success in the sapling layer. In contrast, *P. glauca* generally had negative regeneration success values that decreased towards the boreal end of ecotones ($F_{2,59} = 10.78$, $P = 0.0001$) and were poorer for seedlings than saplings ($F_{1,142} = 19.49$, $P < 0.0001$). These results suggest that locally, boreal conifer regeneration was not limited to the boreal end of ecotones and that performance increased from the seedling to sapling layer.

The two most frequent temperate species, *A. rubrum* and *A. saccharum*, exhibited similar shifts in success by overstory type and size class, but at differing success levels (Fig. 1.3e,f). Regeneration success increased significantly from temperate to boreal overstories for both *A. rubrum* ($F_{2,98} = 44.03$, $P < 0.0001$) and *A. saccharum* ($F_{2,89} = 3.15$, $P = 0.05$). This trend was very strong for *A. rubrum* as success changed from negative to positive across ecotones. *Acer saccharum* showed a smaller increase in success by overstory type and with values always positive or neutral. Regeneration success was also significantly greater in the seedling than sapling layer for both *A. rubrum* ($F_{1,192} = 131.94$, $P < 0.0001$) and *A. saccharum* ($F_{1,168} = 20.95$, $P < 0.0001$). Again, this trend was stronger for *A. rubrum* with more negative success values in the sapling layer and positive values in the seedling layer. Although success varied by species and size class, neither maple was inhibited from establishing in boreal neighborhoods.

Other temperate species with positive regeneration success included *F. nigra* and *O. virginiana* (Fig. 1.3). *Fraxinus nigra* regeneration indicated trends towards higher success beneath boreal overstories ($F_{2,29} = 2.51$, $P = 0.10$) and greater success in the seedling layer ($F_{1,56} = 3.99$, $P = 0.051$). *Ostrya virginiana* exhibited significantly higher regeneration success in the sapling than seedling size class ($F_{1,59} = 34.67$, $P < 0.0001$) but values did not change across ecotones ($F_{2,21} = 0.56$, $P = 0.58$).

Three temperate broadleaf species with low, often negative regeneration success that did not differ by size class were *B. alleghaniensis*, *Q. rubra* and *Tilia americana* (Fig. 1.3g,k,l). The success of *B. alleghaniensis* did not vary by overstory type ($F_{2,17} =$

1.11, $P = 0.35$) while both *Q. rubra* and *T. americana* had better regeneration success with increasing boreal overstory abundance ($F_{2, 36} = 3.24$, $P = 0.051$ and $F_{2, 19} = 10.59$, $P = 0.0008$, respectively).

REGIONAL CLIMATE-MEDIATED REGENERATION SUCCESS

Comparisons of site level regeneration success at the edges and middle of the transition zone revealed responses to climate for several species, though interactions between climate and size class were generally weak (Figs 1.4 and 1.5, Tables S1.3 and S1.4). Within the set of boreal species, the understory-abundant *A. balsamea* responded to both climate variables. Success was poorest at warm sites ($F_{2,67} = 8.50$, $P=0.0005$) and there was some evidence, though marginally significant, of an interaction between temperature and size class ($F_{2,67} = 2.48$, $P=0.09$) (Fig. 1.4a). Response to precipitation also indicated poorest performance at dry sites ($F_{2,67} = 3.58$, $P=0.03$) (Fig. 1.5a). The other boreal conifer, *P. glauca*, did not show a detectable response to temperature ($F_{2,55} = 0.28$, $P=0.75$) (Fig 4b) but did exhibit a weak interaction between precipitation and size class ($F_{2,54} = 2.92$, $P=0.06$) indicating better performance of saplings at drier sites. The boreal broadleaf species, *B. papyrifera* and *P. tremuloides*, did not show significant responses to either climate variable.

For the temperate group, five out of eight species had significant regeneration success relationships with climate (Figs 1.4 and 1.5, Tables S1.3 and S1.4). The four most abundant temperate species responded to summer temperature. *Acer rubrum* was the only temperate species to have greatest regeneration success at cool sites ($F_{2,68} = 3.49$, $P=0.04$) (Fig. 1.4c). In contrast, *Acer saccharum* and *F. nigra* each displayed a

positive relationship with temperature ($F_{2,53} = 3.49$, $P=0.01$ and $F_{2,32} = 3.75$, $P=0.03$, respectively) while *O. virginiana* had a significant interaction between size class and temperature ($F_{2,27} = 5.46$, $P=0.01$) with saplings at warm sites showing the strongest performance (Fig. 1.4d,e,f). The only temperate species with a strong response to precipitation was *A. rubrum* with highest regeneration success at dry sites ($F_{2,68} = 6.43$, $P=0.003$) (Fig. 1.5b). The less abundant *B. alleghaniensis* had poorest response to precipitation at mid sites ($F_{2,25} = 3.48$, $P=0.05$) while *T. americana* interaction between size class and precipitation indicated a weak trend towards greater success by seedlings at wet sites ($F_{2,16} = 2.95$, $P=0.08$).

Discussion

Establishment and persistence of seedlings and saplings are early, yet crucial, steps in forest development and successional change. The research presented here indicates that understory performance, as measured via relative abundance and regeneration success values, in ecotonal temperate-boreal forests varies by species, size class, climate regime and spatial scale. By specifically sampling multiple local ecotones along regional temperature and precipitation gradients, we were able to detect regeneration responses to climate and show that ecotonal forests in this region are likely very sensitive to climate change and are simultaneously exhibiting signs of local expansion and regional shifts in composition. Using the overstory as a baseline, we found that many species, especially abundant ones such as *Abies balsamea*, *Acer rubrum* and *Acer saccharum*, are not inhibited from establishing across local ecotonal

boundaries. Furthermore, performance shifted at larger spatial scales in response to climate with the sharpest changes in regeneration success generally at the warm end of the transition zone. Other species, such as *Populus tremuloides*, failed to exhibit detectable shifts in regeneration across regional climate gradients possibly due to functional traits, including mode of regeneration, seedbed requirements, and other factors, such as browse pressure, having a greater impact on performance. Transition zone forests are forecast to have dramatic compositional shifts by the end of the current century and this research provides an early indication of species likely sensitive to climate change.

ASSESSING HYPOTHESES

Regeneration success of temperate and boreal species both supported and refuted our hypotheses of local and regional shifts in understory performance. Since regeneration success was defined on the basis of understory and overstory relative abundances, high overstory abundance and low regeneration density of boreal *Betula papyrifera*, *Populus tremuloides* and *Picea glauca* created opportunities for positive temperate seedling and sapling regeneration success within boreal neighborhoods. The high regeneration success of *A. rubrum*, *A. saccharum*, *Fraxinus nigra* and *Prunus serotina* within boreal neighborhoods supported our hypothesis of temperate species expanding across local ecotones. On the other hand, higher than predicted success by boreal species in temperate neighborhoods failed to support our hypothesis of boreal regeneration failure and local boreal forest retraction due to the warming trend of the

past 40 years. These results indicate a potential for more mixing of temperate and boreal species in the near-future and thus the expansion of ecotonal stands at the local scale.

The findings of our local ecotone research from a single sampling of trends that have developed over an approximate 20 year period (based on average seedling and sapling age) are comparable to other studies in similar forest types. Two prior studies in the region (Maycock & Curtis 1960; Buell & Martin 1961) also found abundant temperate seedlings in ecotonal stands. The Buell & Martin study, at a single site at the warm and dry end of the transition zone, spanned two decades and documented a resulting spatial shift in the local ecotonal boundary due to temperate expansion and failure of boreal conifers to regenerate. Our findings are also comparable to a more recent long-term ecotone study by Beckage et al. (2008) that solely measured shifts in overstory composition. Our species level regeneration success trends were similar in direction to the change in overstory basal area detected over a 40 year period in that study. Positive regeneration success by *A. saccharum* and *A. balsamea* were similar to the increases in overstory basal area of these two species in the long-term study. The negative regeneration success of *P. glauca* corresponded with a decrease in basal area of the closely related *Picea rubens*. The parallel trends by shade-tolerant species in these studies suggest that regeneration success may be a suitable metric for assessing performance across temperate-boreal ecotones.

At the regional scale, we detected shifts in species performance mostly in line with our climate-mediated hypotheses. For most species, regeneration success was similar at mid and cool sites but differed significantly at the warm edge of the transition

zone. For example, regeneration success of the understory abundant boreal *A. balsamea* declined sharply at warm sites and this trend was somewhat more pronounced for saplings than seedlings. Three relatively abundant temperate species *A. saccharum*, *F. nigra* and *Ostrya virginiana* had positive responses to temperature and appear to be filling the understory niche left vacant by poor *A. balsamea* performance at warm sites. This finding is similar to those from other regional studies of understory performance that found species-level seedling abundances to be shifted north or higher in elevation when compared with overstory abundances (Woodall et al 2009, Lenoir et al. 2009). Lower regeneration success (though always neutral to positive) at cool sites by these temperate species also suggests that their performance is constrained by low summer temperatures. On the other hand, *A. rubrum* showed no temperature constraint and in fact had a strong increase in regeneration success at cool sites. Other factors such as higher understory light levels at cooler sites may be more important for *A. rubrum* success than temperature. Although our research was conducted at the western end of the temperate-boreal transition zone near the prairie-forest border, responses to the precipitation gradient were generally weak, with only two species showing significant responses to dry conditions. This was likely due to the relatively wet conditions, especially at the dry end of the region over the past 30 years (Karl, Melillo & Peterson 2009).

SIZE CLASS TRENDS

Several species showed significant differences in performance by size class, indicating that the choice of size classes included in analyses can influence

interpretations, although trends across local ecotones were always in the same direction and regionally no species exhibited opposing success responses to temperature or precipitation in the two size classes. Performance shifts by size class can perhaps be explained by underlying functional traits such as evergreen foliage, shade-tolerance and palatability. Relative abundance increased from the seedling to sapling layer for *A. balsamea*, *P. glauca* and *O. virginiana* which are all shade-tolerant and non-preferred browse species. Additionally, two of these species are evergreen and greater performance in the sapling layer may be due in part to the compounding photosynthetic area from multiple cohorts of evergreen needles (Lusk 2002) and the persistence of these needle cohorts due to very low levels of browse damage. Characteristics of species with greater seedling than sapling relative abundances include mid shade-tolerance, heavy browse damage and frequent seed crops. These species, such as *A. rubrum*, *F. nigra* and *Q. rubra*, likely are able to establish from seed in most years but are unable to persist in the taller size class due to the shady conditions and over-abundant deer populations (Côté et al. 2004).

FUTURE FORESTS

Tree response to temperature and precipitation ranges across the transition zone can be compared to projected climate change, although they can not be considered a direct substitute and should be considered as a rough guide only after careful consideration of potential caveats. The differences in mean annual temperature, 3.1 °C, and summer temperature, 3.6 °C, between the cold and warm ends of the temperate-boreal transition zone are at the conservative to moderate end of projected warming by

century's end (Christensen et al. 2007; Wuebbles & Hayhoe 2004). Under moderate projections, conditions and species level performance at the warm end of the transition zone will shift north to locations even beyond the current northern limits of ecotonal stands. Our results suggest that the success of temperate species, such as *A. saccharum*, *F. nigra* and *O. virginiana* should increase and that of boreal species such as *A. balsamea* to decrease under this warming scenario. *Acer rubrum* seems especially poised to increase in the future overstory due to its positive performance in boreal neighborhoods, and current high regeneration success at the dry and cool edges of the transition zone.

The lack of a detectable shift in performance by some species implies that a climate threshold was not reached or that other factors currently have much greater impact on performance and in either case larger changes in climate will be required before responses become evident. One such factor that likely affects regeneration sensitivity to climate and potential future forest composition is mode of regeneration, whether vegetative or from seed. New germinants only have the stored energy present in the seed and must quickly grow a sufficient root system and canopy of leaves in order to acquire necessary resources. In contrast, vegetative resprouts have a pre-existing root system and comparably large quantity of stored energy on which to initially rely and buffer against harsh climatic conditions. For example, the abundant *P. tremuloides* regeneration, primarily from root sucker sprouts, did not vary in relative abundance across local ecotones and regeneration success does not appear to be closely tied to the current climatic conditions found across the transition zone. *Populus tremuloides* can

replace itself vegetatively for several centuries (Barnes 1966), long after the climatic conditions needed for regeneration from seed have shifted beyond current range limits (Mitton & Grant 1996). Thus, species that rely at least partially on vegetative reproduction may remain in transition zone forests long after the climate prohibits successful regeneration from seed.

Overall, this research suggests that tree species growing in ecotonal stands across the temperate-boreal transition zone are sensitive to climate at early stages of development and several species are already showing shifts in understory abundance in the direction predicted in response to climate change. Our regeneration success metric likely underestimates sensitivity to regional climate gradients because it only reflects a regeneration response to climate after controlling for the covarying relationships between overstory relative abundance and climatic factors. Whether species response rates and canopy turnover are adequate to keep pace with a rapidly changing climate remain to be seen. Eventual ascension into the canopy depends on many other factors such as the type, size and severity of disturbance. Species specific canopy turnover rates will also influence the direction and rate of forest change. Species able to persist in the overstory for long periods such as *A. saccharum* and *P. glauca* require less frequent replacement than shorter-lived species such as *A. balsamea* and *P. tremuloides* (Kneeshaw & Prevost 2007). Thus, regeneration success may overestimate performance for short-lived species and underestimate success for long-lived trees. Insects, disease and nonnative species, which are themselves responding to a changing climate, may dramatically alter the current forest trajectory (Lovett et al. 2006, Frelich & Reich

2010). Further research is needed to address these issues and continue tracking shifts in forest composition.

Table 1.1. Common tree species present in greater than 10 plots per overstory type in ecotonal temperate-boreal forests of the upper Great Lakes region, USA. Shade-tolerance ratings are based on Burns & Honkala 1990. Browse index is based on the observed proportion of browse damaged branches (see Methods). Regeneration mode is based on observations of stems in plots.

Scientific name	Biome	Leaf-Type	Shade-Tolerance‡	Browse-Index¶	Regeneration Mode	Presence in Overstory Type		
						Temperate (n=68)	Mixed (n=85)	Boreal (n=90)
<i>Betula</i>								
<i>papyrifera</i>	Boreal	Broadleaf	4	1.7	Both	23	56	68
<i>Populus</i>								
<i>tremuloides*</i>	Boreal	Broadleaf	5	1.2	Vegetative	21	62	74
<i>Abies</i>								
<i>balsamea</i>	Boreal	Conifer	1	0.3	Seed	57	76	88
<i>Picea glauca†</i>	Boreal	Conifer	2	0	Seed	36	57	65
<i>Acer rubrum</i>	Temperate	Broadleaf	2	2.0	Both	58	76	84
<i>Acer</i>								
<i>saccharum</i>	Temperate	Broadleaf	1	1.9	Seed	62	65	59
<i>Betula</i>								
<i>alleghaniensis</i>	Temperate	Broadleaf	3	1.8	Seed	31	22	15
<i>Fraxinus nigra</i>	Temperate	Broadleaf	3	2.3	Seed	25	36	30
<i>Ostrya</i>								
<i>virginiana</i>	Temperate	Broadleaf	1	1.0	Seed	34	29	18
<i>Prunus</i>								
<i>serotina</i>	Temperate	Broadleaf	3	0.8	Seed	23	28	25
<i>Quercus rubra</i>	Temperate	Broadleaf	3	2.4	Seed	30	36	35
<i>Tilia</i>								
<i>americana</i>	Temperate	Broadleaf	2	1.9	Both	24	24	16

* includes *Populus grandidentata* and *Populus balsamifera*

† includes *Picea mariana*

‡ from 1-very tolerant to 5-very intolerant

¶ from 0-low to 3-high browse damage

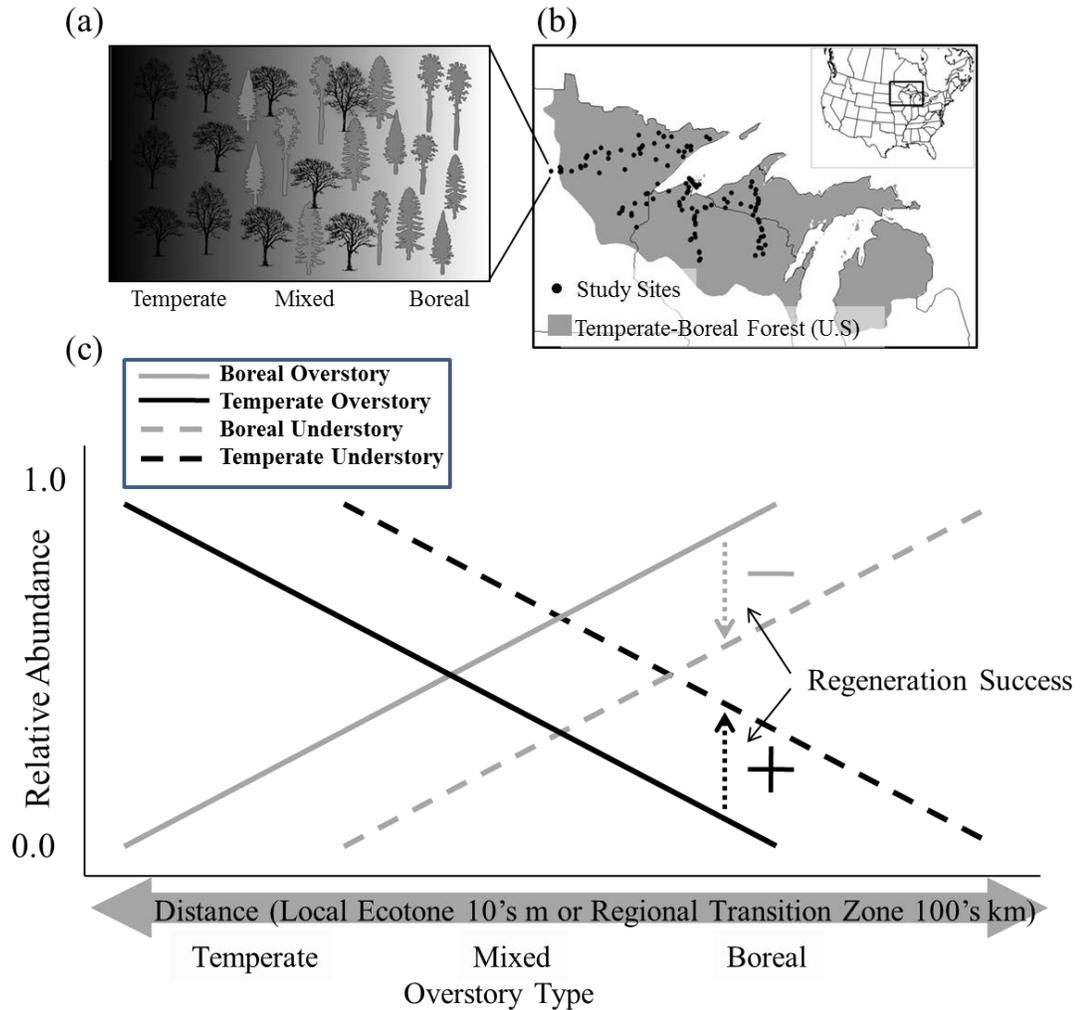


Figure 1.1. Ecotone studies are undertaken at two spatial scales: (a) local ecotones (10's m) and (b) the regional transition zone (100's km). (c) Hypothesized relative abundance shifts (expansion by temperate species and retraction of the boreal forest) between the overstory and understory for temperate and boreal species at all spatial scales. Species level performance, here named regeneration success, is the difference in relative abundance between the understory and overstory layers. Study site locations in the upper Great Lakes region, USA, are shown in the inset map.

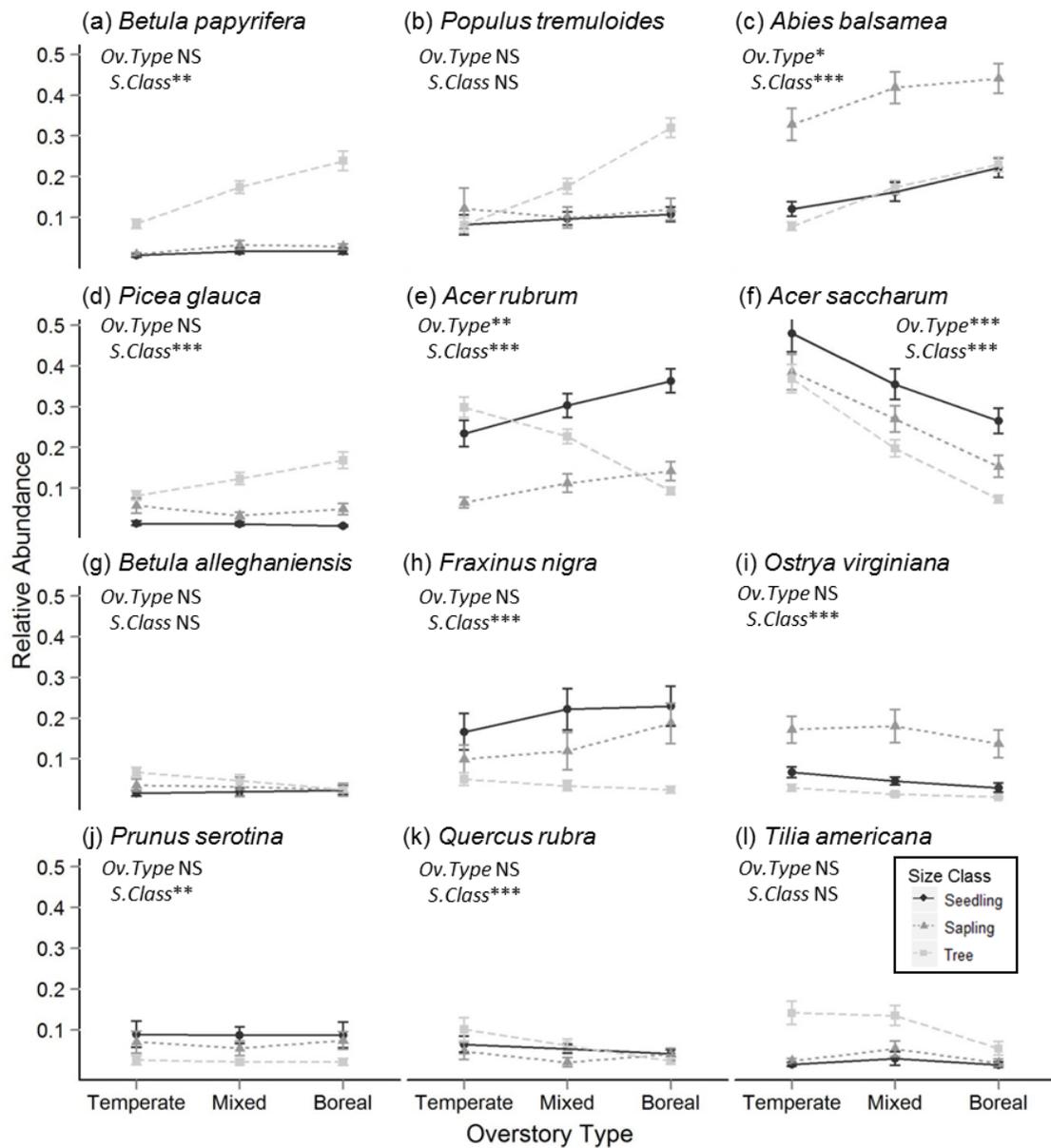


Figure 1.2. Species relative abundance by size class across ecotonal stands. Data are from temperate-boreal forests of the upper Great Lakes region, USA. Overstory type is based on relative abundance of temperate and boreal species in the tree layer. See text for size class and relative abundance classifications. Error bars are ± 1 standard error.

Ov.Type = overstory type. S.Class = size class. NS P-value > 0.05, *P-value < 0.05,
P-value < 0.01, *P-value < 0.001.

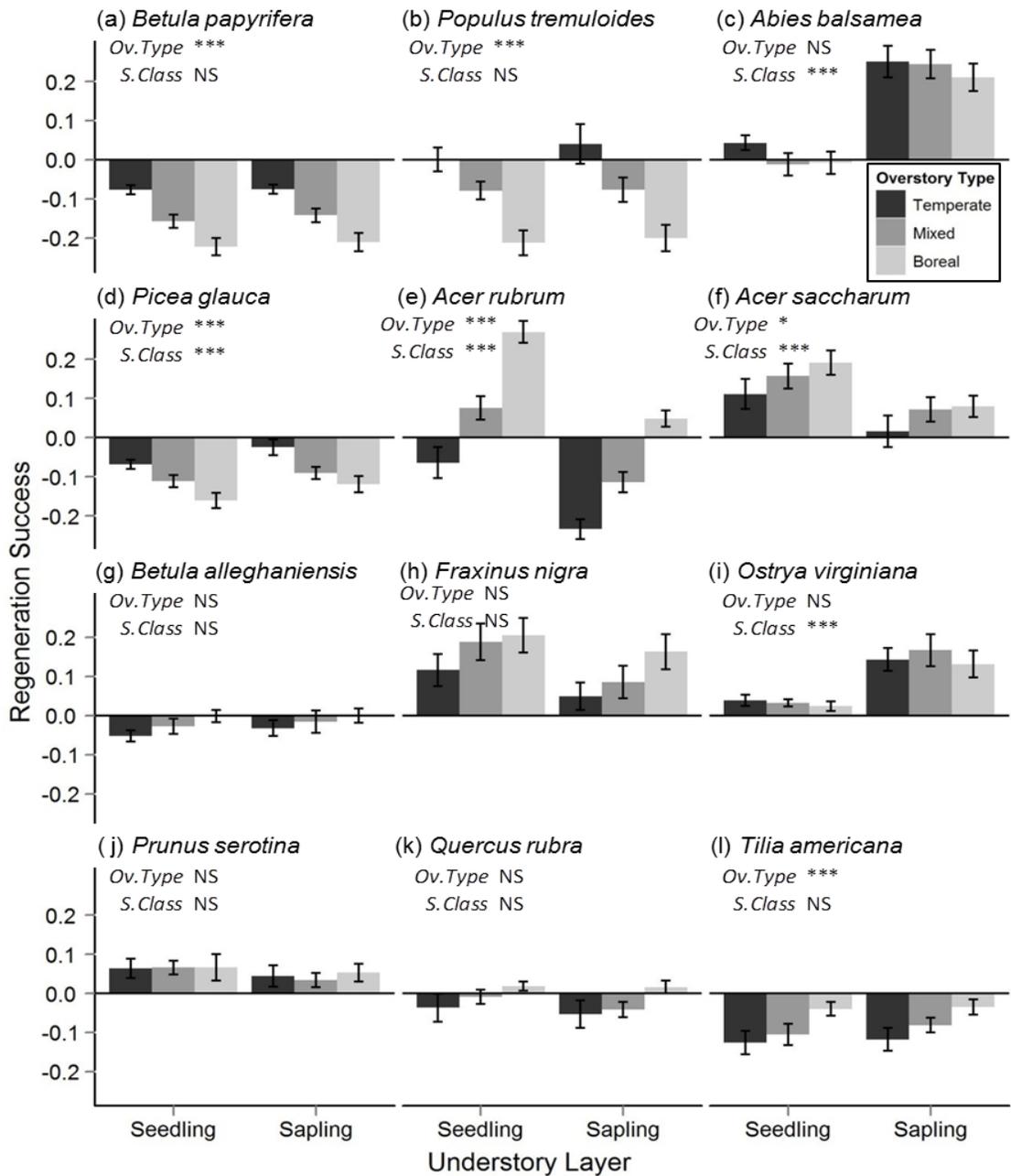


Figure 1.3. Regeneration success (defined as the difference in relative abundance between the understory and overstory) for seedlings and saplings across local ecotones. Data are from temperate-boreal forests of the upper Great Lakes region, USA. See text for size class and relative abundance classifications. Error bars are ± 1 standard error.

Ov.Type = overstory type. S.Class = size class. NS P-value > 0.05, *P-value < 0.05,
P-value < 0.01, *P-value < 0.001.

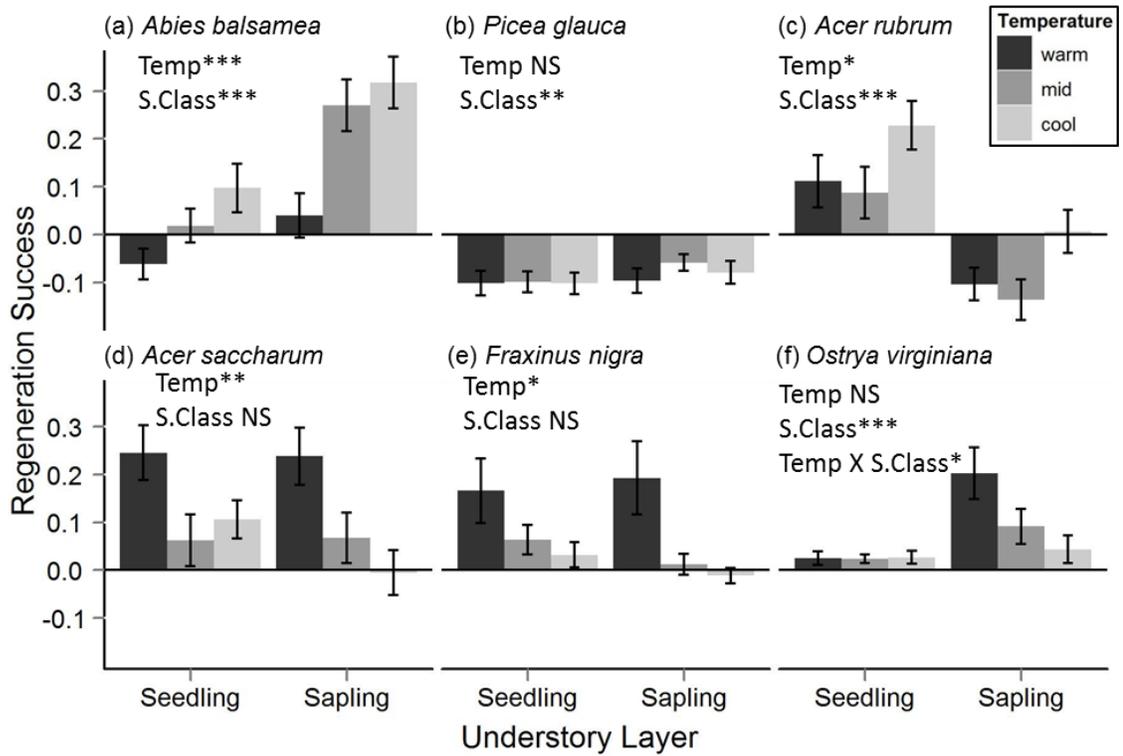


Figure 1.4. Regeneration success (defined as the difference in relative abundance between the understory and overstory) for seedlings and saplings across the regional transition zone by summer temperature classes. Data are from temperate-boreal forests of the upper Great Lakes region, USA. See text for size class and relative abundance classifications. Error bars are ± 1 standard error. Ov.Type = overstory type. S.Class = size class. NS P-value > 0.05 , *P-value < 0.05 , **P-value < 0.01 , ***P-value < 0.001 .

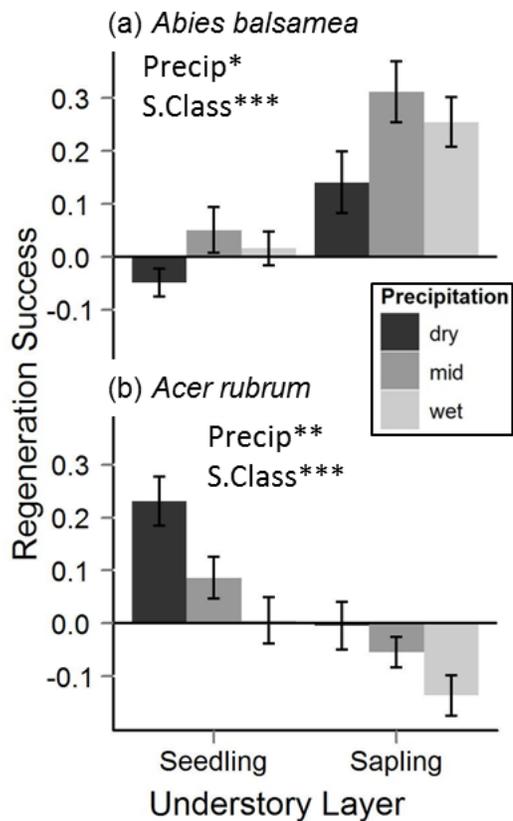


Figure 1.5. Regeneration success (defined as the difference in relative abundance between the understory and overstory) for seedlings and saplings across the regional transition zone by annual precipitation classes. Data are from temperate-boreal forests of the upper Great Lakes region, USA. See text for size class and relative abundance classifications. Error bars are ± 1 standard error. Ov.Type = overstory type. S.Class = size class. NS P-value > 0.05, *P-value < 0.05, **P-value < 0.01, ***P-value < 0.001.

CHAPTER 2

**Partitioning among climate, overstory composition, and understory drivers of tree
regeneration in ecotonal temperate-boreal forests**

Summary

Forest compositional shifts in response to climate change are likely to be initially detectable along ecotonal boundaries where different community types border one another. Furthermore, early signs of forest change should be manifest in the understory tree regeneration layer. Because many other factors in addition to climate, such as seedbed and soil characteristics of the understory environment, overstory composition, and interactions with other understory biota, drive tree regeneration trends, a thorough understanding of the relative importance of all tree regeneration drivers as well as their interrelationships within ecotonal forests is needed. The range limits of several widespread temperate and boreal tree species overlap in the upper Great Lakes region, USA, thus facilitating an observational study over relatively short regional climate gradients to examine the role of climate and other drivers in ecotonal temperate-boreal stands. We used redundancy analysis (RDA) and variation partitioning to quantify the unique, shared, and total explanatory power of tree regeneration drivers. The results showed that all four driver sets (climate 9.5%, understory environment 13.7%, overstory composition 26.3%, and understory biota 13.8%) individually explained a significant portion of tree regeneration compositional variation. Among the strongest individual drivers were overstory *Acer saccharum* and *Populus tremuloides*, soil pH, mean summer temperature, and mean annual precipitation. Partitioning also revealed high confounded or shared explanatory power among driver sets (39-78%), but also that each set contributed significant unique explanatory power not shared with other drivers (22-61%). Suites of associated drivers included cool, moist, sandy, and

acidic conditions; overstory boreal broadleaf species, light availability, shrub abundance, and forb cover; and warm temperatures and graminoid cover. Future forest shifts will depend not only on the rate and direction of climate change but also on the magnitude of interrelationships and responses of other drivers, such as overstory composition and understory biota, to climate change.

Introduction

Tree regeneration layer composition is driven by numerous interrelated and covarying biotic and abiotic ecosystem drivers (Grubb 1977, Arian and Lechowicz 2002, Pickett et al. 2009, McEwan et al. 2011). These factors can be grouped into logical driver sets, such as climate, overstory composition, abiotic understory environment, and understory biota, which due to their interrelationships have varying degrees of overlapping influence on tree regeneration.

For example, climate directly impacts germination, growth, and survival and indirectly affects tree regeneration through its relationships with the other driver sets (Barnes et al. 1998). The composition of the overstory, which itself varies with climate, directly influences propagule availability and strongly affects understory processes and properties including nutrient availability, seedbed conditions, and amount and timing of shading (Frelich et al. 1993, Canham et al. 1994, Finzi et al. 1998a,b). The abiotic understory environment, including seedbed type, soil texture and pH, and light availability, drives not only tree regeneration but also the composition of competing

vegetation layers (Canham et al. 1996, Walters and Reich 1996, Demers et al. 1998). The range of abiotic conditions, such as soil texture, over which a forest type occurs, is partially determined by climate (Henne et al. 2007). Understory biota includes herbaceous and shrub layers and selective browse pressure, for example by white-tailed deer (*Odocoileus virginianus*), that act as filters determining which tree species are able to successfully compete and survive in the regeneration layer (Frelich and Lorimer 1985, Royo and Carson 2006) and that are themselves simultaneously responding to the same conditions as the regeneration layer.

Each driver set can thus be characterized as having both unique influences on tree regeneration that cannot be attributed to other factors and shared explanatory power due to confounded relationships. Regeneration drivers, due to their filtering effects at early stages of development, can have long-term impacts on forest composition and thus understanding the unique and shared explanatory power of these driver sets is critical to estimating compositional shifts within forest types forecast to be sensitive to climate change (Pastor and Post 1988, Prentice et al. 1991, Frelich and Reich 2010).

Climate-mediated changes in forest composition are most likely to be first detected along ecotonal boundaries where vegetation shifts from one community type to another (di Castri et al. 1988). The upper Great Lakes region in North America contains a broad forest transition zone where temperate and boreal tree species reach their northern and southern limits, respectively. Within this zone, the landscape is a mosaic of temperate, boreal, and mixed or ecotonal stands (Pastor and Mladenoff 1992, Goldblum and Rigg 2010). Because ecotonal temperate-boreal forests include species at

or near their temperature and moisture driven range limits, small changes in climate are forecast to have major effects on composition, with tree species shifting their range limits north and east (Iverson and Prasad 1998, Scheller and Mladenoff 2005, Frelich and Reich 2010). However, due to the complex role of climate within ecosystems, determining the influence of climate on tree regeneration has been difficult to ascertain. Furthermore, most research on forest dynamics and underlying drivers has focused on ‘pure’ or ‘homogeneous’ temperate or boreal stands (Forcier 1975, Runkle 1981, Frelich and Reich 1995, Kneeshaw and Bergeron 1996), and far fewer studies have specifically targeted ecotonal stands (Buell and Martin 1961, Barras and Kellman 1998, Diochon et al. 2003, Kneeshaw and Prevost 2007). Quantifying the interrelated roles of tree regeneration drivers within ecotonal temperate-boreal stands is needed in order to better understand which factors are determining composition at vegetation boundaries, especially in light of global change concerns.

The roles of regeneration drivers are often examined independently from one another, however as mentioned above, these drivers are simultaneously responding to one another as well as to other often unmeasured factors. Too much emphasis can be placed on single factors when in reality other covarying factors may at least be partially driving trends. Within observational datasets, this lack of independence among drivers and thus multicollinearity can result in inaccurate and statistically invalid models that exclude important predictor variables (Legendre and Legendre 1998, Graham 2003). There are three main ways to deal with this issue in ecological studies, stratify sampling to minimize confounding, remove collinear variables from models, or purposefully

explore the relationships among drivers and their unique and shared explanatory power (Graham 2003, Borcard et al. 1992). In the present research we undertake both of the latter two methods in order to examine and quantify the explanatory relationships among tree regeneration drivers and then find the parsimonious model that explains understory trends.

The objective of this study was to test the relative importance of tree regeneration drivers within ecotonal temperate-boreal forests. By simultaneously studying four driver sets: climate, abiotic understory environment, overstory composition, and understory biota, we can disentangle and quantify the unique, shared, and total variation in understory composition explained by each driver set. We specifically sampled sites across the northern, southern, and western limits of ecotonal stands in the Great Lakes region of North America to test the hypothesis that tree regeneration composition is sensitive to temperature and precipitation, to assess the degree of overlap in explanatory power among driver sets, to examine the individual drivers that are covarying, and finally to build the most parsimonious model that explains tree regeneration composition of ecotonal temperate-boreal stands.

Materials and methods

STUDY SITES AND EXPERIMENTAL DESIGN

Ecotonal temperate-boreal forest stands were sampled at 124 sites over a three year period (2008-2010) across a 170,000 km² area in northern Minnesota, Wisconsin, and the Upper Peninsula of Michigan, USA (Fig. 2.1a). Within this region, ecotonal

stands are typically narrow bands situated between larger tracts of separate temperate and boreal dominated stands. Selection criteria for study sites included mature, upland forest with established advance regeneration and overstory composition of both temperate and boreal tree species. Stands were typically of second-growth origin, having been harvested 70-100 years ago. There were on average four plots per site, placed at 50 m intervals, designed to capture variation in overstory composition across ecotones. Tree stems were sampled by size class within nested plots. Overstory trees, ≥ 10 cm dbh (diameter at breast height, measured at 1.3 m above the ground surface), were measured within a 10 m radius plot. This plot size was found to capture the local overstory neighborhood area of influence in a similar forest type (Frelich et al. 1993). Understory stems, older than first year germinants and < 10 cm dbh were tallied within a 5 m radius subplot centered inside the overstory plot.

Understory tree regeneration drivers were a priori divided into four explanatory data sets, climate, abiotic understory environment (hereafter referred to as understory environment), overstory composition, and understory biota, based on previous knowledge regarding similarities in the scale and role of individual drivers (Table 2.1). Earthworm disturbance severity was included in the understory environment driver set because nonnative earthworms strongly affect the seedbed environment, specifically the presence and depth of the organic and upper mineral soil horizons (Frelich et al. 2006, Eisenhauer et al. 2007), and thus provide an integrated measure of environmental conditions at the forest floor. The spatial patterning of selected drivers is shown in Fig. 2.1b-1. As weather stations are not available near most study sites, climate data were

extracted from PRISM interpolated climate surfaces (Daly et al. 2008). Five climate variables (1978-2007 averages) considered a priori as likely biologically influential were included as potential drivers: mean annual precipitation, mean summer precipitation (June-August), mean annual temperature, mean summer temperature (June-August), and mean minimum January temperature.

Although the upper Great Lakes region lacks mountain ranges that could create sharp temperature or precipitation gradients, the climate nevertheless exhibits complex patterns due in part to the large lakes themselves. In general, the climate grades from dry and continental to wet and temperate from west to east across the region, however these patterns vary by season. For example, annual precipitation (655-987 mm) increases from west to east while summer precipitation (244-330 mm) shows less variation across the region and in fact is lowest on the downwind (southeast) side of Lake Superior (Fig. 2.1b, c). Thus sites in Michigan had the lowest summer precipitation and highest winter precipitation while western Minnesota sites had generally low precipitation year round.

Similar to precipitation, the direction of temperature trends varied by season across the study region (Fig. 2.1d-f). Although mean annual temperature (2.5-5.6 °C) generally decreased directly with latitude as expected, mean summer and mean minimum January temperatures exhibited differing trends. Summer temperature (15.8-19.4 °C) decreased with latitude in Wisconsin and Michigan, while in Minnesota summer temperature decreased from southwest to northeast. In contrast, mean minimum January temperature (-21.7--14.4 °C) exhibited more of a continental pattern with warm

winters in the south and along Lake Superior and the coldest temperatures at interior Minnesota sites. Thus sites in western Minnesota had relatively warm summer and cold winter temperatures.

The understory environment driver set of eight mainly abiotic variables described conditions in the understory and included seedbed characteristics, soil texture, pH, and available light (Table 2.1). Mineral soil samples of the upper 20 cm were extracted from five random points within each plot and samples were combined. In the lab, soil pH was measured using a water:soil suspension and sand and clay particle fractions were determined with the hydrometer method. Regional variation in soil pH and percent sand are shown in Fig. 2.1g, h. Leaf litter thickness was also sampled at each soil extraction point. The percent cover of leaf litter and moss were visually estimated for each understory subplot. The severity of earthworm disturbance was measured for each plot using a 4 point scale based on the presence and characteristics of the litter and organic layers, exposure of mineral soil, formation of a thick soil A horizon, density of earthworm middens, and presence of worms found during soil collection. Canopy openness at 1 m above ground level was determined at plot center using a spherical concave densiometer.

Overstory composition was calculated based on species basal area. The potential pool of tree species included in the overstory data set was limited to species present in the overstory in more than 50% of sites in order to adhere to statistical testing assumptions. This resulted in six species from three functional groups: boreal broadleaf *Betula papyrifera* Marsh. and *Populus tremuloides* Michx., boreal conifer *Abies*

balsamea (L.) Mill. and *Picea glauca* (Moench) Voss, and temperate broadleaf *Acer rubrum* L. and *Acer saccharum* Marsh. (Table 2.1). Each of these overstory species was present at more than 70% of sites and the set accounted for, on average, 80% of site basal area. The spatial patterns of *A. saccharum* and *P. tremuloides* basal area are depicted in Fig. 2.1i, j.

The understory biota driver set included six herbaceous and woody functional vegetation groups and browse pressure, which reflect direct competitive and trophic interactions (Table 2.1). Graminoid (grasses and sedges) (Fig. 2.1k), forb (broadleaved herbaceous species) (Fig. 2.1l), fern, and low shrub (low, spreading generally rhizomatous woody species such as *Vaccinium* spp. L., *Diervilla lonicera* Mill., and *Rubus* spp. L.) percent cover were estimated within each understory subplot. Tall shrubs included woody species that typically grow into the sapling layer such as *Corylus cornuta* Marsh., *Amelanchier* spp. Medik., and *Acer spicatum* Lam. Tall shrub stem density was measured in two size classes, < 1 m and \geq 1 m in height within each understory subplot. Site browse pressure, primarily from white-tailed deer (*Odocoileus virginianus*), was assessed on a four point scale as the proportion of branches with browse damage on individual maple (*Acer* spp.) stems within the browse layer (0.25 to 2.0 m in height).

STATISTICAL ANALYSES

To explore relationships among ecosystem drivers, we used a multivariate method of variation partitioning with partial and simple Redundancy Analysis (RDA) (Borcard et al. 1992, Økland and Eilertsen 1994, Anderson and Gribble 1998). RDA is a

constrained multivariate ordination technique that is essentially the multivariate extension of multiple regression (Legendre and Legendre 1998). This parametric technique assumes multivariate normal data and a linear relationship among response and explanatory variables. Explanatory variables were transformed as necessary to attain normal distributions. Because there was generally greater site to site variation than within site variation in explanatory variables (N. Fisichelli *unpublished data*) and to avoid pseudoreplication, data presented here are averaged to the site level. The response variables, tree species understory stem densities, were log transformed and then standardized using the Hellinger transformation to optimize model performance (Legendre and Gallagher 2001). Insufficiently sampled tree species, defined as species present in fewer than 10% of sites in the understory, were removed from analyses. Of the 34 species found within plots, six boreal and 13 temperate species were present in > 10% of sites (Table 2.2).

Variation partitioning determines the amount of unique, shared, and total explained variation contributed by each set of explanatory variables. The unique explained variation is that portion explained by a single variable after controlling for all other measured variables. The shared variation is the confounded portion or explained variation that is common to more than one factor. The total variation explained by a variable is the sum of its unique and shared portions. Partitioning is accomplished by running multiple RDAs with differing sets of explanatory variables in order to subdivide the explained variation (Borcard et al. 1992). All variation partitioning calculations were based on adjusted R^2 values that have been shown to be unbiased

estimators and that facilitate valid comparisons among explanatory sets (Peres-Neto et al. 2006). The four explanatory data sets each initially contained five to eight variables. Due to correlations and multicollinearity among variables within each set, a stepwise selection process using two stopping criteria, model adjusted R^2 and variable retention at a permutation P-value of 0.05, was used (Blanchet et al. 2008). Additionally, stepwise selected variables had to have variance inflation factors (VIF) < 10 (Borcard et al. 2011).

After variation partitioning, we ran two additional RDA models. In the first model, all significant drivers of tree regeneration identified during variation partitioning were combined into one data set. The results of this RDA were plotted in order to examine relationships among all explanatory variables. Then, a final parsimonious RDA model was run after stepwise selection (same method as above) of the combined data set. This process identified the smallest number of significant predictors necessary to model understory abundance trends.

Finally, since we are interested in shifts in tree regeneration composition across the region, we assessed both the spatial structure within the data and how well we captured these spatial trends. We used the principle coordinates of neighbor matrices (PCNM) method to model spatial structure present in the study design (Borcard and Legendre 2002, Dray et al. 2006, Borcard et al. 2011). Mean nearest neighbor distance between sites was 10.0 km and the minimum distance was 0.5 km, thus we treat sites as independent sampling units. PCNM eigenfunctions capture spatial trends at all spatial scales of the sampling scheme and generally perform better than polynomial terms of

geographic coordinates (Peres-Neto and Legendre 2010). For all points to remain connected the maximum Euclidean distance to define neighbors was 52.7 km and all pairs of points at a greater distance received a value equal to four times this threshold (Borcard and Legendre 2002). Through principle coordinate analysis of the geographic distance matrix among sites, 76 positive eigenfunctions were created. Stepwise selection, again using model adjusted R^2 and variable retention at a permutation P-value of 0.05, was run to determine the significant eigenvectors that explained the spatial pattern of tree regeneration composition. We then ran a variation partitioning model using two variable sets, the set of individual drivers selected above in the final parsimonious RDA model and the set of PCNM eigenfunctions, to examine the ability of explanatory variables to explain both spatially and non-spatially structured variation in tree regeneration. The significance of all RDA models, RDA axes, and variation partitioning components were tested via permutation procedures (P-value = 0.05). PCNM, variation partitioning, RDA models, and stepwise selection were run using the ‘vegan’ package (v. 1.17-6) (Oksanen et al. 2011) in R (v. 2.12) (R Development Core Team 2008).

Results

EXPLANATORY VARIABLES

Initial stepwise selection procedures within each of the four driver sets chose a total of 19 variables important in explaining understory tree regeneration patterns (Table 2.3). Within the climate set, the final selected variables were summer

temperature and annual precipitation. Additionally, six of eight environmental variables, five of six overstory species, and six of seven understory biota variables were selected. Explanatory power (adjusted R^2) of each individual variable based on RDA analyses is also shown in Table 2.3. *Acer saccharum* basal area, soil pH, summer temperature, *Populus tremuloides* basal area, and annual precipitation were the five strongest individual explanatory variables.

VARIATION PARTITIONING

The results of the variation partitioning indicate that all driver sets had both significant explanatory power and strong interrelationships (Fig. 2.2, see also Fig. S2.1 for complete partitioning among all driver sets). The overall model including all four driver sets had an adj. R^2 of 0.42 and each set of understory drivers contributed significant total and unique explanatory power (all P-values < 0.005). Climate, environment, and biota each individually explained about 10-14% of understory variation, while overstory composition explained the greatest variation, 26%. The unique portions, which represent explanatory power that can only be attributed to individual driver sets, accounted for 22-61% of the explained variation within each driver set with understory biota and overstory composition having the smallest and largest unique proportions, respectively. Conversely and as expected, there was a large amount of shared explanatory power, 39-78% of the explained variation attributed to each driver set.

The extent of shared explanatory relationships among all pairs of driver sets is shown in Fig. 2.3. Climate shared 21-45% of its explanatory power with each of the

other drivers. The understory environment and understory biota sets had similar levels of shared explained variation as climate (ranging from 27-40% for the former and from 31-49% for the latter). Overstory composition, which as a driver set explained the greatest variation, showed the lowest rates of confounding, 8-25%. Overall, these levels of confounding indicate complex relationships among all sets of explanatory variables.

Explanatory relationships among individual variables from all driver sets were explored through a correlation biplot of the full RDA model used in variation partitioning (Fig. 2.4). The biplot reveals the suites of associated variables that are driving tree regeneration trends within the first two RDA axes. Axes 1 and 2 explained 19.7% and 10.9% of total variation, respectively, and together accounted for 73% (30.6/42) of the explained variation; they thus portray the most important relationships. The locations of sampling sites in ordination space were well dispersed and there were no obvious groupings or outliers driving the model. Axis 1 mainly represented variation in overstory composition and related variables. Overstory composition shifted from dominance by *Populus tremuloides*, *Betula papyrifera*, and *Abies balsamea* at the negative end of the axis to *Acer saccharum* at the positive end. Overstory *P. tremuloides*, *B. papyrifera*, and *A. balsamea* were positively associated with understory light levels, low shrub cover, tall shrub density, moss cover, and forb cover. Conversely, *A. saccharum* overstory basal area was negatively related to these variables and positively correlated with leaf litter cover and annual precipitation.

Axis 2 mainly reflected nutrient and climate gradients, with soil pH and summer temperature positively associated and annual precipitation and soil percent sand

negatively associated with the axis. Also, *Acer rubrum* basal area was associated with cool, wet, acidic, and sandy conditions along the negative end of axis 2. Additional variables with positive loadings on axis 2 were graminoids, browse pressure, and earthworm invasion severity. Other relationships among drivers within the first two axes included negative correlations between precipitation and both browse damage and forb cover and between moss cover and both leaf litter cover and earthworm severity.

FINAL PARSIMONIOUS RDA MODEL

The final RDA model included 13 explanatory variables (adj. $R^2 = 0.41$) chosen during the stepwise selection process from the four driver sets (Table 2.4). Both annual precipitation and summer temperature were selected from the climate set. The five overstory tree species and five of six biota variables were chosen. Only one out of six understory environment drivers, soil pH, was selected. Although variation partitioning revealed much confounding among driver sets, two-thirds of individual drivers contributed significantly to the parsimonious model and thus were retained. The first five variables chosen were overstory *Acer saccharum*, soil pH, summer temperature, overstory *Populus tremuloides*, and overstory *Abies balsamea*, and together accounted for 84% of the explained variation (0.34/0.41).

ACCOUNTING FOR SPATIAL PATTERNS

As expected, the PCNM analysis found significant spatial structure in regeneration layer composition. Stepwise selection identified 15 significant PCNM eigenvectors (1-7, 9, 10, 12-14, 24, 54, 60) (adj. $R^2 = 0.24$) that mainly represented broad-scale variation across the region. The set of 14 explanatory variables from the

four driver sets selected above in the final RDA model and the PCNM eigenvectors together explained 44.5% of the variation in the tree regeneration layer (Fig. 2.5). The set of 14 explanatory variables explained the majority, 86.9% (21.2/24.4), of the total spatially structured variation, and overall roughly half (21.0/41.1) of the explained variation in understory composition was spatially structured.

Discussion

Identifying fundamental ecological drivers and gauging their roles in determining the composition of the tree regeneration layer is particularly essential along ecotonal boundaries where composition is predicted to shift rapidly in response to climate change. Through RDA and variation partitioning, we found that the regeneration layer reflects complex suites of associated drivers, including climate, understory environment, overstory composition, and understory biota. Even though there were multilayered interrelationships among driver sets, each exclusively explained a significant unique portion of regeneration compositional variation, underscoring the large number of factors influencing the performance of tree species in the regeneration layer. An initial main goal of this study was to test whether the tree regeneration layer was responding to climate and our results reveal that even given the strengths of other understory drivers, tree regeneration in ecotonal temperate-boreal stands is sensitive to temperature and precipitation gradients. However, other driver sets, such as overstory composition, had greater explanatory power than climate and indicate that the rate and direction of climate-mediated changes in forest composition will depend on the

strengths of these factors. Furthermore, the relative importance of these other driver sets is likely to vary in the future due to direct and indirect relationships with a rapidly changing climate. Although it is difficult to cleanly assign causative effects from a correlative study, our research clearly shows the multitude of factors that must be taken into account when attempting to understand and model tree regeneration dynamics along ecotonal boundaries.

OVERSTORY, ENVIRONMENTAL, AND BIOTIC DRIVERS AND INTERRELATIONSHIPS WITH CLIMATE

Although much current research emphasis is placed on climatic variables, our research clearly shows that the relative strengths of other interrelated drivers must be taken into account when attempting to project changes in forest composition. A recent study by Zhu et al. (2011) using a massive USDA FIA data set found evidence of range contractions at northern range limits, rather than expansions, suggesting that factors other than climate are driving regeneration trends for tree species in the southeast and east-central U.S. Similarly, our analyses indicate that suites of associated drivers including cool, moist, sandy, and acidic conditions; overstory boreal broadleaf species, light availability, shrub abundance, and forb cover; and warm temperatures and graminoid cover are determining tree regeneration trends. Three drivers in particular, current overstory composition, soil pH, and the set of understory biota, appear most likely to interact with a changing climate and drive future forest composition.

The central role of the current overstory has strong implications on the rate of forest change. The high unique explanatory power of overstory composition was likely

mainly due to direct influence on propagule availability. Within closed canopy forest, mean seed dispersal distance for most tree species is less than 20 m (Ribbens et al. 1994), and root suckers and basal sprouts, especially from *P. tremuloides*, *Betula papyrifera*, and *Acer rubrum* were common in the understory (N. Fisichelli *personal observation*). The ability of current advance regeneration to fill future gaps in the canopy will depend on the type and severity of future disturbances, which are themselves partly driven by climate. If the understory is left intact, for example after a wind storm that topples a few canopy trees, then advance regeneration is likely to fill these gaps and thus the current overstory will have great influence on future forest composition. This dynamic has two main implications. First, at the local scale along ecotonal boundaries, temperate species already present in the overstory may be able to make significant expansions through gap dynamics. Secondly and at a larger spatial scale, compositional shifts in the direction predicted by climate change may be slowed by the legacy effect of the current overstory. In boreal dominated areas, more severe disturbances such as intense fires which remove large portions of both the understory and overstory may be required to facilitate the rapid establishment of new species not present in the previous overstory neighborhood and that may be better adapted to the changed climate.

Given the current overstory composition and thus propagule availability, soil pH and related factors are likely to play a major role in determining which tree species (and where) are actually able to respond to a changing climate. For example, nutrient demanding temperate species will likely perform better under warmer temperatures at

less acidic sites. It is important to note here that this response will be constrained by the covarying relationship between soil pH and annual precipitation. Across the region, precipitation increases from west to east as do sulfur and nitrogen concentrations in precipitation and total deposition rates (Lovett 1994). Soils at the eastern end of the study region receive higher concentrations as well as total amounts of acid wet deposition and have lower pH levels. Thus species otherwise inhibited by strongly acidic conditions may be best able to respond to future warming at the western end of the temperate-boreal transition zone, assuming adequate precipitation levels.

While soil pH was a strong understory environment driver, soil sand fraction showed low explanatory power and clay was surprisingly not a significant factor. Sand was negatively related to annual precipitation, i.e., ecotonal temperate-boreal forests were more confined to finer textured soils at drier sites -itself an interesting finding- but were found on a wider variety of textures at wetter sites, analogous to the results of Henne et al. (2007). Wet conditions over the past three decades may have limited the significance of soil texture as a regeneration driver. If the future climate becomes more droughty, mesic ecotonal stands currently on coarse textured soils may shift composition more dramatically towards drought tolerant species than stands on finer textured soils with higher moisture holding capacity. Soil nitrogen has been shown to correlate with soil pH and texture in similar forest types (Mladenoff 1987) and is known to be an important driver of species in this study (Walters and Reich 1997, 2000, Machado et al. 2003). The high explanatory power of soil pH suggests that this variable

reflected the availability of nitrogen and other nutrients, while texture alone may have been a poor proxy for nutrients across our study sites.

Understory biota are likely to play a dynamic role in driving tree regeneration patterns under a global change scenario. The strength of the relationship between tree regeneration and understory biota will vary depending on how understory biota respond to a changing climate. For example, both forb cover and shrub abundance showed a negative relationship with precipitation while graminoid cover increased with temperature across the region. Thus tree species attempting to track climate change and shift their ranges will have to compete with these also climate-sensitive vegetation groups (Royo and Carson 2006, Montgomery et al. 2010). The inhibitory effects of understory biota on expanding tree species could intensify if a biotic driver is able to more rapidly track climate change and establish ahead of lagging tree species. Conversely, if existing understory biota are negatively impacted by the changing climate, expanding tree species may experience reduced competition. Another complicating factor is that some understory biota may be sensitive to different aspects of climate than tree regeneration, such as white-tailed deer responding more to winter conditions (Côté et al. 2004) than summer temperature. The strong relationship between climate and understory biota also implies that overall understory community composition may be shifting with climate. Because species richness in these forests is greatest in the understory, these shifts will affect overall biodiversity and ecosystem functioning (Gilliam 2007).

SEASONAL CLIMATE GRADIENTS

Although not the strongest individual driver set, climate does appear to play an influential role in driving tree regeneration trends. Differences in spatial patterns of annual and seasonal climate variables allowed us to differentiate among the effects of these typically strongly correlated drivers. Annual precipitation showed much greater variation across the region than summer precipitation and the selection of only annual precipitation within our model suggests that differences in precipitation during the dormant season, presumably in the form of snow, were an important driver of regeneration composition. Moisture released from the snowpack during the spring melt likely lengthened the period at the beginning of the growing season when soils were moist and thus conducive to the germination and early survival of many mesic species in this study (Hardy et al. 2001, Henne et al. 2007).

Precipitation played a smaller role than anticipated, likely because both summer and winter regional precipitation over the last 30 years were above the 20th century average (Karl et al. 2009). Thus seedlings establishing and persisting during this relatively wet period have not experienced moisture-driven selective pressures as intense as would be expected during dry conditions. Climate models project wetter winters and drier summers in the future (Wuebbles and Hayhoe 2004, Karl et al. 2009). Assuming that precipitation does not keep pace with future warming and dry summer conditions become more frequent and long-lasting, the influence of seasonal precipitation on tree regeneration will shift from winter to summer dominated trends. Furthermore, because ecotonal temperate-boreal stands in the western Great Lakes region are near their moisture-driven range limit, small changes in precipitation,

especially trends toward drier conditions, will have particularly large impacts on tree regeneration dynamics (Frelich and Reich 2010).

Similar to precipitation, seasonal trends in temperature, namely summer temperature, may be most influential in determining future forest trajectory. Across the study region, temperate-boreal ecotonal stands are only found over a summer temperature range of 4 °C, while predicted regional summer warming over the course of the 21st century is 3-8 °C (Wuebbles and Hayhoe 2004). Thus even under a moderately low CO₂ emissions scenario, forest composition is likely to shift dramatically. Regional warming over the past 30 years has been greatest in winter and spring (Karl et al. 2009), though predictions for the first half of the 21st century are for greater warming during summer months (Wuebbles and Hayhoe 2004). If these predictions bear out and the tree regeneration layer is as sensitive to summer temperature as indicated by our research, then shifts in forest composition may also accelerate in the coming decades.

Interestingly, minimum winter temperature was not shown to add significantly to the explanatory power of the climate driver set even though it may determine the extreme northern range limit of several temperate tree species present in this study (Sakai and Weiser 1973, Arris and Eagleson 1989). Although winter temperature exhibited an east-west trend somewhat similar to annual precipitation, increasing abundance of drought-tolerant temperate (*Quercus* spp.) and boreal (*Populus tremuloides*) species at western sites suggests that composition was responding more to precipitation than winter temperature at these sites. These results further suggest that a modest rise in winter temperatures may not significantly impact tree regeneration

dynamics within the study region. Although, if warming in winter was sufficient to eliminate snowpack and allow soils to freeze deeply, this might become more influential, but our data suggest this has not likely been the case for the variation observed across the study region in the recent past.

SPATIALLY PATTERNED AND UNEXPLAINED VARIATION

Overall our model successfully accounted for most of the spatially patterned variation in regeneration and the majority of unexplained variation was not spatially structured. The unexplained spatial patterning (3%) may be associated with an unmeasured but spatially structured explanatory variable or indicate nonlinear relationships that were not accounted for by monomial predictors. The large majority of unexplained variation (52.1%) did not have a spatial structure and was likely due to unmeasured locally varying factors and stochastic events. Unknown but potentially important local factors include disturbance (Turner et al. 2001) and land-use history (Foster et al. 2003), which can both have long-lasting effects on community composition. Additionally, this study was based on a single sampling period and thus variability in seed production, germination, recruitment, and mortality may have contributed to the residual variation (Beckage et al. 2005).

CONCLUSION

The tree regeneration layer in ecotonal stands responds to multiple interrelated drivers. Continued shifts in climate and especially warming and drying during the summer months are likely to accelerate changes in tree regeneration composition, although this will largely depend on propagule availability, soil nutrient status, and

interactions with other understory biota. Moreover, since these other drivers also have interrelationships with climate, the direction and rate of forest change may hinge on how the importance of these drivers shifts with climate and, for the biotic drivers, on the rate and magnitude of their own responses to climate change. An important future step is to further disentangle the roles of interrelated drivers in order to more precisely quantify their direct and indirect impacts on tree regeneration. Determining the relative importance of covarying drivers will inform management actions aimed at adaptation to climate change (Millar et al. 2007, Frelich & Reich 2009).

Table 2.1. Summary information for explanatory variables within four understory tree regeneration driver sets. Data were collected at 124 ecotonal temperate-boreal forest sites across the upper Great Lakes region, USA.

Variable	Units	Mean	CV(%)	Min	Max
Climate					
Annual temperature	°C	4.37	17.85	2.54	5.60
Summer temperature (JJA)	°C	17.76	3.69	15.84	19.40
Mean minimum January temperature	°C	-17.76	11.95	-21.65	-14.36
Annual precipitation	mm	777.2	8.42	655	986
Summer precipitation (JJA)	mm	296.5	6.22	244	330
Understory Environment					
Sand	%	67.79	41.19	18.50	90.27
Clay	%	8.23	23.53	2.09	39.41
Soil pH		4.59	9.59	3.14	5.87
Earthworm disturbance	0-3 index	1.73	54.24	0	3
Litter depth	cm	1.44	20.73	0.42	3.00
Leaf litter cover	% cover	88.85	13.81	55.37	95
Moss cover	% cover	2.06	52.72	0	42
Canopy openness	%	13.82	52.72	6.37	31.1
Overstory (basal area)					
<i>Abies balsamea</i>	m ² /ha	2.77	39.38	0	13.67
<i>Acer rubrum</i>	m ² /ha	3.01	45.69	0	22.31
<i>Acer saccharum</i>	m ² /ha	2.03	70.04	0	18.94
<i>Betula papyrifera</i>	m ² /ha	1.94	73.03	0	20.39
<i>Picea glauca</i>	m ² /ha	1.79	70.19	0	15.55
<i>Populus tremuloides</i>	m ² /ha	2.30	70.11	0	30.35
Understory Biota					
Graminoids	% cover	3.07	68.95	0	45.08
Forbs	% cover	14.16	31.36	1.44	68.75
Ferns	% cover	7.51	44.87	0	53.81
Low Shrubs	% cover	2.6	58.48	0	33.75
Tall Shrubs < 1m	stems/ha	6225	18.07	0	60478
Tall Shrubs > 1m	stems/ha	465	48.27	0	14722
Browse Pressure	0-3 index	2.27	35.61	1	3

Table 2.2. Common tree species found in the regeneration layer (present at greater than 10% of sites). Regeneration layer stems are older than first year germinants and < 10 cm diameter at 1.3 m above ground level.

Species	Biome	Form	Sites (out of 124)	Mean (stems/ HA)*	CV (%)*	Max (stems/ HA)
<i>Abies balsamea</i>	Boreal	Conifer	116	14009	11.9	109220
<i>Acer rubrum</i>	Temperate	Broadleaf	117	22917	13.5	371627
<i>Acer saccharum</i>	Temperate	Broadleaf	94	28823	17.5	738153
<i>Betula alleghaniensis</i>	Temperate	Broadleaf	31	1345	17.0	37059
<i>Betula papyrifera</i>	Boreal	Broadleaf	53	714	20.8	15120
<i>Fraxinus nigra</i>	Temperate	Broadleaf	58	6314	17.9	97482
<i>Fraxinus pennsylvanica</i>	Temperate	Broadleaf	18	3213	18.9	88864
<i>Ostrya virginiana</i>	Temperate	Broadleaf	56	2781	18.4	29778
<i>Picea glauca</i>	Boreal	Conifer	59	767	16.0	5825
<i>Pinus strobus</i>	Temperate	Conifer	22	1684	17.0	41221
<i>Populus grandidentata</i>	Boreal	Broadleaf	13	480	16.4	1719
<i>Populus tremuloides</i>	Boreal	Broadleaf	91	4984	13.9	54447
<i>Prunus serotina</i>	Temperate	Broadleaf	46	3431	14.2	36136
<i>Quercus macrocarpa</i>	Temperate	Broadleaf	13	1316	14.2	5570
<i>Quercus rubra</i>	Temperate	Broadleaf	61	2233	14.7	26086
<i>Sorbus spp.</i>	Boreal	Broadleaf	15	1835	12.2	18271
<i>Tilia americana</i>	Temperate	Broadleaf	38	1347	15.1	8555
<i>Tsuga canadensis</i>	Temperate	Conifer	20	1763	16.9	21486
<i>Ulmus americana</i>	Temperate	Broadleaf	17	1135	15.4	6366

*Calculated from sites where present

Table 2.3. Explanatory variables selected during stepwise selection procedures for variation partitioning models. Variable selection occurred within each variable set and the order of selection is shown. Individual R^2 are based on RDA models with only the single explanatory variable included and the Hellinger transformed understory tree species stem density as the response variable.

Variable	Acronym	Individual adj. R^2	Within group selection order
Climate			
Summer temperature	Temp	0.055	1
Annual precipitation	PPT	0.040	2
Environment			
Soil pH	pH	0.071	1
Moss	Moss	0.021	2
Earthworm Severity	Worm	0.018	3
Canopy Openness	Light	0.011	4
Leaf Litter	Litter	0.018	5
Sand	Sand	0.015	6
Overstory			
<i>Acer saccharum</i>	AcsaTr	0.165	1
<i>Populus tremuloides</i>	PoptTr	0.055	2
<i>Acer rubrum</i>	AcruTr	0.027	3
<i>Betula papyrifera</i>	BepaTr	0.034	4
<i>Abies balsamea</i>	AbbaTr	0.021	5
Understory Biota			
Forbs	Forbs	0.047	1
Graminoids	Grams	0.035	2
Browse Pressure	Browse	0.023	3
Low Shrubs	L.Shrub	0.030	4
Tall Shrubs <1m	T.Shrub	0.030	5
Ferns	Ferns	0.005	6

Table 2.4. Explanatory variables selected from the combined sets of regeneration drivers for the final RDA model. Variables are in selection order and the model adj. R^2 after inclusion of each successive variable is shown. Only significant predictors ($P < 0.05$) were retained. The response data are the Hellinger transformed stem densities of tree species in the regeneration layer.

Selection order	Variable	Driver set	Model adj. R^2	F-value	P-value
1	<i>Acer saccharum</i>	Overstory	0.165	25.3777	0.005
2	Soil pH	Environment	0.232	11.5799	0.005
3	Summer temperature	Climate	0.290	10.8847	0.005
4	<i>Populus tremuloides</i>	Overstory	0.328	7.7552	0.005
5	<i>Abies balsamea</i>	Overstory	0.344	3.8555	0.005
6	<i>Betula papyrifera</i>	Overstory	0.359	3.789	0.005
7	Tall Shrubs <1m	Biota	0.368	2.6257	0.005
8	<i>Acer rubrum</i>	Overstory	0.377	2.7346	0.005
9	Graminoids	Biota	0.385	2.6139	0.005
10	Annual precipitation	Climate	0.394	2.5534	0.005
11	Browse pressure	Biota	0.401	2.3978	0.005
12	Ferns	Biota	0.405	1.7366	0.03
13	Forbs	Biota	0.409	1.7777	0.04

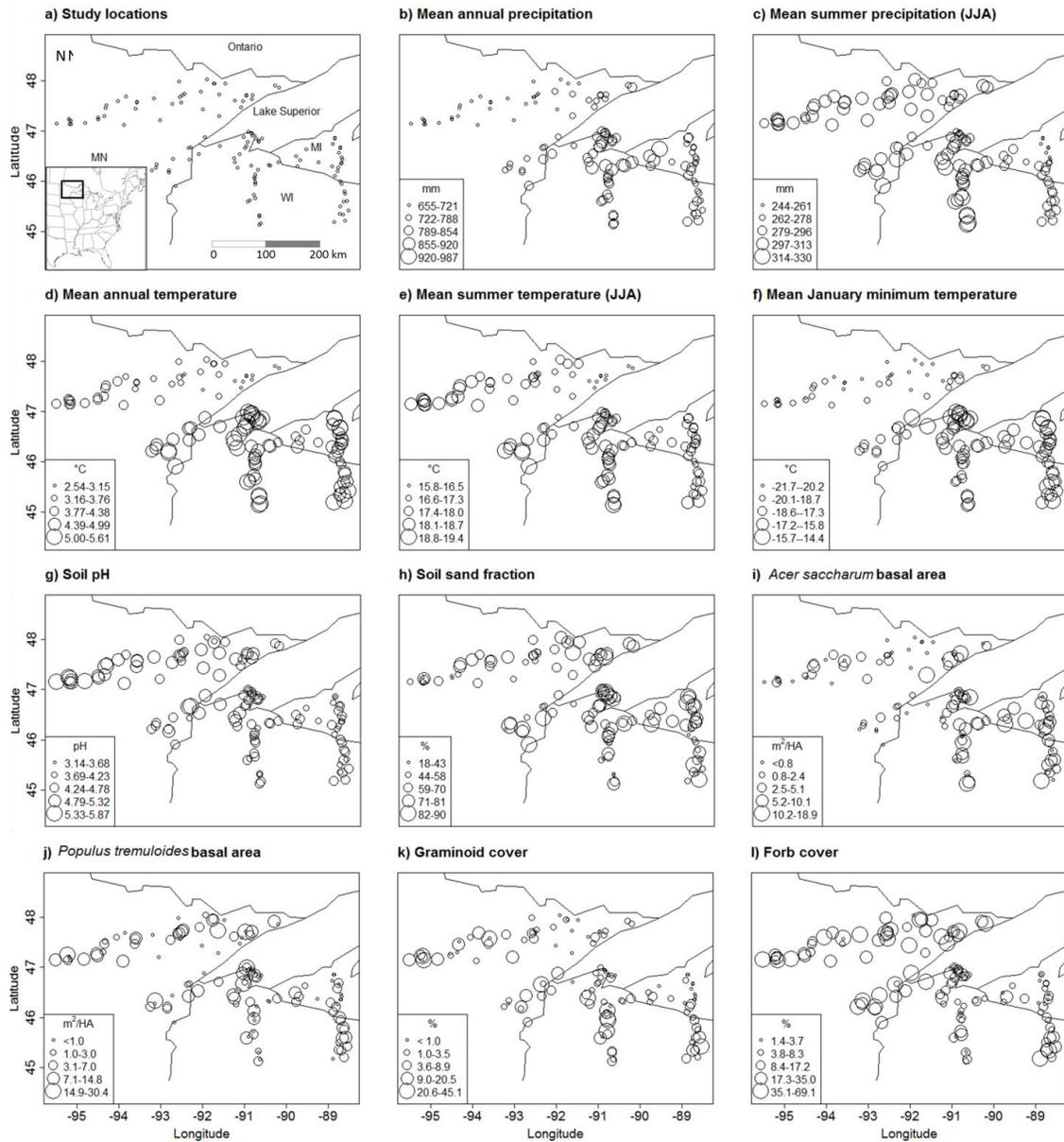


Figure 2.1. Locations of study sites, upper Great Lakes region USA, and spatial patterns of selected understory regeneration drivers. (a) study sites. Climate variables include (b) mean annual precipitation, (c) mean summer precipitation (JJA), (d) mean annual temperature, (e) mean summer temperature (JJA), and (f) mean January

minimum temperature. Understory environment drivers are (g) soil pH and (h) soil sand fraction. Overstory variables include the basal area of (i) *Acer saccharum* and (j) *Populus tremuloides*. Understory biota include the percent cover of (k) graminoids and (l) forbs.

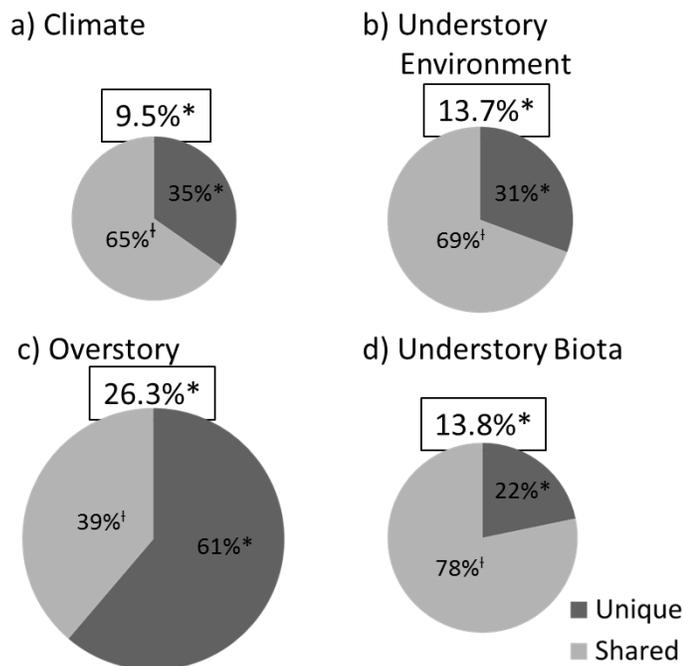
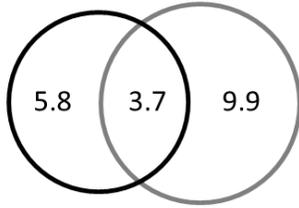
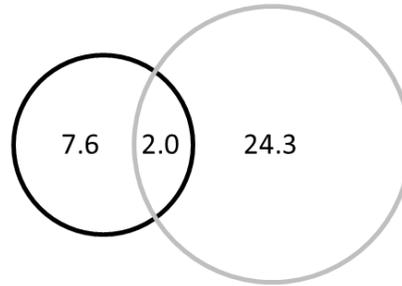


Figure 2.2. Unique, shared, and total variation of the tree regeneration layer explained by (a) climate, (b) understory environment, (c) overstory composition, and (d) understory biota. Values determined through variation partitioning model including all four tree regeneration driver sets. The full variation partitioning model with all 4 driver sets explained 42% of variation in the regeneration layer (based on adj. R^2). Shaded areas within and among circles are proportional to variation explained. See text for specific variables within each driver set. * $P < 0.005$, † cannot be tested.

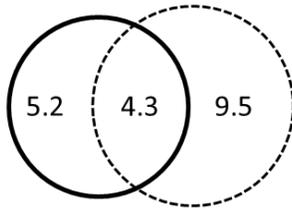
a) Climate + Environment = 19.5%



b) Climate + Overstory = 33.9%



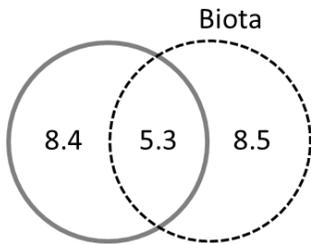
c) Climate + Understory Biota = 19.0%



d) Environment + Overstory = 34.5%



e) Environment + Understory = 22.2%



f) Overstory + Understory Biota = 33.4%

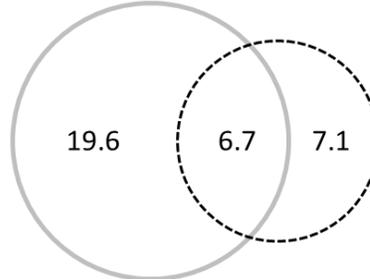


Figure 2.3. Variation partitioning results for all pairs of drivers. Venn diagrams show explanatory relationships among all pairs of tree regeneration driver sets (a-f). Variation explained (%) is based on adj. R^2 . All unique portions (non-overlapping outer section of each circle) explained a significant portion of regeneration layer variation ($P < 0.005$). The overlapping middle sections represent the ‘shared’ portion or variation explained by both drivers. Climate is represented by solid black circles, understory environment by dark gray, overstory by light gray, and understory biota by dashed black circles. The size of each circle section is proportional to the variation accounted for by that element. See text for specific variables within each driver set.

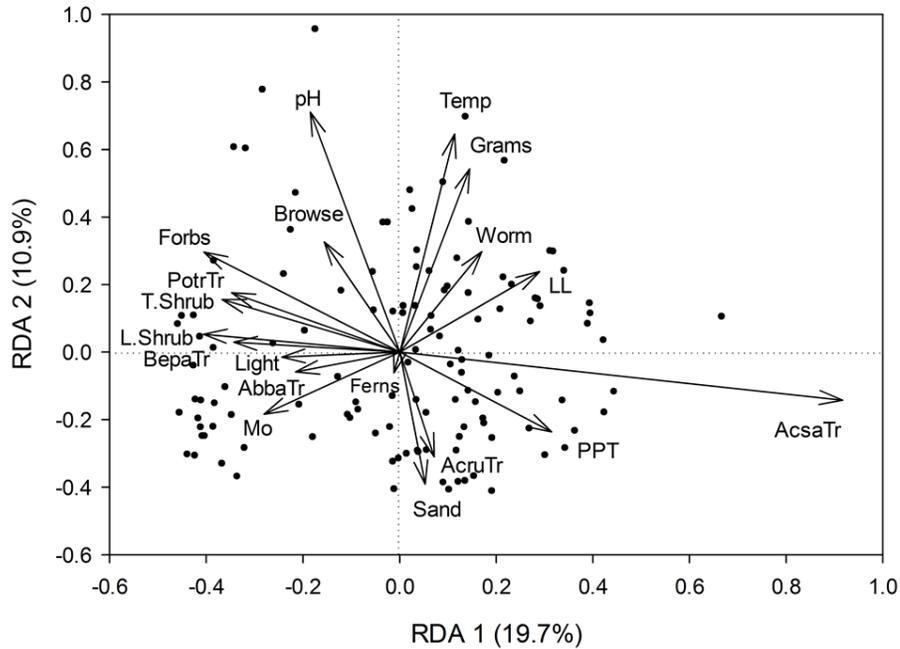


Figure 2.4. Redundancy analysis (RDA) correlation biplot for the 19 significant explanatory variables in four driver sets (climate, understory environment, overstory composition, and understory biota) identified during variation partitioning. The response data are the Hellinger transformed stem densities of tree species in the regeneration layer. Explanatory variables are shown as vectors and sites as points. See Table 2.3 for explanations of acronyms.

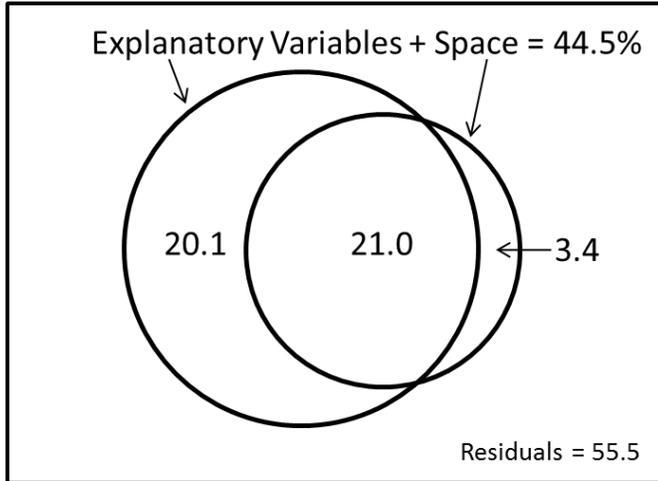


Figure 2.5. Venn diagram depicting the partitioning of variation in the tree regeneration layer among explanatory variables (climate, understory environment, overstory composition, and understory biota) (left circle) and spatial variables (right circle). The explanatory drivers include 13 variables (see Table 2.4) and the spatial set includes 15 principle coordinates of neighbor matrices (PCNM) eigenfunctions selected during stepwise selection procedures. Explained variation percentages are based on adj. R^2 values.

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CHAPTER 3

Deer ‘cool’ sapling growth responses to warmer temperatures near range limits

Summary

Rising temperatures are predicted to cause temperate tree species to expand north into currently boreal dominated forests. Other factors, such as overabundant deer, may hinder temperate expansion. We examined how interactions among temperature, browse pressure, light availability, and initial size impact height and radial growth of naturally regenerated, competing temperate and boreal saplings across their overlapping range limits in central North America. Temperate sapling growth increased and boreal sapling growth decreased with temperature across a regional summer temperature gradient (2.3 °C), causing a rank reversal in growth rates. This suggests that temperature is a key driver of sapling performance and range boundaries. However, under high browse pressure positive temperate responses to temperature were eliminated, pushing the crossover point in growth between temperate and boreal species further south. These results highlight the importance of interactions among global change agents and potential impediments for tree species to track a rapidly changing climate.

Introduction

Global change agents and their interactions and interrelationships with local environmental conditions will drive the future trajectory of forest ecosystems (Chapin et al. 1997; Dietze & Moorcroft 2011; Chapter 2). Forest overstory composition is determined in large part by performance at the younger seedling and sapling stages where survival and growth rates have been shown to be excellent predictors of canopy

layer composition (Pacala et al. 1996; Kobe 1996; Wyckoff & Clark 2002). Sapling performance in understory conditions is primarily driven by light availability, with survival and growth responses partially dependent upon nutrient and moisture availability, and the level of neighborhood competition (Canham et al. 1996; Walters & Reich 1997; Coomes & Grub 2000; Kobe 2006, Montgomery et al 2010). Additionally, global change agents such as rising temperatures and overabundant herbivores may select for differing suites of species, especially near range boundaries (Post & Pedersen 2008; Olofsson et al. 2009; Speed et al. 2011). Given the often stressful growing conditions in the forest understory, including potentially intense browse pressure, tree regeneration responses to warming may be inhibited, creating an extended time lag to climate change. The goal of the current research is to examine how interactions among temperature, browse pressure, light availability, and sapling size influence the growth of temperate and boreal saplings near their shared, climate-mediated range limits.

Species growing near their range limits are likely most sensitive to climate change and apt to exhibit growth responses to small variations in climate (Fritts 1976; Parmesan et al. 2005; Reich & Oleksyn 2008). Several recent studies indicate that tree species abundances are already shifting spatially. Woodall et al. (2009) and Lenoir et al. (2009) found shifts in the latitudinal and elevational distributions of seedlings compared with overstory trees. Research along ecotonal boundaries has shown that the relative abundance of temperate and boreal species in the regeneration layer and overstory varied with climate (Beckage et al. 2008; Chapter 1). These changes in relative abundance are concomitant with the direction predicted by recent warming, although

specific mechanisms causing abundance changes are unclear. Juvenile stages may have narrower climate thresholds than adult stages and thus be more responsive to climate change (Grubb 1977; Jackson et al. 2009; van Mantgem et al. 2009). In addition to shifts in germination, establishment, and early survival, warming temperatures may shift competitive interactions among saplings in favor of those species with more positive growth increases (Woodward 1987). Differential growth responses to temperature are likely most consequential where northern and southern range limits of competing species overlap, such as within the temperate-boreal transition zone. Species at their northern range limits are predicted to exhibit strong positive growth responses to increases in temperature while growth responses at southern limits are less certain, with evidence for positive, flat, and negative responses, depending on species and location (Schenk 1996, Stott & Loehle 1998, Reich & Oleksyn 2008). Even with somewhat positive growth responses to temperature, southern range limits are assumed to be defined by competitive dynamics with faster growing, more warm-adapted species, whereas northern limits are controlled by abiotic stressors such as low temperatures (Woodward 1987).

In addition to climate, other global change agents are also likely to play important roles in determining future forest composition and may facilitate or inhibit climate-mediated forest changes. Herbivore populations are at historically unprecedented levels in many parts of the globe (McCabe & McCabe 1997), such as the temperate-boreal transition zone in the Great Lakes region of North America where white-tailed deer (*Odocoileus virginianus*) densities are roughly 2.5-5 times higher than

prior to European settlement (Rooney & Waller 2003). Through selective and intense herbivory, overabundant deer populations strongly impact the composition of the forest understory and can alter competitive dynamics in favor of less palatable species (Stromayer & Warren 1997; Côté et al. 2004). Within temperate forests, sustained high browse pressure has shifted the understory of hemlock-hardwood forests from the browse-preferred but intolerant *Tsuga canadensis* to the less preferred and more browse-tolerant *Acer saccharum* (Frelich & Lorimer 1985; Salk et al. 2011). In boreal systems, heavy browsing eliminates the regeneration of *Thuja occidentalis* and *Abies balsamea* and facilitates replacement by the unpalatable *Picea glauca* (McInnes et al., 1992, Cornett et al. 2000, Potvin et al. 2003). Chronic browse pressure can also delay ascension above the browse layer for several decades (Vila et al. 2003), and thus curtail the ability of temperate tree species to respond to warming temperatures (Rodenhouse et al. 2009). Recent studies at alpine tree line and within tundra systems indicate that vegetation responses to temperature may be sharply limited by browse pressure (Post & Pedersen 2008; Olofsson et al. 2009; Speed et al. 2011). Similar trends are likely within forest systems such as the temperate-boreal transition zone, where sensitivities to temperature and browse pressure likely vary widely among tree species.

The primary goals of this research were to examine understory temperate and boreal sapling growth responses to temperature across a regional climate gradient, to quantify the role of browse pressure in impacting growth in general and more specifically in response to temperature, and finally to explore interactions between global change agents and the classic predictors of sapling growth, initial size and light

availability (Kobe 1996). We hypothesized that temperate tree species will have positive growth responses to temperature while boreal species will have flat or negative responses. Temperate species will also have more negative responses to browse pressure due to higher palatability and thus higher rates of severe browse damage. The strengths of these drivers and their interactions will influence competitive interactions and thus impact migration potential and future forest composition.

Materials and Methods

FIELD AND LABORATORY

This study included 14 research sites, which span the temperate-boreal transition zone in Minnesota, USA. Maximum distance between the warmest sites in the south and coolest sites in the north is approximately 300 km. Mean annual temperature varies from 3.0 - 5.5 °C, mean summer temperature (JJA) from 16.2 - 19.1 °C, and annual precipitation from 683 - 835 mm (1978 - 2007 period, Daly et al. 2008). Research sites were upland mesic stands with a diverse mixture of temperate and boreal tree species.

Sapling growth rates were studied for five mid to very shade-tolerant species, including two boreal conifers, *Abies balsamea* and *Picea glauca*, and three temperate broadleaf species, *Acer rubrum*, *Acer saccharum*, and *Quercus rubra*, commonly found growing as advance regeneration (Table 3.1). A sixth species, *Tilia americana*, a prolific basal sprouter, was initially included; however, models of sapling growth had extremely poor fits likely because many stems originated from vegetative reproduction, even though obvious basal sprouts were avoided during sampling. Each study site

contained between two and five species and each was present at 7-14 sites. To examine how drivers of growth and their interactions may shift with sapling size, we conducted a stratified random sample of saplings in four height classes (20-50 cm, 50-100 cm, 100-200 cm, and 200-425 cm). Plots within sites were randomly located and a subset or all saplings of a species and size class combination (depending on abundance) were sampled within 15 m of plot center. Our goal for each species was to include ~10 stems per size class at each site, though due to varying abundances, sample size varied between one and 15 stems per size class. As mentioned above, we attempted to include only saplings that appeared to have established from seed (multi-stemmed basal sprouts were avoided).

For each individual stem, we recorded browse damage and light availability. Browse pressure to each sapling was scored on a scale from 0-10 based on the proportion of branches with browse damage (0 = no damage, 10 = all branches with browsed tips) (Frelich & Lorimer, 1985). The temperate broadleaf species generally experienced much higher browse pressure than the boreal conifers (Table 3.2). The majority of browse damage was due to white-tailed deer (*Odocoileus virginianus*), with moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) accounting for a very low percentage of observed damage. Although deer densities are regionally high, we were able to exploit local scale variability in deer abundance and thus browse pressure. Only one deer enclosure at a single site was utilized and these stems only accounted for 1% of the overall sample size. The light environment (percent canopy openness) at the top of each sapling (or at 3 m above ground level for saplings > 3 m in height) was

measured with a LI-COR LAI-2000 plant canopy analyzer (LI-COR Inc., Lincoln, Nebraska) under uniform overcast conditions. Saplings, on average, were growing in intermediate shade (8-12% canopy openness) (Table 3.2). Finally, samples of the upper 20 cm of mineral soil were collected at each plot. Soil pH was measured using a water:soil suspension and sand particle fraction was determined with the hydrometer method.

We assessed the performance of saplings through measures of both height and radial growth. Plots were sampled during the growing season (2009-2010). Terminal leader annual stem elongation (height growth) was determined for up to six years (2005-2010) by measuring the distance between terminal bud scars. Saplings were harvested at 10 cm above ground level and a basal cross-section collected. These were then dried and sanded (up to 1200 grit) and age and ring width measurements, to the nearest 0.01 mm, were made along the radial line that bisected the angle between the longest and shortest radii using a stereomicroscope and a Velmex sliding-stage measuring system (Velmex, East Bloomfield, New York). Although partial rings were detected by examining multiple radii, false rings and missing rings could not be identified through cross-dating due to the suppressed condition of saplings and generally short ring series (Lorimer et al. 1999).

STATISTICAL ANALYSES

To model sapling growth, we utilized linear mixed-effects models with log transformed growth and light data and a Gaussian error distribution. Although other

modeling of sapling growth has used non-linear Michaelis-Menton functions (Pacala et al. 1994; Kobe 1996; Wright et al. 1998), ~95% of saplings in this study were growing in < 20 % full sunlight and thus asymptotic growth rates were rarely achieved.

Preliminary analyses with only light as a predictor indicated better fit by the linear model on log-transformed data than the non-linear model. Mixed-effects modeling permitted us to correctly account for the hierarchical structure of the data, specifically stem level predictors size, light, and browse; plot level soil variables; and site level climate data. We calculated mean annual radial growth from the 5 year period 2005-2009 and mean annual height growth from 2007-2008. Height growth for the full five year period (2005-2009) could not be accurately measured on heavily browsed stems because it was difficult to identify stem lengths going back more than a couple of years. Additionally, since many stems were harvested at the end of the 2009 growing season and most browse damage occurs during winter months, 2008 was the most recent year of growth to experience a full year of browse pressure. Mean summer temperature (June-August) for these years was obtained from PRISM (Daly et al. 2008) 4 km resolution gridded climate data. As understory conditions can change over relatively short periods, such as light levels due to canopy gaps forming and closing, interannual variability in growth response to climate variables is difficult to detect in understory saplings. Thus we use differences among sites to model responses to temperature. Present and past temperatures across the transition zone are compared with future predictions of Kling et al. (2003). In addition to temperature, some sites also spanned a historical precipitation gradient; however there was only minor site to site variation in

precipitation during the 5 year period of interest and preliminary analyses found precipitation to be a poor predictor of growth (data not shown). Preliminary analyses using soil variables (texture and pH) also yielded poor results, likely also due to insufficient variation across sites, and thus these predictors were dropped from further analyses.

Our final set of potential predictors included initial size (log transformed radius in 2004, square root transformed height prior to 2007), light availability (log transformed % canopy openness), browse damage (0-10 index, treated as a continuous variable), and summer temperature (JJA °C) (Table 3.2). Correlations among predictors were generally weak. The strongest relationships were decreasing browse damage with increasing size ($r = -0.26$), due to the inability of deer to browse the entire canopies of tall stems, and an inverse relationship between understory light and temperature ($r = -0.34$). The change in understory light was due to a slight increase in basal area of temperate broadleaf species, such as *A. saccharum*, with temperature ($r = 0.33$) and inverse relationship between basal area of thin canopied early-successional boreal broadleaf species, such as *Populus tremuloides*, and temperature ($r = -0.28$).

In addition to these main effects we examined five *a priori* selected two-way browse and temperature interactions: size by browse, light by browse, browse by temperature, size by temperature, and light by temperature. Because *Picea glauca* received essentially zero browse pressure, only combinations of three main effects and two interactions were possible for this species. For each species, we fit models of varying complexity from a simple model only including size as a predictor to a model

with all four main effects and five interactions. Model parameters were fit using maximum likelihood estimation which finds the set of parameter values that make the observed data most likely to have occurred (Bolker 2008). We evaluated models through comparisons of small sample corrected Akaike information criteria (AICc), which assesses model performance based on goodness-of-fit and a penalty for the number of model parameters (Burnham & Anderson 2002). For each species, we present results from the model with lowest AICc (see Tables S3.1, S3.2 for comparisons among models via Δ AICc). Predictors were centered and models checked for multicollinearity; all variance inflation factors (VIFs) were < 2 indicating no collinearity issues (Zuur et al. 2009). Parameter estimates of top models were assessed via t-values and prediction intervals calculated through model fitting. Data were analyzed using the 'nlme' package (v. 3.1) (Pinheiro et al. 2009) in R (v. 2.12) (R Development Core Team 2008).

Results

Sapling radial and height growth models indicated strong support for the inclusion of initial size, light, browse, temperature, and interactions (Tables 3.3, S3.3) (tables and figures in main text present height growth data; see supplementary material for corresponding radial growth tables and figures). Complexity of top models varied from including only two fixed effects (size and light) for *Picea glauca* radial growth to eight terms including four interactions for *Acer saccharum* radial growth. As expected, initial size and understory light levels were strong predictors for all species. Browse

interactions were included in both height and radial growth models for each of the four browsed species and temperature or temperature interactions in 9 of 10 growth models for the five study species. Radial and height growth model parameters and the strength and direction of coefficients were generally similar within species. For example, the top *Quercus rubra* height and radial growth models included identical parameters.

Strong temperature or temperature interactions were detected for all species over the 2.3 °C summer temperature gradient (Tables 3.3, S3.3, Figs. 3.1, S3.1). Growth declined with temperature for the two boreal conifers, with the reduction in growth more pronounced for *Abies balsamea* than *P. glauca* (Fig. 3.1a,b). Height growth also decreased somewhat more rapidly with temperature for *A. balsamea* saplings in high rather than low light microsites. All three temperate broadleaf species exhibited neutral to positive growth responses to temperature, depending on the level of the interacting predictor (Fig. 3.1c-f). We observed strong positive *Acer rubrum* height growth and *Acer saccharum* height and radial growth responses to temperature when browse pressure was low, but increasing browse pressure strongly reduced these positive growth responses. Heavily browsed stems displayed essentially no growth response to temperature, and at warm sites this pressure resulted in growth reduction of 50% or more compared with unbrowsed stems. For moderately shade-tolerant *Quercus rubra*, height and radial growth responses to temperature increased with decreasing stem size and there was moderate evidence for increased positive response under higher light availability. At warmer sites, height growth of higher light *Q. rubra* stems was

approximately twice as great as low light stems, whereas there was no difference in growth by light levels at cooler sites.

In addition to the browse by temperature interactions, the effects of browse pressure also varied with size and light availability (Tables 3.1, S3.3, Figs. 3.2, S3.2). Heavy browse damage reduced height and radial growth by 50% or more for potentially fast growing stems of all four browsed species. Although browse damage was generally low for *A. balsamea* (mean browse index < 1), growth was strongly reduced where browse damage was high, with smaller stems exhibiting greater height growth reduction than tall stems due to direct browsing of the terminal leader (Fig. 3.2a), while conversely, larger diameter *A. balsamea* stems showed greater radial growth sensitivity to browse than smaller stems. Browse pressure also more negatively impacted height and radial growth of large than small *Q. rubra* stems (Fig. 3.2b), and strongly negated height and radial growth responses to increasing light levels for both *A. rubrum* and *A. saccharum* (Fig. 3.2c,d).

Interspecific variations in palatability and thus level of browse damage as well as differing responses to temperature resulted in strong shifts in relative performance across the temperate-boreal transition zone (Fig. 3.3). Under low browse pressure (index = 0), height growth was generally greater for the boreal conifers than temperate broadleaf species at cool sites while temperate species exhibited relatively higher growth rates at warm sites, resulting in a rank reversal of growth rates (Fig. 3.3a). However, under high browse pressure (each species assigned its 80th percentile browse rating) temperate species height growth was uniformly low and as a result lower than

that of boreal conifers at all but the warmest sites (Fig. 3.3b). These growth patterns across the temperate-boreal transition zone can be compared with recent and predicted temperature changes (Fig. 3.3c).

Discussion

The results of this research underscore the importance of interactions among global change agents in driving forest composition and potential response rates to climate change. Eventual overstory composition is the result of species level performance and competitive interactions at multiple early life stages (Pacala et al. 1996; Poorter 2007). Radial and height growth are integrated measures of plant performance and inclusion of temperature and browse as strong explanatory variables in both sets of analyses bolsters the evidence that these factors are important drivers of plant productivity and forest dynamics. As hypothesized, all temperate broadleaf species responded positively to temperature while the boreal conifer temperature-growth relationships were generally negative. Decreasing growth by both temperate and boreal saplings as they approach their range limits suggests that temperature-mediated competitive dynamics are a key driver of sapling performance, forest composition, and range boundaries across the temperate-boreal transition zone. However, heavy browse pressure can eliminate positive temperate growth responses to warmer temperatures, tilting growth rates in favor of less palatable boreal species and possibly hindering the ability of temperate species to track climate change. Comparable reductions in growth due to browse damage and temperature limitations indicate that the potential impacts of

both factors are similar in magnitude across the temperate-boreal transition zone. Thus, successional trajectories could lead in multiple directions, depending on the relative strengths and variability of drivers over space and time (Rodenhuse et al. 2009).

Projected climate change indicates the potential for large temperate and boreal tree range shifts (Iverson et al. 2008). In order for species to expand their range limits and track a rapidly changing climate, they will need to not only contend with the abiotic environment at a new site, but also endure biotic interactions with extant species. Thus, in addition to likely seed dispersal limitation, competition with other plants already present on site and trophic interactions with abundant herbivores could further reduce tree migration rates. The importance of competition is predicted to exceed moderate climate variation and dispersal ability, at least over the near future (Clark et al. 2011, Xu et al. 2012). However, for temperate and boreal species growing together as advance regeneration, competitive dynamics appear to be tightly linked with climate. This sensitivity was illustrated by growth responses to temperature and rank reversals in relative performance across a relatively narrow temperature gradient (2.3 °C). It is important to point out that this trend only was apparent when browse pressure was low. Thus even though boreal conifers exhibited reduced growth with temperature, their relative performance increased with increasing browse pressure on competing temperate saplings. Browsing may further indirectly impact the ability of temperate species to track climate change by extending the time required to grow up through the browse layer and capture canopy gaps. Finally, growth responses to temperature also shifted

with stem size and light conditions, demonstrating that the rate and direction of forest change will depend on a multitude of interacting factors.

Decreasing growth with increasing temperature for the two boreal conifers indicated that not only are these species unable to keep pace with the growth of temperate species but they are also more stressed as they approach their southern range limits. These results suggest that abiotic stressors at least partially determine southern range limits for boreal conifers in the advance regeneration layer. A study of several western North American shade-tolerant conifers found similar results with higher low light growth in the coolest climatic regions (Wright et al., 1998). In Europe, *Pinus sylvestris* in the southern part of its range showed decreased growth and survival with modest warming in transplant experiments (Reich & Oleksyn 2008). These results may reflect a tradeoff between photosynthetic rates and respiration costs with varying temperature and light regimes (Adams & Loucks 1971, Tjoelker et al. 1998), or the increased frequency of drought and/or heat stress events (Reich & Oleksyn 2008), or both. If warming is accompanied by reduced soil moisture, then drought-intolerant species such as *Abies balsamea* will be unable to respond to otherwise enhanced growing conditions. For example, the greater decline in growth with temperature by higher light *A. balsamea* stems suggests that increases in temperature within sunny gaps were likely accompanied by lower soil moisture that may have swamped any potential benefit of higher understory light levels. Similarly, the lack of response by low light *Quercus rubra* stems to temperature may also indicate that increasing respiratory costs with increasing temperature were not met by low light photosynthetic rates.

Mean summer temperature has warmed by roughly 0.5 °C across the study region over the past few decades (based on 20 year averages) and is predicted to warm another ~1.7 °C by about 2030 (Kling et al. 2003), suggesting continued temperature-mediated shifts in the competitive interactions among temperate and boreal species in the coming decades, depending on browse levels (Fig. 3.3). Summer warming of the magnitude predicted for the end of the 21st Century, 3-8 °C (Kling et al. 2003), will eventually cause the relative performance of boreal saplings to be much poorer than temperate species across most if not all of the current temperate-boreal transition zone, regardless of browse intensity. As temperatures continue to increase across this region, the influence of browse pressure will shift from facilitating the resilience of boreal conifers to driving competitive interactions among expanding temperate species. As deer are likely to also respond to climate change by expanding northward (Côté et al. 2004), the importance of future deer-plant interactions at and beyond the current northern limit of the temperate-boreal transition zone will depend in part on the direction and rate of changing climatic conditions, with summer temperatures influencing plant growth rates and winter conditions driving browse pressure levels (Rodenhouse et al. 2009).

Our research revealed natural spatial heterogeneity in browse pressure across the landscape that is sufficient to modify sapling growth trends of all browsed species and thus potentially influence the spatial pattern of temperate tree expansion. This heterogeneity was likely due to local differences in winter deer yarding behavior and winter conditions. Although northern portions of the study region are reported to have

lower deer densities (2-6 deer km⁻¹) than southern areas (6-12 deer km⁻¹) (MN DNR 2009), our measure of deer browse pressure showed no correlation ($r = 0.01$) with temperature, indicating that lower regional deer densities alone do not necessarily equate with enhanced performance for temperate species at fine scales such as used in this study. Some of the cooler sites may have increased browse pressure due to extended browsing over a longer, harsher winter, and deer concentrating in areas where snow depth is low (Dumont et al. 2005). This increased browse pressure may inhibit the ability of temperate species to expand in these areas. On the other hand, low browse pressure at two cool sites located in the lake-effect snowbelt caused by Lake Superior may facilitate temperate expansion. Deer avoid the deep snows of this area during winter when most browse damage occurs (Frelich & Lorimer 1985), thus minimizing growth loss and improving the relative performance of more palatable broadleaf temperate species.

In addition to growth, mortality rates are an important driver of understory dynamics (Pacala et al. 1994, Wyckoff & Clark 2002). Saplings can spend decades in the understory as advance regeneration, as evidenced by the fact that the lowest median age of any of our study species was 16 years (*A. rubrum*), maximum age for each species was greater than 45 years, and the maximum height was < 5 m. Although we did not directly measure mortality rates, probability of mortality increases with decreasing growth, especially at very low growth rates (Kobe 1996, Wyckoff & Clark 2002). Thus, slow growing stems (small size, low light, high browse pressure, or near temperature limits) may be surviving near their physiological limits and further stress could cause

mortality. For example, increased browse damage at northern range limits for temperate species and warmer temperatures at southern range limits of boreal species may increase the probability of mortality, thus altering relative performance in addition to changes due to growth rates.

All saplings in this observational study were naturally established advance regeneration growing in typical forest understory conditions and these results demonstrate that natural variation in drivers across the narrow temperate-boreal transition zone can cause detectable changes in growth rates and relative performance of competing saplings. Although warming temperatures are predicted to result in large range limit shifts, the outcome of competitive interactions among saplings will depend on multiple factors including browse pressure, understory light levels, and even sapling size. Enhanced growth by temperate species in response to temperature was most detectable under favorable growing conditions, including low browse pressure and high light. Thus, any efforts at facilitating forest compositional changes will need to address these interactions, especially the ‘cooling’ effects of browse pressure.

Table 3.1. Summary data for the two boreal conifer and three temperate broadleaf study species. Species selected were common as advance regeneration in temperate-boreal transition zone forests. Stem age and radial growth were determined from basal cross-sections harvested 10 cm above ground level.

Species	Sites	Stems	Shade-tolerance*	Age			Radial growth (mm yr ⁻¹)			Height growth (cm yr ⁻¹)		
				median	min	max	mean(sd)	min	max	mean(sd)	min	max
<i>Abies balsamea</i>	14	509	1	23	3	61	0.50(0.42)	0.03	3.03	9.0(7.2)	0.1	41.8
<i>Picea glauca</i>	8	218	2	23	5	77	0.59(0.43)	0.04	2.23	7.5(5.7)	1.1	25.8
<i>Acer rubrum</i>	7	178	2	16	2	49	0.28(0.18)	0.03	1.00	8.8(8.9)	0.1	46.5
<i>Acer saccharum</i>	14	553	1	18	3	72	0.23(0.13)	0.05	1.13	6.6(6.6)	0.1	39.1
<i>Quercus rubra</i>	7	156	3	18	2	45	0.22(0.19)	0.04	1.03	8.0(7.4)	0.5	33.5

*Shade-tolerance: 1 (high) - 5 (low) (based on Burns & Honkala 1990)

Table 3.2. Summary information for explanatory variables used in sapling radial and height growth models. Summer temperature is based on the months of June-August, 2005-2009.

Species	Initial Radius (mm)			Initial height (cm)			Light (canopy openness %)			Browse pressure (0-10 scale)			Summer Temp. (JJA °C)	
	mean(sd)	min	max	mean(sd)	min	max	mean(sd)	min	max	mean(sd)	min	max	min	max
<i>Abies balsamea</i>	6.24(4.22)	0	22.29	124.9(76.9)	3.2	366.7	9.4(7.8)	0.8	39.7	0.7(1.7)	0	9	17.0	19.3
<i>Picea glauca</i>	7.74(5.83)	0	31.27	126.6(76.1)	0	382.5	8.6(7.1)	0.7	39.8	0(0.1)	0	1	17.0	19.3
<i>Acer rubrum</i>	3.38(2.37)	0	13	126.6(101.6)	0	454.4	12.5(10.2)	1.5	39.2	3.0(3.2)	0	9	17.0	18.7
<i>Acer saccharum</i>	3.76(2.73)	0	18.35	146.5(105.5)	2.4	453.0	8.2(5.5)	0.5	30.5	2.7(2.9)	0	9	17.0	19.3
<i>Quercus rubra</i>	3.48(2.30)	0	11.06	112.4(93.9)	8.6	403.7	11.6(8.1)	1.3	37.3	3.4(3.4)	0	9	17.0	19.3

Table 3.3. Fixed effects parameter estimates from linear mixed-effects models of sapling height growth for each of the five study species. r^2 is the squared correlation coefficient between observed and modeled values.

<i>Abies balsamea</i> ($r^2 = 0.77$)				
Parameter	Value	SE	t-value	P-value
Intercept	2.033	0.058	35.12	<0.0001
sqrt(initial size)	0.119	0.006	20.51	<0.0001
log(light)	0.345	0.034	10.14	<0.0001
Browse	-0.049	0.019	-2.58	0.010
Temperature (JJA)	-0.294	0.078	-3.78	0.003
Size X Browse	0.013	0.004	3.42	0.001
Light X Temp	-0.082	0.042	-1.94	0.053
<i>Picea glauca</i> ($r^2 = 0.64$)				
Parameter	Value	SE	t-value	P-value
Intercept	1.923	0.041	47.09	<0.0001
sqrt(initial size)	0.088	0.009	9.29	<0.0001
log(light)	0.355	0.045	7.85	<0.0001
Temperature (JJA)	-0.128	0.052	-2.46	0.049
<i>Acer rubrum</i> ($r^2 = 0.43$)				
Parameter	Value	SE	t-value	P-value
Intercept	1.966	0.078	25.14	<0.0001
sqrt(initial size)	0.052	0.013	4.03	<0.0001
log(light)	0.425	0.072	5.88	<0.0001
Browse	-0.080	0.019	-4.29	<0.0001
Temperature (JJA)	0.327	0.113	2.89	0.028
Light X Browse	-0.066	0.021	-3.17	0.002
Browse X Temp	-0.056	0.025	-2.27	0.025
<i>Acer saccharum</i> ($r^2 = 0.46$)				
Parameter	Value	SE	t-value	P-value
Intercept	1.689	0.082	20.48	<0.0001
sqrt(initial size)	0.019	0.008	2.34	0.020
log(light)	0.284	0.060	4.77	<0.0001
Browse	-0.070	0.013	-5.52	<0.0001
Temperature (JJA)	0.103	0.110	0.94	0.368
Light X Browse	-0.045	0.016	-2.77	0.006
Browse X Temp	-0.036	0.016	-2.31	0.021
<i>Quercus rubra</i> ($r^2 = 0.53$)				
Parameter	Value	SE	t-value	P-value
Intercept	1.806	0.124	14.54	<0.0001
sqrt(initial size)	0.043	0.017	2.53	0.013
log(light)	0.379	0.081	4.70	<0.0001
Browse	-0.067	0.018	-3.77	<0.0001
Temperature (JJA)	0.089	0.150	0.59	0.574
Size X Browse	-0.010	0.005	-1.94	0.054
Size X Temp	-0.034	0.013	-2.63	0.010
Light X Temp	0.189	0.098	1.93	0.056

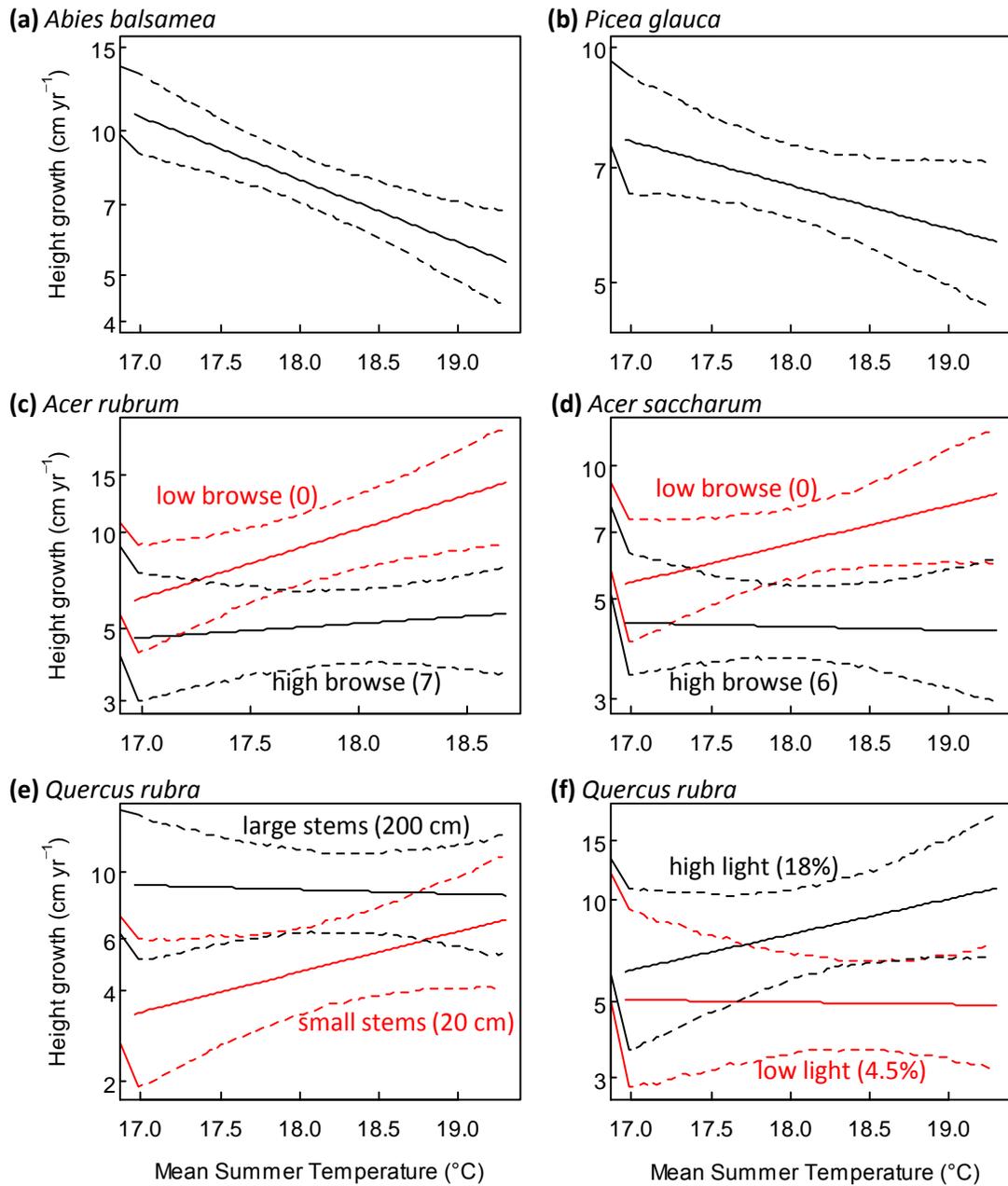


Figure 3.1. Height growth responses to mean summer temperature and temperature interactions across the temperate-boreal transition zone. Boreal conifers (a) *Abies balsamea* and (b) *Picea glauca* exhibited negative growth responses to the main effect of temperature. High browse pressure eliminated positive growth responses to

temperature for the temperate broadleaf species (c) *Acer rubrum* and (d) *Acer saccharum*. Temperate *Quercus rubra* height growth responses to temperature varied by (e) sapling size and (f) light availability. Low (red) and high (black) values of interacting factors are assigned their 20th and 80th percentile values, respectively. Dashed lines represent approximate 95% prediction intervals.

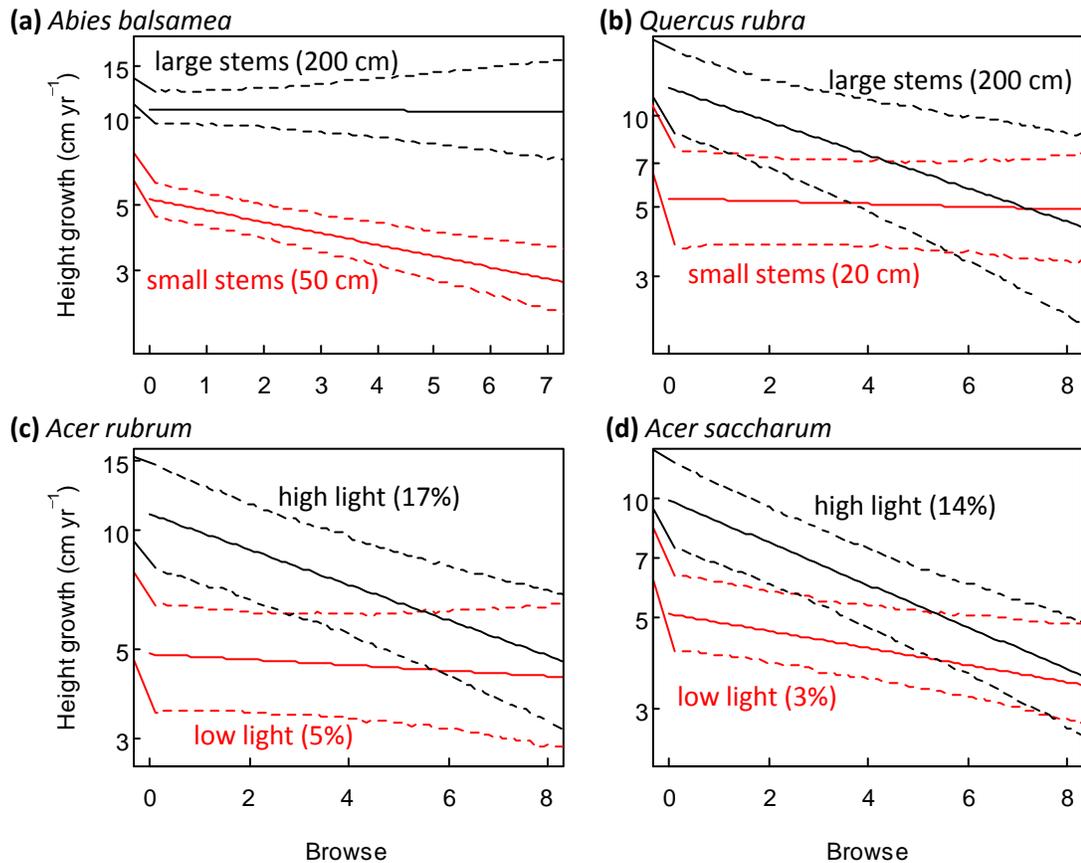


Figure 3.2. Height growth responses to browse interactions. (a) *Abies balsamea* and (b) *Quercus rubra* height growth responses to increasing browse damage varied by sapling size. Increasing browse pressure also eliminated height growth responses to increasing light availability for (c) *Acer rubrum* and (d) *Acer saccharum*. Low (red) and high (black) values of interacting factors are assigned their 20th and 80th percentile values, respectively. Dashed lines represent approximate 95% prediction intervals.

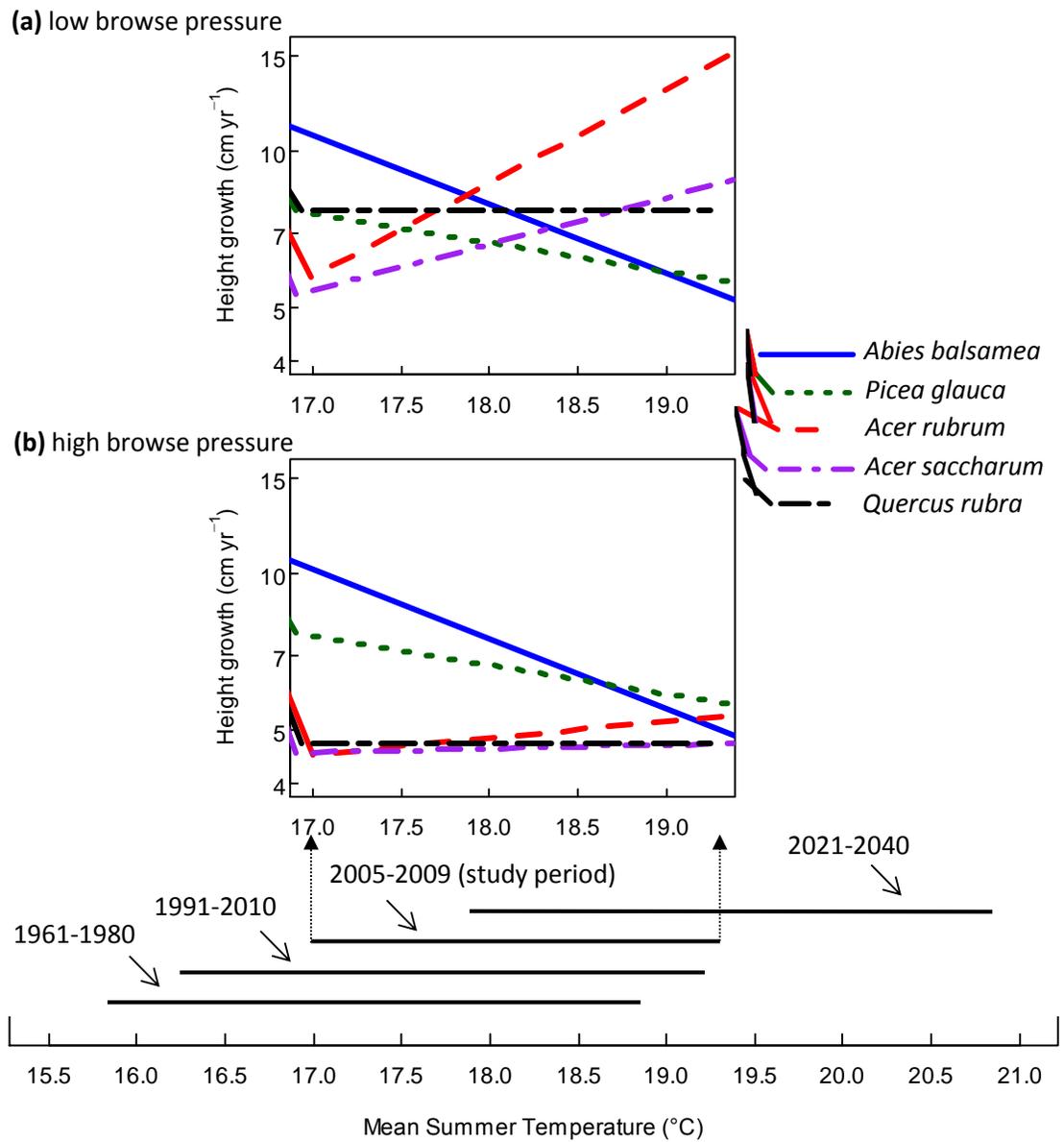


Figure 3.3. Height growth responses to temperature of all five species at (a) low and (b) high browse pressure. (c) comparisons of recent past and predicted future temperatures across the temperate-boreal transition zone. Low and high browse pressure for each

species were determined based on 20th and 80th percentile values, respectively. Future temperatures based on Kling et al. (2003).

Conclusions

Overall, the research within this dissertation shows that both temperate and boreal tree regeneration are sensitive to climate across the regional temperate-boreal transition zone, with performance shifts detectable across mean summer temperature gradients as narrow as 2.3 °C. Abundance and growth responses indicate that even moderate climate change will cause shifts in the relative performance of competing temperate and boreal regeneration. Because overstory composition is partially the result of species performance and interactions during the seedling and sapling stages, observed shifts in performance support predictions of climate-mediated changes in forest composition. Negative boreal conifer growth and abundance relationships to warmer temperatures suggest that the greatest changes in the near future will be at the warm end of the transition zone. Temperate species were not shown to be inhibited from establishing within boreal dominated neighborhoods when overstory temperate trees were present, indicating that understory conditions alone within boreal neighborhoods were not sufficient to exclude temperate species. Thus, temperate species appear likely to be able to expand within boreal dominated neighborhoods through typical gap dynamics. However, the strong role of the current overstory as a regeneration driver implies that a lack of sufficient temperate seed rain will slow compositional shifts within heavily boreal dominated stands. In addition to overstory neighborhood effects, seedbed conditions, mode of regeneration, light availability, competition with herbaceous and woody shrub species, and especially browse pressure will all impact regeneration performance and the rate and direction of forest change.

Continued research is needed to further elucidate tree regeneration dynamics and drivers and track forest compositional shifts across the temperate-boreal transition zone.

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APPENDIX A, Supplementary information for Chapter 1

Table S1.1. ANOVA tests of relative abundance shifts by overstory type and size class across local ecotones. Overstory types are temperate, mixed, and boreal and are based on tree layer relative abundances (see Methods for definitions). Size classes are seedlings, < 1 m in height, and saplings, ≥ 1 m height and <10 cm dbh.

Species	Size Class			Overstory Type			S.Class X Ov.Type		
	df	F	P	df	F	P	df	F	P
<i>Betula papyrifera</i>	1,144	7.60	0.007	2,53	0.82	0.444	2,144	0.35	0.704
<i>Populus tremuloides</i>	1,154	2.99	0.086	2,59	0.11	0.894	2,154	0.18	0.834
<i>Abies balsamea</i>	1,218	86.26	<0.0001	2,100	4.70	0.011	2,218	1.01	0.366
<i>Picea glauca</i>	1,155	30.00	<0.0001	2,59	0.53	0.594	2,155	0.30	0.740
<i>Acer rubrum</i>	1,215	195.86	<0.0001	2,98	5.64	0.005	2,215	0.78	0.459
<i>Acer saccharum</i>	1,183	24.66	<0.0001	2,89	14.54	<0.0001	2,183	1.01	0.365
<i>Betula alleghaniensis</i>	1,65	0.24	0.628	2,17	0.12	0.884	2,65	0.71	0.493
<i>Fraxinus nigra</i>	1,88	30.83	<0.0001	2,29	1.96	0.159	2,88	0.94	0.396
<i>Ostrya virginiana</i>	1,78	38.62	<0.0001	2,21	1.62	0.222	2,78	0.45	0.638
<i>Prunus serotina</i>	1,73	7.21	0.009	2,26	0.02	0.985	2,79	0.32	0.726
<i>Quercus rubra</i>	1,98	16.28	0.0001	2,36	0.32	0.725	2,98	0.97	0.385
<i>Tilia americana</i>	1,61	0.93	0.339	2,19	1.43	0.263	2,61	0.30	0.743

Table S1.2. ANOVA tests of regeneration success shifts by overstory type and size class across local ecotones. Regeneration success is the difference in relative abundance between the overstory and understory layers. Overstory types are temperate, mixed, and boreal and are based on tree layer relative abundances (see Methods for definitions). Size classes are seedlings, < 1 m in height, and saplings, \geq 1 m height and <10 cm dbh.

Species	Size Class			Overstory Type			S.Class X Ov.Type		
	df	F	P	df	F	P	df	F	P
<i>Betula papyrifera</i>	1,139	3.12	0.080	2,53	12.57	<0.0001	2,139	0.25	0.781
<i>Populus tremuloides</i>	1,147	0.29	0.590	2,59	12.57	<0.0001	2,147	0.26	0.773
<i>Abies balsamea</i>	1,206	128.53	<0.0001	2,100	0.80	0.451	2,206	0.76	0.470
<i>Picea glauca</i>	1,142	19.49	<0.0001	2,59	10.78	0.0001	2,142	0.74	0.481
<i>Acer rubrum</i>	1,192	131.94	<0.0001	2,98	44.03	<0.0001	2,192	0.27	0.767
<i>Acer saccharum</i>	1,168	20.95	<0.0001	2,89	3.15	0.048	2,168	0.29	0.752
<i>Betula alleghaniensis</i>	1,50	0.06	0.945	2,17	1.11	0.351	2,50	1.54	0.221
<i>Fraxinus nigra</i>	1,56	3.99	0.051	2,29	2.51	0.099	2,56	0.88	0.422
<i>Ostrya virginiana</i>	1,59	34.67	<0.0001	2,21	0.56	0.579	2,59	0.39	0.682
<i>Prunus serotina</i>	1,39	0.01	0.940	2,26	0.16	0.849	2,39	0.14	0.872
<i>Quercus rubra</i>	1,53	0.87	0.356	2,36	3.24	0.051	2,53	1.35	0.268
<i>Tilia americana</i>	1,49	1.35	0.251	2,19	10.59	0.001	2,49	0.37	0.692

Table S1.3. ANOVA tests of regeneration success shifts by summer temperature

regime and size class across the regional transition zone. Regeneration success is the difference in relative abundance between the overstory and understory layers. Overstory types are temperate, mixed, and boreal and are based on tree layer relative abundances (see Methods for definitions). Size classes are seedlings, < 1 m in height, and saplings, \geq 1 m height and <10 cm dbh . Mean summer temperature (JJA, 1978-2007) is based on Daly et al. (2008).

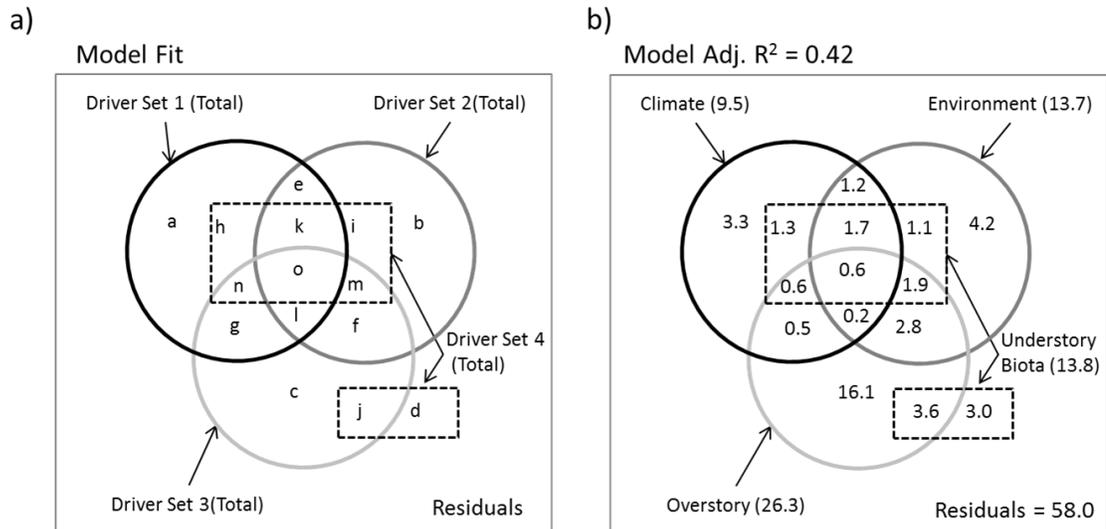
Species	Summer Temp			Size Class			Temp X S.Class		
	df	F	P	df	F	P	df	F	P
<i>Betula papyrifera</i>	2,52	2.12	0.130	1,51	0.06	0.808	2,51	0.49	0.618
<i>Populus tremuloides</i>	2,54	1.11	0.337	1,51	0.20	0.655	2,51	1.79	0.178
<i>Abies balsamea</i>	2,67	8.50	0.001	1,67	42.81	<0.0001	2,67	2.48	0.092
<i>Picea glauca</i>	2,55	0.28	0.755	1,54	7.74	0.007	2,54	1.41	0.253
<i>Acer rubrum</i>	2,68	3.49	0.036	1,63	95.39	<0.0001	2,63	0.06	0.946
<i>Acer saccharum</i>	2,53	5.24	0.008	1,50	2.95	0.092	2,50	2.01	0.144
<i>Betula alleghaniensis</i>	2,25	1.92	0.168	1,19	0.66	0.426	2,19	1.92	0.175
<i>Fraxinus nigra</i>	2,32	3.75	0.034	1,20	1.45	0.243	2,20	1.56	0.235
<i>Ostrya virginiana</i>	2,32	2.54	0.094	1,27	19.55	0.0001	2,27	5.46	0.010
<i>Prunus serotina</i>	2,26	1.18	0.324	1,17	3.39	0.083	2,17	0.38	0.692
<i>Quercus rubra</i>	2,35	0.47	0.632	1,20	0.38	0.544	2,20	2.59	0.100
<i>Tilia americana</i>	2,23	0.81	0.459	1,18	0.51	0.483	2,18	0.36	0.705

Table S1.4. ANOVA tests of regeneration success shifts by precipitation regime and size class across the regional transition zone. Regeneration success is the difference in relative abundance between the overstory and understory layers. Overstory types are temperate, mixed, and boreal and are based on tree layer relative abundances (see Methods for definitions). Size classes are seedlings, < 1 m in height, and saplings, \geq 1 m height and <10 cm dbh. Mean annual precipitation (1978-2007) is based on Daly et al. (2008).

Species	Annual Precipitation			Size Class			Precip X S.Class		
	df	F	P	df	F	P	df	F	P
<i>Betula papyrifera</i>	2,52	1.91	0.158	1,51	0.02	0.894	2,51	1.75	0.185
<i>Populus tremuloides</i>	2,54	1.12	0.332	1,50	1.17	0.285	2,50	0.37	0.695
<i>Abies balsamea</i>	2,67	3.58	0.033	1,66	56.84	<0.0001	2,66	0.46	0.633
<i>Picea glauca</i>	2,55	0.21	0.812	1,54	10.60	0.002	2,54	2.92	0.063
<i>Acer rubrum</i>	2,68	6.43	0.003	1,63	54.50	<0.0001	2,63	2.01	0.142
<i>Acer saccharum</i>	2,52	2.34	0.107	1,49	8.62	0.005	2,49	0.11	0.899
<i>Betula alleghaniensis</i>	2,25	3.48	0.047	1,21	0.02	0.900	2,21	1.51	0.243
<i>Fraxinus nigra</i>	2,32	1.20	0.315	1,25	4.64	0.041	2,25	0.96	0.398
<i>Ostrya virginiana</i>	2,32	0.77	0.473	1,27	13.04	0.001	2,27	1.43	0.256
<i>Prunus serotina</i>	2,26	0.26	0.774	1,16	0.51	0.487	2,16	0.26	0.774
<i>Quercus rubra</i>	2,35	1.28	0.291	1,20	2.66	0.119	2,20	1.00	0.385
<i>Tilia americana</i>	2,23	1.92	0.169	1,16	0.00	0.968	2,16	2.95	0.081

APPENDIX B, Supplementary information for Chapter 2

Figure S2.1. Venn diagrams of variation partitioning among four sets of explanatory variables. (a) diagram showing the partition of variation into 15 explained portions (a-o) and one unexplained portion (residuals). Polygons a-d indicate unique explained variation, polygons e-j, k-n, and o depict explained variation shared by two, three, and all four explanatory variables, respectively. (b) variation partitioning of the tree regeneration layer by climate, understory environment, overstory composition, and understory biota. Explained variation (%) is based on adj. R^2 values.



APPENDIX C, Supplementary information for Chapter 3

Table S3.1. Height growth model rankings based on AICc. Top models ($<2 \Delta AICc$), base (size+light), browse (size+light+browse), temperature (size+light+temperature), and additive (size+light+browse+temperature) models are shown for comparison.

Model parameter symbols: S = initial size, L= canopy openness (light), B = browse pressure, T = mean summer temperature (JJA °C 2007-2008). Two letters combined represent two-way interactions.

Table S3.1.

		Model Parameters	$\Delta AICc$
<i>Abies balsamea</i>			
		S + L + B + T + SB + LT	0
		S + L + B + T + SB + ST	1.37
		S + L + B + T + SB	1.68
(additive)		S + L + B + T	11.53
(browse)		S + L + B	20.13
(temperature)		S + L + T	29.55
(base)		S + L	38.66
<i>Picea glauca</i>			
(temperature)		S + L + T	0
(base)		S + L	3.06
<i>Acer rubrum</i>			
		S + L + B + T + LB + BT	0
(additive)		S + L + B + T	8.02
(browse)		S + L + B	10.68
(base)		S + L	21.44
(temperature)		S + L + T	22.40
<i>Acer saccharum</i>			
		S + L + B + T + LB + BT	0
		S + L + B + LB	2.10
(browse)		S + L + B	3.99
(additive)		S + L + B + T	5.29
(base)		S + L	28.73
(temperature)		S + L + T	29.36
<i>Quercus rubra</i>			
		S + L + B + T + SB + ST + LT	0
		S + L + B + T + ST + LT	1.52
		S + L + B + T + SB + ST	1.56
(browse)		S + L + B	3.18
(additive)		S + L + B + T	5.04
(base)		S + L	9.23
(temperature)		S + L + T	10.85

Table S3.2. Radial growth model rankings based on AICc. Top models (<2 Δ AICc), base (size+light), browse (size+light+browse), temperature (size+light+temperature), and additive (size+light+browse+temperature) models are shown for comparison. Model parameter symbols: S = initial size, L= canopy openness (light), B = browse pressure, T = mean summer temperature (JJA °C 2005-2009). Two letters combined represent two-way interactions.

	Model Parameters										Δ AICc					
<i>Abies balsamea</i>																
	S	+	L	+	B	+	T	+	SB	+	LB	0				
(additive)	S	+	L	+	B	+	T					25.68				
(temperature)	S	+	L	+	T							27.45				
(browse)	S	+	L	+	B							29.46				
(base)	S	+	L									31.46				
<i>Picea glauca</i>																
(base)	S	+	L									0				
(temperature)	S	+	L	+	T							2.12				
<i>Acer rubrum</i>																
	S	+	L	+	B	+	T	+	LB	+	ST	0				
(additive)	S	+	L	+	B	+	T					15.64				
(browse)	S	+	L	+	B							19.68				
(temperature)	S	+	L	+	T							20.00				
(base)	S	+	L									21.69				
<i>Acer saccharum</i>																
	S	+	L	+	B	+	T	+	SB	+	LB	+	BT	+	ST	0
	S	+	L	+	B	+	T	+	SB	+	LB	+	ST			1.6
(additive)	S	+	L	+	B	+	T									17.34
(temperature)	S	+	L	+	T											18.43
(browse)	S	+	L	+	B											20.82
(base)	S	+	L													22.22
<i>Quercus rubra</i>																
	S	+	L	+	B	+	T	+	SB	+	ST	+	LT			0
	S	+	L	+	B	+	T	+	SB	+	ST					0.39
	S	+	L	+	B	+	SB									0.62
(browse)	S	+	L	+	B											14.85
(additive)	S	+	L	+	B	+	T									16.53
(temperature)	S	+	L	+	T											29.35
(base)	S	+	L													30.97

Table S3.3. Fixed effects parameter estimates from linear mixed-effects models of sapling radial growth for each of the five study species. r^2 is the squared correlation coefficient between observed and modeled values.

<i>Abies balsamea</i> ($r^2 = 0.70$)				
Parameter	Value	SE	t-value	P-value
Intercept	-1.054	0.073	-14.51	<0.0001
log(initial size)	0.683	0.046	14.81	<0.0001
log(light)	0.432	0.045	9.66	<0.0001
Browse	-0.088	0.028	-3.11	0.002
Temperature (JJA)	-0.235	0.098	-2.39	0.034
Size X Browse	-0.133	0.029	-4.59	<0.0001
Light X Browse	-0.075	0.018	-4.25	<0.0001
<i>Picea glauca</i> ($r^2 = 0.73$)				
Parameter	Value	SE	t-value	P-value
Intercept	-0.810	0.059	-13.77	<0.0001
log(initial size)	0.635	0.053	12.08	<0.0001
log(light)	0.528	0.049	10.81	<0.0001
<i>Acer rubrum</i> ($r^2 = 0.41$)				
Parameter	Value	SE	t-value	P-value
Intercept	-1.496	0.045	-33.26	<0.0001
log(initial size)	0.306	0.078	3.93	0.0001
log(light)	0.299	0.056	5.36	<0.0001
Browse	-0.036	0.014	-2.48	0.015
Temperature (JJA)	0.264	0.067	3.94	0.0077
Light X Browse	-0.069	0.015	-4.51	<0.0001
Size X Temp	0.241	0.114	2.12	0.036
<i>Acer saccharum</i> ($r^2 = 0.44$)				
Parameter	Value	SE	t-value	P-value
Intercept	-1.631	0.054	-30.13	<0.0001
log(initial size)	0.034	0.043	0.80	0.427
log(light)	0.155	0.039	3.95	0.0001
Browse	-0.024	0.009	-2.77	0.006
Temperature (JJA)	0.183	0.072	2.53	0.027
Size X Browse	-0.046	0.015	-3.09	0.002
Light X Browse	-0.025	0.011	-2.33	0.020
Browse X Temp	-0.021	0.011	-1.91	0.057
Size X Temp	-0.157	0.050	-3.14	0.002
<i>Quercus rubra</i> ($r^2 = 0.64$)				
Parameter	Value	SE	t-value	P-value
Intercept	-1.877	0.092	-20.44	<0.0001
log(initial size)	0.311	0.109	2.84	0.005
log(light)	0.549	0.076	7.23	<0.0001
Browse	-0.071	0.014	-4.94	<0.0001
Temperature (JJA)	0.092	0.112	0.82	0.444
Size X Browse	-0.132	0.032	-4.16	0.0001
Size X Temp	-0.294	0.107	-2.74	0.007
Light X Temp	0.149	0.092	1.61	0.109

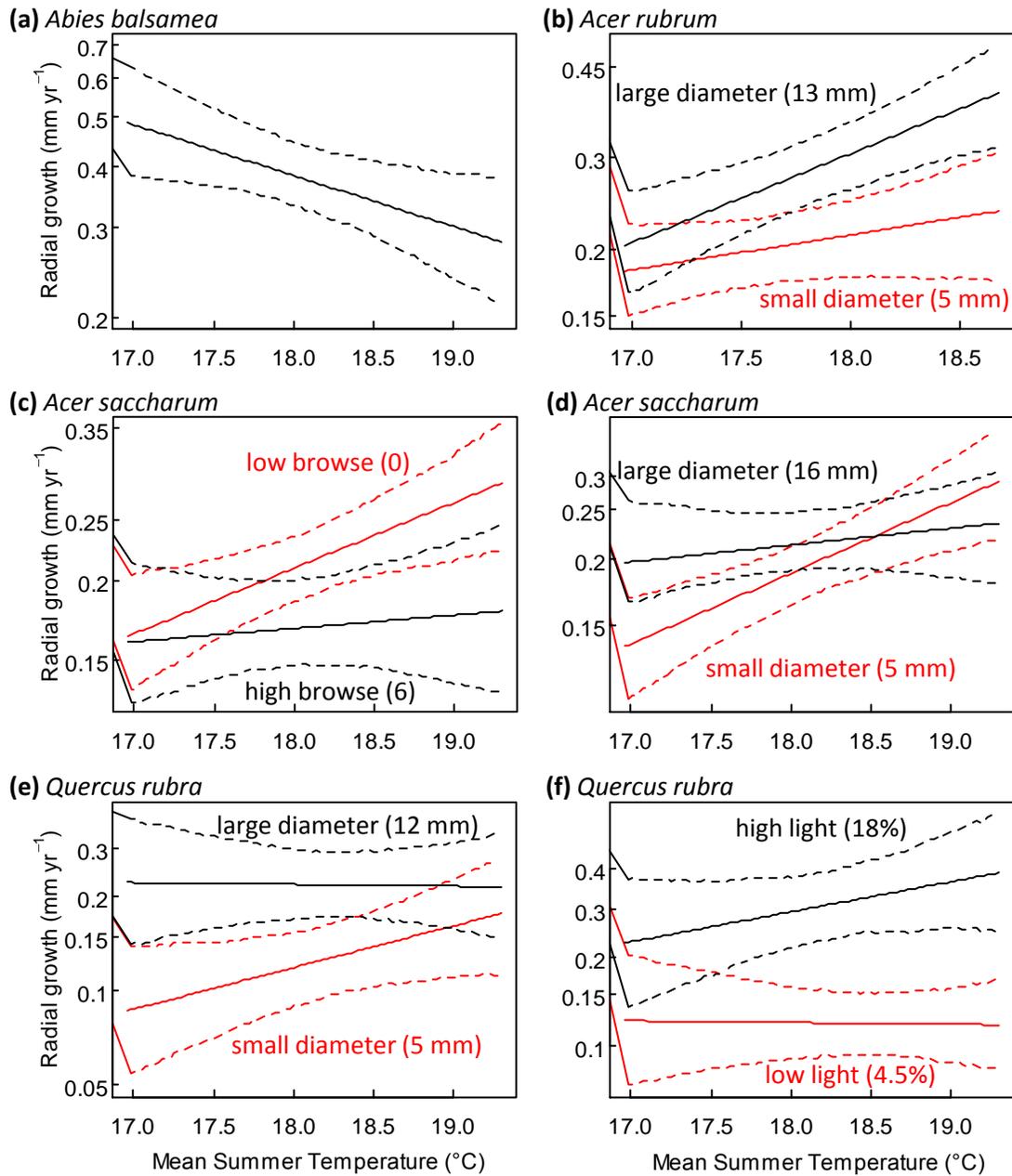


Figure S3.1. Radial growth responses to summer temperature and temperature interactions across the temperate-boreal transition zone. (a) Boreal conifer *Abies balsamea* growth response to the main effect of temperature was negative. Radial growth responses to temperature varied by initial sapling size for (b) *Acer rubrum*, (d)

Acer saccharum, and (e) *Quercus rubra*. (d) high browse pressure eliminated positive radial growth responses to temperature for *Acer saccharum*. (f) radial growth responses to temperature increased with increasing light for *Quercus rubra*. Low (red) and high (black) values of interacting factors are assigned their 20th and 80th percentile values, respectively. Dashed lines represent approximate 95% prediction intervals.

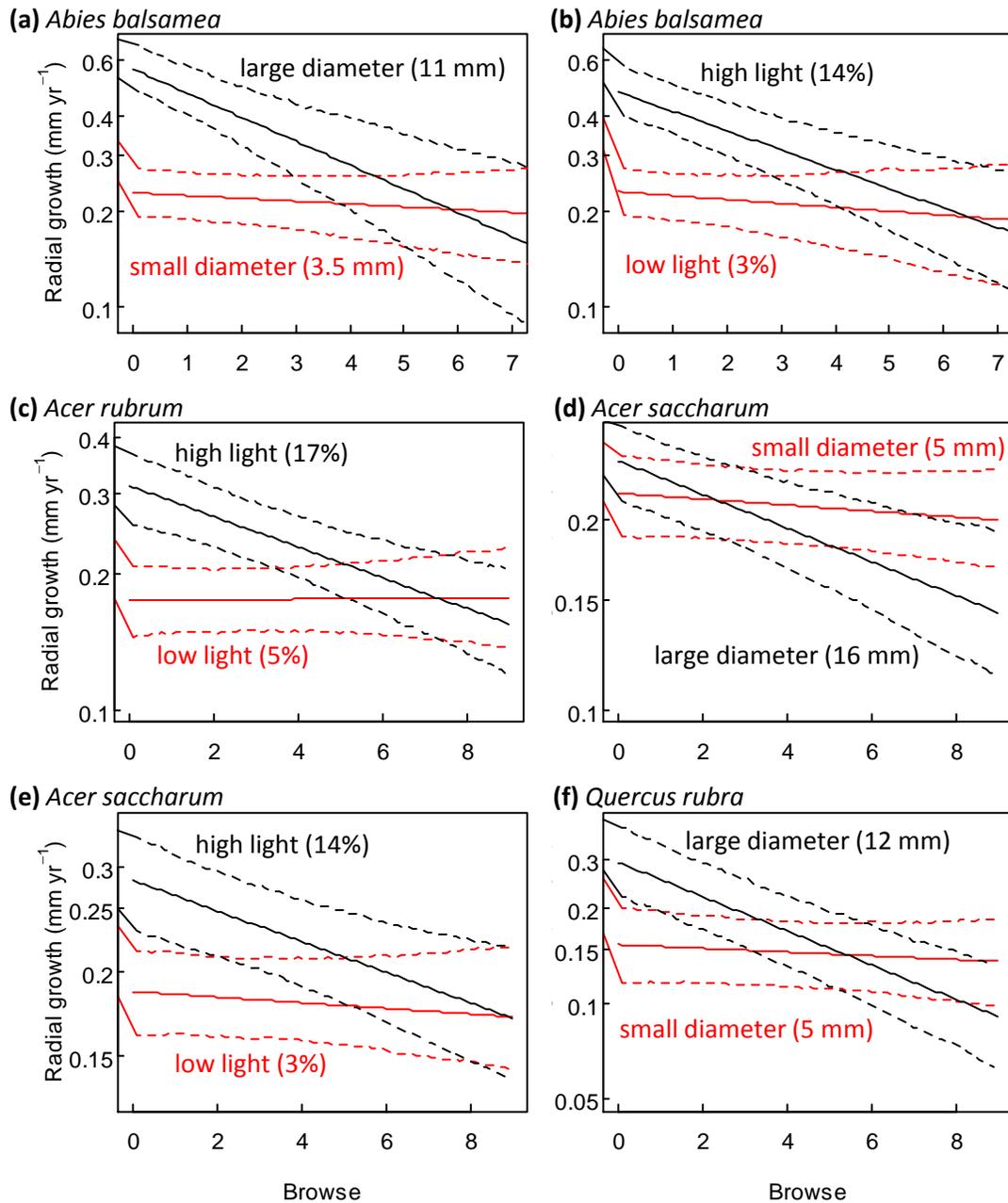


Figure S3.2. Radial growth responses to browse interactions. Radial growth reductions due to increasing browse pressure were greater for large than small diameter stems of (a) *Abies balsamea*, (d) *Acer saccharum*, and (f) *Quercus rubra*. High browse pressure also eliminated growth responses to increasing light for (b) *Abies balsamea*, (c) *Acer*

rubrum, and (e) *Acer saccharum*. Low (red) and high (black) values of interacting factors are assigned their 20th and 80th percentile values, respectively. Dashed lines represent approximate 95% prediction intervals.