Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine

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Abstract

Because species affect ecosystem functioning, understanding migration processes is a key component of predicting future ecosystem responses to climate change. This study provides evidence of range expansion under current climatic conditions of an indigenous species with strong ecosystem effects. Surveys of stands along the northern distribution limit of lodgepole pine (*Pinus contorta* var. *latifolia*) in central Yukon Territory, Canada showed consistent increases in pine dominance following fire. These patterns differed strongly from those observed at sites where pine has been present for several thousand years. Differences in species thinning rates are unlikely to account for the observed increases in pine dominance. Rates of pine regeneration at its range limits were equivalent to those of spruce, indicating a capacity for rapid local population expansion. The study also found no evidence of strong climatic limitation of pine population growth at the northern distribution limit. We interpret these data as evidence of current pine expansion at its range limits and conclude that the northern distribution of lodgepole pine is not in equilibrium with current climate. This study has implications for our ability to predict vegetation response to climate change when populations may lag in their response to climate.

Introduction

A major scientific challenge is to understand the causes, mechanisms, and ecosystem consequences of species migration in response to global environmental change. Modern and paleoecological studies show that changes in species distributions can dramatically alter the structure and functioning of ecosystems, especially when a species has unique effects on environment or disturbance regime (Vitousek *et al.*, 1987; D'Antonio & Vitousek, 1992; Hu *et al.*, 2001). Plant species migrate individualistically, with rates that vary in time and space (Davis, 1981; Webb, 1987; Huntley, 1991). Such variations can reflect differences in climate forcing, climate response, and dispersal behavior. Improving our understanding of how dispersal dynamics (e.g. Clark *et al.*, 1998) and climate (e.g. Davis *et al.*, 1986) interact to drive migration rates is an important component of predicting future ecosystem response to global change.

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Many vegetation models predict that plant species will migrate in response to future changes in climate (e.g. Kirilenko & Solomon, 1998; Shafer *et al.*, 2001; Malcolm *et al.*, 2002). These models frequently depict expected range distributions in equilibrium with climate, but are poor indicators of transient species responses because they rarely consider non-climatic factors that affect distribution patterns and migration rates (Loehle & LeBlanc, 1996; Kirilenko & Solomon, 1998). The climate response functions that usually form the basis of these models are derived from current species distribution patterns (e.g. Woodward & Williams, 1987; Lenihan, 1993), a technique that implicitly assumes that current species distributions are in equilibrium with the climate and directly reflect climate limitation of growth or survival (Loehle & LeBlanc, 1996).

This study examines the population dynamics of a boreal tree species (lodgepole pine, *Pinus contorta* ssp. *latifolia*) at its northern distribution limits in order (a) to assess whether its current distribution limits appear to be in equilibrium with climate or other limiting factors,

and (b) if non-equilibrium is suggested, to gain insight into the population processes that occur along a transient distribution limit. The motivation for a study on lodgepole pine arises from earlier research on Holocene pollen records, which show that lodgepole pine appears to have arrived at sites in central Yukon Territory, Canada as recently as 300–400 years BP (MacDonald & Cwynar, 1986, 1991). These dates represent the latest stage of an 1800 km northward migration that began near the southern border of Canada about 12 000 years BP (MacDonald & Cwynar, 1986; MacDonald et al., 1998). Lodgepole pine does not occur further north or west in interior Alaska, although the healthy growth and cone production of planted pines in this area (Alden, 1988) suggest that suitable habitat and climatic regime are present. These studies indicate that lodgepole pine may be continuing its Holocene expansion into modern time and that its northern distribution limits may not represent an equilibrium with the current climate.

Continued migration of lodgepole pine has implications for understanding species migration response to long-term changes in climate and the roles played by migration lags in determining transient assemblages of vegetation communities. The presence of a non-equilibrium distribution edge would imply that empirical estimates of the climate envelope of this species (Lenihan, 1993; Thompson et al., 1999; Sykes, 2001) may be biased in their representation of the full potential range of the species. The migration dynamics of lodgepole pine are also important to consider with respect to changes in boreal ecosystem functioning. Boreal pines (lodgepole and jack pine, *Pinus banksiana*) have a unique set of traits that affect ecosystem processes in ways that are different from those of alternative forest dominants such as spruce (*Picea*) or deciduous trees (*Populus* and *Betula*). Changes in the distribution of pine would therefore be expected to have important feedbacks to ecosystem dynamics.

In this study, we test the hypothesis that lodgepole pine is currently migrating by comparing pine regeneration dynamics between sites located along the northern edge and those in the interior of its range in the Yukon Territory, Canada. Estimates of local expansion rates and relationships between expansion and site conditions provide additional information on the population processes occurring along the range edge of this species.

Materials and methods

Study area

The current distribution of interior lodgepole pine follows along the Rocky Mountain chain in North America from a southern limit in Colorado, USA to a northern limit in central Yukon Territory, Canada (Wheeler & Guries, 1982). Our sampling focuses on the northern populations of pine located in the Yukon Territory and along the Yukon/British Columbia border (Fig. 1). The regeneration of lodgepole pine is commonly associated with fire (Lotan & Perry, 1983), so we focused our sampling specifically on recently burned forest patches.

We used a multi-step procedure to select sample sites along the edge and in the interior of the northern lodgepole pine range. We first identified all road-accessible burns between 5 and 50 years of age in southern and central Yukon Territory using federal fire inventory maps (Indian and Northern Affairs Canada,
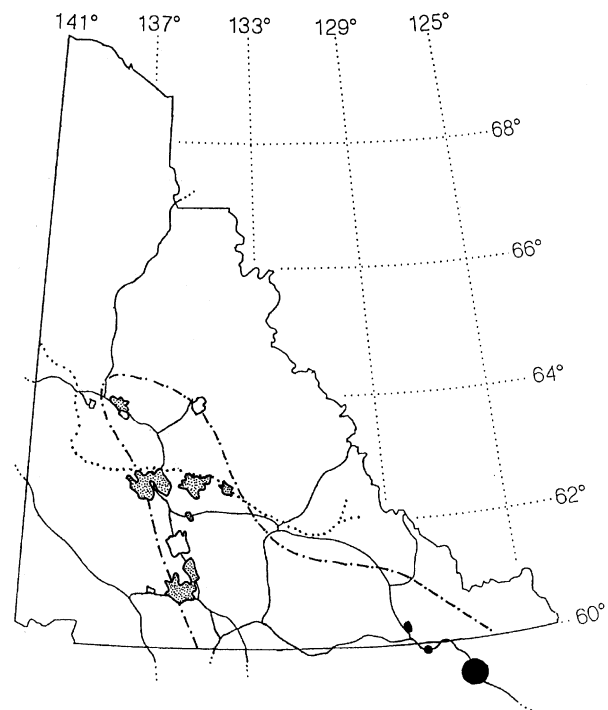

Fig. 1 Map of the Yukon Territory, showing the location of sample burns (oblong shapes) and lodgepole pine distribution limits (dash-and-dot line). Solid lines show roads and the dotted line indicates the Pelly River. The burns that are shown fit our criteria of accessibility, age restrictions, and preservation of deadwood. Unfilled shapes indicate burns where no pine was found ($n = 5$), stipple-filled shapes indicate burns with scattered pine present ($n = 6$), and solid-filled shapes indicate burns in areas of pine dominance ($n = 3$). Burn locations are based on the Yukon Fire History database (Indian and Northern Affairs Canada, unpublished). Locations of burns in British Columbia are approximate. Lodgepole pine distribution limits are drawn to encompass published pine sample locations in the Yukon Territory (Wheeler & Guries, 1982; MacDonald & Cwynar, 1986; Cody, 1996).

Whitehorse, Yukon). We visually inspected burns to determine whether deadwood from the recent fire was sufficiently well preserved to identify the genus of prefire individuals. We classed the resultant set of burns into one of three categories describing their position relative to the current pine distribution, as follows: (1) outside range: no evidence of pine being present, (2) range interior: burns occurred in or adjacent to stands dominated (>50% cover) by mature lodgepole pine, and (3) range edge: sites with trace amounts of mature pine but with no dominant pine stands >0.5 ha (Fig. 1). The resulting distribution of burns in these classes is generally consistent with published range maps of lodgepole pine (Wheeler & Guries, 1982; Cody, 1996). However, it is important to note that pine is not evenly distributed within those range limits and the species is absent from many areas that appear to be suitable habitat (J. Johnstone, personal observations).

We sampled all road-accessible burns along the range edge that met our sample criteria, plus two additional, isolated burns that were accessed by boat along the Pelly River (Fig. 1). The resultant range edge sample included six burns, ranging in age from 6 to 48 years. Within each burn, we sampled stands where pine was present in the prefire community, as evidenced by standing dead pine trees. In three of the burns, we sampled all accessible pine stands; in burns where pine was more widespread, we selected stands to represent the range of observed pine regeneration densities. We measured a total of 17 stands, with 1–5 stands burn^{-1}. All the selected stands experienced 100% mortality of standing trees as a result of the most recent fire. Ages of the prefire stands ranged from 60–130 years.

We sampled three burns located in the interior of the pine range along the Yukon/British Columbia border (Fig. 1). These burns were the closest burns to the pine range edge that fit our sample criteria. Pollen records indicate that pine has been present in the area for 2500–5000 years (MacDonald & Cwynar, 1986, 1991). Samples from the burns were obtained at sites where postfire vegetation succession had been documented in an earlier study (Oswald & Brown, 1990). All three burns occurred in the same year, and were sampled 19 years after burning. In total, 24 stands were sampled that ranged in age from 70–130 years when they burned (Oswald & Brown, 1990; unpublished data).

Sample procedures

For sites along the pine range edge, we sampled five randomly positioned $2 \times 50\,m^2$ transects (0.05 ha) within a 0.25 ha area in each stand and counted the total number of seedlings or saplings of each tree species. We pooled seedlings of black and white spruce (*Picea mariana* and *P. glauca*) because small seedlings of these two species could not be differentiated. In all but the oldest stands, aspen (*Populus tremuloides*) trees were the tallest individuals, followed by pine and then spruce. Species size distributions showed only occasional evidence of seedling establishment occurring later than 10 years after the burn, supporting our expectations of even-aged stands. We recorded observations of dead postfire seedlings as we encountered them. For dead seedlings, we assessed whether mortality was caused by herbivory or some other factor by looking for evidence of browsed stem tips or compensatory branching.

We documented the composition and basal diameters of all trees in the prefire community from standing or fallen deadwood that had been rooted within a sampling transect prior to the fire. Genus determinations of dead trees were based on cone, bark, and branching morphology. Dead trees of uncertain identity (6% of all sampled trees) were allocated to species categories according to the proportional composition of identified individuals. Black and white spruce were pooled because some black spruce individuals lack cones and cannot be readily differentiated from dead white spruce trees. We did not count trees that were dead at the time of the fire, judging from deep charring patterns on the bole. Together, pine, spruce, and aspen accounted for 99% of tree composition in both pre- and postfire stands.

We measured organic-layer depths at 55 points at 5 m intervals along the center line of each transect. The upper 15 cm of mineral soil was sampled using a 2.5 cm corer at five random points for laboratory analysis of soil pH and gravimetric moisture content at field capacity. The age of the prefire stand was determined from annual ring counts of 5–10 basal disks or tree cores (30 cm above the uppermost roots) obtained from a mixture of dead pine and spruce trees systematically sampled to represent the largest, and hence oldest, trees in the stand.

For sites in the range interior, we measured prefire basal diameters and postfire stem density in a single $10 \times 10\,m$ plot within each stand. The plots were established 1 year after the sites were burned, and were haphazardly selected to represent a range of prefire stand compositions and site conditions. Soil and site characteristics were measured at the time of plot establishment and are presented elsewhere (Oswald & Brown, 1990). All stands had lodgepole pine present in either the pre- or postfire community, and were dominated by pine, spruce, or a mixture of the two. Spruce, pine, and aspen represented 99% and 96% of stems in prefire and postfire stands, respectively.

Data analysis

We tested for differences in the general pattern of succession between pine range edge and range interior sites by calculating the frequency of positive, neutral, or negative shifts in the proportion of pine relative to the total conifer count (pine + spruce) and of aspen relative to the total stem count (pine + spruce + aspen). Composition shifts were calculated as pairwise differences in the proportion of a given species in pre- and postfire communities, respectively, within a stand. The use of pairwise, proportional differences allowed us to com-
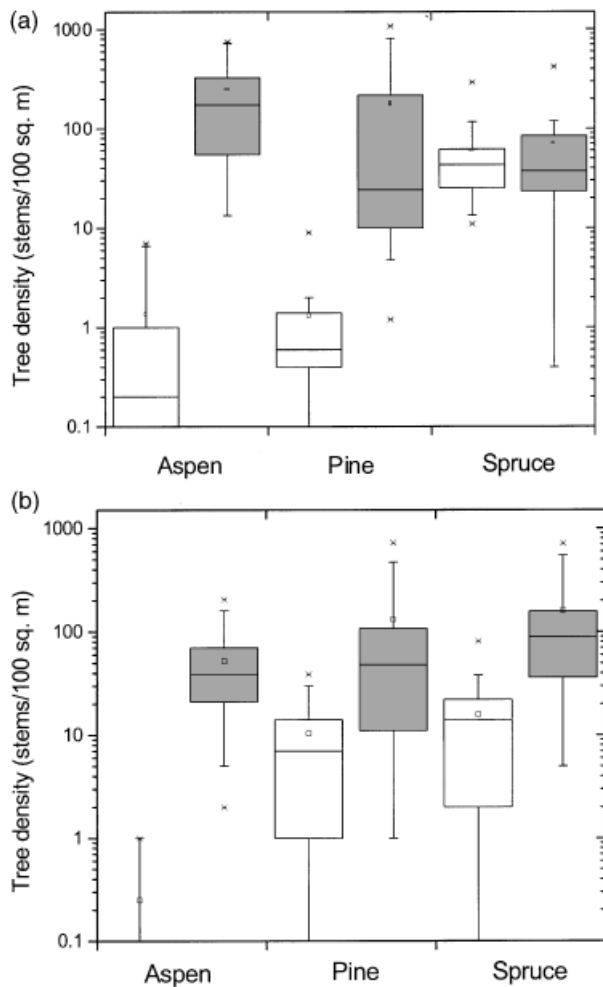
pare succession changes consistently across sites that spanned four orders of magnitude in species densities (Fig. 2). Pairwise differences were classed into five categories of change, ranging from a decrease of >50% to an increase of >50%, and significant differences in the distribution of observations were tested with a χ^2 test statistic (Conover, 1999). Summaries of mean pine : spruce ratios omitted stands with zero values for spruce because of its position in the denominator.

We evaluated possible relationships between postfire regeneration density and prefire and site characteristics at the pine range edge using the Spearman rank correlation coefficients, with a conservative significance threshold of $\alpha = 0.01$. We used a rank-based correlation statistic because several variables had non-normal distributions that were not satisfactorily corrected with transformations. Site variations in the slope and aspect were minimal and these characteristics were not included in the correlation analysis.

Results

Stands sampled along the edge of the pine range (Fig. 1) were dominated by white or black spruce at the time of burning, with minor components of lodgepole pine and trembling aspen (Fig. 2). Stem densities in both study areas show a general pattern of increased density following fire. This is a common pattern in forest succession, where initial recruitment occurs at high densities and stands subsequently thin through density-dependent mortality. There was substantial overlap in the ranges of species densities observed at sites along the pine range edge and in the range interior, although aspen was generally more common at the range edge sites.

Despite the similarity in absolute stem densities between the pine range edge and range interior, pairwise comparisons of species composition before and after fire indicate significant differences in successional trajectory between the two regions. Sites in the pine range interior frequently showed no change in conifer composition after fire, and of those that did, there was an equal tendency of increasing or decreasing pine dominance (Fig. 3). Sites along the pine range edge, however, showed a significantly different pattern ($\chi^2 = 20.7$, $P < 0.001$), in which 90% of the sampled stands experienced an increase in the proportion of pine after fire, and no stands showed a decrease in pine. This change represents a shift in the pine : spruce ratio at the pine range edge from a mean $\pm$ SE of 0.05 ± 0.02 ($n = 17$) in prefire stands to 4.79 ± 2.19 ($n = 16$) in postfire stands. In contrast, there was no significant shift in the mean pine : spruce ratio at sites in the range interior, with prefire communities averaging 2.72 ± 1.19

Fig. 2 Box plot of prefire (white boxes) and postfire (shaded boxes) stem densities of aspen, spruce, and pine measured in stands located (a) along the lodgepole pine range edge ($n = 17$), and (b) in the interior of the lodgepole pine range ($n = 23$). The box area encompasses the 25% and 75% quartiles, the sample median is designated as a horizontal line inside the box, and the sample mean is shown as an open square. Bars extending from the box encompass 95% of the observations, and additional ticks show extreme observations.
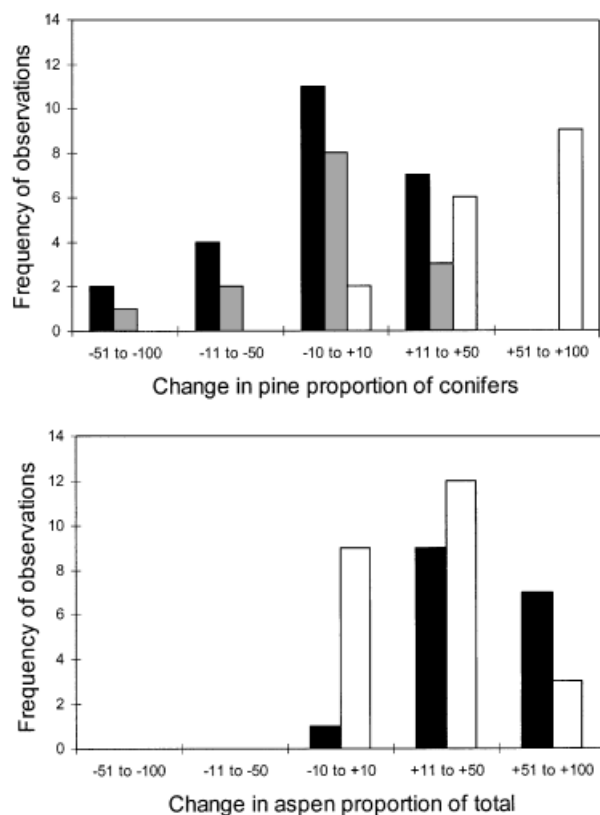
Fig. 3 Histograms showing the frequency of different classes of change in postfire stand composition relative to prefire composition. Changes in (a) the proportion of pine relative to total conifers, and (b) the proportion of aspen relative to total tree counts are shown separately for sites from the pine range edge (white bars) and range interior (black bars). Proportional changes in pine are also shown for a subset of range interior sites (gray bars; see results section).

($n = 20$) and postfire communities averaging 1.78 ± 0.54 ($n = 23$).

It could be argued that the above comparisons are biased because stands with very little prefire pine at the range edge are being compared with stands covering a wide range of prefire pine densities in the range interior. To account for this, we performed the same comparisons using only those range interior sites that had prefire pine : spruce ratios falling within the range observed at the range edge sites (0–0.3). The resulting subset of 14 range interior sites shows a pattern of conifer composition change that is very similar to the full set of sites (Fig. 2). The average pine : spruce ratios for this subset of interior sites significantly increased from prefire (mean $\pm$ SE of 0.07 ± 0.03, $n = 10$) to postfire (0.77 ± 0.09, $n = 13$) communities, but this increase was significantly lower than that observed at the pine range edge (Wilcoxon paired-ranks test, $Z = -3.45$, $P = 0.006$, $n = 10, 16$).

The observed changes in aspen dominance following fire were more consistent between study areas than the changes in pine (Fig. 3). The majority of sites in both regions showed an increase in the proportion of aspen following disturbance, and no sites exhibited a decrease in the proportion of aspen. There was, however, a greater frequency of stands showing a positive increase in aspen dominance in the range edge area compared to the range interior ($\chi^2 = 7.5$, $0.05 > P > 0.01$), probably related to the generally greater abundance of aspen at the range edge sites (Fig. 2). Postfire aspen densities (but not pine or spruce densities) were negatively correlated with postfire stand ages of sites along the pine range edge (Spearman $r = -0.78$, $P = 0.0002$).

Pine regeneration density at sites along the pine distribution edge was not significantly correlated with any of the environmental or stand factors that we measured, with the exception of soil moisture content at field capacity. Both pine and spruce densities tended to be higher on soils with greater moisture-holding capacity ($r = 0.77$ and 0.67, $P = 0.0003$ and 0.0035, respectively).

Discussion

We observed large increases in aspen density after fire at the majority of our sample sites (Fig. 2). A pulse of high aspen recruitment after disturbance is a common feature of normal succession development in boreal stands and reflects aspen's capacity for prolific root-sprouting (Zasada et al., 1992; Greene & Johnson, 1999). The fact that all our sites had low densities of prefire aspen is consistent with studies showing high rates of aspen mortality over time, particularly in mixed deciduous/conifer stands (Greene & Johnson, 1999; Yao et al., 2001). The negative correlation that we observed between aspen densities and postfire stand age provides additional support that substantial thinning of aspen was occurring during early succession at our sites.

In contrast to aspen, we expect stable patterns of relative dominance among conifers to be established shortly after fire and to persist through stand maturity. Trees in the boreal forest commonly establish during a brief 3–7 year window after fire, which is then followed by several decades of low recruitment (Lavoie & Sirois, 1998; Greene & Johnson, 1999; Gutsell & Johnson, 2002). Any subsequent changes in canopy dominance that occur through succession are largely the result of species differences in growth rate and mortality (Van Cleve & Viereck, 1981; Gutsell & Johnson, 2002). There is little evidence that later establishment of understory trees is likely to alter patterns of canopy dominance in

frequently burned forests (Johnson & Fryer, 1989; Gutsell & Johnson, 2002).

Both pine and spruce have the capacity to dominate mature sites in the Yukon Territory (Oswald & Brown, 1986). Pine frequently has higher initial growth rates than spruce, and is thus able to reach the canopy earlier and establish dominance (Eis *et al.*, 1982; Gutsell & Johnson, 2002). In northern British Columbia, heights of white spruce do not begin to exceed those of lodgepole pine until 100 years of age (Eis *et al.*, 1982). Although there are no published fire cycle estimates for our study area, the mean fire return intervals for nearby areas in Alaska and Alberta are estimated to range between 40–130 years (Yarie, 1981; Larsen, 1997). The mean prefire age of the stands we sampled was approximately 80 years (range 50–130 years). Given the current fire cycle, successional trajectories are too short to allow spruce to exclude pine competitively from the canopy of mature stands.

At least two factors, self-thinning and herbivory, could alter conifer composition following initial establishment, but are unlikely to lead to spruce dominance during the relatively short intervals between fires. Firstly, pine seedlings self-thin more rapidly than does spruce, but thinning rates decline dramatically once canopy dominance is established (Yao *et al.*, 2001). Pine reaches the canopy earlier than spruce because of its faster growth rate (Eis *et al.*, 1982; Wang *et al.*, 1994). Thinning is therefore unlikely to reverse strong hierarchies in conifer dominance within the current fire cycle or to explain the 40-fold increase in median pine abundance in post- and prefire stands at the pine distribution edge. Secondly, density-independent sources of mortality, such as herbivory, could reduce initial pine densities. Herbivory was most pronounced at one 48 year old site, where snowshoe hares caused 50% mortality in pine and <5% mortality in spruce. Although this site represents an extreme level of herbivory (herbivory-induced mortality at other sites was always <5% for both pine and spruce), initial pine densities were high enough such that pine was still the dominant conifer when we sampled. Future herbivory at this site is expected to be limited because the surviving pine saplings have reached heights above those accessible to hares. In summary, although thinning and herbivory may influence stand densities, the hierarchies of conifer dominance observed in postfire recruitment are likely to be maintained through succession to mature stands.

Succession in the boreal forest is commonly characterized as following a pattern of stand self-replacement, and mature forest composition is expected to vary little across multiple disturbance cycles in the absence of extreme disturbance events (Van Cleve & Viereck, 1981; Payette, 1992; Frelich & Reich, 1999). Even when forest composition is locally stable, however, we would expect individual stands to show some variability in composition after disturbance. Such variability can easily arise due to stochastic variations in seed availability, substrate conditions, mortality agents, or other factors (e.g. Zasada *et al.*, 1992). The pattern of conifer compositional change we observed at sites in the pine range interior is highly consistent with this type of dynamic equilibrium. There was no indication of a directional shift in conifer composition associated with fire disturbance at these sites, as similar numbers of sites showed positive vs. negative changes in pine relative abundance. This pattern held even when only sites with low initial pine abundance were examined. Instead, patterns of variation in species composition at these sites appear to be related to variations in environmental conditions (Oswald & Brown, 1990).

In contrast, sites along the pine range edge showed consistent, large increases in the relative proportion of pine following fire and consequently, a strong directional shift in conifer composition. The magnitude of observed increases in pine dominance at the range edge were, on average, four-fold larger than those observed for range interior sites with low prefire pine abundance. These large increases in pine abundance at the range edge are dramatic enough that many of the stands we sampled appear to be switching from dominance by spruce to dominance by pine within a single disturbance cycle. Such a clear directional shift strongly indicates a non-equilibrium succession dynamic in these stands. We suggest that the most reasonable explanation for this pattern is local population expansion associated with species migration. The movement of species range limits is expected to involve repeated colonization events, followed by population increases where site conditions are suitable (e.g. Clark *et al.*, 1998). Our observations of large, directional shifts in composition are consistent with expectations of local population increases along an active migration zone. Pollen records suggest that pine range limits reached central Yukon during the past millennium (MacDonald & Cwynar, 1986, 1991), and current population expansions may simply represent the latest stages of Holocene pine migration. An alternative explanation, that pine is responding to recent trends of increased warming (Serreze *et al.*, 2000) or fire disturbance (Weber & Flannigan, 1997), is also plausible, provided that populations at the range edge are more strongly limited by these factors than those in the range interior.

The lack of unique relationships between pine regeneration and environmental conditions provides additional indirect support for current migration

activity. If pine were limited to its current distribution by site factors or climate, we would expect its regeneration performance to be more sensitive to environmental variations than spruce, whose range limits extend well beyond our study area. Our analysis indicated, however, that both pine and spruce are sensitive to the same site factors (soil moisture capacity). This relationship presumably reflects a positive effect of moisture availability on young seedling survival (Zasada et al., 1992).

A comparison of absolute tree regeneration densities (Fig. 2) indicates that pine populations at the range edge have a recruitment capacity that is similar to that of spruce, despite low prefire densities of pine that might ordinarily be interpreted as an indication of marginal site conditions for pine growth. Variations in pine regeneration density among range-edge sites were not correlated with prefire pine basal area, an index of on-site seed source strength (Greene & Johnson, 1999). Most of the stands we sampled were hundreds to thousands of meters distant from any nearby pine stands, so local seed rain would have been the primary seed source for postfire pine regeneration. If seed availability is not an important driver of pine regeneration success, then single dispersal events that allow one or a few pine individuals to establish in a stand can have rapid and strong effects on future population densities. The presence of isolated prefire populations of pine capable of large increases in population size fits a model of migration in which recurrent establishment and growth of outlier populations provides the primary mechanism of expansion. If the relatively slow Holocene migration rates of interior lodgepole pine (MacDonald et al., 1998) represent a lag behind potential environmental limits, our data suggest that these lags are more likely to be associated with low rates of dispersal success, rather than intrinsically low rates of population increase. In particular, the strong dependence of pine regeneration on fire disturbance (Lotan & Perry, 1983), combined with a patchy distribution of fires and habitat in the mountainous Cordilleran landscape may limit the frequency with which successful long-distance establishment events occur for this species.

Pine expansion into spruce-dominated forests is likely to cause significant changes in ecosystem processes such as fire regime, forest productivity, and carbon storage. In western Canada, pine forests burn more frequently (Larsen, 1997) and generate larger fires (Cumming, 2001) than spruce forests. The serotinous cones of lodgepole pine store and release seed in response to heat, allowing pine to rapidly re-establish following fire (Lotan & Perry, 1983). This generates self-replacing stands with frequent fires and low soil carbon storage throughout the range of lodgepole pine (Lotan & Perry, 1983). Pine has higher nitrogen use efficiency than spruce (Bothwell et al., 2001) and produces higher volumes of wood when grown on poor-quality sites (Wang et al., 1994). Jack pine stands in central Canada are characterized by lower levels of organic layer accumulation and carbon storage on the forest floor than spruce stands (Trumbore & Harden, 1997). Because of these strong ecosystem effects, continued migration of lodgepole pine could have important feedbacks to ecosystem functioning in spruce-dominated boreal forests that would not be predicted from direct effects of climate on ecosystem processes.

Conclusions

This study is one of the first examples of which we are aware that documents current range expansion activity of an indigenous species in a relatively pristine natural environment. Observations of postfire stand regeneration at the edge and interior of the lodgepole pine range in the Yukon Territory provide strong evidence of non-equilibrium pine population expansion at its northern distribution limits. In conjunction with pollen records that estimate the arrival dates of pine in central Yukon to within the past millennium (MacDonald & Cwynar, 1986, 1991), this research suggests that lodgepole pine is continuing a trajectory of northern range expansion initiated in the early Holocene. This study has implications for how we interpret models of vegetation response to climate change. It provides an example of a species whose current range limits do not appear to be in equilibrium with modern climate and thus violates the assumptions implicit in the development of the climate response functions used in many biogeographical models. The rapid rates of population growth that we observed for pine at its range limits also suggest that limitations on local expansion rates are unlikely to account for the slow migration rate of interior lodgepole pine during the Holocene. Instead, we hypothesize that dispersal dynamics and regeneration niche are factors likely to constrain pine migration dynamics. Our ability to predict future ecosystem responses to climate change at time scales relevant to society depends on improving our understanding of the mechanisms, such as disturbance-dependent migration that may cause species migration rates to lag behind their potential climate limits. Because of the important effects of species on ecosystem processes, species differences in migration behavior may emerge as a key factor controlling transient ecosystem response to global change.

Acknowledgements

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