

1 **Title:** Satellite-based evidence for shrub and graminoid tundra expansion in northern Quebec
2 from 1986-2010.

3
4 **Running Title:** Shrub Expansion in Northern Quebec

5
6 Authors: K.M. McManus¹, D.C. Morton², J.G. Masek², D. Wang³, J.O. Sexton³, J. Nagol³, P.
7 Ropars⁴, S. Boudreau⁴

8
9 **Affiliations:**

10 ¹ Environmental Earth System Science, Stanford University

11 ² Biospheric Sciences Laboratory, NASA Goddard Space Flight Center

12 ³ Department of Geographical Sciences, University of Maryland, College Park

13 ⁴ Département de biologie, Northern Research Chair on Disturbance Ecology, Centre
14 d'études nordiques, Université Laval

15
16
17
18 **Corresponding Author:** Kelly M. McManus, Stanford University, Department of Global
19 Ecology. 260 Panama Ave, Stanford, CA 94305. email: mcmanusk@stanford.edu

20
21
22 **Keywords:** Arctic ecosystems, climate-induced vegetation response, Landsat, remote
23 sensing, time-series analysis

26 **Abstract**

27 Global vegetation models predict rapid poleward migration of tundra and boreal forest vegetation
28 in response to climate warming. Local plot and air-photo studies have documented recent
29 changes in high-latitude vegetation composition and structure, consistent with warming trends.
30 To bridge these two scales of inference, we analyzed a 24-year (1986-2010) Landsat time series
31 in a latitudinal transect across the boreal forest-tundra biome boundary in northern Quebec
32 province, Canada. This region has experienced rapid warming during both winter and summer
33 months during the last forty years. Using a per-pixel (30 m) trend analysis, 30% of the
34 observable (cloud-free) land area experienced a significant ($p < 0.05$) positive trend in the
35 Normalized Difference Vegetation Index (NDVI). However, greening trends were not evenly
36 split among cover types. Low shrub and graminoid tundra contributed preferentially to the
37 greening trend, while forested areas were less likely to show significant trends in NDVI. These
38 trends reflect increasing leaf area, rather than an increase in growing season length, because
39 Landsat data were restricted to peak-summer conditions. The average NDVI trend (0.007/yr)
40 corresponds to a leaf-area index (LAI) increase of ~ 0.6 based on the regional relationship
41 between LAI and NDVI from the Moderate Resolution Spectroradiometer (MODIS). Across the
42 entire transect, the area-averaged LAI increase was ~ 0.2 during 1986-2010. A higher area-
43 averaged LAI change (~ 0.3) within the shrub-tundra portion of the transect represents a 20-60%
44 relative increase in LAI during the last two decades. Our Landsat-based analysis subdivides the
45 overall high-latitude greening trend into changes in peak-summer greenness by cover type.
46 Different responses within and among shrub, graminoid, and tree-dominated cover types in this
47 study indicate important fine-scale heterogeneity in vegetation growth. Although our findings
48 are consistent with community shifts in low-biomass vegetation types over multi-decadal time

49 scales, the response in tundra and forest ecosystems to recent warming was not uniform.

50 **1.0 Introduction**

51

52 Climate exerts a primary control on the extent of forest cover and other vegetation types within
53 Arctic and sub-Arctic ecosystems. Recent warming has been most rapid at high latitudes, and
54 stronger warming expected in the next century may shift the distribution of vegetation types at
55 these latitudes (IPCC 2007). Dynamic global vegetation models (DGVMs) predict a
56 temperature-induced growth response in high-latitude ecosystems, leading to a poleward or
57 upslope expansion of boreal forest and an increase in the boreal forest carbon sink over the
58 course of the 21st century (Emanuel *et al.* 1985; Pastor & Post 1988; Prentice & Fung 1990;
59 White *et al.* 2000; Parmesan & Yohe 2003; Lucht *et al.* 2006; IPCC 2007). In many of these
60 scenarios, the vegetation response to warming is both widespread and rapid during the 21st
61 century, which suggests that early signs of warming-induced biome shifts might already be
62 observable.

63

64 Coarse-resolution satellite data and field observations have provided intriguing evidence for
65 climate-driven shifts in vegetation type and condition since the mid-20th century. Vegetation
66 index data from the coarse-resolution Advanced Very High Resolution Radiometer (AVHRR)
67 have suggested widespread increases in high-latitude vegetation greenness and net primary
68 productivity (NPP) since the 1980's (Myneni *et al.* 1997; Goetz *et al.* 2005; Bunn & Goetz 2006;
69 Pouloit *et al.* 2009; Wang *et al.* 2011). AVHRR-based studies of high-latitude greening typically
70 use seasonally-integrated vegetation indices. Thus, it is not clear whether these satellite-based
71 “greening” trends reflect increased peak-summer vegetation cover or lengthening growing
72 seasons (including trends in spring snow cover). These studies also lack the spatial resolution to

73 delineate stand-level changes in vegetation composition or extent (Masek 2001) and suffer to
74 varying degrees from issues associated with instrument calibration and sampling (e.g., Running
75 *et al.* 2004; Gallo *et al.* 2005).

76

77 Field studies using plot measurements or repeat aerial photography suggest that recent climate
78 warming has led to expansion of shrub cover within tundra biomes (Van Wijk *et al.* 2004; Tape *et*
79 *al.* 2006; Jagerbrand *et al.* 2006; Tremblay 2010; Ropars & Boudreau 2012). However, the extent
80 to which such local trends contribute to or characterize larger, systemic change in Arctic and sub-
81 Arctic vegetation remains unknown. Within the boreal forest biome, evidence for climate-driven
82 change is less conclusive. A meta-analysis of pan-boreal treeline studies indicated that northward
83 or altitudinal expansion of forest is evident in over half of study sites with coincident warming
84 trends (Harsch *et al.* 2009), yet variation in treeline form (e.g. diffuse, abrupt, island, and
85 krummolz) suggests a diversity of responses to local conditions as well as climate (Harsch &
86 Bader 2011). Recent studies demonstrate the possibility to link field observations and satellite-
87 based trends in vegetation productivity (e.g., Beck *et al.* 2011); however, higher-resolution
88 satellite observations are likely needed to directly scale individual tree or stand-scale growth
89 responses to satellite resolution. Large area coverage with high resolution time series is also
90 desirable since coarse or moderate resolution satellite data indicate a diversity of trends in tundra
91 ecosystems and primarily negative (browning) trends over boreal forest in North America (Bunn
92 & Goetz 2006; Pouliot *et al.* 2009; Zhao & Running 2010).

93

94 In this study, we use fine-scale Landsat observations to quantify vegetation changes within and
95 among plant cover types over the past quarter-century. Our study considers a latitudinal transect

96 across the forest-tundra biome boundary in northern Quebec, a region that has experienced rapid
97 warming in both winter (November-April) and summer (May-October) seasons during the
98 satellite era, from the early 1970s onwards (Fig. 1). Unlike previous satellite-based studies of
99 vegetation greening, we carefully selected time series of peak-summer Landsat data to evaluate
100 changes in vegetation composition and structure rather than changes in phenology. The study
101 had three specific aims: 1) identify changes in high-latitude tundra and forest cover types over a
102 period of pronounced warming using time series of Landsat Normalized Difference Vegetation
103 Index (NDVI); 2) analyze the magnitude and distribution of change by cover type; and 3) assess
104 the underlying ecological mechanisms of a trend in greenness by plant cover type and terrain
105 attributes.

106

107

108 **2.0 Materials and Methods**

109

110 **2.1 Data**

111 We assembled a Landsat time series transect across the forest-tundra biome boundary in northern
112 Quebec to assess changes in summer vegetation cover during 1986-2010 (Fig. 1). The transect
113 spanned 9 adjacent Landsat frames, covering an area of 260,000 km². The time series of Landsat
114 data for each frame in the transect was selected to minimize the impact of phenology on trends in
115 summer vegetation cover over the 24-year period (Fig. 2). We used the average growing season
116 phenology during 2001-2006 from the MODIS phenology product (MCD12Q2, Zhang *et al.*
117 2003) to select the peak growing season greenness for each Landsat data frame. Within this
118 narrow window of peak greenness (day of year 185-215, or July 4 – August 3 in non-leap years),
119 images were selected to minimize cloud cover and variability in the date of image acquisition. A
120 total of 52 Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+)
121 images were acquired from the United States Geological Survey (glovis.usgs.gov) and Canadian
122 Centre for Remote Sensing (ccrs.nrcan.gc.ca) Landsat Data Archives, with an average of 6
123 Landsat scenes per frame (Fig. 2).

124

125 Landsat data were converted from radiance to surface reflectance using the Landsat Ecosystem
126 Disturbance Adaptive Processing System (LEDAPS), an automated atmospheric correction
127 approach to account for absorption and scattering by atmospheric trace gases (O₃, O₂, CO₂, NO₂,
128 and CH₄), aerosols, and water vapor (Masek *et al.* 2006). The LEDAPS system also generates a
129 cloud mask layer. For this study, we implemented additional masking procedures for water
130 (Band 4 reflectance <0.12), thin cirrus clouds (Band 1 reflectance >0.08), and contrails (Band 6

131 brightness temperatures). Finally, the Normalized Difference Vegetation Index (NDVI) was
132 calculated from the masked red and near-infrared surface reflectance data for each scene (Tucker
133 1979). Time series of NDVI for each Landsat frame were used to detect trends in forest and
134 tundra vegetation during 1986-2010.

135

136 Temperature trends in Boreal North America area were analyzed using monthly mean
137 temperatures from the University of East Anglia Climatic Research Unit Time Series 3.1 (CRU
138 TS3.1, <http://badc.nerc.ac.uk/data/cru>). The CRU TS3.1 product is a gridded $0.5^\circ \times 0.5^\circ$ product
139 based on meteorological station data (see Mitchell & Jones 2005). Monthly mean temperatures
140 were averaged for winter (November-April) and summer (May-October) seasons; previous
141 studies have shown that warming winter temperatures may be important for recent treeline
142 advances (e.g., Harsch et al., 2009). Simple linear regression was used to estimate trends in
143 mean winter and summer temperatures for 1971-2008 and 1970-2009, respectively. The total
144 change in winter and summer temperatures during 1970-2009 was estimated using linear trends
145 on a per-pixel basis. Finally, seasonal temperature changes were averaged for each 0.5° latitude
146 bin to estimate the gradients in winter and summer temperatures within the Landsat transect
147 during this period.

148

149

150 ***2.2 Trend Detection***

151 Trends in mid-summer NDVI were assessed on a per-pixel basis using least-squares regression.
152 For a time series of n scenes, only pixels with n or $n-1$ observations were evaluated for trends in
153 NDVI over time. Selecting pixels with one missing data value allowed for the use of some

154 cloud-filtered data and post-2003 Landsat ETM+ data while minimizing the potential for
155 spurious trend detection. In regions with overlapping coverage from adjacent Landsat frames,
156 the denser time series was selected to assess trends in NDVI over time. For each 30-meter pixel,
157 the slope and statistical significance of the linear regression in NDVI values were evaluated
158 using a Student's t-test at 95% confidence level.

159

160 Large-scale disturbances from fire and wood harvest are common in North American boreal
161 forests. Although climate warming may influence disturbance rates in boreal forests, the focus of
162 this work was to detect vegetation changes in undisturbed regions. Therefore, we used two
163 approaches to exclude large-scale disturbances from the analysis of NDVI trends. First, the
164 earliest cloud-free Landsat MSS image for each scene (1972-1976) was used to digitize burn scar
165 perimeters for fires prior to the start of each Landsat TM/ETM+ time series (~1986). These
166 areas were eliminated from further analysis. Second, within the Landsat TM/ETM+ time series
167 (1986-2010), a thresholding approach was used to eliminate areas with strong increases or
168 decreases in NDVI (absolute changes greater than 0.08 NDVI) between successive images.

169

170 The sensitivity of the Landsat NDVI trend detection approach to real changes in vegetation cover
171 depends, in part, on the uncertainty in the original radiometric observations (measurement
172 errors). Recent improvements to Landsat calibration, including cross calibration of Landsat-4, -5,
173 and -7 data using an absolute radiometric scale (Markham & Helder in press), have reduced
174 uncertainties associated with comparing Landsat data from different sensors. The uncertainty of
175 the LEDAPS atmospherically corrected products is the greater of 0.5% absolute reflectance or
176 5% of the recorded reflectance value (1σ), similar to the NASA Moderate Resolution Imaging

177 Spectroradiometer (MODIS) sensors (Masek *et al.* 2006). The resulting uncertainty in any given
178 NDVI observation is thus ~ 0.02 (1σ). Based on Monte Carlo modeling of MODIS NDVI trend
179 detection using noisy time series (Wang *et al.* 2012), we expect that actual NDVI trends greater
180 than ± 0.003 NDVI yr^{-1} can be reliably mapped given the Landsat measurement errors and the
181 typical number of observations for each frame in the transect.

182

183 Increases in NDVI over time are generally associated with increases in leaf area index (LAI)
184 (Turner *et al.* 1999). Because changes in LAI may be more easily compared to modeled or
185 measured vegetation changes, we developed relationships between NDVI and LAI using the
186 MODIS/Aqua LAI product (MYD15A2, Knyazikhin *et al.* 1999) and NDVI product
187 (MYD13A1, Huete *et al.* 2002). First, trends in 2002-2010 MODIS LAI and NDVI were
188 assessed independently across the northern United States and Canada, using the same linear
189 regression and t-test approach as the analysis of trends in Landsat NDVI. Data quality layers
190 were used to restrict the analysis to LAI estimates from the radiative transfer algorithm and
191 highest quality NDVI observations. Pixels with statistically significant linear trends in both
192 MODIS LAI and MODIS NDVI were selected to derive estimates of the change in LAI per unit
193 NDVI. The larger (continental) geographic area allowed over 200,000 MODIS NDVI-LAI pairs
194 to be collected for comparison.

195

196 ***2.3 Spatial Analysis of NDVI Trends***

197 Trends in Landsat NDVI during 1986-2010 were assessed by cover type using forest and tundra
198 land cover classifications derived from circa 2000 Landsat imagery. North of the tree line,
199 designated as the Rivière aux Feuilles, tundra cover types were classified based on the CCRS

200 Northern Land Cover of Canada dataset
201 (http://www.ccrs.nrcan.gc.ca/optical/landcover2000_e.php). The Canadian Forest Service's
202 Earth Observation for Sustainable Development of Forests (EOSD) classification was used to
203 analyze trends in NDVI by cover type for portions of the time series transect south of tree line
204 (http://www4.saforah.org/eosdlcp/nts_prov.html). Land cover information from the two
205 classification products was merged to create a harmonized classification for the study region with
206 six vegetation classes, barren or exposed bedrock, and water (Table 1). Trends were further
207 analyzed by latitude by comparing the mean NDVI trend between adjacent (north-south) scenes.
208 Trends in NDVI and temperature were tested for correlation with latitude using Pearson's
209 product-moment correlation coefficient.

210

211 Finally, trends in Landsat NDVI for each cover type were further evaluated by slope, aspect, and
212 elevation. Topographic information was derived from the Shuttle Radar Topography Mission
213 (SRTM) 3 Arc Second Filled Finished-B product (USGS 2006; www.landcover.org). The
214 relationship between slope, elevation, and aspect with positive non-disturbed NDVI trend
215 occurrence was explored for a random sample of positive and no-trend observations (equal to
216 10% of total observations of each) using a binomial generalized linear model (R version 2.11.0,
217 R Core Development Team 2010).

218

219

220

221

222 3. Results

223 The Landsat study area covered 26 million ha in a transect across the forest-tundra biome
224 boundary. Approximately 70% of the transect had a sufficient number of cloud-free Landsat
225 observations to assess trends in peak-season NDVI. Of this “observable” portion, one-third
226 (34%) of the area experienced a statistically significant trend in NDVI during 1986 – 2010 based
227 on the T-test criterion (Fig. 3a). The remaining observable area either had small NDVI trends
228 that were not significantly different from zero or exhibited significant year-to-year variability
229 that precluded statistical confidence.

230

231 Almost all of the statistically significant NDVI trends were positive. Large-scale forest
232 disturbance events prior to or during the study period, including forest fires and timber harvests,
233 accounted for 3.2% of the area with significant NDVI trends. Excluding these disturbances,
234 98.95% of the remaining trend area had positive (greening) trends and only 1.05% of the trend
235 area exhibited negative (browning) NDVI trends (Fig. 3a). The mean positive trend was an
236 increase $0.007 \text{ NDVI yr}^{-1}$ for a total increase of 0.17 NDVI over the entire 24-year time series
237 (Fig. 3b). Positive NDVI trends were concentrated north of the treeline; nearly half (48%) of the
238 observed area north of treeline had a statistically significant positive NDVI trend compared to
239 only 25% of observable area south of treeline. Latitude and the frequency of statistically
240 significant NDVI trends were positively correlated (Pearson’s $R = 0.819$, $P = 0.0248$), although
241 the magnitude of the NDVI trend was not correlated with latitude (Fig. 4, Table 2). Temperature
242 trends, both annual and cumulative, were not significantly correlated with trends in NDVI
243 abundance or magnitude (Table 2).

244

245 NDVI trends showed significant associations with specific land cover types (Fig.5, Table 3).
246 Low shrubs and graminoid tundra contributed preferentially to the observed greening trend. Out
247 of the area showing a positive NDVI trend, 38% occurred in regions classified as either
248 low/dwarf shrubs or graminoid tundra, even though these types only make up 22% of the study
249 area. Within the total area of tall shrubs, 30% of observations showed a positive trend. The rate
250 of NDVI increase for all cover types was broadly similar, varying from 0.0055 NDVI year⁻¹ for
251 sparsely vegetated areas to 0.0075 NDVI yr⁻¹ for graminoid tundra. Although forests comprise
252 the majority of the southern portion of the transect, they contributed less than 10% to the overall
253 greening trend. Within forests, 15% of total observations showed a positive trend, with a mean
254 increase of 0.0064 NDVI yr⁻¹. In contrast, 50-60% of the low/dwarf shrub and graminoid tundra
255 areas showed significant NDVI increases.

256

257 Positive trends in peak summer NDVI correspond to an increase in LAI over time. Using
258 MODIS data for the study region, statistically significant changes in NDVI between 0.005 - 0.01
259 yr⁻¹ corresponded to changes in LAI of ~0.02 (mode) to 0.03 (median) LAI yr⁻¹ (Fig. 6). This
260 relationship between MODIS LAI and NDVI was invariant across the multiple cover types
261 occurring in the study region. We applied a value of 0.025 LAI yr⁻¹ to those Landsat NDVI
262 trends not associated with disturbance, assuming that areas not exhibiting significant trends
263 experienced no change in LAI. The resulting estimate of the area-averaged LAI change across
264 the transect was 0.2 LAI over the 24-year record. However, for tundra cover types in the
265 northern portion of the transect, the estimated 24-year LAI increase was *ca.* 0.3. Tundra and
266 shrub-tundra LAI values generally fall in the range of 0.5 to 1.5 (Asner *et al.* 2003; Beringer *et*

267 *al.* 2005; Williams 2008), thus an LAI increase of 0.3 translates to roughly a ~20-60% increase
268 in leaf area over two decades.

269 Geographically, the highest magnitude of NDVI change occurred proximal to and north of the
270 regional treeline, which roughly coincides with the Rivière aux Feuilles (Fig. 3b). Greening
271 trends were less abundant in the forested regions in the southern half of the transect, and trends
272 decayed in frequency and magnitude along the northern edge bordering the Hudson Strait.

273

274 Topography was an important predictor of greening trends over the study domain (Table 4).

275 While the landscape is generally flat, locations with higher slopes and elevations were negatively
276 correlated with the frequency of detecting greening trends. North- and northeast- facing slopes
277 were least likely to exhibit a positive trend, and western and southwestern facing slopes were the
278 most likely. Stronger NDVI trends were detected along two major rivers, the Rivière aux
279 Feuilles and the southern reaches of the Rivière Arnaud. Topographic associations between
280 valley bottoms and vegetation growth likely reflect more favorable edaphic conditions along the
281 channel banks, as well as more sheltered microclimates and available water.

282

283 Most cover types exhibited consistent linear changes in NDVI over the 24-year study period.

284 The temporal distribution of the Landsat images did not support a regional, year-by-year analysis
285 of greening trends. Instead, we divided observations into “early” (1985-1990), “mid” (1998-
286 2001), and “late” (2008-2010) intervals to evaluate rates of NDVI change by cover type over
287 time (Fig. 7). Most classes maintained similar rates of NDVI change during both early and late
288 intervals. However, in wetland and tall shrub classes, NDVI increases were slower in the later
289 period.

290

291 4. Discussion

292

293 Using time series of Landsat data, we found a strong mid-summer greening trend across the
294 northern Quebec area. This trend corresponds to significant increases in peak growing season
295 leaf area. Graminoid and shrub-tundra classes contributed nearly 60% of the greening trends
296 identified in this study. These low-biomass vegetation types experienced a 20-60% relative
297 increase in green leaf area over the 24-year study period—a rapid and significant increase
298 relative to existing phytomass. Whether these LAI gains reflect the growth of individual plants,
299 an increase in the density of individuals, or community-scale changes such as shifts from
300 graminoid- to shrub-dominated tundra remains an important area for further study. Large and
301 persistent changes in LAI identified in this study may also alter biophysical feedbacks, including
302 seasonal changes in albedo (e.g., Randerson *et al.* 2006; Bonan 2008), snow cover, and turbulent
303 fluxes (e.g., Lee *et al.* 2011).

304

305 Changes in shrub and graminoid tundra in this study are consistent with regional evidence of
306 shrub expansion in tundra ecosystems (Ropars & Boudreau, 2012) and similar findings across
307 North America (Chapin 1995, Sturm *et al.* 2001; Tape *et al.* 2006, Jagerbrand 2005; Van Wijk *et*
308 *al.* 2004). A recent air photo analysis for a region west of our transect revealed increases in
309 dwarf birch (*Betula glandulosa* Michx.) shrub cover up to 47% over a 51-year period (1957-
310 2008), with larger changes on low-altitude sandy terraces than on exposed hilltops (Ropars &
311 Boudreau, 2012). The Landsat data suggest that this shrub expansion is not isolated, but
312 widespread across the tundra region of northern Quebec. Quebec and Alaska were the only
313 regions in North America with strong warming trends in both winter and summer semesters

314 during 1970-2009, and both regions have consistent reports of increasing shrub cover during the
315 satellite era. We did not identify strong correlations between the magnitude of recent
316 temperature changes and increases in fractional cover, possibly due to consistent and strong
317 (1.5°-2.5°) warming across the entire study region. Given favorable climatic conditions,
318 landscape heterogeneity and species-level responses may be stronger predictors of vegetation
319 change.

320

321 Biophysical mechanisms operating at the local scale may contribute to observed NDVI/LAI
322 increases in tundra cover types. First, snowdrifts are more likely to form at lower elevations,
323 trapping organic debris and leaf litter (Fahnestock *et al.* 2000). Snow protects newly-established
324 shrubs from harsh winter conditions, and warmer soil temperatures under deep snow may
325 increase microbial activity that mobilizes additional nutrients for shrub growth (Sturm *et al.*
326 2005). A positive feedback between shrub cover and snow is consistent with larger LAI
327 increases at lower slopes and elevations in this study. In more sparsely vegetated cover types,
328 dominated by lichen, mosses, and bryoids, another feedback cycle between the lichen-caribou-
329 woody plant communities may be important. Caribou trampling destroys the lichen and exposes
330 mineral soil, allowing for an increase in seedling establishment for dominant subarctic tree and
331 shrub species such as black spruce (*Picea mariana*; Dufour-Tremblay & Boudreau 2011) and
332 dwarf birch (*B. glandulosa*; Ropars & Boudreau, 2012). The activity of the Leaf River Caribou
333 Herd in western subarctic Quebec peaked during the mid-1990s to mid-2000s (Dufour-Tremblay
334 & Boudreau, 2011; Alexandre Truchon-Savard, pers. comm.), suggesting that browsing and soil
335 disturbances from large herbivores may contribute to the patterns of shrub and graminoid tundra
336 changes in this study. The availability of bare soil, whether from caribou disturbance or other

337 disturbances like frost boils or cryoturbation, combined with milder conditions more favorable
338 for seed production and seedling establishment, may allow for the encroachment of woody
339 species and other vascular vegetation into sparsely vegetated areas.

340

341 This study found less conclusive evidence for vegetation changes within forest areas. While
342 most observations of NDVI trend within the forested parts of the transect were positive, a much
343 smaller area showed a statistically significant trend compared to graminoid- and shrub-
344 dominated regions. In contrast to the shrub expansion studies, evidence for northern advance of
345 treeline into tundra has been mixed (Harsch *et al.* 2009). At the treeline, a positive temperature
346 trend may not necessarily correlate with the northward expansion of trees, given the influence of
347 water availability, soil properties, competition, or pests on the spatial arrangement of trees
348 (Meunier *et al.* 2007). Furthermore, the responsiveness of non-tree species in forest
349 communities, such as shrubs, to a positive temperature trend may be suppressed by tree cover
350 (Boudreau & Villeneuve-Simard 2012). Although within-stand changes in forest leaf area were
351 less common, it is possible that expansion of tree species into tundra communities dominated by
352 tall shrubs or other functional groups contributed some of the observed changes in other
353 vegetation classes reported in the study. Additional field studies in areas of recent change are
354 needed to identify the contributions from the growth of existing individuals (Gamache & Payette
355 2004; Beck *et al.* 2011) and establishment of new individuals (e.g., Danby & Hik 2007) to recent
356 increases in vegetation cover.

357

358 Observed NDVI trends in forest may reflect recovery from historic disturbances, despite efforts
359 to mask out large-scale disturbances from fires and forestry operations visible during the Landsat

360 era. In eastern Canada, severe fires sharply reduce LAI, and vegetation regrowth occurs over
361 century timescales, during which post-fire succession is likely to overshadow climate-driven
362 trends in vegetation (Girard *et al.* 2008). Two other factors may contribute to the lack of
363 observed forest greening within a time series of Landsat data. First, the establishment and
364 growth of trees is an inherently slower process compared to growth of existing individuals (e.g.,
365 Danby & Hik 2007), and the 24-year Landsat record may not be long enough to identify changes
366 within forest stands. Second, forested areas tend to have higher initial NDVI values. Since
367 NDVI saturates at modest LAI values (~3.0), small LAI increases within existing forest stands
368 may not be obvious from the remote sensing data.

369

370 DGVMs suggest poleward migration of biomes as a long-term response to climate warming
371 (Lucht *et al.* 2006). The observed association between shrub cover types and increased NDVI is
372 generally consistent with the concept that woody plants can take advantage of warmer conditions
373 and grow more vigorously. In areas of mixed graminoid and shrub cover types, the competitive
374 advantage of shrubs should lead to a long-term shift in composition, and ultimately a poleward
375 shift in the biome boundary. However, the satellite data do not yet provide unambiguous
376 evidence for geographic biome shifts as opposed to simply increasing LAI within existing biome
377 distributions. As noted by others, the ability of vegetation communities to expand their range
378 depends not just on increased productivity, but on overcoming a host of ecological constraints
379 (Rozenzweig *et al.* 2008). Particularly in the boreal environment of Canada, small lakes and
380 rocky outcrops present innumerable fine-scale barriers to propagation and expansion. The poor
381 reproductive capacity of frontier tree species such as *Picea mariana* may also somewhat explain
382 observed lags between warming and vegetation growth, both above and below the subarctic

383 treeline (Gamache & Payette 2004), although an increase in seed viability was noticed near the
384 treeline in recent years (Dufour-Tremblay & Boudreau, 2011). These fine-scale barriers to forest
385 expansion constitute macro-scale “resistance” to biome shifts that are not considered in the
386 current generation of DGVMs.

387

388 Our results complement previous studies of high-latitude vegetation change using moderate or
389 coarse-resolution satellite data (e.g., Pouliot *et al.* 2009). We used Landsat time series to
390 subdivide the overall greening trend into increases in LAI for specific cover types. The Landsat-
391 based approach in this study could be expanded to evaluate climate-driven shifts in vegetation in
392 other regions, within the limits of the existing Landsat data archive (Goward *et al.* 2006). High-
393 resolution time series over the 35+ year Landsat record provide invaluable observational data to
394 refine and benchmark ecological models. However, there are several important limitations of
395 this work that could be addressed in future studies. First, given the uncertainties in the MODIS
396 LAI product in high-latitude areas, the uncertainties in the derived MODIS NDVI-LAI
397 relationship, and the difficulties of scaling field-observed LAI to satellite resolution, area-
398 averaged LAI increases in this study should be interpreted cautiously. Second, we evaluated
399 trends in Landsat NDVI by cover type using vegetation classification data from a snapshot in
400 time (circa 2000). Classification information from 2000 may already incorporate growth of
401 woody vegetation during 1986-2000, such that areas classified as shrublands in 2000 had lower
402 amounts of woody cover at the beginning of the study period. Third, multispectral remote
403 sensing has limited sensitivity to subtle changes in composition and structure, especially in
404 closed-canopy forest conditions. The addition of hyperspectral imagery (to map compositional
405 gradients) and LiDAR(to map structure) would provide a more comprehensive benchmark of

406 current conditions for future studies of climate-driven vegetation changes. Finally, we identified
407 linear changes in NDVI over the Landsat study domain. Non-linear greening or browning
408 responses to recent climate warming may therefore be underestimated in this study.

409

410 Using time series of Landsat observations, we mapped widespread vegetation greening in
411 northern Quebec over the last 24 years. The observed NDVI increases were concentrated in
412 graminoid and shrub-tundra areas, leading to an area-averaged LAI increase of ~0.2 across the
413 entire transect, or ~0.3 for the northern tundra-dominated portion. The latter figure represents a
414 20-60% relative increase compared to typical shrub-tundra LAI values. These findings expand
415 the spatial extent of previous field and air photo studies used to characterize changes in shrub
416 cover. Our results also provide a fine-scale evaluation of the contribution of different cover
417 types to trends detected from coarse-resolution satellite data. The coincidence of the shrub
418 greening trend with an area of rapid winter and summer warming supports the hypothesis that
419 warmer temperatures favor the growth of woody plants at high latitudes (Sturm *et al.* 2001;
420 2005; Tape *et al.* 2006). In contrast, positive NDVI trends within forested areas were less
421 common, suggesting that the forest response to recent warming may be occurring more slowly,
422 or that Landsat data alone may be insufficient to identify growth responses in these ecosystems
423 and additional data (e.g., LiDAR) may be needed to characterize temperature-induced vegetation
424 changes within boreal forest communities.

425

426

427

428 **6. Acknowledgements**

429 This work was supported by the NASA Terrestrial Ecology Program. We thank M.A. Wulder for

430 guidance on land cover information for eastern Canada, and we appreciate comments and

431 suggestions on a previous version of this manuscript from H. Margolis and an anonymous

432 reviewer.

433

434

435

436

437 **7. References**

- 438
- 439 Asner GP, Schurlock J, and Hicke JA (2003) Global synthesis of leaf area index observations:
440 implications for ecological and remote sensing studies. *Global Ecology & Biogeography*, **12**,
441 191-205.
- 442
- 443 Beck SA, Horning S, Goetz SJ, Loranty MM, Tape KD (2001) Shrub Cover on the North Slope
444 of Alaska: a circa 2000 Baseline Map. *Arctic, Antarctic, and Alpine Research* **43**, 355-363.
- 445
- 446 Beringer J, Chapin FS, Thompson CC, McGuire AD (2005) Surface energy exchanges along a
447 tundra-forest transition and feedbacks to climate. *Agricultural and Forest Meteorology*, **131**,
448 143-161.
- 449
- 450 Bonan GB (2008) Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of
451 Forests. *Science*, **320**, 1444-1449.
- 452
- 453 Boudreau S & Villeneuve-Simard MP (2012) Dendrochronological evidence of shrub growth
454 suppression by trees in a subarctic lichen woodland. *Botany* **90**, 151-156.
- 455
- 456 Bunn AG & Goetz SJ (2006) Trends in satellite-observed circumpolar photosynthetic activity
457 from 1982 to 2003: the influence of seasonality, cover type, and vegetation density. *Earth*
458 *Interactions*, **10**, 1–19.
- 459
- 460 Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KJ, and Laundre JA (1995) Responses of
461 arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.
- 462
- 463 Danby RK & Hik DS (2007) Variability, contingency and rapid change in recent subarctic alpine
464 tree line dynamics. *Journal of Ecology*, **95**, 352-363.
- 465
- 466 Doufour-Tremblay G & Boudreau SB (2011) Black spruce regeneration at the treeline ecotone:
467 synergistic impacts of climate change and caribou activity. *Canadian Journal of Forest*, **41**, 460-
468 468.
- 469
- 470 Emanuel WR, Shugart HH, Stevenson MP (1985) Climate change and the broad scale
471 distribution of terrestrial ecosystem complexes. *Climatic Change*, **7**: 29-43.
- 472
- 473 Gallo K, Ji L, Reed B, Eidenshink J, Dwyer J (2005). *Remote Sensing of the Environment*, **99**,
474 221-231.
- 475
- 476 Gamache I & Payette S (2004) Height growth response of tree line black spruce to recent climate
477 warming across the forest-tundra of eastern Canada. *Journal of Ecology*. **92**, 835-845.
- 478
- 479 Girard F, Payette S, Gagnon R (2008) Rapid expansion of lichen woodlands within the closed-
480 crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada.
481 *Journal of Biogeography*. **35**, 529-537.
- 482

483 Goetz SJ, Bunn AG, Fiske GJ, Houghton RA (2005) Satellite-observed photosynthetic trends
484 across boreal North America associated with climate and fire disturbance. *Proceedings of the*
485 *National Academies of Science*, **102**, 13521-5.

486

487 Goward S, Arvidson T, Williams D, Faundeen J, Irons J, Franks S (2006) Historical record of
488 Landsat global coverage: Mission operations, NSLRSDA, and international cooperator stations.
489 *Photogrammetric Engineering & Remote Sensing*, **72**, 1155-1169.

490

491 Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global
492 meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040–1049.

493

494 Harsch MA & Bader MY (2011) Treeline form – a potential key to understanding treeline
495 dynamics. *Global Ecology and Biogeography*, **20**:582-596.

496

497 Huete A, Didan K, Miura T, Rodriguez EP, Gao X, Ferreira LG (2002) Overview of the
498 radiometric and biophysical performance of the MODIS vegetation indices. 195-213.

499

500 IPCC (2007) *Climate change 2007:Impacts, adaptation and vulnerability. Contribution of*
501 *Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate*
502 *Change* Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE, eds. Cambridge
503 University Press: 211-272.

504

505 Jagerbrand AK, Lindblad KEM, Bjork RG, Alatao JM, Molau U (2006) Bryophyte and lichen
506 diversity under simulated environmental change compared with observed variation in
507 unmanipulated alpine tundra. *Biodiversity and Conservation*, **15**, 4453-4475.

508

509 Knyazikhin Y, Glassy J, Privette JL, *et al.* MODIS Leaf Area Index (LAI) and Fraction of
510 Photosynthetically Active Radiation Absorbed by Vegetation (FPAR) Product (MOD15)
511 Algorithm, Theoretical Basis Document, 126 pp., NASA Goddard Space Flight Center,
512 Greenbelt, Md., 1999.

513

514 Kullman L (2001) 20th Century Climate Warming and Tree-Limit Rise in the Southern Scandes
515 of Sweden. *Ambio*, **30**, 72-80.

516

517 Lee X, Goulden ML, Hollinger DY, *et al.* (2011) Observed increase in local cooling effect of
518 deforestation at higher latitudes. *Nature*, **479**, 384-387.

519

520 Lucht W, Schaphoff S, Erbrecht T, Heyder U, Cramer W (2006). Terrestrial vegetation
521 redistribution and carbon balance under climate change. *Carbon Balance and Management*, **1**,
522 1-6.

523

524 Markham BL & Helder D (in press) Forty-year calibrated record of earth-reflected radiance from
525 Landsat: a review, *Remote Sensing of the Environment*.

526

527 Masek JG (2001) Stability of boreal forest stands during recent climate change: evidence from
528 Landsat satellite imagery. *Journal of Biogeography*, **28**, 967-976.

529

530 Masek JG, Vermote EF, Saleous N, *et al.* (2006) A Landsat surface reflectance data set for North
531 America, 1990-2000. *Geoscience and Remote Sensing Letters*, **3**, 68-72.

532

533 Meunier C, Sirois L, Bégin Y (2007) Climate and *Picea mariana* seed maturation relationships: a
534 multi-scale perspective. *Ecological Monographs*, **77**, 361-376.

535

536 Mitchell TD & Jones PD (2005) An improved method of constructing a database of monthly
537 climate observations and associated high-resolution grids. *International Journal of Climatology*,
538 **25**, 693-712.

539

540 Myneni RB, Keeling CD, Tucker CJ, Asrar G (1997) Increased plant growth in the northern high
541 latitudes from 1981 to 1991. *Nature*, **386**, 698-702.

542

543 Pastor J & Post WM (1988) Response of northern forests to CO₂-induced climate change.
544 *Nature*, **334**, 55-58.

545

546 Parmesan C & Yohe G (2003) A globally coherent fingerprint of climate change impacts across
547 natural systems. *Nature*, **421**, 37-42.

548

549 Pouliot D, Latifovic R, Olthof I (2009) Trends in vegetation NDVI from 1 km AVHRR data over
550 Canada for the period 1985-2006. *International Journal of Remote Sensing*, **30**, 149-168.

551

552 Prentice KC & Fung IY (1990) The sensitivity of terrestrial carbon storage to climate change.
553 *Nature*, **346**, 48-50.

554

555 Randerson JT, Liu H, Flanner MG, *et al.* (2006) The impact of boreal forest fire on climate
556 warming. *Science*, **314**, 1130-1132.

557

558 Ropars P, & Boudreau S (2012) Shrub expansion at the forest-tundra ecotone: spatial
559 heterogeneity linked to local topography. *Environmental Research Letters* **7** (015501).

560

561 Rosenzweig C, Karoly D, Vicarelli M, *et al.* (2008) Attributing physical and biological impacts
562 to anthropogenic climate change. *Nature*, **453**, 353-357.

563

564 Running SW, Nemani RR, Heinsch FA, Zhao M, Reeves M, Hashimoto H (2004). A continuous
565 satellite-derived measure of global terrestrial primary production. *BioScience*, **54**, 547-560.

566

567 Sturm M, Racine C, Tape K (2001) Climate change – increasing shrub abundance in the Arctic.
568 *Nature*, **411**, 546-547.

569

570 Sturm M, Schimel J, Michaelson G, Welke JM (2005) Winter biological processes could help
571 convert Arctic tundra to shrubland. *Bioscience*, **55**, 17-26.

572

573 Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the
574 Pan-Arctic. *Global Change Biology*, **12**, 686-702.

575
576 Tremblay B (2010) Augmentation récente du couvert ligneux érigé dans les environs de
577 Kangiqsualujuaq (Nunavik, Québec). MSc thesis, Université du Québec à Trois-Rivières, Trois-
578 Rivières, Québec, Canada.
579
580 Tucker CJ (1979) Red and Photographic Infrared Linear Combinations for Monitoring
581 Vegetation, *Remote Sensing of Environment*, **8**,127-150.
582
583 Turner DP, Cohen WB, Kennedy RE, Fassnacht KS, & Briggs JM (1999) Relationships between
584 leaf area index and Landsat TM spectral vegetation indices across three temperate zone sites.
585 *Remote Sensing of Environment*, **70**, 52–68.
586
587 University of East Anglia Climatic Research Unit (CRU) [Phil Jones, Ian Harris]. CRU Time
588 Series (TS) high resolution gridded datasets, [Internet]. NCAS British Atmospheric Data Centre,
589 2008. http://badc.nerc.ac.uk/view/badc.nerc.ac.uk_ATOM_dataent_1256223773328276
590
591 Van Wijk MT, Clemmensen KE, Shaver GR, *et al.* (2004) Long-term ecosystem level
592 experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and
593 differences in ecosystem and plant type responses to global change. *Global Change Biology*, **10**,
594 105 -123 .
595
596 Wang D, Morton D, Masek J, *et al.* (2012) Impact of sensor degradation on the MODIS NDVI
597 time series. *Remote Sensing of Environment*.**119**, 55-61.
598
599 Wang X, Piao S, Ciais P, Li J, Friedlingstein P, Koven C, Chen A (2011) Spring temperature
600 change and its implication in the change of vegetation growth in North America from 1982 to
601 2006. *Proceedings of the National Academies of Science*, **108**, 1240-1245.
602
603 White A, Cannell MGR, Friend AD (2000) The high-latitude terrestrial carbon sink: a model
604 analysis. *Global Change Biology*, **6**, 227-245.
605
606 Williams M, Bell R, Spadavecchia L, Street LE, van Wijk MT (2008) Upscaling leaf area index
607 in an Arctic landscape through multi-scale observations. *Global Change Biology*, **14**, 1517-1530.
608
609 Zhang X, Friedl MA, Schaaf CB, Strahler AH, Hodges JCF, Gao F, Reed B, Huete A (2003)
610 Monitoring vegetation phenology using MODIS. *Remote Sensing of Environment*, **84**, 471-475.
611
612 Zhao M and Running SW (2010) Drought-Induced Reduction in Global Terrestrial Net Primary
613 Production from 2000 Through 2009. *Science*, **329**, 940 – 943.
614
615

Table 1. Harmonization scheme for a simplified vegetation classification of the study area, based upon the Canadian Centre for Remote Sensing (CCRS) Northern Land Cover of Canada and the Canadian Forest Service Earth Observation for Sustainable Development of Forests (ESOD) datasets.

| CCRS classification | EOSD classification | Harmonized Classification |
|--|---|--------------------------------------|
| Tussock graminoid tundra | Herbaceous (grasses, crops, forbs, graminoids; 20% ground cover) | Graminoid |
| Wet sedge | | |
| Moist to dry non-tussock graminoid/ dwarf shrub tundra | | Low & dwarf shrub |
| Prostrate dwarf shrub | | |
| Low shrub (< 40cm; >25% cover) | | |
| Tall shrub (>40cm; >25% cover) | Shrub- tall (>2m; 20% ground cover) Shrub- low (<2m; 20% ground cover) | Tall shrub |
| | Coniferous: Dense, Open, and Sparse ¹ Broadleaf: Dense, Open, and Sparse ¹ Mixed Wood: Dense, Open, and Sparse ¹ | Forest |
| Sparsely vegetated bedrock | Bryoids (bryophytes and lichen; 20% ground cover or 1/3 of vegetation) | Sparse vegetation |
| Sparsely vegetated till-colluvium | | |
| Bare soil with cryptogam crust-frost boils | | |
| Wetlands | Wetland- Coniferous Wetland- Broadleaf Wetland- Mixed Wood Wetland- Shrub- Tall Wetland- Shrub- Low | Wetlands |
| Barren | Rock/rubble Exposed land (<5% vegetation) | Barren & exposed surfaces |
| Water | Water | Water |
| Ice/snow | Cloud | No data |
| Shadow | Shadow | |
| No data | Snow/ice No data | |

617 ¹ Coniferous, broadleaf, and mixed wood classes were further subdivided in the EOSD classification as dense (>60%
618 crown closure), open (26-60% crown closure), and sparse (10-25% crown closure).
619
620
621
622
623
624
625
626
627

Table 2. Correlation coefficients for the relationships among latitude, summer and winter temperature (T) changes (1970-2009), and Landsat NDVI trends (1986-2010), summarized at 0.5° resolution.

| Variables | Latitude | Winter T Change | Summer T Change |
|------------------------|----------|-----------------|-----------------|
| Latitude | - | | |
| Winter T Change | 0.39 | - | - |
| Summer T Change | 0.47 | - | - |
| Fraction + NDVI Trend | 0.82* | 0.19 | 0.28 |
| Fraction - NDVI Trend | -0.71 | -0.56 | -0.64 |
| Fraction no NDVI Trend | -0.81* | -0.17 | -0.26 |
| Positive NDVI Trend | -0.62 | -0.04 | -0.19 |
| Negative NDVI Trend | -0.34 | -0.23 | -0.38 |

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 3. Positive Landsat NDVI trends by land cover class for the Quebec study region.

| Class | Fraction of study area | Fraction of positive NDVI trend area | Fraction of class with positive NDVI trend | Mean annual positive NDVI trend (± 1 S.D.) |
|-----------------------------|------------------------|--------------------------------------|--|---|
| Barren and exposed surfaces | 8.0 | 8.1 | 35.0 | $6.0 \times 10^{-2} \pm 2.2 \times 10^{-2}$ |
| Sparse vegetation | 16.5 | 15.7 | 32.7 | $5.5 \times 10^{-2} \pm 2.8 \times 10^{-2}$ |
| Tall shrubs | 25.6 | 23.1 | 31.0 | $7.5 \times 10^{-2} \pm 3.5 \times 10^{-2}$ |
| Wetlands | 2.5 | 2.1 | 28.7 | $5.9 \times 10^{-2} \pm 3.9 \times 10^{-2}$ |
| Forest | 20.9 | 9.7 | 16.0 | $6.4 \times 10^{-2} \pm 3.8 \times 10^{-2}$ |
| Low and dwarf shrubs | 14.1 | 23.1 | 56.5 | $6.3 \times 10^{-2} \pm 2.3 \times 10^{-2}$ |
| Graminoid | 8.3 | 14.6 | 60.8 | $7.5 \times 10^{-2} \pm 2.7 \times 10^{-2}$ |
| Water | 4.2 | 3.5 | 28.2 | $5.6 \times 10^{-2} \pm 2.4 \times 10^{-2}$ |

632

Table 4. Topographic coefficients derived from generalized linear model (GLM) fit of greening trends. Based upon Landsat data from 1985-2010 for northern Quebec.

| Binomial GLM: Positive non-disturbed trend/no trend. | | |
|--|------|-----------------------------|
| | | <i>Estimate^c</i> |
| Intercept | | 1.282 |
| Slope ^a | | -0.03651 |
| Elevation ^a | | -0.006545 |
| Aspect ^b : | | |
| | Flat | -0.5449 |
| | N | -0.08753 |
| | NE | -0.1102 |
| | E | -0.1271 |
| | SE | -0.07817 |
| | S | -0.04362 |
| | SW | 0.05415 |
| | W | 0.08525 |
| | NW | NA |
| ^a continuous; ^b ordinal | | |
| ^c p-values for all variables < 2e-16 | | |

633
 634
 635
 636
 637
 638
 639
 640
 641
 642
 643
 644
 645
 646
 647
 648
 649
 650
 651
 652
 653

Fig. 1. Changes in mean winter (left) and summer (right) temperatures between 1970 and 2009 across Boreal North America based on the CRU TS3.1 dataset. The locations of the Landsat transect (white) and boreal forest biome (green) are also shown.

654 Figure 2. The temporal distribution of the Landsat data (1985-2010) used in this study. Each
655 panel represents a frame (path-row location), and the images used are shown by year (x-axis) and
656 day of year (y-axis). Images were selected within a window of peak greenness (day of year 185-
657 215) whenever high quality, minimal cloud-covered images were available. Closed circles
658 indicate Landsat-5 TM data; open circles indicate Landsat-7 ETM+ data.

659

660 Figure 3. a. Locations of positive, negative, and no NDVI trend across the study region, based
661 upon Landsat data from 1985-2010 for northern Quebec. White regions signify that data were not
662 in sufficient quantity to determine a statistical trend. Red regions denote areas of known
663 disturbances; b. The magnitude of trend across the study region.

664

665 Figure 4. The mean annual NDVI trend by latitude (top). Trends in winter and summer
666 temperatures (1970-2009) and fraction of NDVI change by latitude (bottom).

667

668

669 Figure 5. (left) The fraction of observable (non cloud) study area experiencing positive,
670 negative, or no trend in Landsat NDVI (1986-2010); (right) distribution of land cover types
671 among the area experiencing positive (greening) trend.

672

673 Figure 6. (a) Relationship between MODIS and Landsat NDVI (aggregated to 500m resolution)
674 for pixels showing a statistically significant, positive NDVI trends; (b) Relationship between
675 MODIS NDVI and LAI trends for the northern US and Canada. For the range of NDVI changes
676 considered in this study (0.005-0.01 NDVI/yr), the corresponding modal and median values of
677 LAI change are 0.02 and 0.03 LAI/yr, respectively.

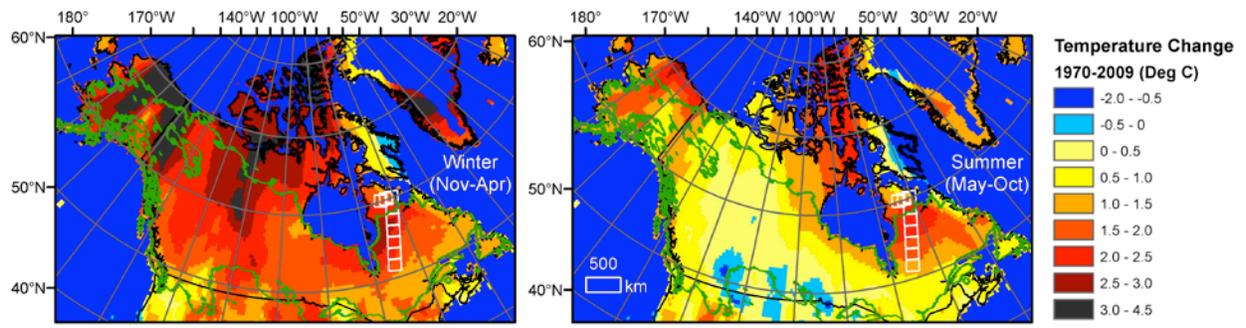
678

679 Figure 7. Mean NDVI values per class for 1986, 2000, and 2010 reference periods. Data for
680 each Landsat frame in the time series transect were selected within ± 2 years of these reference
681 years.

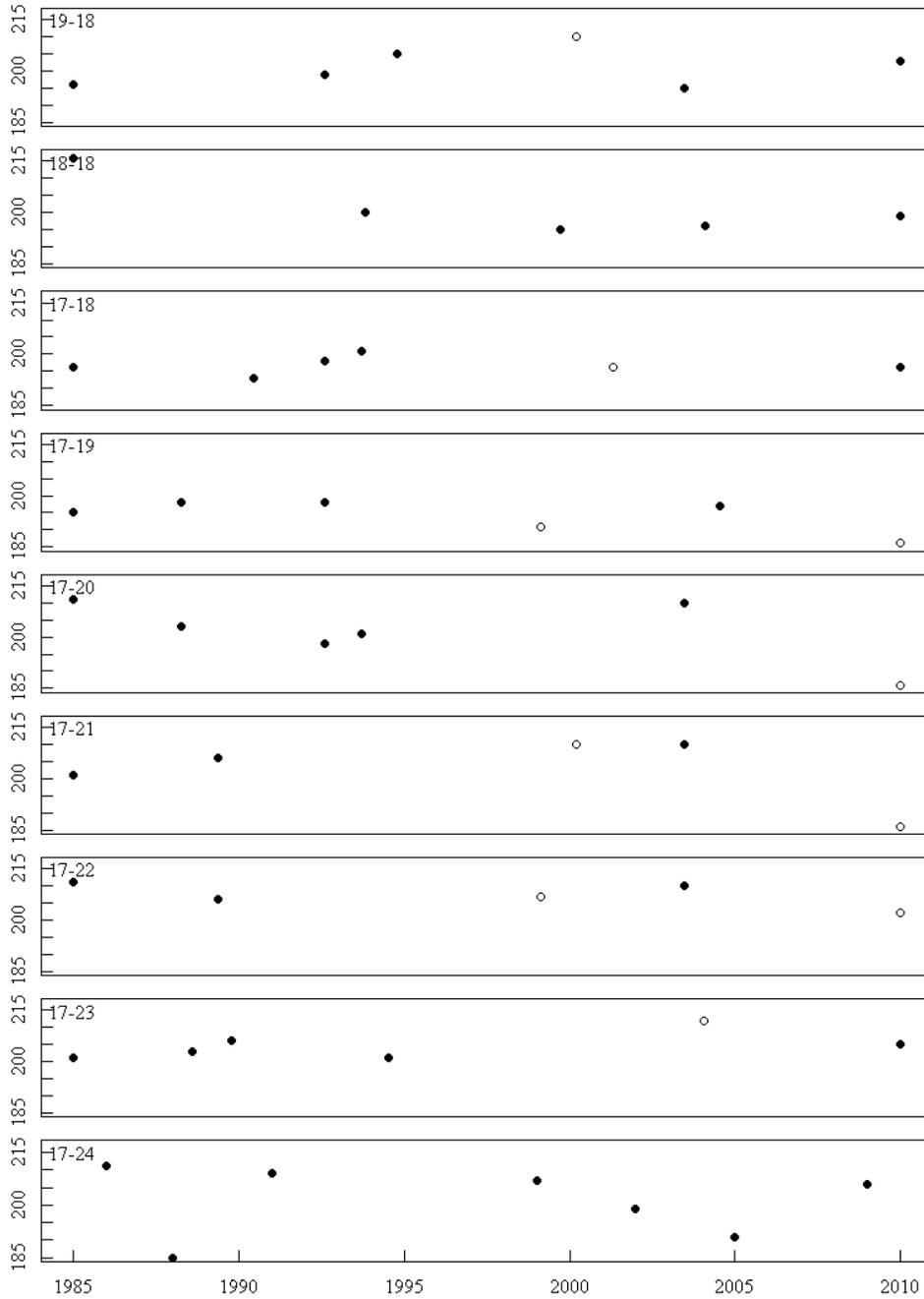
682

683

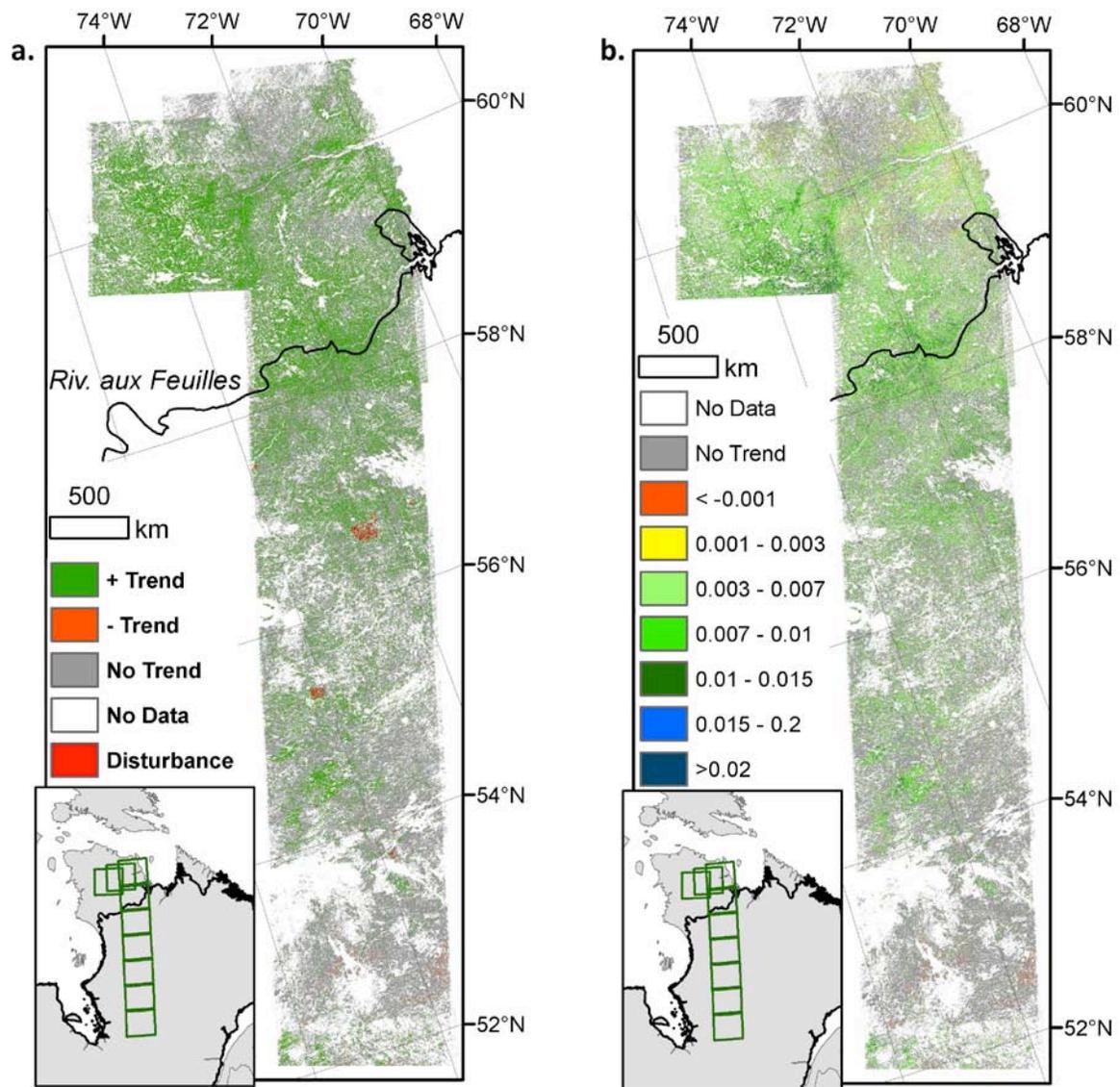
684



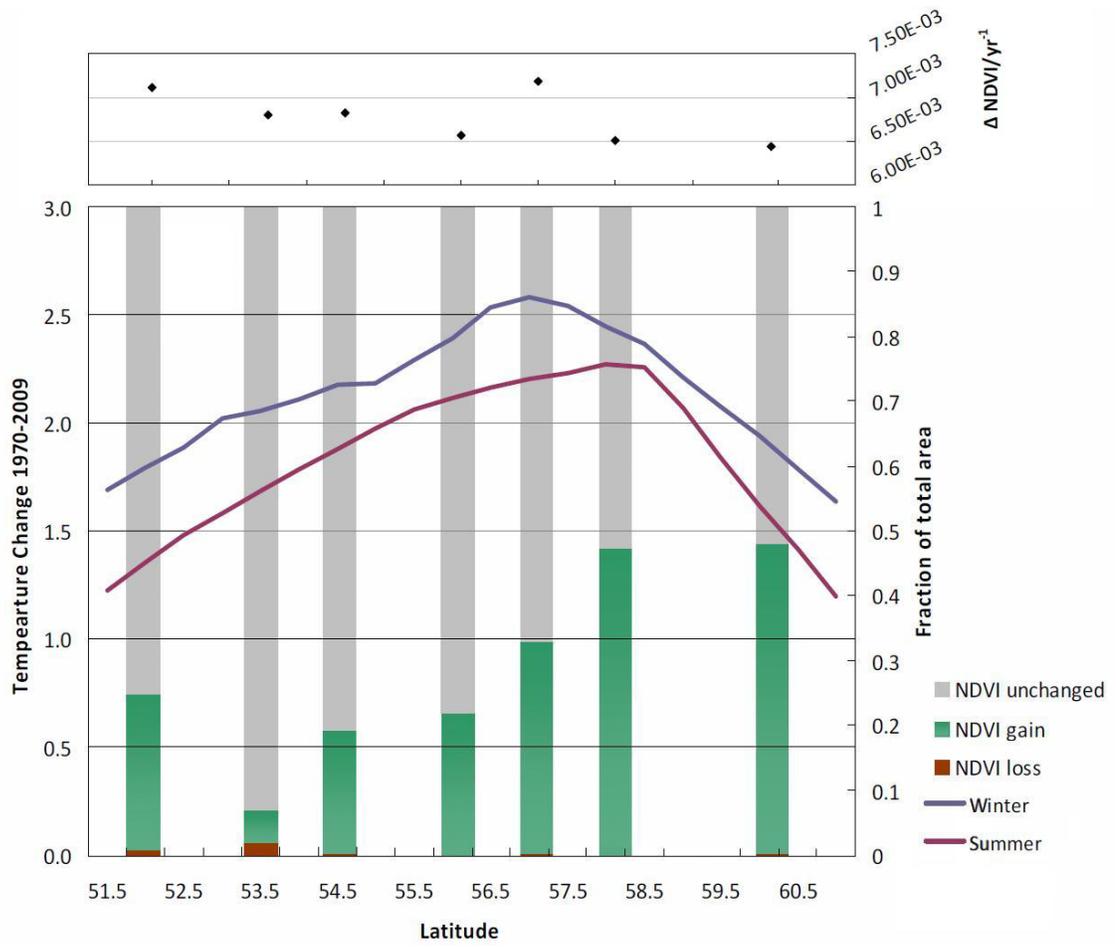
685
686 Fig. 1
687



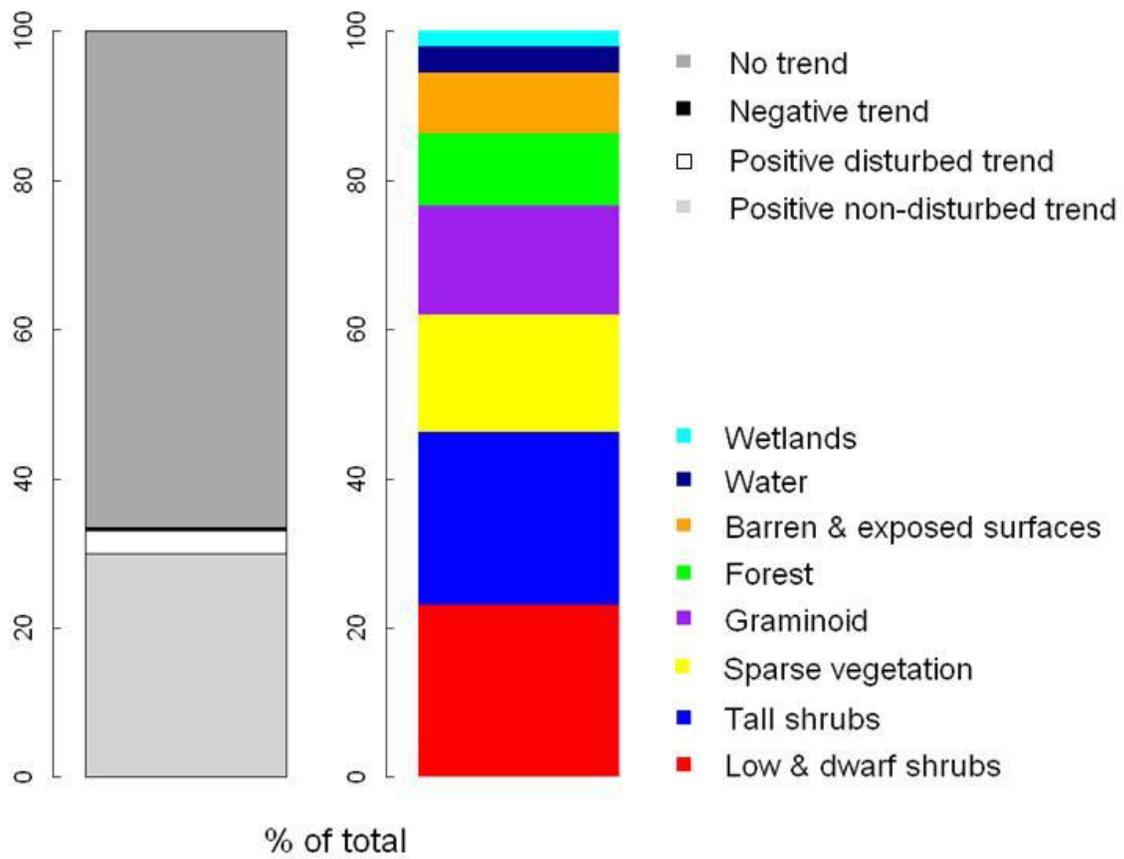
688
689 Fig. 2
690



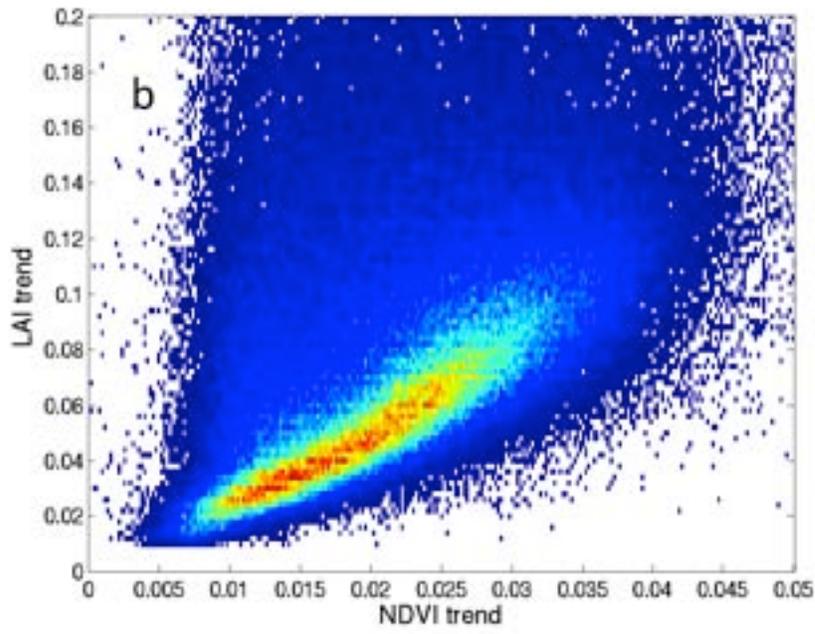
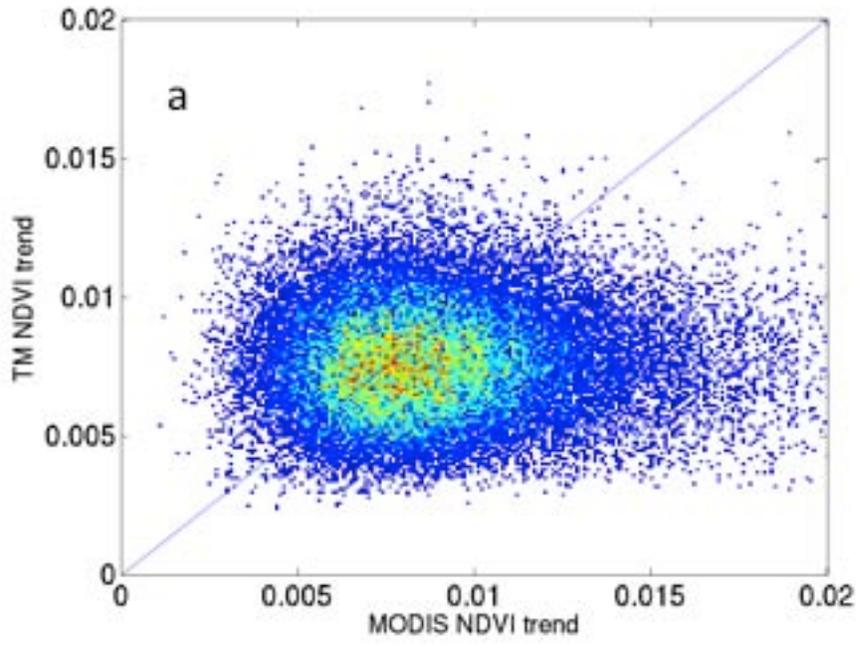
691
 692 Fig. 3
 693



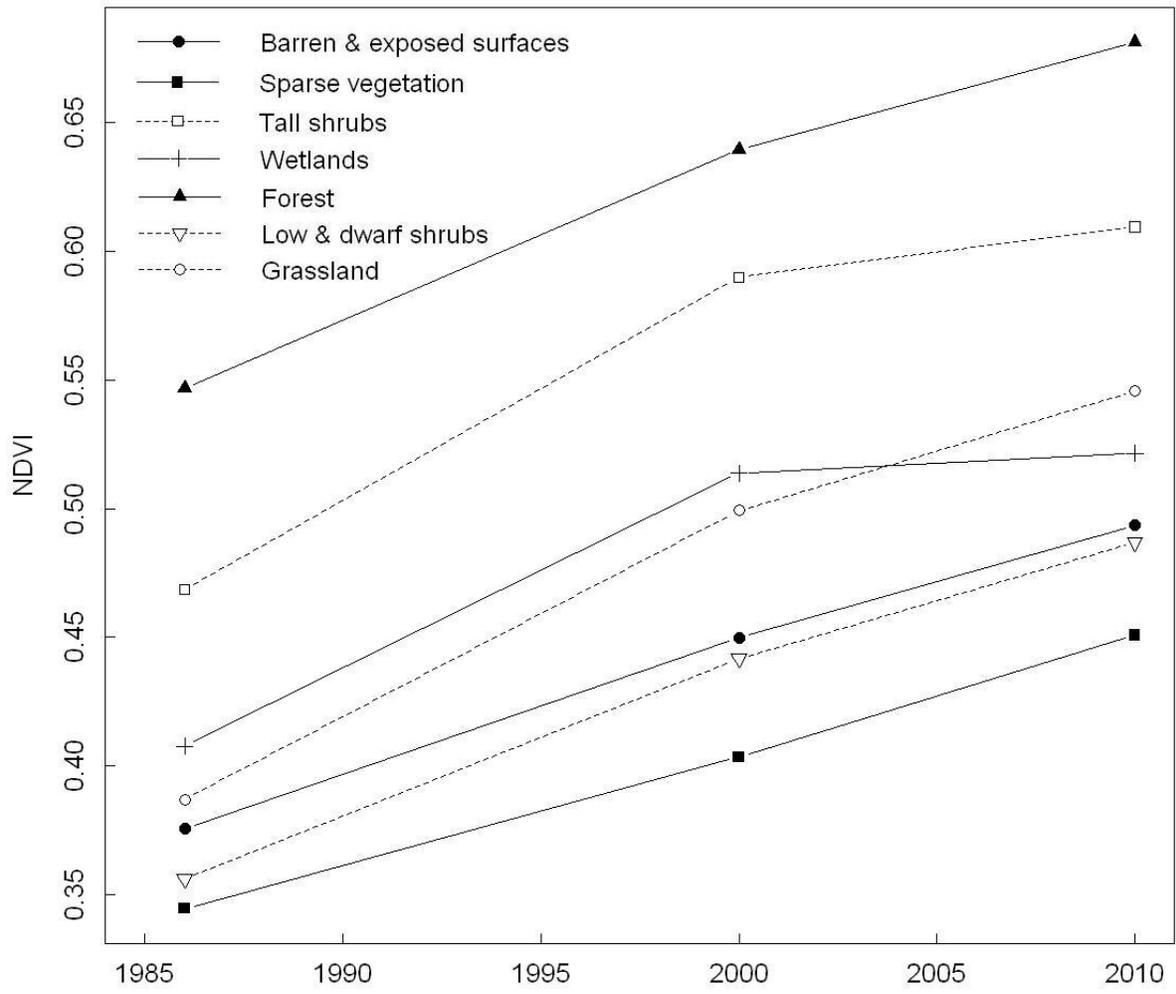
694 Fig 4.
 695
 696



697
698 Fig. 5
699



700
701 Fig. 6
702



703
704 Fig. 7