Title

Turf Wars: Biodiversity Benefits from Forest Understory Turf Transplants

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Statement of Authorship

All authors collected data, ZM analyzed the data and wrote the manuscript.

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Abstract

Restoration can increase biodiversity in anthropogenically degraded areas. These efforts can be divided into three categories: composition, structure, and function. The purpose of this study was to assess increases in biodiversity from transplants of forest understory turf in the Regreened forests of Sudbury, Ontario, Canada. We sampled understory vegetation plots within 6-year-old established transplants and comparison controls under coniferous and deciduous canopy cover in Regreened forests, as well as reference sites representing transplant donor sites and transplants immediately after installation, for measures of the three categories of biodiversity. We measured alpha diversity of the understory vegetation, decomposition through a cotton strip assay, and soil temperature variation. We found that transplants were highly successful in increasing compositional and structural biodiversity, but less successful in increasing function. It is our hope that these results will influence future focuses in the methodology of turf translocation to maximize biodiversity benefits.

Key words: Turf transplants; restoration ecology; forest; understory; vegetation; biodiversity; ecosystem function.

Main Text

Introduction

Reductions in biodiversity caused by anthropogenic impact are of large concern for the longevity of ecosystems. Biodiversity can be broken down into three hierarchical categories: composition, structure, and function (Franklin 1988). Composition refers to the types of organisms and habitats present, structure refers to their spatio-temporal organization, and function refers to how these factors impact fundamental processes such as nutrient cycling and microclimatic variation (Noss 1990). Restoration usually increases biodiversity relative to the degraded landscape, although not to the same extent as is present in a healthy reference site (Benayas *et al*. 2009). A large emphasis has traditionally been placed on measuring biodiversity in terms of composition and structure, but function has become a larger aspect of restoration science in recent years (Aerts 2011).

This study focused on the reclamation efforts of the Sudbury Regreening Program in Sudbury, Ontario, Canada. As a consequence of intensive logging, open bed roasting for ore extraction, and subsequent soil erosion, over 820 km^2 of Sudbury was reduced to barren or semi-barren land by the 1970's (Courtin 1994). This denuding of the landscape was followed by large scale reclamation through the collaborative efforts of the municipal, provincial, and federal governments alongside the local community, academia, and the mining industry from the 1970's to the present (Winterhalder 1985; City of Greater Sudbury 2012; VETAC 2010, 2015). The major problems which prevented revegetation included low soil pH, high concentrations of bioavailable metal species, and low nutrient concentration in poorly developed soils (Winterhalder 1985). High soil temperatures were also an issue, as the temperature of barrens relative to undisturbed forests can be significantly more variable (Kozlov and Zvereva 2007). The key methods used in the establishment of vegetation included applications of dolomitic limestone to raise soil pH, fertilizers to increase nutrient content, native seed mixtures to increase soil cover, stabilization, followed by plantings of tree seedlings (Winterhalder 1985). Between 1979 and 2015, the City of Sudbury succeeded in planting nearly 10,000,000 trees and developed large canopy covers (VETAC 2015), significantly increasing the biodiversity of Sudbury under all three of the hierarchical categories.

A remaining problem in the anthropogenic forests of Sudbury is the lack of development of the forest understory layer. Although in a healthy forest, the understory represents on average 80% of the total plant species richness (Gillam 2007), much less analytic emphasis is usually placed on the contributions of the understory to ecosystem function (Aerts 2011). The diversity of the understory layer is integral to nutrient cycling and energy flow in forest ecosystems (Gilliam 2007), and has also been shown to have a strong influence on soil biota diversity and functionality (Eisenhauer *et al*. 2011; Zhao *et al* 2014). To further complicate this issue, natural understory development in anthropogenic forests has been shown to be radically different between coniferous and deciduous forests in terms of composition and functionality, with conditions in coniferous forests often preventing establishment of some herbaceous species (Aubin *et al* 2008). It is thus expected that natural colonization would occur in the forests of Sudbury, but that it would be extremely slow and differential between canopy types (Braun 2007, Aubin *et al.* 2008; VETAC 2010).

This slow colonization of understory vegetation has been aided by translocation and establishment of turf transplants (hereafter, transplants). Transplants of forest understory have been an aspect of large scale Regreening operations since 2010. Small, 10cm thick plots of soil, rich in its biota and seed bank, are translocated from healthy "donor" sites to set up larger plots in degraded "recipient" sites within the reclaimed forests of Sudbury (VETAC 2010). Between 2010 and 2015, 121 sites and nearly 1.5 ha of land have received transplants (VETAC 2015). Transplants have been shown to be successful in increasing the compositional and structural biodiversity in multiple degraded communities such as alpine trails and roadsides (Conlin and Ebersole 2001; Bay and Ebersole 2006; Aradottir and Oskarsdottir 2013), tropical savannahs (Le Stradic *et al*. 2016), and temperate heathland (Box *et al*. 2011). The effect of environmental variables on the successful establishment of transplant plots in Sudbury itself has additionally been studied (Santala *et al*. 2015). Success in these studies is generally high although inevitably imperfect, as some complications and discrepancies exist relative to the donor sites. There is thus significant evidence of transplants increasing compositional and structural diversity in their recipient sites, but much less emphasis has been placed on how transplants impact function within the recipient site.

The purpose of this study was to assess the effectiveness of transplants in increasing local biodiversity under different forest types in terms of not only composition and structure, but also function. At the understory level, we used measures of alpha diversity for composition and structure, and decomposition and temperature alleviation at the soil level as measures of function. We compared established transplants with local comparison sites under deciduous and coniferous canopy cover, and additionally compared these to reference sites representing potential donor sites and transplant recipient sites immediately after translocation. We hypothesized that: (1) there would be an increase in compositional and structural biodiversity, although to a lesser degree than the reference sites (Conlin and Ebersole 2001; Bay and Ebersole 2006; Box *et al*. 2011; Aradottir and Oskarsdottir 2013; Santala *et al*. 2015; Le Stradic *et al*. 2016), (2) decomposition would be increased as a result of the correlation between soil functionality and understory diversity (Eisenhauer *et al.* 2011; Zhao *et al*. 2014), (3) that increased understory vegetation cover from transplants would decrease variation in soil temperatures (Winterhalder 1985; Kozlov and Szereva 2007; Zhao *et al.* 2014), and (4) coniferous forests would have lesser transplants success than deciduous forests due to decreases in nutrient availability, cooler temperatures, and other differences in environmental variation between the two forest types (Aubin et al. 2008).

Methods

Study Design

We sampled 4x4m plots in the understory of forests from 3 locations in Sudbury in July and August, 2016. The sites were located at Jane Goodall Reclamation Trail, Kelly Lake Trail, and Lake Laurentian Conservation Area/ Laurentian University (“Laurentian”). Each location had 2 sample plots where transplants had been established in 2010; one under a coniferous tree canopy and one under a deciduous tree canopy. At each location, we sampled an additional 2 plots without transplants to serve as comparisons. We selected these comparison plots so they were under the same respective forest canopy types as, and within 50m of, each of the transplant plots. The Laurentian location required the separation of the coniferous and the deciduous forest sites to, respectively, Lake Laurentian Conservation Area and the Laurentian University Outdoor Classroom, a distance of approximately 3 km. Both other forest comparisons were within 1 km from each other within a location and abiotic properties did not differ significantly between sites within a location (data not shown).

Aside from these 12 plots, we sampled 3 plots under mixed forest in each of 2 additional locations to be used for further comparison. The first was located 50 km south of Sudbury in an undisturbed forest on Crooked Lake Road. These plots had understory turf that met the criteria to be potentially used as donor sites (VETAC 2010; Peter Beckett, personal communication), and thus represented a pre-transplant condition for a donor site. The second, at Wanapitei Lake Provincial Park, was representative of recently transplanted plots established within one month prior to sampling. The reference plots were not sampled for all of the factors outlined below due to time constraints (Table 1).

The chosen sites allowed comparison between of Regreened forest understory *without* transplants to: healthy *donor* sites, transplant recipient sites immediately *after translocation*, and transplant recipient sites after *longer term establishment*. This gave us a total of six site types. We used the factorial design of all four combinations of forest type ("coniferous" and "deciduous") and plot type ("transplant" and "comparison") for our core analysis and compared these additionally to the reference forest plots representing the "pre-transplant/donor" and "recent-transplant" conditions (Table 1). Because each of the reference conditions had three plots within a single location, they were deemed non-independent. We thus excluded the reference plots from statistical analyses where non-independence violates test assumptions and compared reference sites to the treatments qualitatively. All statistical analyses were performed using R (version 3.2.4; R Core Team, 2016).

Vegetation Surveys

We identified all of the understory vegetation species within each plot and estimated their percent cover. We defined the understory as any plant which was less than 1m in height (Gilliam 2007). These included mosses, lichens, herbs, ferns and tree seedlings. For species with only a single individual or very low cover, we assigned covers of 0.5% and 1%, respectively. We estimated cover for all other species as total leaf area to the nearest 5% of the total plot area through a consensus amongst two observers on opposite sides of the plot. For each plot we used the sum of the percent cover for all species present as a measure of total understory percent cover. Some estimates of the total understory percent cover in a plot exceed 100% due to overlap of the understory vegetation.

In addition to the understory vegetation, we also quantified canopy percent cover as a proxy for light penetrance to the forest floor. We estimated canopy percent cover as the average of 5 measurements using a spherical crown densiometer (Model-C); one in each corner of the four corners of the plot and one in the centre.

We used separate two-way analyses of variance (ANOVAs) to test for differences based on forest cover and plot type, and a Tukey HSD *post hoc* test for pairwise comparisons between site types. As two measures of alpha-diversity for the composition of the understory vegetation, we compared species richness and Simpson's Diversity Index (*1-D*) according to the equation

$$D = \sum_{i}^{S} {P_i}^2 \qquad \text{Eq. 1}$$

where *D* is Simpson's Dominance Index, measured as the sum of the square of the proportion, *P*, for each species, *i*. We used Simpson's Diversity Index (*1-D*) because it is less sensitive than the Shannon-Weiner Diversity Index to the inclusion of rare species in analysis (Heip *et al.* 1998), and rare species were common in our study. We used the same analyses to test additionally for differences in total understory percent cover and canopy percent cover.

Decomposition

We used decomposition of cellulose as a measure of soil functionality. In order to quantify cellulose decomposition rates for each plot, we used bagged cotton strips made from bulk artists' fabric (Tiegs *et al*. 2013). We cut 10 strips from swatches of 72" wide unprimed #12 canvas (Curries, Product #CC12A72F) 6cm long by 6 threads wide each, and placed them in individual compartments within a 20x20cm, heat sealed, 50µm mesh bag (No-see-um netting, Jennis Fabrics Pattern NNOSEE9). We chose this mesh size to ensure changes in the structural integrity of the strips were due to microbial degradation and not macroinvertebrate grazing. At each of the treatment plots we cut the organic soil layer in an approximately 30x30cm square on three sides so that it could be pulled back to create a small excavation situated on top of the mineral soil horizon. We chose this location in order to minimize disturbance to the understory vegetation. We placed one bag in each of these excavations and left it to incubate for 28 days. We kept one of these bags as a control, and incubated it at ambient temperature in our lab on a windowsill with natural day and night cycles for the same period of time as the treatment bags. After the incubation period, we recollected the bags, washed the strips with 80% ethanol, brushed them clean with a small paintbrush, dried them for 24-48 hours in an oven at 40^{o}C, and measured the maximum break force of each strip in kilograms of force (kgf) using a tensiometer (Model Imada DS2-50N). To additionally test whether decomposition was uniform across the entire surface of the strip, we cut each strip in half before breaking them and compared the two halves across all sites using a paired t-test. We then took the mean of both halves for all of the 10 strips for each plot and the control. Consequently, this gave us a single measure of average break force for each plot and for the control. In order to use break force as a measure of decomposition, we standardized each plot average by the control average according to the equation,

$$TL = \frac{100}{t}\left(1 - \frac{f_s}{f_c}\right) \qquad \text{Eq. 2}$$

where *TL* is the percent tensile strength loss per day (percent decomposition per day), *t* is the incubation time in days, f_s is the average break force for the treatment strips (kgf), and f_c is the average break force for the control strips (in kgf). We used a two-way analysis of variance (ANOVA) to test for differences based on forest cover and plot type and a Tukey HSD *post hoc* test for pairwise comparisons between site types.

Temperature

In order to compare soil and air temperature in each plot and between site types, we used Thermochron iButton™ temperature loggers (Model DS1922L-F5# Maxim Integrated). We taped one logger to a nearby tree at approximately 2m above the ground and placed one logger in the same excavations as the cotton strip bags for the same 28-day incubation period as the strips. The loggers took measurements of temperature once every hour. The soil logger at one site (LU-Dt) was discounted due to suspected tampering by an animal over the incubation period. We used separate three-way analyses of variance (ANOVAs) to test for differences in the coefficient of variation over the whole incubation period and the average daily maximum temperature between forest cover, plot type, and logger location (in soil or air). We also used a Tukey HSD *post hoc* test to examine pairwise comparisons between site types and logger locations.

Results

Vegetation Surveys

We found higher understory vegetation alpha diversity in transplant plots than comparison plots (Figure 1). There was a significant effect of plot type (c < t; $p < 0.001$), with no effect of forest type ($p = 0.66$), on species richness, which was reflected in the pairwise comparisons (all pairwise c to t, $p < 0.05$; Figure 1A). Qualitatively, the reference plots had species richness higher than the comparison plots, but lower than the transplant plots (c < p,r < t). There were no direct pairwise significant differences between site types in terms of Simpson's Diversity Index (all pairwise $p > 0.05$; Figure 1B), but there was, similar to species richness, a significant effect of plot type (c < t; $p = 0.03$), with no effect of forest type ($p = 0.30$). Grouped into plot type, transplant Simpson's Diversity index was also, qualitatively, slightly higher than the reference sites, although with some overlap of standard deviations (p,r < t). There were no significant differences in total understory percent cover ($p_{forest} = 0.11$, $p_{plot} = 0.12$, all pairwise $p > 0.05$; Figure 1C) or in canopy percent cover ($p_{forest} = 0.33$, $p_{plot} = 0.56$, all pairwise $p > 0.05$; Figure 1D) between forest and plot type.

Decomposition

We did not find any significant differences in decomposition between our site types. There was no significant difference between the average break strength on either half of the same strip ($t_{124} = -0.55$, $p = 0.58$), indicating uniform decomposition across strips. This justified us pooling both halves of each strip in estimating the average decomposition rate per sample plot. There was no significant effect of forest type ($p = 0.48$) or plot type ($p = 0.44$) on the standardized cellulose decomposition rate measured from the cotton strip assay, and no significant pairwise differences between site types (Figure 2; all pairwise $p > 0.05$;).

Temperature

There were significant differences between the air and soil temperature logger locations (Figure 3). There was a significant effect of logger location on the coefficient of variation (soil < air; $p < 0.01$), with no significant effect of forest type or plot type ($p_{forest} = 0.25$, $p_{plot} = 0.95$; Figure 3A). This was reflected in the pairwise comparisons (all pairwise soil to air $p < 0.05$, all pairwise soil to soil $p > 0.05$, all pairwise air to air $p > 0.05$). Similarly, there was a significant effect of logger location on the average daily maximum temperature (soil < air; $p < 0.01$) with no effect of plot type ($p = 0.44$; Figure 3B). However, contrasting the coefficient of variation, there was a significant effect of forest type on the average daily maximum temperature (C < D; $p < 0.01$). This was not reflected in pairwise comparisons (all pairwise soil to air $p < 0.05$, all pairwise soil to soil $p > 0.05$, all pairwise air to air $p > 0.05$).

Discussion

We sampled plots in the understory of forests in Sudbury to measure the success of understory vegetation transplants in increasing biodiversity in terms of composition, structure and function. We found a significant increase in species richness and Simpson's Diversity in the transplant plots compared to both the comparison sites and also the reference sites, as well as a minor increase in percent cover, although this was not statistically significant (Figure 1A, 1B, 1C). The lower comparison plot diversity is consistent with previous research and the successful establishment of the transplants (Conlin and Ebersole 2001; Bay and Ebersole 2006; Box *et al*. 2011; Aradottir and Oskarsdottir 2013; Santala *et al*. 2015; Le Stradic *et al*. 2016). However, the higher diversity in our 6-year-old established plots (t) relative to the recent transplant plots (Rr) and the potential donor sites (Rp), contrasted the hypothesis that the reference sites would have higher alpha diversity than the transplant sites. This is an odd occurrence receiving less attention in other works. In some studies, it has been found that species richness and percent cover in transplant plots relative to donor/reference sites can not only be similar, but actually higher after a period of several years (Bay and Ebersole 2006; Santala *et al.* 2015). This ranges from a mild increase to a significant increase as we observed in our results (aside from percent cover, specifically), and has been argued as anomalous in both of the cited works. While this is a definite possibility, it could also be argued that the transplanted plots, in addition to their desirable ability to colonize the surrounding area, are also colonized by existing vegetation in the area. This finding lends further support to the increase in compositional and structural diversity already associated with transplants in degraded areas.

Contrasting the strong support for our first hypothesis, we found no support for an increase in function within the transplant plots for either metric we used. There was no statistically significant increase in soil decomposition rates (Figure 2) and no significant decrease in average daily maximum temperature or the temperature coefficient of variation (Figure 3) in transplant recipient sites. This finding contrasts the expectations of the study by Eisenhauer *et al*. (2011). From a survey of forest understory vegetation, soil macroarthropods and soil microbes, they found a significant positive correlation of understory plant species richness with microbial biomass, basal respiration, and varying types of macroarthropods. This is a result which agrees with the findings of Zhao *et al.* (2014), whom found that removal of understory plants resulted in decreased soil microbial phospholipid fatty acid (PLFA) content and also nematode diversity, an effect which was partially explained by changed in soil temperature regimes. This result was, again, not echoed in our results.

Some potential caveats of our methods may explain discrepancies from these previously published results and limit the interpretation of our results. First, our incubation period was approximately one month, and after this time some sites did not have decomposition significantly greater than the lab-incubated controls (standardized percent decomposition ≤ 0). If we had incubated strips for a longer period of time, perhaps a trend would have become more evident. Second, we only sampled for the function of microbial decomposition, while macroinvertebrates play a key in the decomposition process (Stork and Eggleton 1992). If we had additionally used a decomposition assay which also accounted for macroinvertebrate grazing, we could have gained a more realistic estimate of decomposition within sites. Third, we had no method of comparing the established transplants to our reference sites as a result of a lack of decomposition assays in those plots due to time constraints (Table 1). Nevertheless, a possible explanation for our results is thus that disturbance of the transplant turf during translocation prevented establishment of microbial communities, rendering similar decomposition rates to that of the degraded soils in the comparison sites. In this case, we would have expected significantly higher decomposition rates in the reference sites relative to the transplants and comparisons, regardless of plant species richness or cover, although our experimental design does not permit us to test this hypothesis. However, if this was indeed the most likely explanation for our observations, it would have significant implications and identify a need for alteration of procedures used in the transplantation process to maximize biodiversity benefits in transplant recipient sites.

In regards to our third hypothesis, changes in microclimatic temperature as a result of changes in vegetation are supported by several other studies. Zhao *et al*. (2014), again, found that removal of understory vegetation altered soil temperatures and thus impacted soil communities. Kozlov and Szereva (2007) summarized that temperatures are much more variable in industrial barrens relative to undisturbed reference forests. Although the established canopies of Sudbury's regreening efforts undoubtedly alleviate harsh temperatures at the soil level, it might have been expected that the understory vegetation also contributed the dampening of temperature oscillations. This was not supported by our results, which indicate that the vegetation cover provided by the transplants do not function in influencing temperature (Figure 3) despite similar percent canopy covers between site types (Figure 1D).

Our final hypothesis was that coniferous forests would have less transplant success than deciduous forests. This, again, was not supported by our results, but has been previously reported. Aubin *et al.* (2008) sampled understory vegetation in forests regrown on formerly agricultural land. They distinguished between plantations, anthropogenically grown forests similar to that of Sudbury, and “naturally revegetated” forests, and found that mature deciduous plantations had developed understories more similar to that of the “natural” condition, whereas mature coniferous plantations developed less extensive understories. This was hypothesized to be due to colder, less nutrient rich conditions in coniferous understories. Although we did find evidence of coniferous understories being slightly colder than deciduous understories (Figure 3B), this did not seem to inhibit transplant success adversely.

In conclusion, our study of the Regreened forests of Sudbury reiterates some previous notions regarding translocation of turf for the purposes of increasing biodiversity and raises some new concepts. First, transplants are capable of increasing compositional and structural diversity relative to the surrounding, degraded landscape, and also possibly even relative to the donor sites. Second, transplants likely increase functional diversity less than previously assumed. Our observed lack of increase in decomposition may be due to flaws in our methodology, but is equally likely to be a result of damage to microbial communities during translocation and installation. Transplants are also unlikely to function in alleviation of microclimatic temperature variation at the soil level, although this may be due to the redundancy of being beneath the tree canopy in our system. Finally, despite theoretical predictions and mild climatic differences, we find no difference in terms of transplant success between coniferous and deciduous cover. It is our hope that these findings can contribute to the adaptive management of the Sudbury Regreening Program, and also to the increase of biodiversity in other areas by similar methodologies.

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Tables and Figures

Table 1. Acronyms and factors measured for each of the study sites. Y and N correspond to "measured" and "not measured", respectively. Forest types C, D, and R correspond to "coniferous", "deciduous", and "reference (mixed)", respectively. Plot types c, t, p, and r correspond to "comparison", "(established) transplant", "pre-transplant/donor", and "recent-transplant", respectively.

	Treatment Locations			Reference Locations	
Factor	Jane Goodall	Kelly Lake	Laurentian University	Crooked Lake	Wanapitei Lake
Site Acronym	JG	KL	LU	CL	WL
Forest Type(s)	C, D	C, D	C, D	R	R
Plot Type(s)	c, t	c, t	c, t	p	r
Total Sample Plots	4	4	4	3	3
Site Type(s)	Cc, Ct, Dc, Dt	Cc, Ct, Dc, Dt	Cc, Ct, Dc, Dt	Rp	Rr
Understory Vegetation *(Species composition and percent cover)*	Y	Y	Y	Y	Y
Canopy *(Percent cover)*	Y	Y	Y	Y	N
Decomposition *(Cellulose strips)*	Y	Y	Y	N	N
Temperature *(Soil and air throughout decomposition strip incubation period)*	Y	Y	Y	N	N

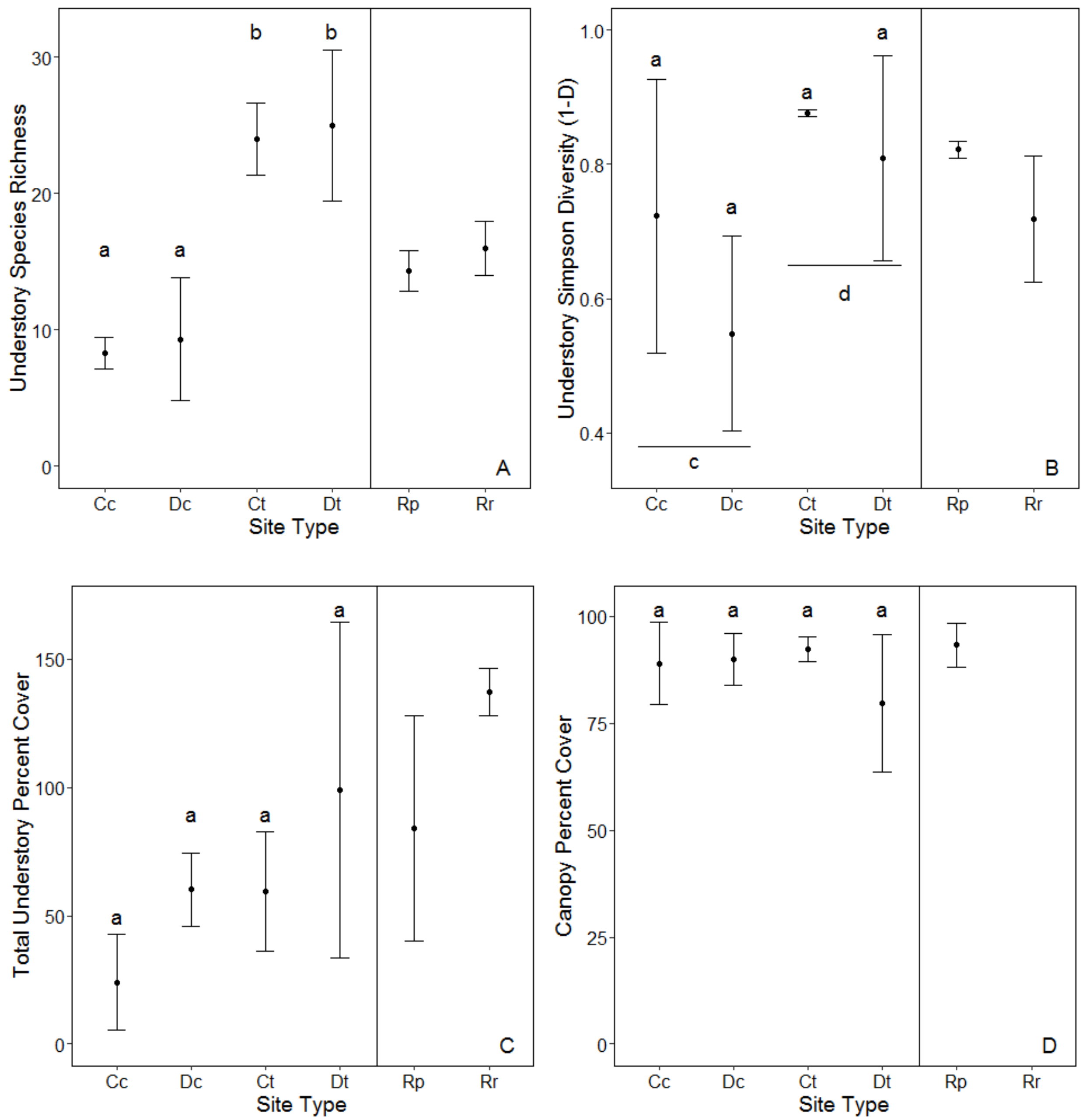

Figure 1. Vegetation indices by site type for understory species richness (A), understory Simpson's Diversity Index (B), total understory percent cover (C), and canopy percent cover (D); showing means and standard deviations. Site types labeled according to acronyms in Table 1. Letters "a" and "b" denote significant pairwise differences ($p < 0.05$). Letters "c" and "d" denote significant group effects ($p < 0.05$). Vertical line separates factorial site types from reference site types, the latter of which were not included in statistical analyses for lack of independence in measures.

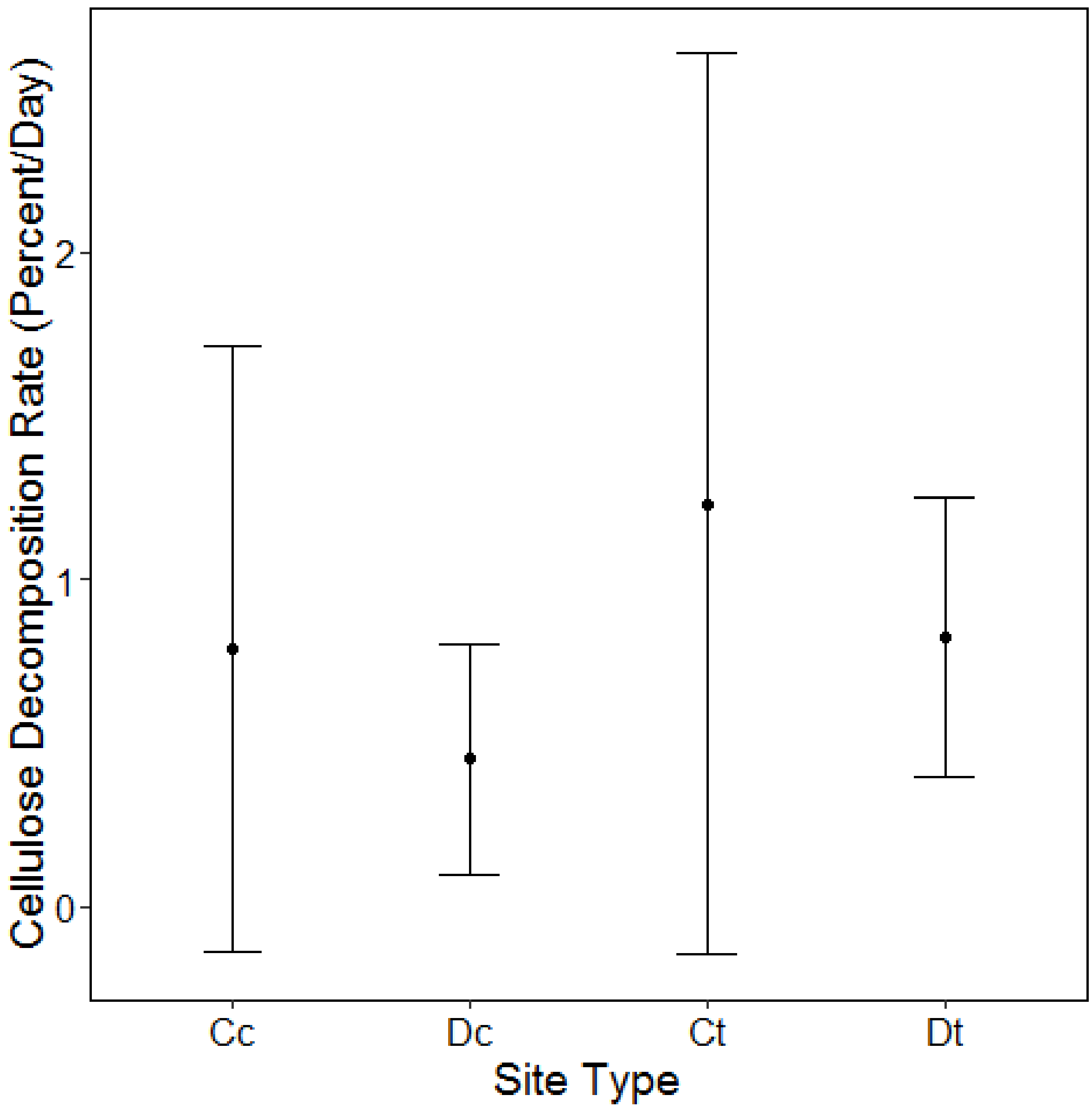

Figure 2. Cellulose decomposition rate by site type showing means and standard deviations. Site types labeled according to acronyms in Table 1. No significant differences are present between site types.

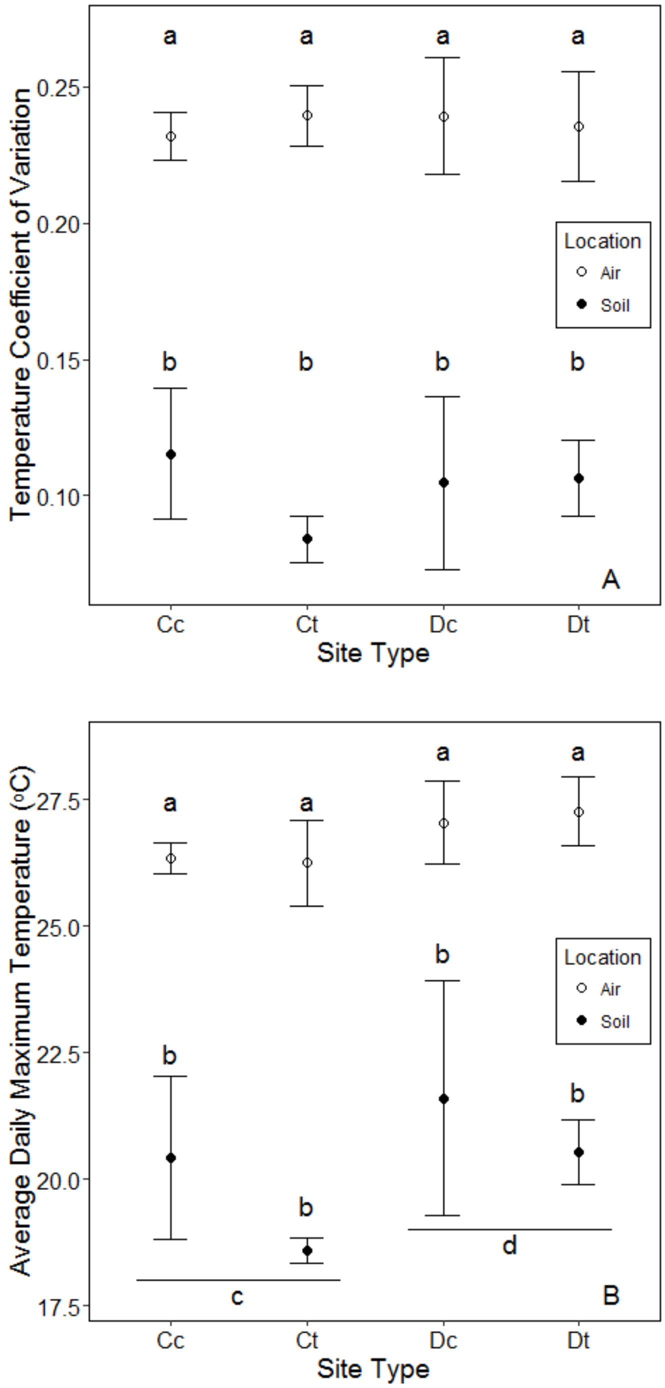

Figure 3. Temperature data by site type and logger location as the coefficient of variation over the entire time series (A) and the average daily maximum temperature in ºC (B); showing means and standard deviations. Site types labeled according to acronyms in Table 1. Letters “a” and “b” denote significant pairwise differences ($p < 0.05$). Letters “c” and “d” denote significant group effects ($p < 0.05$).