Identifying understory diversity and resilience patterns with the depth-to-water index in boreal mixedwood forests

by

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Abstract

For the purpose of informing biodiversity conservation efforts in managed landscapes, we explored whether and how understory plant communities (abundance, diversity, composition) were related to a topographic moisture index, called depth-to-water, in the boreal mixedwood forests of northwestern Alberta. As a measure of resilience, we also examined if these relationships were changed by retention harvesting, 15 years after harvesting. Sample plots were placed along the depth-to-water moisture gradient in three forest types: coniferous, mixedwood, and deciduous, and in four retention harvesting treatments: unharvested (control), 50% retention, 20% retention, and clearcut (2% retention). Understory diversity, abundance, and composition were measured for each plot.

In unharvested stands, we found understory attributes were related to the depth-to-water index with the relationships varying among forest types. In coniferous stands, we found higher diversity and abundance (cover) on drier sites. In deciduous and mixedwood stands, understory abundance was higher on drier sites, but diversity was not related to the depth-to-water index. Lastly, composition was significantly, but weakly, related to the depth-to-water index in all three forest types.

Harvesting affected the relationships between understory variables and the depth-to-water index; again, effects differed between forest types. Coniferous stands were the least resilient forest type, as most relationships between understory attributes and the depth-to-water index in these stands were affected by harvesting. For instance, harvested coniferous stands had higher diversity on wetter sites, rather than on drier sites as was seen in the unharvested stands. Mixedwood stands were the most resilient forest type–only the relationship between composition and depth-to-water was affected by harvesting. In deciduous stands, relationships of abundance and composition with depth-to-water were changed by harvesting. The relationship between abundance and depth-to-water was weaker in harvested, as compared to unharvest, deciduous stands. Within the stands, resilience also varied along the depth-to-water gradient. Wetter sites were less resilient in coniferous and mixedwood stands, while drier sites were less resilient in deciduous stands. Our study shows that the depth-to-water index can be used to identify understory distribution and resilience; hence it can be useful for identifying areas to be targeted for conservation.

Dedication

For my family.

Thank you for the support, encouragement, and guidance. ☺

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Chapter 1: General Introduction

Despite increasing efforts to conserve biodiversity and a better awareness of conservation issues, global biodiversity indicators continue to show a declining trend and pressures on the environment, such as consumption and pollution, continue to increase (Butchart et al. 2010, Tittensor et al. 2014). According to a report by the Convention on Biological Diversity, the world's governments were unable to significantly reduce biodiversity losses and meet the 2010 conservation targets (SCBD 2010). In addition, we still face continued loss in most habitats and an increased risk of extinction for threatened species (SCBD 2010). This is concerning since biodiversity is known to drive ecosystem functions and services and is key to ecosystem resilience and recovery after disturbances (Cardinale et al. 2012, Mori et al. 2017). To improve conservation efforts we need to continue addressing research gaps in conservation of biological diversity. For example, to identify which areas to target for conservation, we need to improve our ability to identify diversity patterns across a landscape; this requires a better understanding of factors driving biodiversity. Since anthropogenic activity continues to expand, we also need to better understand how this affects biodiversity. Lastly, we can take advantage of the latest technology and develop additional tools for managing biodiversity. In this thesis, I tackle these issues with a focus on understory vegetation in the boreal forest.

1.1 About the boreal forest

Dubbed Earth's "second lung" (Warkentin and Bradshaw 2012), the boreal forest encompasses approximately a third of the global forest cover and is a unique biome which provides irreplaceable ecosystem goods and services. Boreal forests are found at high latitudes, where temperatures can remain below 0˚C for more than half a year (Gauthier et al. 2015). They are characterized by cold-tolerant trees, mostly from the *Abies, Larix, Picea, Pinus, Populus,* and *Betula* genera (Gauthier et al. 2015). Although tree diversity is low in boreal forests, they still host a diverse set of organisms and multiple trophic levels. As one of the world's last "intact" forests (Badiou et al. 2013), the boreal is a significant carbon reservoir, with over 35% of the world's terrestrial carbon stored within boreal forests (Moen et al. 2014). Boreal forests also play an important role in the livelihoods of communities and the economies of countries, which rely on nonrenewable and renewable resources provided by the forests. For countries, like Canada, industries which occur in boreal forests, such as forestry, oil, and gas industries, are vital for the economy (Ruckstuhl et al. 2008). Additionally, parts of the boreal continue to be inhabited by indigenous peoples who rely on the forest for resources (Bradshaw et al. 2009).

Although the boreal forest is characterized by low densities of human population, it is still vulnerable to anthropogenic activities. Natural disturbances, such as wildfires and insect outbreaks, are essential drivers of ecosystem processes and biodiversity in the boreal (Brandt et al. 2013; Gauthier et al. 2015), but anthropogenic disturbances are having an increasingly important influence on these ecosystem processes and biodiversity. For instance, clear-cut harvesting reduces the structural diversity of a stand and leads to a different regeneration trajectory from that of a natural disturbance, like a wildfire (Venier et al. 2014, Gauthier et al. 2015). Notably, wildfires or insect outbreaks leave behind live residual trees and deadwood, which provide habitat or a growing substrate for organisms and allow nutrients to be distributed back into the soil (Venier et al. 2014); in contrast, harvesting often removes most trees and woody debris. By removing downed woody debris, sites necessary for the establishment of some understory species are lost and we risk reducing the understory diversity (Venier et al. 2014). In this thesis, I focus on forestry in Canada's boreal region, where almost a third of the world's boreal forest is located (Badiou et al. 2013), and explore the potential for conservation in these managed landscapes.

1.2 The road to improving forestry

In Canada, forestry is progressing northwards into areas formerly considered too remote and inaccessible (Badiou et al. 2013). Minimizing the ecological costs that come with forestry will require an integration of conservation principles in forestry practices. Fortunately, increasing awareness of harvesting effects on the boreal forest has led to shifting paradigms in forest management (Venier et al. 2014). Initially, timber was the sole focus of forestry and forests were managed to ensure a constant supply (Wiersma et al. 2015). With time, forest management has focused more on ensuring not just a supply of timber, but rather a more diverse set of ecosystem services, including wildlife habitat and recreational services (Wiersma et al. 2015). Today, sustainable forest management is the dominant paradigm, with a focus on "broader ecological values" and ensuring "long-term ecological integrity of ecosystems" (Wiersma et al. 2015). One approach to attaining sustainability in forest management is natural disturbance-based management (Drever et al. 2006). This approach involves imitating the effects of natural disturbances in order to maintain or restore the habitat heterogeneity found within unmanaged forests; this can help maintain key ecological processes (Drever et al. 2006). For example, variable retention harvesting applies this approach at a stand-scale by leaving behind patches of live trees in a harvested stand (Drever et al. 2006). In this thesis, I will focus on the practice of variable retention harvesting and how it affects understory vegetation.

Retention harvesting was developed in the 1980s in the Pacific Northwest forests of the US and is now one of the leading sustainable alternatives to traditional clear-cutting practices (Gustafsson et al. 2012). It involves permanently retaining both dead and live trees in a harvested area (Gustafsson et al. 2012). Retention harvesting differs from other silvicultural techniques in its focus on what is retained rather than what is harvested (Lindenmayer et al. 2012). Trees are retained for three main purposes: to maintain the presence of resident organisms, to create heterogeneity in stand structure, and to serve as "stepping stones" to aid the movement and dispersal of organisms through the disturbed landscape (Franklin et al. 1997).

Studies have shown that retention forestry can successfully mitigate biodiversity losses associated with harvesting. Retention cuts can support similar levels of total species richness as unharvested forests (Mori and Kitagawa 2014) and, when compared with clearcuts, retention cuts support higher levels of species richness (Fedrowitz et al. 2014). Retained forest patches provide refugia for forest-associated organisms and their effects are evident even 20 years after harvest, as forest-associated organisms continue to thrive within these patches (Fedrowitz et al. 2014, Baker et al. 2015). In addition, harvesting leaves behind open, disturbed sites which are ideal for colonization by early-seral species. Thus, sites with retention-harvesting host more early-seral species than unharvested sites

(Fedrowitz et al. 2014). These pioneer species are also an important part of the forest diversity, even though conservation practices may overlook these species (Swanson et al. 2011). Although these studies show retention patches can maintain forest-associated organisms, it is important to note that they do not conserve all forest-associated species (Fedrowitz et al. 2014; Mori and Kitagawa 2014). Reserves continue to be crucial to biodiversity conservation. These studies merely show the ability of retention harvesting to mitigate at least some of the biodiversity losses associated with clear-cutting.

Most studies on retention harvesting have focused on the effects of the proportion of the trees retained and their spatial arrangement (aggregated or dispersed) in a harvest unit. Intuitively, higher levels of retention should provide more benefits. Studies have found that higher levels of retention are associated with reduced compositional changes and fewer losses of forest specialists in the understory vegetation of stands (Craig and Macdonald 2009, Gustafsson et al. 2012, Halpern et al. 2012). Overall, researchers have suggested 5-10% retention as a bare minimum, but strongly recommend higher retention levels (Craig and Macdonald 2009, Work et al. 2010, Gustafsson et al. 2012, Pinzon et al. 2012). In retention harvesting, retained trees can be spatially arranged either in aggregates or dispersed throughout the harvested site. Areas within a retention patch undergo minimal understory compositional changes, but the benefits of the retained trees are localized to the retention patch (Halpern et al. 2012). Combining aggregate retention with dispersed retention can ensure the benefits of retention harvesting are distributed throughout the stand (Halpern et al. 2012).

While research has improved and guided the practice of retention forestry by recommending retention levels and arrangement, there has been relatively little research into where to best place retention patches to achieve maximum benefit. In some guidelines, an even spatial distribution across a harvest unit is suggested, to assist in dispersal of organisms (Gustafsson et al. 2012). Lindenmayer et al. (2012) suggests that the distribution of retained trees should be designed to mimic the biological legacies and microhabitats left behind by natural disturbances. Halpern et al. (2012) suggests placing residual trees in a manner that utilizes the heterogeneity in forest structure or topography to maximize habitat diversity in the post-harvest landscape. To further guide the placement of retention harvesting, we need a better understanding of how biodiversity is distributed in the landscape. In addition, understanding which areas may be more sensitive to harvesting can guide how harvesting intensity should be varied within a landscape. Remote-sensing technology can potentially assist with this, since it is capable of providing fine-resolution data across a landscape. In this thesis, I explore using remotely-sensed data to identify how understory diversity and resilience change within a forest stand.

1.3 On the importance of the understory vegetation

The understory vegetation is an important component of forested ecosystems, though it encompasses a small portion of a forest's biomass and is often overlooked (Gilliam 2007). It affects wildlife, the overstory community, and ecosystem functioning in a forest. Understory vegetation provides food and habitat for wildlife and a reduction in understory biodiversity can mean the loss of important food sources (Deal 2001). The herbaceous community competes with saplings, thereby affecting the regeneration of overstory trees and overstory composition (Gilliam 2007; Nilsson and Wardle 2005). Nutrient cycling is also affected by the understory community since the litter of understory plants tends to contain high concentrations of key nutrients, decompose rapidly, and is deposited annually (Nilsson and Wardle 2005). Lastly, the understory vegetation accounts for most of the plant diversity found within boreal and temperate forests. For example, in the eastern boreal forests of Canada, there are only about 20 canopy tree species but over 200 understory species (Gilliam 2007; de Grandpre et al 2003).

Understory vegetation distribution is shaped by the availability of resources, such as light and water (Witte et al. 2004). Availability of these resources is, in turn, shaped by abiotic and biotic factors, such as canopy composition and topography. For example, deciduous (broadleaf) trees allow for higher light transmission and higher nitrogen availability to the understory, as compared to conifer trees (Hart and Chen 2006, Jerabkova et al. 2006, Macdonald and Fenniak 2007). Thus, stands dominated by deciduous trees allow for higher shrub and forb diversity (Macdonald and Fenniak 2007). Studies have also shown that these forest types occupy sites with slightly different moisture levels, with coniferous stands on wetter areas and deciduous stands on drier areas (Albani et al. 2005, Nijland et al. 2015). Lastly, these stands differ in how they respond to disturbances. For example, Macdonald and Fenniak (2007) found that the understory of deciduous stands is more resistant to the effects of harvesting, while the understory in conifer-dominated stands is more sensitive. In brief, different canopy compositions can indicate different environmental conditions and support slightly different understory assemblages, with these assemblages responding differently to disturbances (Hart and Chen 2006, Macdonald and Fenniak 2007).

Topography also plays a strong influence on the understory vegetation. Topography affects plant distribution by influencing the transportation and storage of water and the amount of incoming solar radiation (Bridge and Johnson 2000; Chipman and Johnson 2002; Moeslund et al 2013b). In boreal forests, in particular, topography plays a large role in determining soil moisture, because precipitation and evaporation do not vary much across a landscape (Zinko et al. 2005). Moisture, in turn, affects vegetation distribution by influencing water and nutrient availability (Moeslund et al. 2013b). Since vegetation distribution is influenced strongly by topography and moisture, we can potentially use these variables to predict patterns of understory vegetation diversity.

1.4 The depth-to-water (DTW) index: a topographical moisture index

Topographically-derived moisture indices provide a measure of moisture across a landscape at a fine resolution and are now becoming increasingly available. Studies have shown topographically-derived hydrological indices to be correlated with variation in plant species richness and vegetation associations, even in areas of low topographic relief (Zinko et al. 2005, Hiltz et al 2012, Moeslund et al. 2013a, Moeslund et al 2013b). For example, Moeslund et al. (2013a) showed Topographic Wetness Index (TWI)—a topographic hydrological index—was significantly related to species richness in the dry grasslands of Denmark, where topographic relief is minimal. Likewise, Zinko et al. (2005) showed understory species richness was related to TWI in the boreal forest. However, in that study TWI was at a large resolution, derived from 20-m digital elevation data. Other studies have explored the use of moisture values derived from remotely-sensed data to predict vegetation distribution and guide conservation efforts (e.g., Sass et al. 2012). However, more research is needed to extend the use of hydrological indices to predict vegetation patterns in managed landscapes, such as those utilized for forestry.

The depth-to-water (DTW) index is one such topographically-derived moisture index that has been shown to be better at predicting soil moisture than the commonly used TWI (Murphy et al. 2009, Agren et al. 2014). For example, Murphy et al. 2011 found that DTW better captured patterns in soil drainage ($R^2 = 0.64$) and soil type ($R^2 = 0.62$) than TWI ($R^2 = 0.25$ for soil drainage and $R^2 = 0.23$ for soil type). DTW values are a measure of the probability of soil saturation; areas with low DTW values have a higher probability of having surface water for most of the year (Murphy et al. 2007). Thus, areas predicted to have surface water will have a DTW value of zero (Murphy et al. 2009). The DTW values used in this study are derived from Light Detection and Ranging (LIDAR)-based digital elevation models (DEM), which provide topographic values at a fine spatial resolution. Hence, the DTW values in this study are available at a spatial resolution of 1.0 m (Nijland et al. 2015).

DTW not only predicts soil moisture, but studies have also shown DTW is related to key forest attributes. For example, DTW has been shown to be related to post-harvesting vegetation regrowth (Nijland et al. 2015), vegetation classifications (Murphy et al. 2011, Hiltz et al. 2012), and soil drainage class (Oltean et al. 2016). The DTW index is currently used in forestry for risk-management to guide infrastructure development (e.g. roads) and minimize soil disturbance (Agren et al 2014). However, additional studies are needed to examine its ability to characterize patterns in vegetation biodiversity in managed landscapes. In Alberta, the DTW index has been derived for the managed boreal forests north of Peace River—an area that includes the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area (White et al. 2012).

1.5 Can DTW answer the "where" of retention harvesting?

The objective of this thesis is to explore if depth-to-water index can be used to help inform decisions about where to place retention harvesting, in three forest types: conifer-dominated (>70% coniferous trees), mixedwood (30-60% coniferous trees), and deciduous stands (>70% deciduous (broadleaf) trees). For example, high levels of retention could be placed in locations so as to more effectively lifeboat biodiversity or in locations where communities would be more sensitive to harvesting. One thing that would help in deciding 'where' retention should be placed is if we better understood patterns of variation in plant community composition and diversity across the landscape – and if we had some tools to help us map these. In the first chapter, we explore if a relationship exists between the depth-to-water index and understory vegetation attributes, such as diversity and composition, in the three forest types mentioned above. If these are related, depth-to-water can potentially be used to predict diversity patterns of understory vegetation and thus guide the placement of retention harvesting in managed landscapes. In the second chapter, we examine if harvesting affects the relationship between depth-to-water and these understory attributes, 15 years after harvest and how these effects might change with forest type. Since undisturbed forests are becoming more uncommon, it is useful to determine how disturbance might change these relationships and if topographic indices are useful in identifying patterns of resilience. More importantly, these results can show how disturbance affects the understory vegetation along a moisture gradient and if wetter or drier sites are more or less affected by harvesting. For this study, resilience is defined as an ecosystem's ability to absorb the changes brought on by a disturbance (e.g., retention harvesting) and maintain existing ecological relationships (sensu Holling 1973). We use the maintenance of the DTW-understory relationship in harvested stands as a measure of resilience.

Chapter 2: Utilizing the depth-to-water index to identify understory vegetation patterns in the boreal

2.1 Introduction

In forest ecosystems, understory vegetation comprises only a small portion of total plant biomass and thus its ecological importance is often overlooked (Gilliam 2007). However, understory vegetation serves many important functions in a forest, with effects on wildlife, the overstory community, and ecosystem functioning (Deal 2001, Nilsson and Wardle 2005, Gilliam 2007). Most importantly, the understory vegetation accounts for most of the plant diversity found in temperate and northern forests. For example, in the eastern boreal forests of Canada, there are only approximately 20 canopy tree species, while the understory vegetation is comprised of over 200 species (Gilliam 2007; de Grandpré et al 2003).

An important driver of understory vegetation is topography. Topography affects plant distribution by influencing the transportation and storage of water and the amount of incoming solar radiation (Bridge and Johnson 2000; Chipman and Johnson 2002; Moeslund et al 2013b). In boreal forests, in particular, topography plays a large role in determining soil moisture, because precipitation and evaporation do not vary much across a landscape (Zinko et al. 2005). Soil moisture, in turn, affects vegetation distribution by influencing water availability, soil nutrient availability and nutrient uptake (Rodriguez-Iturbe et al. 2001, Araya et al. 2013, Moeslund et al. 2013b). Since moisture and topography influence vegetation patterns, we can potentially use them to predict understory distribution patterns.

Topography and moisture can now be mapped over large areas of land at a fine resolution through the use of topographically-derived moisture indices. Such indices have been shown to be correlated with variation in plant species richness and vegetation assemblages, even in areas of low topographic relief (Zinko et al. 2005, Hiltz et al 2012, Moeslund et al. 2013a, Moeslund et al 2013b). For example, Moeslund et al. (2013a) showed Topographic Wetness Index (TWI)—a topographic hydrological index—was significantly related to species richness in the dry grasslands of Denmark, where topographic relief is minimal. They found higher richness on drier sites. Zinko et al. (2005) likewise showed understory species richness was related to TWI in the boreal forest. However, they found higher richness on wetter sites. In addition, their TWI was at a large resolution, derived from 20-m digital elevation data. In this study, we explore the use of another topographically-based moisture index—the depth-to-water index.

The depth-to-water (DTW) index is a moisture index that has been shown to be better at predicting soil wetness than the commonly used TWI (Murphy et al. 2009, Agren et al. 2014). The depth-to-water index is currently used in forestry for risk management to guide infrastructure development and minimize soil disturbance (Agren et al 2014). It is not only related to soil properties, but also vegetation types, as studies have also shown its usefulness in predicting moisture-based vegetation classifications (Murphy et al. 2011, Hiltz et al. 2012). However, additional studies are needed to examine its ability to predict plant diversity.

The objective of this study was to evaluate the usefulness of the depth-to-water index for characterizing biodiversity patterns of the vascular understory vegetation in the northern boreal mixedwood forests of Alberta. We tested whether the depth-to-water index is related to understory attributes in an area where topographic relief is minimal. The wettest portions of the study area are covered by peatlands, and we excluded these from our study. Therefore, we explored if the depth-to-water index is useful over a relatively narrow range of topography and thus moisture conditions. We asked: is depth-to-water related to understory diversity, abundance, and composition in three forest types—conifer-dominated, mixedwood stands, and deciduous (i.e., broadleaf)-dominated stands? The three forest types we study are known to occupy slightly different positions on the landscape, with conifer stands on wetter areas, followed by mixedwood stands, and lastly deciduous stands on drier areas (Albani et al. 2005, Nijland et al. 2015). In addition, the understory composition tends to differ between the three different forest types (Hart and Chen 2006, Macdonald and Fenniak 2007). Thus, we hypothesized that the relationship between depth-to-water and understory vegetation would vary with forest type. As Zinko et al. (2005) found higher understory richness on wetter sites in the boreal forest we expected to see the same trend in our study. However, their study used TWI at a coarser resolution than our study and TWI is known to be sensitive to digital elevation model (DEM) resolution (Agren et al. 2014); thus it is also possible that our results will show different trends. Lastly, we hypothesized composition would vary with the depth-to-water gradient as understory species vary in their moisture preferences (Ellenberg 1988, Moeslund et al. 2013b).

2.2 Methods

Study area

The study was conducted at the Ecosystem-based Management Emulating Natural Disturbance (EMEND) experimental area, located about 90 km northwest of Peace River in northwestern Alberta, Canada (56˚46' 13" N, 118˚22'28"W). It is situated in the Lower Boreal Highlands subregion of Alberta (Natural Regions Committee 2006). The mean annual temperature in the region is -1 °C and the mean annual precipitation is 495 mm, with 68% falling during the growing season (Natural Regions Committee 2006). Soils are mainly "fine-textured luvisols on glaciolacustrine deposits" (Kishchuk et al 2014). The dominant tree species are *Populus tremuloides*, *Populus balsamifera*, and *Picea glauca* (Natural Regions Committee 2006).

EMEND was established to examine the effects of variable retention harvesting on biodiversity, ecosystem function, and forest regeneration (Spence et al. 1999). Harvesting treatments were applied to 10-ha 'compartments' in four forest types, with three replicates for each forest type. For this study, we focused only on unharvested compartments in three forest types: conifer-dominated (>70% conifer canopy cover), deciduous (i.e. broadleaf)-dominated (>70% deciduous canopy cover), and mixedwood (conifer and deciduous canopy cover, each composing 35-65%).

Depth-to-water (DTW) values

For this study, we use the depth-to-water (DTW) index as a measure of site moisture. DTW values are a measure of the probability of soil saturation; areas with low

DTW values have a higher probability of having surface water for most of the year (Murphy et al. 2007). The lower the DTW value the wetter the site, with areas predicted to have surface water having a DTW value of 0 (Murphy et al. 2009). Calculation of the DTW index begins with a Light Detection and Ranging (LIDAR)-based digital elevation model (DEM) combined with a hydrographic data layer, which identifies the locations of surface water (lakes, rivers, etc.) (Murphy et al. 2007). A flow accumulation network, based on the DEM, is developed using the D8 flow algorithm (Jenson and Domingue 1988) to determine flow direction. Additional stream locations are also predicted based on a flow initiation threshold, which varies from 0.5 to 16 ha. When flow accumulation at a cell has reached the flow initiation threshold, stream flow is assumed to begin at that cell. Streams and cells with water accumulation above the initiation threshold are given a DTW value of 0 and are used as hydrologic source cells for subsequent calculation of the DTW value (Murphy et al. 2007, Dr. Wiebe Nijland, personal communication, March 10, 2015). Each cell in the landscape is then assigned to a hydrologic source cell, which is the closest cell with surface water (i.e., a cell with DTW value = 0, also called a source cell) (Murphy et al. 2007). The DTW value is then calculated as the change in elevation and the horizontal distance between each cell in the landscape and its respective hydrologic source cell (Murphy et al. 2007). The equation used is $\text{DTW} = \left[\sum \frac{d_{zi}}{d_{xi}} a\right] x_c$, where $\frac{d_{zi}}{d_{xi}}$ represents the slope of a cell, a is a multiplier that accounts for the distance between a cell and its corresponding surface water, and x_c is the resolution of the grid.

Using a different initiation threshold creates a different set of DTW values for a given landscape. A low initiation threshold results in a landscape with more predicted streams. This means more cells in a landscape are close to cells with surface water (i.e., source cells) and more areas are therefore predicted to be wet. In contrast, higher flow initiation thresholds (i.e., 16 ha of water accumulation needed to start a flowing channel) produce more conservative estimates of moisture. Thus, DTW values based on a 0.5 ha flow initiation threshold will suggest that a greater proportion of the landscape is likely to be wet than would DTW values based on a 16 ha flow initiation threshold.

DTW values for this study were extracted from the Wet Areas Mapping (WAM) Tool based on LIDAR data collected in Aug. 2008, using a Leica ALS 50-II, with an average density of 2 points/m^2 (Nijland et al. 2015). Ground returns were rasterized into a DEM using a triangulated irregular network, with a final spatial resolution of 1.0 m (Nijland et al. 2015). Additional details of the LIDAR data and the derivation of WAM can be found in Nijland et al. (2015) and Murphy et al. (2007).

Plot selection

We selected 8 – 12 sampling locations within (or just outside) each of the three replicate compartments for each of the three forest cover types to capture a range of depth-to-water values within each compartment, using the mapped DTW data (in ArcGIS; ESRI, Redland CA). Sampling locations were stratified by DTW values to ensure even distribution along the DTW gradient. Each compartment had approximately 5-9 sampling locations on the wetter portion of the DTW gradient (DTW <1) and three sampling locations on the drier portion (DTW >1). Thus we had approximately 35 sampling locations per forest cover type and a total of 112 sampling locations. We limited our plots to the merchantable forest areas of EMEND to ensure our results can be used by forestry companies. Sampling locations were later located in the field using a high precision Global Positioning System (the SX Blue GPS II, Geneq Inc., Montreal, Quebec) that was capable of providing sub-meter accuracy.

Vegetation data

Vegetation data were collected in the summers of 2014 and 2015. At each sampling location, we established a 2x2 m quadrat. Within this we visually estimated the cover of each vascular plant species. Cover values were to the nearest 0.5% from 0 to 1, to the nearest 1% from 1 to 20, and to the nearest 5% from 20 to 100. Plants with trace amounts were assigned 0.1%. Vascular plants included woody shrubs and trees less than 1.3 m tall. Vegetation sampling was conducted by three teams and frequent calibration checks were conducted among teams to ensure consistency in visual estimates. Plants were identified to species, when possible, or were collected and pressed for identification later in the lab. Plants which lacked necessary reproductive parts were left at the genus level (e.g. *Salix* sp.

and *Carex* sp.) or left as numbered unknowns (e.g. unknown 1). Nomenclature follows Moss (1983).

Three types of vegetation response variables were examined: diversity, abundance, and community composition. Three measures of diversity were calculated: species richness, Shannon's diversity number, and Simpson's diversity number for each plot using the vegan package in R (Oksanen et al. 2016). Hill's numbers were used for the diversity indices, as they are in units of effective number of species (Hill 1973, Jost 2006). Thus the exponent of Shannon's entropy was used for Shannon's diversity number, hereafter referred to as Shannon's diversity, and the inverse of the Gini-Simpson index was used for Simpson's diversity number, hereafter referred to as Simpson's diversity. Abundance was quantified by cover; cover values were summed for all species within each plot to produce a total vegetation cover for each plot. Since species tended to overlap within each plot, total cover values exceeding 100% were possible. Cover was also summed for shrubs and forbs (included trailing woody species and low growing plants with a woody rootstock, e.g., *Cornus canadensis*) separately for each plot. Community composition was represented by cover values for each species in each plot.

Data analyses

To determine DTW values for each sample plot, ArcGIS was used to create a buffer with a radius of 2.5 m around each plot. The DTW values within these buffers were then extracted and averaged. This was done since DTW values were at a smaller resolution (1 m^2) than our plot size (4 m^2). This process was repeated for seven DTW estimates based on different initiation thresholds: 0.5 ha, 1 ha, 2 ha, 4 ha, 8 ha, 12 ha, and 16 ha. Since the DTW is not linear, the natural log of the average DTW value was used as the predictor variable (with addition of 0.1 to all values).

We used linear mixed effects models, with a Gaussian distribution, to analyze the relationship of vegetation diversity and abundance with DTW values. DTW values, forest type, and their interaction were used as fixed factors and compartment as a random factor. In preliminary analyses, the interaction between forest type and DTW was significant for some response variables (Appendix A) indicating that the influence of DTW on the response variables differed between forest types. Thus, subsequent analyses for all response variables were conducted for each forest type separately, with DTW as the only fixed factor. Species richness, Shannon's diversity, Simpson's diversity, total understory cover, forb cover, and shrub cover were our response variables. Analyses were done with the nlme package in R (Pinheiro et al. 2016). Residuals were examined to ensure normality and homogeneity of variance.

Models were run separately for the seven different initiation thresholds to determine which threshold was optimal for each response variable, in each forest type. Thus, for each response variable seven models (seven initiation thresholds) were compared and the optimal model was determined by the lowest Akaike Information Criterion (AIC) value. We then used the optimal model for each response variable to determine if DTW was significantly related to that response variable ($\alpha = 0.05$).

Redundancy analysis (RDA) was used to examine the relationship between community composition and log-transformed (natural log) DTW values. Community composition included cover values for each species (or genus, see above) found within the plots. A Hellinger transformation was applied to the species abundance data for the analysis. For the RDA, a full initial model was run including DTW values from all the different initiation thresholds. Forward selection was then conducted to determine which initiation threshold explained the most variation in community composition. The first significant initiation threshold identified by the forward selection was then used as the sole predictor variable in a parsimonious and final RDA model. RDAs were run separately for each forest type. Redundancy analysis was conducted using the vegan package in R (Oksanen et al. 2016). Species with important contributions to the ordination analysis were identified using the equilibrium contribution circle (Borcard et al. 2011). This method identifies species, whose vectors are longer than the radius of the equilibrium contribution circle (Borcard et al. 2011). All statistical analyses were conducted using the R statistics programming environment version 3.2.3 (R Core Team 2015).

2.3 Results

Responses of diversity

In conifer-dominated stands, higher initiation thresholds had stronger relationships with diversity values than did lower initiation thresholds (Table 2.1, Appendix B). The optimal model for species richness included depth-to-water (DTW) values based on the 16-ha initiation threshold as the predictor variable. Based on this model, species richness was significantly positively related to DTW (16 ha), with drier areas (higher DTW values) having higher richness (Table 2.1; Figure 2.1a). For both Shannon's and Simpson's diversity the optimal model was the one including the DTW (12 ha). Both diversity indices were significantly and positively related to DTW, with higher diversity on drier sites (i.e., higher DTW values) (Figure 2.1b, 2.1c).

In mixedwood and deciduous stands, the best models for diversity were those with DTW values based on lower initiation thresholds (Table 2.1a, Appendix B). In mixedwood stands, the best model for species richness used DTW based on 1 ha initiation threshold as a predictor variable, but this relationship was not significant (Figure 2.1a). For both diversity indices the optimal model included DTW based on 0.5 ha initiation threshold. Neither of these models was significant (Figure 2.1b, 2.1c). In deciduous stands, the best models for species richness, and both diversity indices were the ones with DTW at the 0.5 ha initiation threshold. However, none of these were significant (Table 2.1, Figure 2.1a-c).

Responses of abundance

In the conifer stands the best models for total understory cover and forb cover included DTW based on the 16 ha initiation threshold (Table 2.1, Appendix B). Total understory cover was significantly positively related to DTW (16 ha), with drier areas (higher DTW values) having higher understory cover (Table 2.1, Figure 2.2a). Forb cover was not significantly related to DTW (Table 2.1, Figure 2.2b). The optimal model for shrub cover included DTW (2 ha) as the predictor variable (Table 2.1, Appendix B). Shrub cover was significantly positively related to DTW, with higher shrub cover on drier sites (higher DTW values) (Figure 2.2c).

In mixedwood stands, the best model for understory cover included DTW (0.5 ha) values, while the optimal model for forb cover included DTW (4 ha) values (Table 2.1, Appendix A). None of these was significant (Figure 2.2a, b). The optimal model for shrub cover included DTW (1 ha) values (Table 2.1, Appendix B). According to this model, shrub cover was significantly, positively related to DTW (1 ha), with drier sites (higher DTW values) having higher shrub cover (Figure 2.2c).

In deciduous-dominated stands, the optimal model for understory cover included DTW based on the 1 ha initiation threshold (Table 2.1, Appendix B). According to this model, understory cover was significantly positively related to DTW (1 ha), with drier sites (higher DTW values) having higher understory cover values (Figure 2.2a). The best model for forb cover included DTW based on the 8 ha initiation threshold (Table 2.1, Appendix B); however, this model was not significant (Figure 2.2b). The best model for shrub cover used DTW based on the 2 ha initiation threshold as the predictor variable, with shrub cover being significantly positively related to DTW (Table 2.1). Higher shrub cover was found on sites with higher DTW values (i.e. drier sites) (Figure 2.2c).

Responses of community composition

Community composition in all three forest types was significantly related to DTW (Table 2.2). In conifer-dominated stands, the optimal DTW value was the one based on the 8 ha initiation threshold (as determined by forward selection), with the final RDA having an adjusted R^2 of 0.040. In mixedwood stands and deciduous-dominated stands, DTW based on the 16 ha initiation threshold was the first predictor variable selected, with the final RDAs having adjusted R^2 values of 0.058 and 0.091, respectively.

In conifer-dominated stands, the 1st RDA axis was negatively correlated with DTW (8 ha) values (Figure 2.3a). Wetter plots were located towards the higher end of the RDA axis 1. The plots also showed considerable spread along the 1st principal component (PC) axis, which was not related to the DTW gradient. *Equisetum sylvaticum* and *Equisetum arvense* were associated with the wetter portions of the DTW gradient, while *Aralia nudicaulis*, *Rubus pubescens*, and *Rosa acicularis* were associated with the drier portions (Figure 2.3b). *Cornus canadensis* and *Linnaea borealis* were associated with higher values on the 1st PC axis, while *Equisetum arvense* and *Elymus innovatus* were associated with lower values on the 1st PC axis.

In mixedwood stands, the 1st RDA axis was also negatively correlated with DTW (16 ha) (Figure 2.4a). The plots also showed considerable spread along the 1st PCA axis which was not related to the DTW gradient. *Elymus innovatus*, *Rosa acicularis* and *Shepherdia canadensis* were associated with drier portions of the DTW gradient (Figure 2.4b). *Calamagrostis canadensis* and *Mitella nuda* were associated with the wetter portions. Similar to conifer-dominated stands, *Cornus canadensis* and *Linnaea borealis* were associated with higher values on the 1st PC axis. *Viburnum edule* and *Aralia nudicaulis* were associated with lower values on the 1st PC axis.

In deciduous-dominated stands, the 1st RDA axis was negatively correlated with DTW (16 ha) (Figure 2.5a). The plots also showed considerable spread along the 1st PCA axis, which was not related to the DTW gradient. In contrast to the mixedwood stands, *Elymus innovatus* was associated with the wetter portions of the DTW gradient in deciduous stands. *Viburnum edule, Rubus idaeus,* and *Ribes triste* were associated with the drier end of the gradient (Figure 2.5b). *Viburnum edule* was also associated with higher values on the 1st PC axis, while *Calamagrostis canadensis* was associated with lower values on the 1st PC axis. In the RDA, compartment 940 was separated from the other deciduous compartments. This separation may be due to compartment 940's geographical separation from the other compartments (approximately 10 km north of the two other compartments) or to damage caused by beaver activity near some of the wetter plots in compartment 940.

2.4 Discussion

Depth-to-water (DTW) values were related to attributes of the vascular understory plant community in all the forest types we sampled. As hypothesized, the relationships differed between forest types. Depth-to-water (DTW) was significantly related to diversity, abundance, and composition in conifer-dominated stands, while in deciduous and mixedwood stands, only abundance and composition were significantly related to depth-to-water values. The optimal flow initiation threshold differed among response variables and between forest types. Higher initiation thresholds were better for response variables in conifer-dominated stands while lower initiation thresholds were better for response variables in both mixedwood and deciduous stands.

Diversity and DTW values

Contrary to Zinko et al.'s (2005) findings, we found that diversity was positively related to DTW in conifer-dominated stands, with drier sites having higher diversity. Zinko et al. (2005) had found higher understory richness on the wetter sites of a Swedish boreal forest. The difference in the direction of the relationship between moisture and diversity in our study may be due to differences in the resolution of the digital elevation data used to derive the topographic hydrological indices. Zinko et al. (2005) used a topographic wetness index (TWI) derived from a 20-m resolution digital elevation model (DEM), while our study used DTW values derived from a 1-m resolution DEM. Our findings did agree with those of Moeslund et al. (2013a), who also used a finer resolution TWI. They found TWI to be a significant predictor of vascular plant richness in grasslands; like our study, they found that drier sites had higher richness.

The decline in diversity in the wet sites of conifer stands may be due to water levels exceeding plant tolerance at these sites. Since conifer-dominated stands were already on the wetter portions of the DTW gradient (Nijland et al. 2015), it is possible that the wettest sites within these stands are too wet for some plant species (Moeslund et al. 2013b). In contrast, deciduous and mixedwood stands tend to be on relatively drier sites (Nijland et al. 2015) and it may be that the wettest sites in these stands do not exceed the range of tolerance for most plant species. Thus, we see a relationship between diversity and DTW only in conifer-dominated stands. The decline in diversity may also be due to limited nitrogen availability on the wetter sites. In sites approaching soil saturation, availability of inorganic nitrogen is known to decrease with increasing soil moisture (Araya et al. 2013, Moeslund et al. 2013b), as microbes responsible for mineralization require optimal levels of soil water and soil oxygen (Araya et al. 2013). In addition, studies have shown that conifer-dominated stands have limited nitrogen availability due to conifer litter quality (Lindo and Visser 2003). Since coniferous stands already have low levels of nitrogen available for plant use, a decline in nitrogen availability may further limit the growth of most plants. In contrast, deciduous stands tend to have higher rates of mineralization and have higher nitrogen availability than conifer stands (Lindo and Visser 2003, Jerabkova et al. 2006). Due to the higher nutrient levels in deciduous and mixedwood stands, a decline in mineralization rates due to higher moisture levels may not significantly hinder plant growth as nutrient levels may be sufficient even in the wetter sites. This may be another reason why only conifer-dominated stands showed a relationship between diversity and DTW.

Abundance and DTW values

Abundance of understory vegetation was positively related to DTW values in all three forest types. Most studies focus on the relationship between diversity and topographic moisture indices (Zinko et al. 2005, Moeslund et al. 2013a, Oddershede et al. 2015); here we show topographic indices are also related to understory abundance. Interestingly, understory abundance was related to DTW in forest types which did not show a significant relationship between diversity and DTW. This suggests abundance may be more responsive to changes in moisture availability than is diversity. The changes in abundance along the moisture gradient may reflect the preference of shrubs for relatively drier sites. Our results for total understory cover in both conifer-dominated and deciduous-dominated stands seem to be driven mainly by shrub cover, since forb cover did not show any pattern along the moisture gradient. The high cover values for shrubs on relatively drier sites may reflect the site preferences of the common shrub species in the area, for example, *Rosa acicularis*, *Viburnum edule*, etc. (Beckingham et al. 1996).

Composition and DTW values

As hypothesized, community composition was also significantly, but weakly, related to DTW. This agrees with multiple studies that also found that topography and moisture were related to vegetation composition in various ecosystems. Moeslund et al. (2013a) found topography to be related to vegetation composition in grasslands, while Schietti et al. (2014) found another topographically-based moisture index to be related to tree composition in a tropical forest. In addition, Murphy et al. (2011) and Hiltz et al. (2012) have shown the depth-to-water index can be used to predict moisture-based vegetation community types (e.g., mesic, hygric).

Our community composition analysis agrees with the suggestion above that increased shrub abundance on drier sites drives the total understory cover trends. In the ordination analysis, shrubs like *Viburnum edule*, *Rubus sp.*, and *Rosa acicularis* were associated with relatively drier sites in all forest types. Nijland et al. (2015) found a similar trend with post-harvesting vegetation re-growth being higher on drier and more productive sites, with vegetation re-growth defined as vegetation between 0.5 to 6 m in height, as determined by LIDAR-derived vegetation structure data. Interestingly, *Elymus innovatus* was associated with drier sites in mixedwood stands but was associated with wetter sites in deciduous stands. This may be due to the tendency for mixedwood stands to be located on wetter sites than deciduous stands. For example, all the plots in the mixedwood stands had an average DTW value (based on the 16 ha initiation threshold) of 1.79, while the average DTW (16 ha) value for plots in the deciduous stands was 7.37 (Appendix D). A similar trend occurs with *Calamagrostis* canadensis, which is associated with drier sites in conifer-dominated stands; however, in mixedwood stands it is associated with wetter sites. Again, this may be due to conifer-dominated stands tending to be located on wetter sites than mixedwood stands. In conifer-dominated stands, horsetails were associated with wetter sites, which can be expected since horsetails prefer higher soil moisture (Beckingham et al. 1996). The species composition analysis shows DTW is capable of distinguishing changes in moisture availability that are reflected in the vegetation.

In our study, DTW values did not explain a high proportion of the variation found in the understory composition. The low variation explained by DTW values is to be expected since moisture is not the only driver of understory vegetation. Availability of other key resources, such as nutrients and light, also drives understory vegetation (Hart and Chen 2006). These resources are affected by canopy composition and cover, minor disturbances, such as insect outbreak or tree mortality, and competitive interactions within the plant community (Hart and Chen 2006, Gilliam 2007). It is possible that by using DTW along with other key variables, such as canopy cover and nutrient availability, more variation in understory composition could be explained. For example, Alexander et al. (2016) found TWI had a low accuracy for predicting vegetation associations when used as the only predictor variable. However, the prediction accuracy increased when TWI was combined with other topographic variables, such as slope, aspect, surface curvature, and topographic position index. In addition, when combined with other variables, they found TWI was the most important variable for classifying vegetation associations (based on misclassification rate if TWI was omitted). Future studies could explore the use of DTW values along with other drivers of vegetation to predict understory composition patterns within stands.

The influence of forest type

Forest type had a strong influence on the relationship between understory vegetation and DTW values, with these relationships differing among forest types. This was not particularly surprising given that these forest types differ in both understory species composition and environmental conditions (Hart and Chen 2006, Macdonald and Fenniak 2007). For example, deciduous stands allow for higher light transmission to the understory and deciduous leaf litter allows for higher nutrient availability than does conifer litter in conifer-dominated stands (Hart and Chen 2006). This leads to deciduous stands being more suitable for fast-growing herbaceous species, while conifer stands tend to allow for higher bryophyte cover (Hart and Chen 2006). Different species may dominate or may be present in different forest types and thus how these forest types respond to a moisture gradient can differ (Hart and Chen 2006). The differences in the moisture-vegetation relationships may also be due to the differences in environmental conditions created by the overstory composition. For example, as we mentioned the nitrogen-poor conditions of conifer stands may be the mechanism behind plant diversity decline on the wetter sites of conifer stands, while no such trend was evident in deciduous and mixedwood stands. Lastly, these forest types occupied slightly different positions on the depth-to-water gradient, with coniferous stands being on the wetter sites (Nijland et al. 2015, Albani et al. 2005). This difference may have resulted in the understory of coniferous stands being more driven or affected by moisture than in the other stands; thus we had more significant understory-DTW relationships in the conifer-dominated stands.

The optimal initiation threshold varied with forest type; higher initiation thresholds tended to be better in conifer-dominated stands, while lower initiation thresholds were better for deciduous and mixedwood stands. Lower initiation thresholds identify ephemeral streams or areas which temporarily have surface water, while higher initiation thresholds identify areas that are wet for most of the year (Murphy et al. 2011, Agren et al. 2014). This implies that in deciduous and mixedwood stands, any area which is wet, even if it is only temporarily wet, is important for driving vegetation patterns. On the other hand, in conifer-dominated stands, vegetation was more driven by areas that are more likely to have standing water for most of the year (i.e. areas identified as wet by higher initiation thresholds). This may be because conifer-dominated stands had a large proportion of ephemerally wet areas and it is possible that only higher initiation thresholds are able to truly capture a moisture gradient in these stands (Figure 2.6). The differences in the optimal initiation threshold may also be due to differences in how water moves through the litter of each forest type. Studies have shown that the structure of conifer litter allows for faster drainage through the litter layer, while the plate-like structure of broadleaf (deciduous) litter tends to store more water and allows for more horizontal movement of water (Sato et al. 2004, Swallow and Quideau 2013). Thus, the conifer litter may be more permeable than the deciduous litter and allow for faster drainage. Agren et al. (2014) suggested that higher initiation thresholds (i.e. 16 ha) are more appropriate for areas with high substrate permeability, while lower initiation thresholds (i.e. 0.5 ha) are more suitable for areas which drain slowly. Our results would support this, with the permeability of the litter layer affecting which initiation threshold is best. In conifer stands, it was only the shrub abundance model that had the optimal DTW values based on a lower initiation threshold (the 2-ha initiation threshold). This may be because shrubs have a deeper rooting depth and may not be as affected by the availability of water in the litter layer (Canadell et al. 1996). These results show the usefulness of the different initiation thresholds. By changing the initiation threshold, we were able to explore the importance of different types of water sources (ephemeral vs. permanent) and adjust for changes in litter type. Other topographic moisture index studies were unable to explore this and thus may have missed significant moisture-vegetation relationships. When exploring the use of depth-to-water index, future studies should compare different initiation thresholds if possible.

2.5 Conclusion

Our study shows the depth-to-water (DTW) index is related to various vegetation attributes and thus these results contribute to the growing body of research exploring the potential use of the DTW index for predicting key forest attributes. As previously mentioned, DTW values have been shown to be related to multiple soil attributes and vegetation regrowth (Agren et al. 2014, Nijland et al. 2015, Oltean et al. 2016). Our study shows DTW is also related to understory attributes—diversity, abundance, and composition, even on sites with relatively mild topographic relief. In addition, our results show that these relationships differ among forest types. Future research can expand on this study by testing the predictive ability of DTW values for understory vegetation diversity and cover values. In addition, studies could further explore the relationship between DTW and the distribution of rare or invasive plants, which can be useful for conservation and management purposes. Lastly, future studies can explore how the relationships between understory vegetation and DTW are affected by major disturbances, such as wildfire or harvesting.

2.6 Tables

Table 2.1: Results of linear mixed effects models describing the relationship of understory vascular species richness, Shannon's diversity, Simpson's diversity, total understory cover, forb cover, and shrub cover with depth-to-water (DTW) values (natural log transformed for analysis), in conifer-dominated (CDOM), mixedwood (MIX), and deciduous-dominated (DDOM) stands. The models included are the best models for each response variable in each forest type, based on the Akaike Information Criterion (AIC) value (see Appendix B). The initiation threshold used, F-values, degrees of freedom, and p-values for the effect of DTW, and the coefficient and standard error for the influence of DTW are included. DTW p-values in bold indicate DTW was significant (α = 0.05).

Forest type	Response Variable	Predictor Variable	F-value	Degrees of freedom	DTW p-value	DTW coefficient	Standard error
CDOM	Species Richness	ln(DTW 16 ha)	19.23	35	**<0.001**	3.24	0.74
CDOM	Shannon Diversity	ln (DTW 12 ha)	15.61	35	**<0.001**	2.35	0.59
CDOM	Simpson Diversity	ln (DTW 12 ha)	15.61	35	**<0.001**	1.99	0.50
MIX	Species Richness	ln (DTW 1 ha)	2.52	34	0.122		
MIX	Shannon Diversity	ln (DTW 0.5 ha)	2.25	34	0.143		
MIX	Simpson Diversity	ln (DTW 0.5 ha)	2.01	34	0.165		
DDOM	Species Richness	ln (DTW 0.5 ha)	0.68	30	0.416		
DDOM	Shannon Diversity	ln (DTW 0.5 ha)	0.13	30	0.722		
DDOM	Simpson Diversity	ln (DTW 0.5 ha)	0.0006	30	0.981		
CDOM	Total Cover	ln (DTW 16 ha)	12.00	35	**0.001**	16.27	4.69
CDOM	Forb Cover	ln (DTW 16 ha)	2.62	35	0.114		
CDOM	Shrub Cover	ln (DTW 2 ha)	5.44	35	**0.026**	5.19	2.23

Forest type	**Response Variable**	**Predictor Variable**	**F-value**	**Degrees of freedom**	**DTW p-value**	**DTW coefficient**	**Standard error**
MIX	Total Cover	ln (DTW 0.5 ha)	1.84	34	0.184		
MIX	Forb Cover	ln (DTW 4 ha)	1.86	34	0.181		
MIX	Shrub Cover	ln (DTW 1 ha)	13.19	34	**<0.009**	7.61	2.09
DDOM	Total Cover	ln (DTW 1 ha)	4.87	30	**0.0352**	6.68	3.03
DDOM	Forb Cover	ln (DTW 8 ha)	3.37	30	0.0763		
DDOM	Shrub Cover	ln (DTW 2 ha)	28.52	30	**<0.001**	8.11	1.52

Table 2.2: Results of constrained ordination (redundancy analysis with a hellinger transformation applied to species cover values) examining the relationship of understory vascular plant community composition with the natural log of depth-to-water (DTW) values for conifer-dominated stands (CDOM), mixedwood stands (MIX) and deciduous-dominated stands (DDOM). The DTW values used were based on the optimal initiation threshold (determined by forward selection). Adjusted R^2 and significance are included ($\alpha = 0.05$).

Forest Type	**Predictor variables**	**Adjusted R^2**	**p-value**
CDOM	Ln of DTW (8 ha) values	0.040	0.001
MIX	Ln of DTW (16 ha) values	0.058	0.001
DDOM	Ln of DTW (16 ha) values	0.091	0.001

2.7 Figures

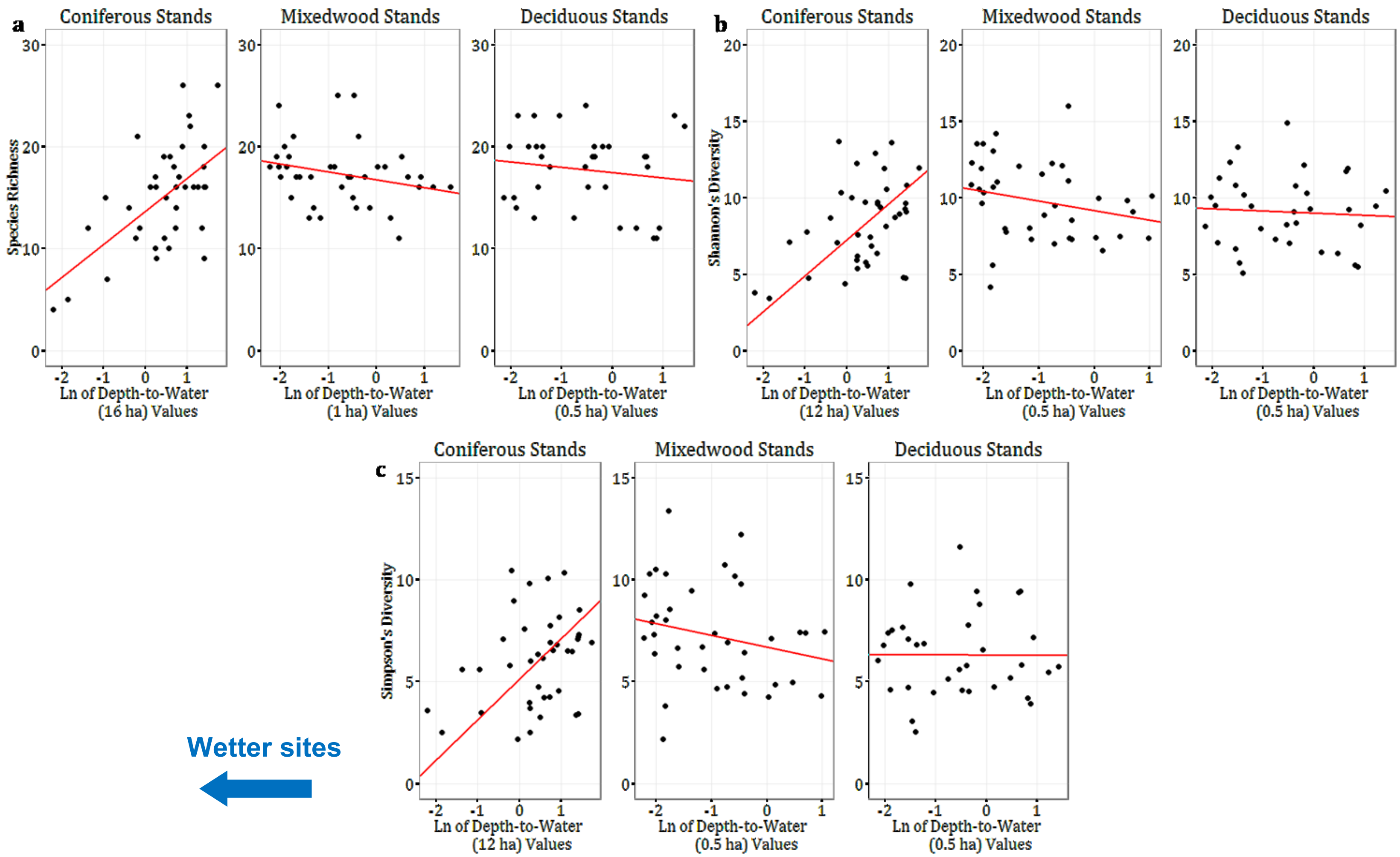


Figure 2.1: Species richness (**a**), Shannon's diversity (**b**), Simpson's diversity (**c**)(per 4 m^2 plot) as a function of the natural log of depth-to-water (DTW) values for the optimal initiation threshold (e.g., 16 ha, see Appendix 2B and Table 2.1) for coniferous, mixedwood, and deciduous stands. Lower DTW values represent wetter sites. The regression line from the results of the mixed effects model analysis is shown. The p-values are given for significant relationships (α = 0.05).

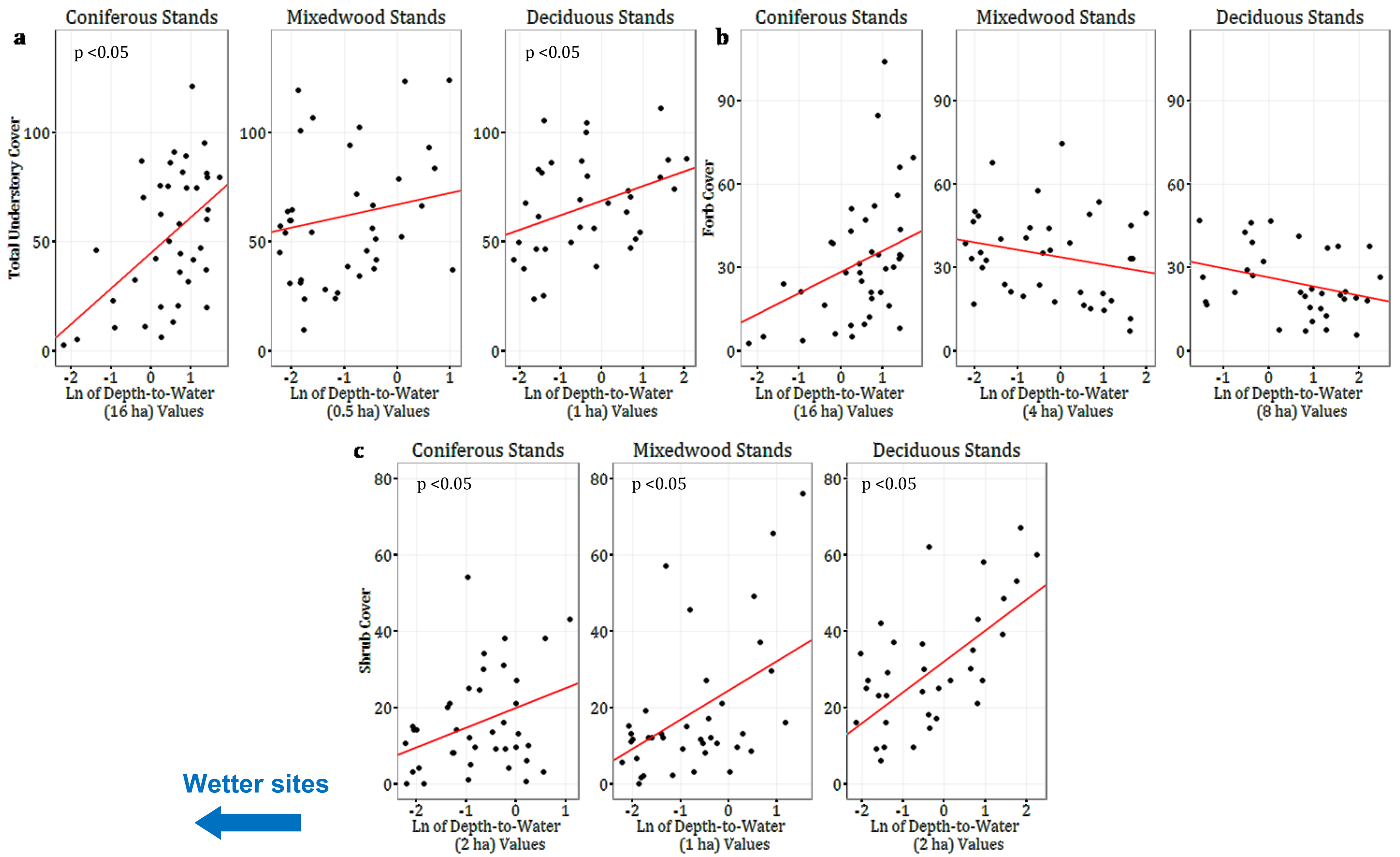


Figure 2.2: Total understory cover (**a**), forb cover (**b**), shrub cover (**c**) (per 4 m^2 plot) as a function of the natural log of depth-to-water (DTW) values for the optimal initiation threshold (e.g., 16 ha, see Appendix B and Table 2.1) for coniferous, mixedwood, and deciduous stands. Lower DTW values represent wetter sites. The regression line from the results of the mixed effects model analysis is shown. The p-values are given for significant relationships (α = 0.05).

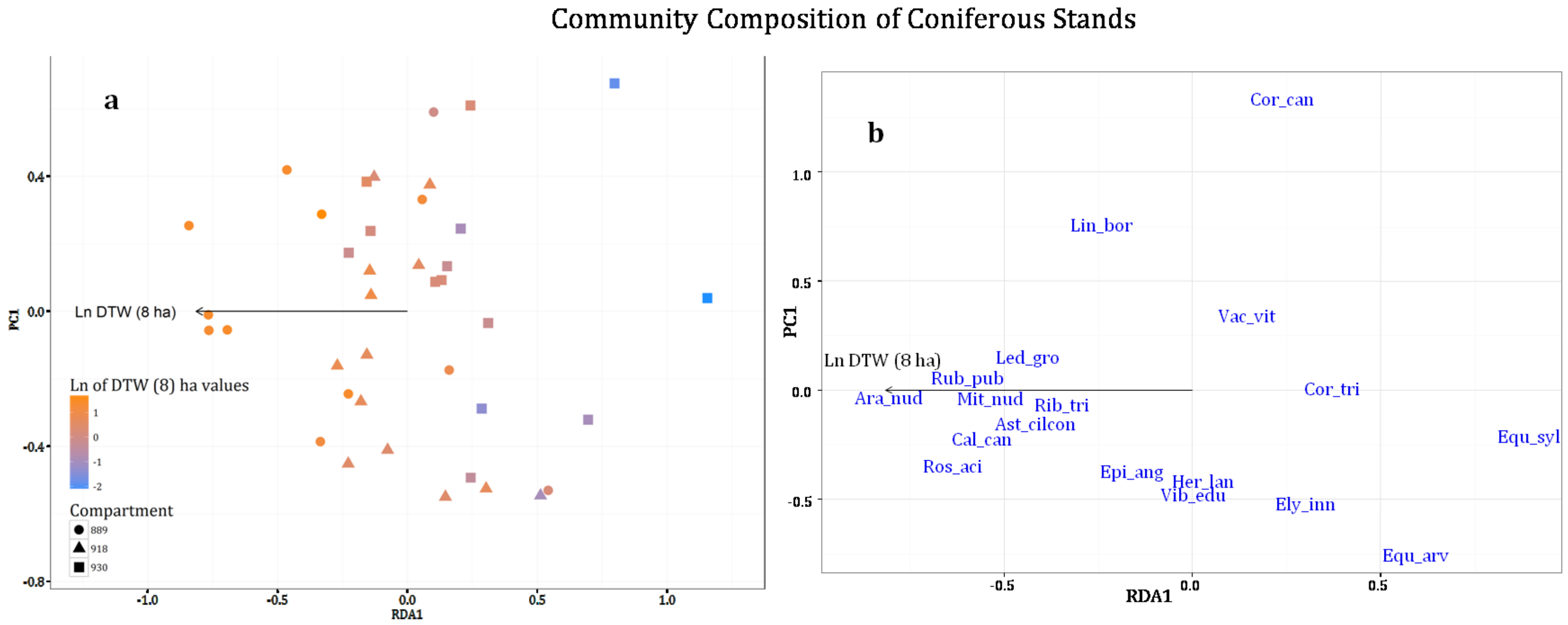


Figure 2.3: (a) Results from constrained ordination (redundancy analysis with a hellinger transformation applied to species abundances) examining the relationship between the vascular understory community composition and the natural log of depth-to-water (DTW) values, based on an 8-ha initiation threshold, in conifer-dominated stands (adjusted $R^2 = 0.040$). The arrow indicates the vector for DTW (8 ha) values, with lower DTW values representing wetter sites. Symbols represent plots, with the shape representing the compartment they are located in and the color representing the DTW (8 ha) value for that plot. **(b):** Understory species which had an important contribution to the ordination analysis (species with vectors longer than the equilibrium contribution circle based on Borcard et al. (2011)) are represented by six letter codes (first three letters of genus and species epithet; see Appendix C).

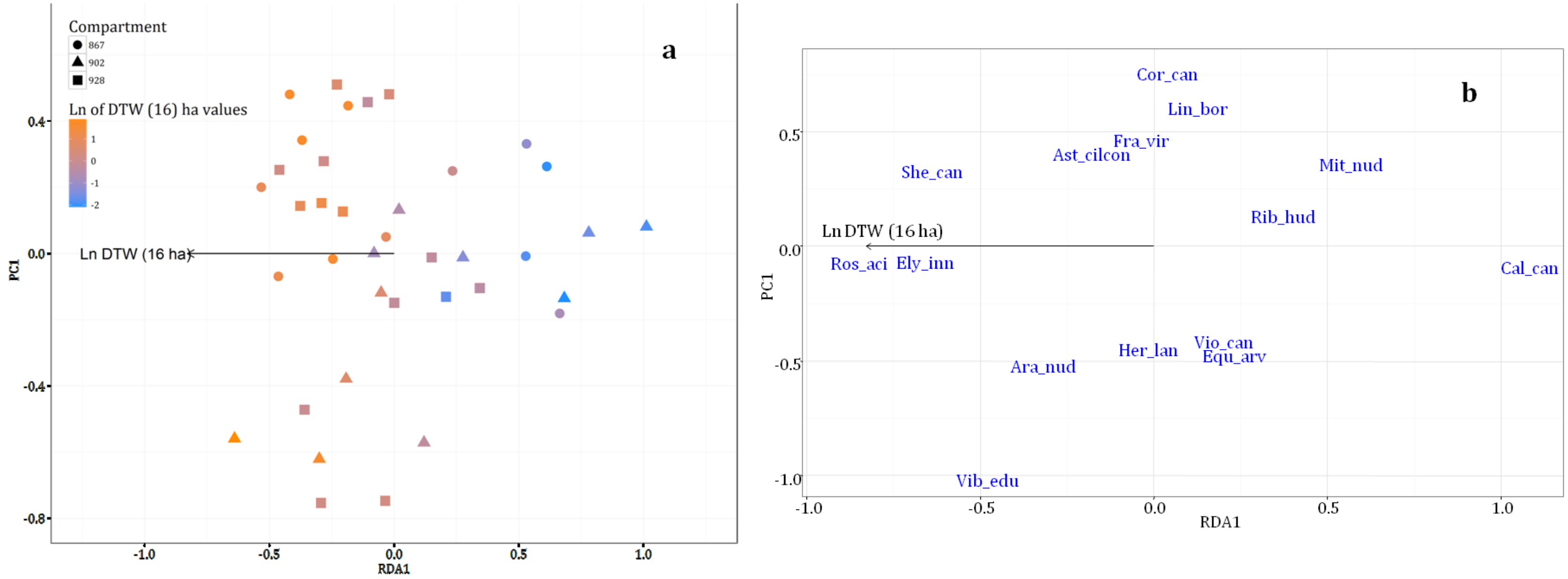


Figure 2.4: (a) Results from constrained ordination (redundancy analysis with a hellinger transformation applied to species abundances) examining the relationship between the vascular understory community composition and the natural log of depth-to-water (DTW) values, based on a 16-ha initiation threshold, in mixedwood stands (adjusted $R^2 = 0.058$). The arrow indicates the vector for DTW (16 ha) values, with lower DTW values representing wetter sites. Symbols represent plots, with the shape representing the compartment they are located in and the color representing the DTW (16 ha) value for that plot. **(b)** Understory species which had an important contribution to the ordination analysis (species with vectors longer than the equilibrium contribution circle based on Borcard et al. (2011)) are represented by six letter codes (first three letters of genus and species epithet; see Appendix C).

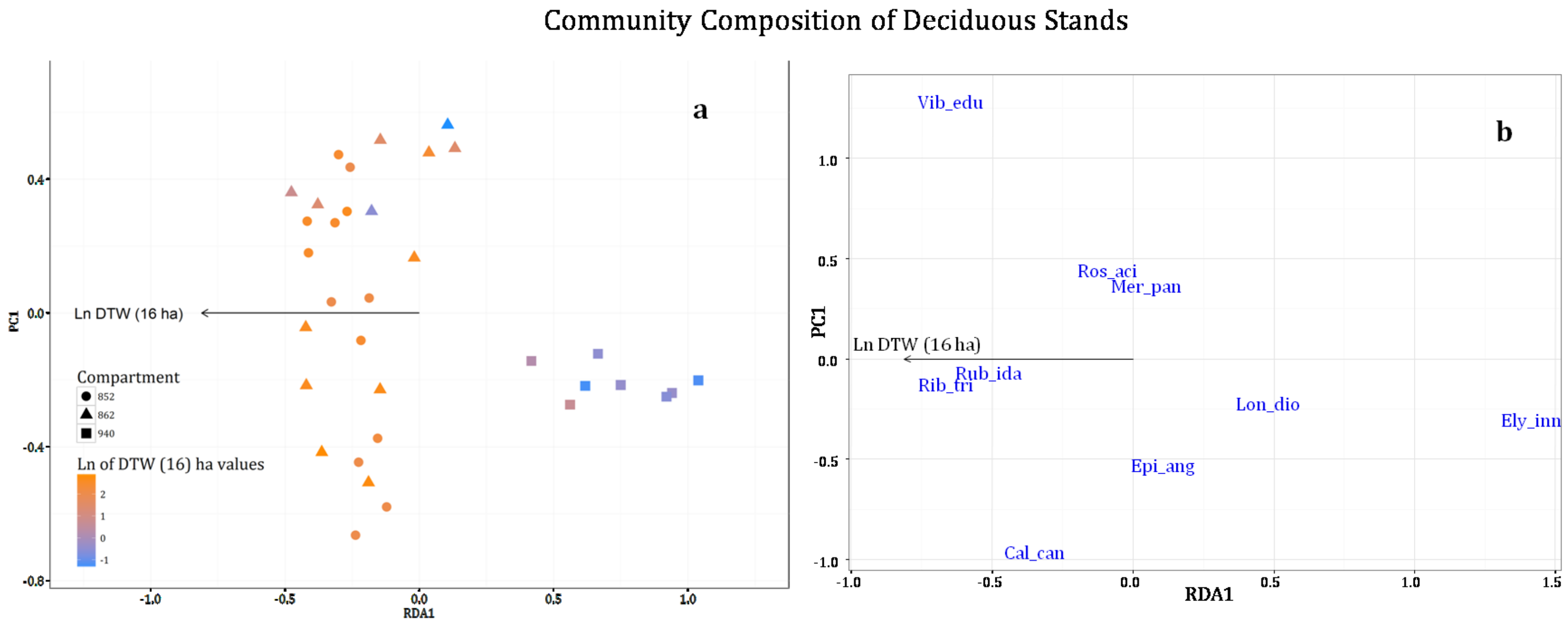


Figure 2.5: (a) Results from constrained ordination (redundancy analysis with a hellinger transformation applied to species abundances) examining the relationship between the vascular understory community composition and the natural log of depth-to-water (DTW) values, based on a 16-ha initiation threshold, in deciduous-dominated stands (adjusted R2 = 0.091). The arrow indicates the vector for DTW (16 ha) values, with lower DTW values representing wetter sites. Symbols represent plots, with the shape representing the compartment they are located in and the color representing the DTW (16 ha) value for that plot. **(b)** Understory species which had an important contribution to the ordination analysis (species with vectors longer than the equilibrium contribution circle based on Borcard et al. (2011)) are represented by six letter codes (first three letters of genus and species epithet; see Appendix C).

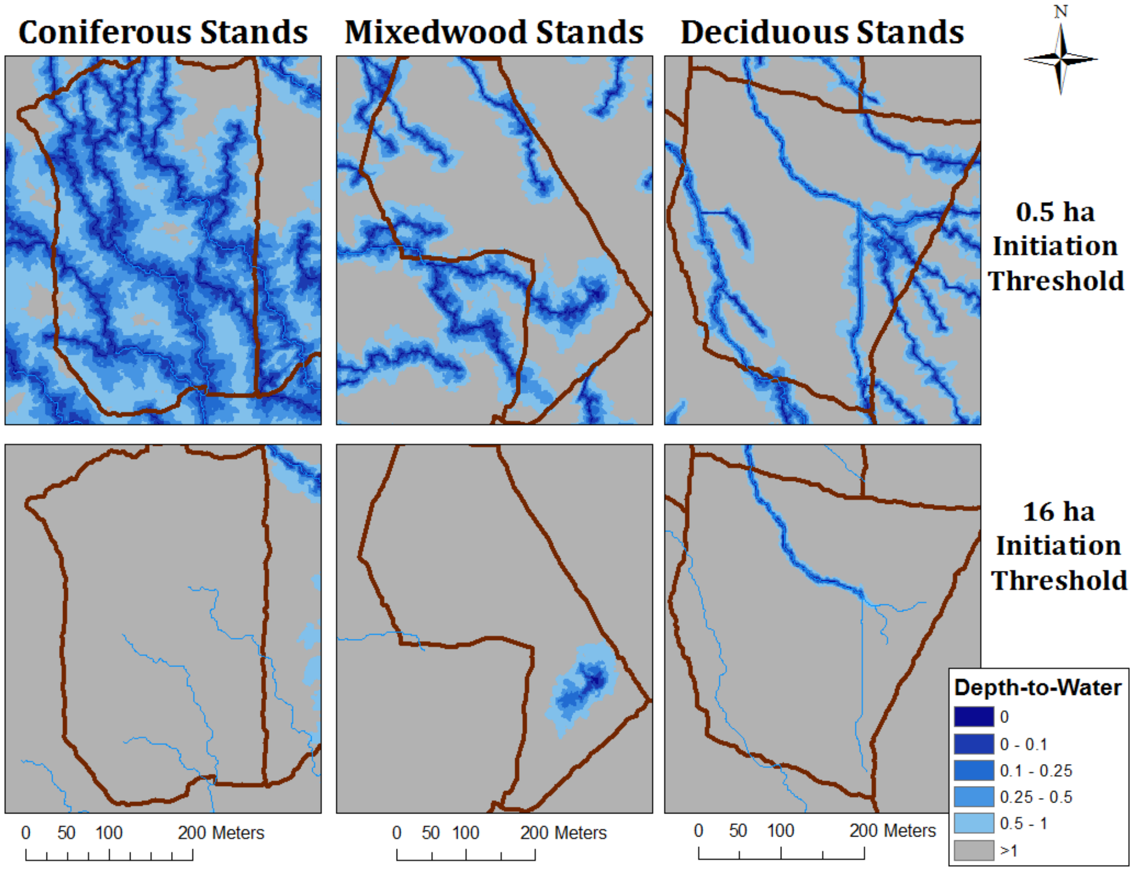


Figure 2.6: Depth-to-water index based on a 0.5 ha and 16 ha initiation threshold in an example compartment for coniferous, mixedwood, and deciduous stands. Coniferous stands tended to have more predicted wet areas than the other two forest types, especially at the lower initiation thresholds.

Chapter 3: The effects of retention harvesting on the relationship between understory vegetation and the depth-to-water index

3.1 Introduction

Resource availability influences understory plant communities and is controlled by abiotic and biotic factors. Studies have drawn on this and have successfully used moisture indices derived from remotely-sensed data to identify patterns of understory diversity and composition across a landscape (Zinko et al. 2005, Moeslund et al. 2013a, Oddershede et al. 2015). For example, in the previous chapter, we demonstrated the use of the depth-to-water index to identify patterns in understory diversity, abundance, and composition in three boreal mixedwood forest types. These results can be useful for guiding conservation efforts in managed landscapes. However, little is known about how the relationships between topographically-based moisture and understory vegetation are affected by disturbances and thus if these remotely-sensed data continue to be useful on disturbed landscapes.

Natural disturbances, such as wildfire, are important drivers of ecosystem processes in the boreal forest and are partly responsible for the maintenance of the biodiversity found within the boreal (Brandt et al. 2013; Gauthier et al. 2015). With increasing attention to the development of forest practices that maintains a diversity of ecological values, alternatives to clear-cutting have been developed to emulate the effects of these natural disturbances. For example, retention harvesting is the leading sustainable alternative to traditional clearcutting practices (Gustafsson et al. 2012) and it involves the retention of live and dead trees, much like how a fire leaves behind patches of unburned forests. The retained trees serve as “stepping stones” to assist in the movement and dispersal of organisms (Franklin et al. 1997). They also provide refugia for forest specialists and help create heterogeneity in stand structure (Franklin et al. 1997). Studies have shown that retention harvesting can help mitigate biodiversity losses, when compared with clearcut harvesting. It can maintain similar levels of richness as unharvested forests (Mori and Kitagawa 2014) while supporting higher levels of richness than clearcuts (Fedrowitz et al. 2014). The retained patches can provide refugia to forest obligates, even 20 years after harvest (Fedrowitz et al. 2014, Baker et al. 2015). At the same time, retention harvesting creates disturbed sites ideal for early-seral species (Fedrowitz et al. 2014). However, few studies have examined how the effects of retention harvesting might vary across sites, such as variation in moisture as indicated by the remote-sensing technologies described above. This is highly relevant to making decisions about how different levels of retention harvesting–including areas protected from any harvesting–might best be deployed across the landscape.

Although retention forestry is thought to be effective for mitigating biodiversity losses, it still involves a disturbance that will result in changes in the environmental conditions and understory vegetation of a stand. For example, harvesting increases light and nutrient availability, allowing for the establishment of early-seral species (Hart and Chen 2006). How these early-seral species respond to moisture availability could differ from how later-seral species might respond; thus potentially changing how the understory is related to a moisture gradient. In addition, regeneration of a different dominant tree species can change the composition of a stand. For example, studies have shown that a spruce canopy is often replaced by aspen after a disturbance, since aspen regenerates (and grows) more quickly than spruce on disturbed sites (Awada et al. 2004, Gartner et al. 2011). This could result in changes to the understory composition of a stand (Craig and Macdonald 2009). In this study, we define resilience as an ecosystem's ability to absorb the changes brought on by a disturbance (e.g., retention harvesting) and maintain existing ecological relationships (sensu Holling 1973). We use the maintenance of the DTW-understory relationship in harvested stands as a measure of resilience.

In this study, we asked how the relationship between the depth-to-water (DTW) index, a topographic moisture index, and understory diversity, abundance, and composition, was affected by retention harvesting. We also examined if the effect of harvesting differed between three boreal mixedwood forest types: conifer-dominated, mixedwood, and deciduous (broadleaf)-dominated stands. Since the studied stands were harvested 15-years prior to the study, we considered similarity in the depth-to-water and understory vegetation relationship between unharvested reference stands and the harvested stands as an indication of resilience. We hypothesized that harvesting would affect the relationship between depth-to-water and understory, even 15 years after harvesting. Since our previous chapter's results showed the relationship between depth-to-water and understory vegetation differed between forest types, we hypothesized that the effects of harvesting would also differ between forest types. Studies have shown that conifer-dominated stands are more affected by harvesting than the other forest types (Macdonald and Fenniak 2007, Pinzon et al. 2012); thus, we expect conifer-dominated stands to be the least resilient, with the slope of the relationship between understory attributes and the depth-to-water index differing between the harvested and unharvested treatments.

3.2 Methods

Study area

The study was conducted at the Ecosystem-based Management Emulating Natural Disturbance (EMEND) experimental area, located about 90 km northwest of Peace River in northwestern Alberta, Canada (56˚46' 13" N, 118˚22'28"W). It is situated in the Lower Boreal Highlands subregion of Alberta (Natural Regions Committee 2006). The mean annual temperature in the region is -1 °C and the mean annual precipitation is 495 mm, with 68% falling during the growing season (Natural Regions Committee 2006). Soils are mainly "fine-textured luvisols on glaciolacustrine deposits" (Kishchuk et al 2014). The dominant tree species are *Populus tremuloides*, *Populus balsamifera*, and *Picea glauca* (Natural Regions Committee 2006).

EMEND was established to examine the effects of variable retention harvesting on biodiversity, ecosystem function, and forest regeneration (Spence et al. 1999). Six levels of harvesting were implemented in four forest types with three replicates for each combination, with treatments applied to 10-ha 'compartments'. Harvesting was conducted in the winter of 1998/1999. Within each compartment, 20 m wide retention strips were established between 5 m wide machine corridors, with the harvesting equipment limited to the machine corridors; thus minimal disturbance of the forest floor occurred in the retention strips. The retention strips were partially harvested to attain the prescribed retention level for each compartment. Trees were removed without bias towards any species or size. For this study, we focused on unharvested (control), 50% retention, 20% retention, and clearcut (2% retention) treatments in three forest types: conifer-dominated (>70% conifer canopy cover), mixedwood (conifer and deciduous canopy cover, each composing 35-65%), and deciduous-dominated (>70% deciduous (i.e., broadleaf) canopy cover).

Depth-to-water (DTW) values

For this study, we used the depth-to-water (DTW) index as a measure of site moisture. DTW values are a measure of the probability of soil saturation; areas with low DTW values have a higher probability of having surface water for most of the year (Murphy et al. 2007). The lower the depth-to-water (DTW) value the wetter the site, with areas predicted to have surface water having a DTW value of 0 (Murphy et al. 2009). Calculation of the depth-to-water index (DTW) begins with a Light Detection and Ranging (LIDAR)-based digital elevation model (DEM) combined with a hydrographic data layer, which identifies the locations of surface water (lakes, rivers, etc.) (Murphy et al. 2007). A flow accumulation network, based on the DEM, is developed using the D8 flow algorithm (Jenson and Domingue 1988) to determine flow direction. Additional stream locations are also predicted based on a flow initiation threshold, which varies from 0.5 to 16 ha. When flow accumulation at a cell has reached the flow initiation threshold, stream flow is assumed to begin at that cell. Streams and cells with water accumulation above the initiation threshold are given a DTW value of 0 and are used as hydrologic source cells for subsequent calculation of the depth-to-water value (Murphy et al. 2007, Dr. Wiebe Nijland, personal communication, March 10, 2015). Each cell in the landscape is then assigned to a hydrologic source cell, which is the closest cell with surface water (i.e., a cell with DTW value = 0, also called a source cell) (Murphy et al. 2007). The depth-to-water value is then calculated as the change in elevation and the horizontal distance between each cell in the landscape and its respective hydrologic source cell (Murphy et al. 2007). The equation used is $\mathrm{DTW} = \left[\sum \frac{d_{zi}}{d_{xi}} a\right] x_c$, where $\frac{d_{zi}}{d_{xi}}$ represents the slope of a cell, a is a multiplier that accounts for the distance between a cell and its corresponding surface water, and x_c is the resolution of the grid.

Using a different initiation threshold creates a different set of DTW values for a given landscape. A low initiation threshold results in a landscape with more predicted streams. This means more cells in a landscape are close to cells with surface water (i.e., source cells) and more areas are therefore predicted to be wet. In contrast, higher flow initiation thresholds (i.e., 16 ha of water accumulation needed to start a flowing channel) produce more conservative estimates of moisture. Thus, DTW values based on a 0.5 ha flow initiation threshold will suggest that a greater proportion of the landscape is likely to be wet than would DTW values based on a 16 ha flow initiation threshold.

DTW values for this study were extracted from the Wet Areas Mapping (WAM) Tool based on LIDAR data collected in Aug. 2008, using a Leica ALS 50-II, with an average density of 2 points/m^2 (Nijland et al. 2015). Ground returns were rasterized into a DEM using a triangulated irregular network, with a final spatial resolution of 1.0 m (Nijland et al. 2015). Additional details of the LIDAR data and the derivation of WAM can be found in Nijland et al. (2015) and Murphy et al. (2007).

Plot selection

We selected 8-12 sampling locations within (or just outside) each of the three replicate compartments for each forest cover type and treatment combination to capture a range of DTW values within each compartment, using the mapped DTW values (in ArcGIS; ESRI, Redland CA). Sampling locations were stratified by DTW values to ensure even distribution along the DTW gradient. Each compartment had approximately 5-9 sampling locations on the wetter portion of the DTW gradient and three sampling plots on the drier portion. Thus we had approximately 30 sampling locations for each forest type and treatment combination and a total of 373 sampling locations. We limited our plots to the merchantable forest areas of EMEND to ensure our results can be used by forestry companies. Sites were precisely located in the field using a high precision Global

Positioning System (the SX Blue GPS II, Geneq Inc., Montreal, Quebec) that was capable of providing sub-meter accuracy.

Vegetation data

Vegetation data were collected in the summers of 2014 and 2015. At each sampling location, we established a 2x2 m quadrat. Within this, we visually estimated the cover of each vascular plant species. Cover values were to the nearest 0.5% from 0-1, to the nearest 1% from 1 to 20, and to the nearest 5% from 20 to 100. Plants with trace amounts were assigned 0.1%. Vascular plants included woody shrubs and trees less than 1.3 m tall. Vegetation sampling was conducted by three teams and frequent calibration checks were conducted among teams to ensure consistency in visual estimates. Plants were identified to species, when possible, or were collected and pressed for identification later in the lab. Plants which lacked necessary reproductive parts were left at the genus level (e.g. *Salix* sp. and *Carex* sp.) or left as numbered unknowns (e.g. unknown 1). Nomenclature follows Moss (1983).

Three types of response variables were examined: diversity, abundance, and community composition. Three measures of diversity were calculated: species richness, Shannon's diversity number, and Simpson's diversity number for each plot using the vegan package in R (Oksanen et al. 2016). Hill's numbers were used for the diversity indices, as they are in units of effective number of species (Hill 1973, Jost 2006). Thus the exponent of Shannon's entropy was used for Shannon's diversity number, hereafter referred to as Shannon's diversity, and the inverse of the Gini-Simpson index was used for Simpson's diversity number, hereafter referred to as Simpson's diversity. Abundance was quantified by cover; cover values were summed for all species within each plot to produce a total vegetation cover for each plot. Since species tended to overlap within each plot, total cover values exceeding 100% were possible. Cover was also summed for shrubs and forbs (included trailing woody species and low growing plants with a woody rootstock, e.g., *Cornus canadensis*) separately for each plot. Community composition was represented by cover values for each species in each plot.

Data analyses

To determine DTW values for each plot, ArcGIS was used to create a buffer with a radius of 2.5 m around each plot. The DTW values within these buffers were then extracted and averaged. This was done since DTW values were at a smaller resolution (1 m^2) than our plot size (4 m^2). This process was repeated for seven DTW estimates based on different initiation thresholds: 0.5 ha, 1 ha, 2 ha, 4 ha, 8 ha, 12 ha, and 16 ha. Since the DTW is not linear, the natural log of the average DTW value was then used as the predictor variable (with addition of 0.1 to all values).

We used linear mixed effects models with a Gaussian distribution to analyze the relationship of vegetation diversity and abundance to DTW values and harvesting treatment. Analyses were carried out separately for each forest type, using the nlme package in R (Pinheiro et al. 2016). Species richness, Shannon's diversity, Simpson's diversity, total understory cover, forb cover, and shrub cover were our response variables. Depth-to-water values, harvesting treatment, and their interaction were used as fixed factors and compartment as random factor. Residuals were examined to ensure normality and homogeneity of variance.

Models were run separately for the different initiation thresholds to identify the optimal initiation threshold for each response variable. Thus, for each response variable seven models (seven initiation thresholds) were compared and the optimal model was determined by the lowest Akaike Information Criterion (AIC) value. We then used the optimal model for each response variable to determine if DTW, harvesting treatment, or their interaction were significantly related to that response variable ($\alpha = 0.05$). When the interaction term was significant, post-hoc analyses were conducted using the lsmeans package in R (Lenth 2016), to compare slopes (vegetation as a function of DTW) among harvesting treatments.

Redundancy analysis (RDA) was used to examine the relationship between community composition, log-transformed (natural log) DTW values, harvesting treatment, and the interaction between DTW values and harvesting. Community composition included cover values for each species (or genus, see above). A hellinger transformation was applied to the species abundance data for the analysis. For the RDA, a full initial model was run with only the DTW values from all the different initiation thresholds as predictor variables. Forward selection was then conducted to determine which initiation threshold explained the most variation in community composition. The first significant initiation threshold identified by the forward selection was then used in a final RDA model with harvesting treatment and the interaction between harvesting treatment and DTW values as predictor variables. RDAs were run separately for each forest type. Redundancy analysis was conducted using the vegan package in R (Oksanen et al. 2016). Species with important contributions to the ordination analysis were identified using the equilibrium contribution circle (Borcard et al. 2011). This method identifies species whose vectors are longer than the radius of the equilibrium contribution circle (Borcard et al. 2011). All statistical analyses were conducted using the R statistics programming environment version 3.2.3 (R Core Team 2015).

We do not address differences among retention levels alone since other studies have thoroughly investigated this (see Craig and Macdonald 2009, Halpern et al. 2012). In addition, a comprehensive analysis on the effects of retention harvesting on the understory vegetation at EMEND, 15 years post-harvest, is currently in preparation.

3.3 Results

Responses of diversity and abundance

In conifer-dominated stands, species richness was related to depth-to-water (DTW) but there was no significant effect of harvesting treatment or harvesting by depth-to-water interaction (Table 3.1). However, for Shannon's and Simpson's diversity, and total and forb cover, the relationship with DTW varied with harvesting (significant DTW by harvesting interaction) (Table 3.1). Species richness was significantly negatively related to DTW, with wetter sites (lower DTW values) having higher richness (Figure 3.1). For Shannon's and Simpson's diversity, DTW, harvesting, and their interaction were all significant predictor variables (Table 3.1). In both cases, the three harvested treatments had negative slopes, while the control (unharvested) treatment had a positive slope (Table 3.1; Figure 3.2). Harvested stands had higher diversity at wetter sites (lower DTW values), while unharvested stands had lower diversity at wetter sites (Figure 3.2). Post-hoc analyses for both response variables showed the slope for the 20% retention was significantly different from the slope for the unharvested stands while the other two harvesting treatments had intermediate values for slope (Table 3.1)

For both total understory cover and forb cover, there was a significant depth-to-water by harvest treatment interaction (Table 3.1). Harvested stands showed almost no relationship or a slightly negative relationship between total understory cover and DTW, while unharvested stands showed a positive relationship with lower understory cover and forb cover on wetter sites (lower DTW values) (Figure 3.3). Post-hoc analyses showed all retention treatments had significantly different slopes as compared to unharvested stands, but did not differ from one another (Table 3.1). None of the predictor variables were significant for shrub cover (Table 3.1).

In mixedwood and deciduous stands, species richness, Shannon's and Simpson's diversity were significantly related to DTW, but harvesting treatment and the interaction were not significant predictors (Table 3.1). For both stands, species richness, Shannon's and Simpson's diversity were negatively related to DTW; i.e., higher diversity at wetter sites (lower DTW values) (Figures 3.4a, b, c, 3.6).

For both total understory cover and shrub cover in mixedwood stands, only DTW was a significant predictor (Table 3.1). Total understory cover and shrub cover were positively related to depth-to-water (i.e., lower cover on wetter sites (lower DTW values)), across all harvesting treatments (Figure 3.4d, e). Forb cover was significantly related to both harvesting treatment and DTW values but there was no significant interaction (Table 3.1). Forb cover was positively related to DTW (i.e., lower cover on wetter sites) regardless of harvesting treatment (Figure 3.5). Although the slope for the 50% retention appears to be negative and different from the other treatments, there was no significant interaction between the depth-to-water index and harvesting treatment; thus the slopes did not significantly differ between the harvesting treatments.

In deciduous stands, total understory cover was significantly related to harvesting treatment and the interaction between harvesting and DTW values (Table 3.1). Post-hoc analyses showed the 20% retention and unharvested stands had significantly different slopes for total understory cover versus DTW, while the other two harvesting treatments had intermediate values for slope (Table 3.1). In harvested stands, the DTW-cover relationship had a negative slope, with higher cover values on wetter sites (lower DTW values) (Figure 3.7a). In contrast, in the unharvested stands, total understory cover was positively related to DTW, with lower cover values on wetter sites (lower DTW values) (Figure 3.7a). Forb cover was significantly positively related to DTW values, with higher forb cover on wetter sites (lower DTW values) (Table 3.1, Figure 3.8). For shrub cover, both DTW values and the interaction between harvesting treatment and DTW were significant (Table 3.1). Post-hoc analysis showed the slope for the relationship of shrub cover to DTW in unharvested stands was significantly different from the slope for the 20% retention and clearcut treatments (Table 3.7b); the slope for the 50% retention treatment did not differ from any of the other treatments. For both unharvested and harvested stands, DTW was positively related to shrub cover (i.e., lower shrub cover on wetter sites) (Figure 3.7b); however, unharvested stands had a much steeper slope (Table 3.1, Figure 3.7b).

For conifer-dominated stands, the optimal model for species richness and shrub cover included the DTW values based on 1-ha initiation threshold (Appendix E). For both Shannon's and Simpson's diversity the optimal model included DTW values based on the 0.5-ha initiation threshold. The optimal model for total understory cover and forb cover included DTW values based on the 16-ha initiation threshold (Table 3.1, Appendix E). In mixedwood stands, the optimal initiation threshold was 0.5-ha for all diversity and abundance variables (Table 3.1, Appendix E). In deciduous-dominated stands, the optimal initiation threshold was 0.5 ha for the diversity variables and 1 ha for the abundance variables (Table 3.1, Appendix E).

Responses of community composition

Community composition in all three forest types was significantly related to the natural logarithm of DTW, harvesting treatment, and their interaction (Table 3.2). The optimal initiation thresholds, as determined by forward selection were 12 ha, 8 ha, and 16 ha for conifer-dominated, mixedwood, and deciduous-dominated stands, respectively (Table 3.2). The adjusted R^2 for the final RDAs were 0.096, 0.106, and 0.107 for conifer-dominated, mixedwood, and deciduous-dominated stands, respectively (Table 3.2).

In conifer-dominated stands, the 2nd RDA axis was positively correlated to DTW (12 ha) values; wetter plots were located towards the lower end of RDA axis 2 (Figure 3.9a). The harvesting treatment was correlated with the 1st RDA axis; plots in control stands were located towards the higher end of RDA axis 1, well separated from the harvested treatments, which were located towards the lower end of RDA axis 1 and were not strongly separated from one another. *Viburnum edule* and *Rubus idaeus* were associated with the drier portions of the DTW gradient, while *Equisetum arvense* and *Salix bebbiana* were associated with the wetter portions of the DTW gradient (Figure 3.9b). *Equisetum sylvaticum, Vaccinium vitis-idaea, Equisetum arvense,* and *Cornus canadensis* were associated with the unharvested stands, while "early successional" species, such as *Calamagrostis canadensis* and *Epilobium angustifolium* were associated with the harvested stands (Figure 3.9b).

In mixedwood stands, the 1st RDA axis was positively correlated to DTW (8 ha) values; wetter plots were located towards the lower end of RDA axis 1 (Figure 3.10a). The harvesting treatment was correlated to the 2nd RDA axis (Figure 3.10a). Clearcut plots were located on the higher end of the 2nd RDA axis, while plots in the control were located on the lower end of the 2nd RDA axis. Much like the conifer-dominated stands, plots in the unharvested stands were strongly separated from the harvested stands. *Rosa acicularis* and *Viburnum edule* were associated with the drier portions of the DTW gradient, while *Equisetum arvense* and *Linnaea borealis* were associated with the wetter portions of the DTW gradient (Figure 3.10b). *Epilobium angustifolium* was associated with clearcuts, while *Linnaea borealis, Mitella nuda* and *Cornus canadensis* were associated with control plots.

In deciduous-dominated stands, the 1st RDA axis was positively correlated to the general DTW (16 ha) index for all harvesting treatments; wetter plots were located towards the lower end of RDA axis 1 (Figure 3.11a). However, within each harvesting treatment, the DTW gradient was more correlated with the 2nd RDA axis. Drier plots for both 20% retention and clearcut stands were located towards the higher end of RDA axis 2, while drier plots for the 50% retention stands were located towards the lower end of RDA axis 2. The harvesting treatments were correlated with the 2nd RDA axis (Figure 3.11a). Unlike the conifer-dominated stands, there was no clear separation between plots in harvested and unharvested stands. However, higher values along the RDA axis 2 were associated with the 20% retention treatment, while lower values were associated with the 50% retention and clearcut stands. *Elymus innovatus, Epilobium angustifolium* and *Cornus canadensis* were associated with the wetter portions of the DTW gradient, while *Viburnum edule, Rubus idaeus* and *Ribes oxyacanthoides* were associated with the drier portions of the DTW gradient (Figure 3.11b). *Heracleum lanatum* and *Calamagrostis canadensis* were associated with the drier portions of 50% retention stands, while *Rosa acicularis* was associated with the drier portions of the clearcut stands (Figure 3.11b).

3.4 Discussion

Our results supported our hypothesis that harvesting would affect the relationship between understory attributes and depth-to-water (DTW) and that these effects would vary between the three forest types. We found that the relationship between diversity and DTW was more resilient than was the relationship of abundance or composition and DTW. As hypothesized, conifer-dominated stands were the least resilient forest type, with harvesting affecting the relationship to DTW for almost all understory attributes. Mixedwood stands were the most resilient, with harvesting only affecting the relationship between understory composition and DTW.

Resilience by forest type

Conifer-dominated stands were the least resilient forest type, with only the relationship between species richness and DTW being unaffected by harvesting. In harvested conifer stands, diversity increased towards the wet end of the DTW gradient, while in unharvested controls the opposite was true; this suggests that increases in diversity associated with harvesting occurred preferentially in wetter sites. Abundance in unharvested stands increased towards the wetter portions of the DTW gradient. In contrast, abundance in the harvested treatments remained relatively constant across the gradient or increased towards the wet end of the DTW gradient at a more gradual slope than in the unharvested controls. This suggests that harvesting affected abundance in both the wet and dry ends of the DTW gradient. The reduction in abundance towards the drier sites of the harvested treatments may be caused by aspen regeneration limiting light availability and thus understory growth on these sites. The increased diversity and abundance towards the wetter sites of harvested stands is likely due to the establishment of early-successional species in the wetter sites. The species composition analysis supported this with ruderal species, such as *Achillea millefolium, Vicia americana,* and *Salix bebbiana*, being associated with the wet areas in conifer-dominated stands. In addition, in the ordination analysis, separation of the plots by harvesting treatment was more evident in the wetter portions of the DTW gradient than in the drier portions. Based on this, wet areas in conifer-dominated stands seem to be more sensitive to harvesting than dry areas.

Mixedwoods were the most resilient forest type, with only forb cover and the relationship between composition and depth-to-water being affected by harvesting. Even in the ordination analysis, the vectors representing the interaction between harvesting and depth-to-water were acutely angled from each other and thus they do not differ greatly between treatments. Much like in the conifer-dominated stands, separation of the plots by harvesting treatment was more evident in the wetter portions of the DTW gradient than in the drier portions; this implies that composition in wetter areas was more sensitive to harvesting than in the drier areas. The relationship between understory composition and DTW was less resilient than the relationships of abundance and diversity with DTW as these were not affected by harvesting in mixedwood stands. The resilience of the mixedwood stands contributes to evidence showing the importance of maintaining mixedwood forest types within the boreal mixedwood region (Cavard et al. 2011).

Deciduous stands were of intermediate resilience, as only the relationship between diversity and DTW was unaffected by harvesting. In unharvested deciduous stands, total understory cover and shrub cover increased towards the dry end of the DTW gradient. However, in harvested stands, total understory cover decreased towards the dry end of the DTW gradient and shrub cover increased towards drier sites, but at a more gradual slope. This indicates that losses in understory abundance due to harvesting occurred more preferentially on drier sites. This trend may be mainly driven by a reduction in the cover of the most common shrub, i.e. *Rosa acicularis*, towards the drier sites of harvested compartments. The species composition analysis supports this with shrubs associated with the drier portions of the depth-to-water gradient, showing the preference of shrubs for drier sites. Deciduous stands were the only forest type that did not show a clear separation between harvested and unharvested stands in the ordination analysis. However, it was also the only forest type to show a strong divergence of the vectors representing the interaction between depth-to-water and harvesting. The interaction vectors imply that the compositional changes along the DTW gradient in the 50% treatment differs from that of the 20% and clearcut treatments. This shows that harvesting intensity can influence how harvesting changes DTW-understory relationship–a trend which was not as evident in the other response variables. In contrast to coniferous and mixedwood stands, separation of the plots by harvesting treatment in deciduous stands was more evident in the drier portions of the depth-to-water gradient than in the wetter portions, implying that composition was more resilient in wetter sites. Thus, in deciduous stands, the results of both the composition and abundance analysis indicate that the wetter portions of the DTW gradient are more resilient than the drier portions.

It is unsurprising that conifer-dominated stands were least resilient, since previous studies have shown deciduous-dominated stands to be relatively resistant to the effects of variable retention harvesting. For example, 2-yrs after harvesting in the same study site, Macdonald and Fenniak (2007) found no change in the understory vascular plant species richness of harvested deciduous stands, while conifer-dominated and mixedwood stands showed a reduction in species richness. Other organisms also show a similar trend. Pinzon et al. (2012) looked at ground-dwelling spider assemblages 7 years after harvest and found that in deciduous-dominated stands the only significant differences were between lower retention harvesting treatments and unharvested stands; in conifer-dominated stands, on the other hand, even higher retention treatments were significantly different from unharvested stands. Here we show that even 15 years after harvest, the effects of harvesting are still evident in conifer-dominated stands; in our case this was manifest as a difference in relationship between diversity and DTW values as compared to unharvested stands.

The role of aspen regeneration

A factor that could help explain the observed responses is the effect of site moisture on forest redevelopment, notably vegetative regeneration of aspen. Studies have shown aspen's preference for drier areas (Albani et al. 2005, Nijland et al. 2015). At the EMEND experimental area, post-harvesting canopy cover and overall vegetation regrowth (vegetation between 0.5 to 6 m in height) was higher in the drier portions of the DTW gradient (Nijland et al. 2015). This was attributed to greater aspen regrowth on drier sites (Nijland et al. 2015). In conifer-dominated stands, reduced aspen regeneration in the wetter sites could allow for continued high levels of light availability in the understory leading to the continued presence of early-successional species in the wetter areas. This would account for the wetter sites being less resilient than the drier sites in conifer-dominated stands. In addition, limited light availability on the drier sites of harvested conifer stands may be limiting understory growth and thus the decrease in understory abundance on these sites. While shrubs are known to be particularly susceptible to the effects of harvesting and slow to recover (Halpern et al. 2012), recovery of shrub cover on the drier sites of deciduous stands may be especially delayed because of increased competition with aspen regeneration on drier sites. This could explain the decrease in shrub cover on drier sites in the harvested stands and account for the drier sites being less resilient than the wetter sites in deciduous stands.

Aspen regeneration may also explain why conifer-dominated stands were the least resilient of the three forest types. A shift from conifer-dominated trees to a deciduous canopy could cause substantial and long-term shifts in the understory composition. Only the regeneration of conifer saplings and re-establishment of a conifer canopy would restore the conditions suitable for the pre-harvest understory vegetation of conifer-dominated stands. This is also noted by Pinzon et al. (2012) and they suggest higher retention levels or larger patch sizes are needed in conifer-dominated stands, in order to better meet the habitat requirements of conifer forest specialists. As other studies have suggested (Work et al. 2010, Pinzon et al. 2012), our results provide additional evidence of the need for less intense harvesting on conifer-dominated stands, especially in wetter areas, as they are slower to recover than the other forest types.

In contrast to the previous chapter's findings, the best models for diversity in conifer-dominated stands included depth-to-water values based on low initiation thresholds (i.e., 0.5 and 1 ha). Unlike the diversity models, the best models for abundance in conifer-dominated stands continue to use DTW values based on a 16 ha initiation threshold; and these variables did not exhibit a strong relationship with DTW values in the harvested stands. The shift in the optimal threshold in conifer-dominated stands may be due to the shift to aspen dominance in harvested conifer-dominated stands. A shift to aspen dominance in the harvested conifer stands could result in the understory responding to DTW in a manner similar to the understory in deciduous and mixedwood stands. In contrast, there was no shift in optimal initiation thresholds in the deciduous-dominated and mixedwood stands, where harvesting did not change litter type. The best models for understory diversity and abundance in deciduous and mixedwood stands continued to include DTW values based on 0.5 and 1 ha (low initiation thresholds), even in the harvested stands.

3.5 Conclusions

Our study shows that the relationship between understory vegetation and the depth-to-water (DTW) index is affected by harvesting, with conifer-dominated stands appearing to be particularly sensitive, even 15 years after harvesting. Our results also show topographic indices continue to be useful in identifying understory patterns on disturbed sites. In addition, through this study we were able to see how resilience might change along a moisture gradient within upland stands—a topic sparsely studied (but see Dynseius et al. 2009 and MacDonald et al. 2014, 2015). Our results suggest that harvesting intensities should be reduced on wetter sites of conifer-dominated stands and on drier sites of deciduous stands, as these areas seem to be less resilient. In general, harvesting intensity did not have a strong influence on how understory and DTW relationships were changed by harvesting. It is possible that differences due to harvesting intensity may be stronger shortly after harvesting, but are weakened as the forest regenerates. Future studies can compare our results with the effects of natural stand-replacing disturbances such as wildfires. This would allow us to compare the effects of natural and anthropogenic disturbances on moisture-understory relationships. It could also show if the effects of wildfires vary along a moisture gradient, much like in retention harvesting, and if similar resilience patterns occur. This can be particularly useful for guiding restoration efforts or improving retention harvesting’s ability to emulate natural disturbances.

3.6 Tables

Table 3.1: Results of linear mixed models describing the relationship of understory vascular plant species richness, Shannon's diversity, Simpson's diversity, total understory cover, forb cover, and shrub cover with depth-to-water (DTW) values (natural log transformed for analysis), harvesting treatment, and their interaction, in conifer-dominated (CDOM), mixedwood (MIX), and deciduous-dominated (DDOM) stands. The models included are the best models for each response variable in each forest type, based on the Akaike Information Criterion (AIC) value (see Appendix E). The initiation threshold used, coefficient for the influence of DTW, and p-values for the effect of DTW, harvesting treatment and their interaction are included (also see Appendix G for F-values and degrees of freedom for each predictor variable and standard errors for the DTW coefficient). DTW coefficients in bold indicate DTW was significant (α = 0.05). Treatment and interaction p-values in bold also indicate significance (α = 0.05). Slopes for the relationship between DTW and the response variable are given for each harvesting treatment when the interaction was significant. Letters indicate significant differences in slope between harvesting treatments.

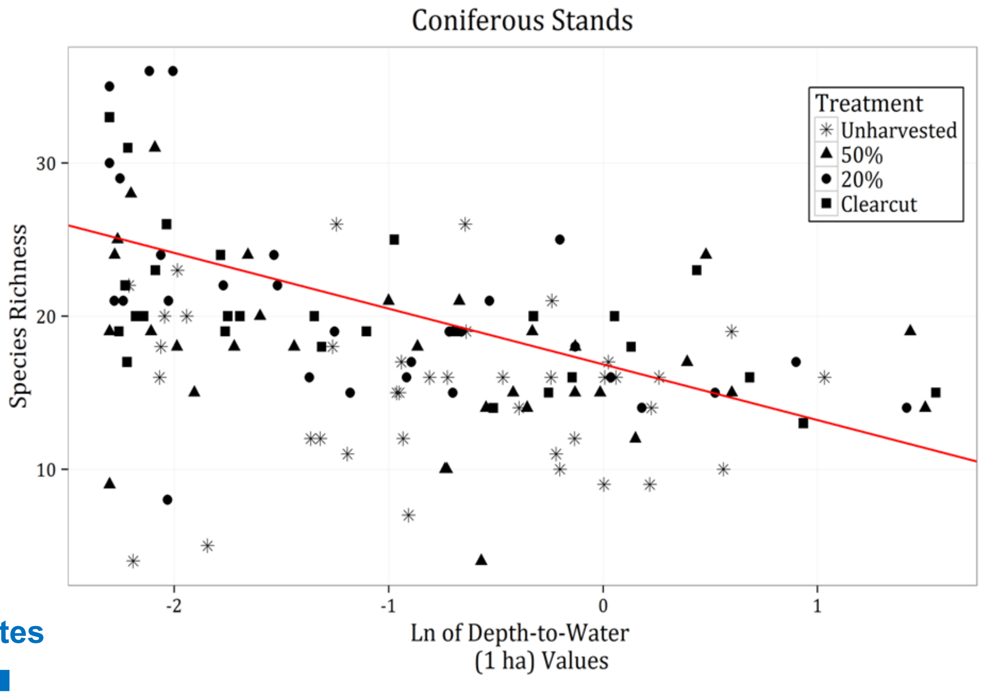
Forest type	**Response Variable**	**DTW initiation threshold**	**DTW coefficient**	**DTW p-value**	**Treatment p-value**	**Interaction p-value**	**Clearcut slope**	**20% slope**	**50% slope**	**Control slope**
CDOM	Species Richness	1 ha	**-3.638**	**<0.001**	0.0639	0.1088				
CDOM	Shannon Diversity	0.5 ha	**-2.721**	**<0.001**	**0.0265**	**0.0177**	-4.068^{ab}	-4.972^{a}	-2.480^{ab}	1.0211^{b}
CDOM	Simpson Diversity	0.5 ha	**-1.688**	**0.001**	**0.0462**	**0.0336**	-2.714^{ab}	-3.084^{a}	-1.726^{ab}	1.294^{b}
CDOM	Total Cover	16 ha	-0.112	0.107	0.5364	**0.0003**	0.520^{a}	-0.052^{a}	-1.387^{a}	7.583^{b}
CDOM	Forb Cover	16 ha	-1.817	0.715	0.1270	**0.0011**	-0.682^{a}	-0.847^{a}	-1.976^{a}	4.519^{b}
CDOM	Shrub Cover	1 ha	2.220	0.082	0.7098	0.3213				

Forest type	**Response Variable**	**DTW initiation threshold**	**DTW coefficient**	**DTW p-value**	**Treatment p-value**	**Interaction p-value**	**Clearcut slope**	**20% slope**	**50% slope**	**Control slope**
MIX	Species Richness	0.5 ha	**-1.672**	**0.014**	0.7582	0.7342				
MIX	Shannon Diversity	0.5 ha	**-1.846**	**<0.001**	0.6271	0.4688				
MIX	Simpson Diversity	0.5 ha	**-1.389**	**0.001**	0.5499	0.6836				
MIX	Total Cover	0.5 ha	**7.178**	**0.001**	0.6213	0.9819				
MIX	Forb Cover	0.5 ha	**5.176**	**0.028**	**0.0205**	0.3332				
MIX	Shrub Cover	0.5 ha	**2.480**	**<0.001**	0.8856	0.0994				
DDOM	Species Richness	0.5 ha	**-1.930**	**0.003**	0.8909	0.1653				
DDOM	Shannon Diversity	0.5 ha	**-1.435**	**0.001**	0.4432	0.2881				
DDOM	Simpson Diversity	0.5 ha	**-1.168**	**0.008**	0.5154	0.3624				
DDOM	Total Cover	1 ha	-3.075	0.228	**0.0199**	**0.0352**	-1.380^{ab}	-2.627^{a}	-1.232^{ab}	5.993^{b}
DDOM	Forb Cover	1 ha	**-4.769**	**0.020**	0.4437	0.1703				
DDOM	Shrub Cover	1 ha	**1.254**	**<0.001**	0.5387	**0.0055**	0.889^{a}	1.071^{a}	2.749^{ab}	7.083^{b}

Table 3.2: Results of constrained ordination (redundancy analysis with a hellinger transformation applied to species abundance values) examining the relationship of understory vascular plant community composition with the natural log of depth-to-water (DTW) values, harvesting treatment, and their interaction for conifer-dominated stands (CDOM), mixedwood stands (MIX), and deciduous-dominated stands (DDOM). The DTW values used were based on the optimal initiation thresholds (determined by forward selection). Adjusted R^2 and significance are included ($\alpha = 0.05$).

Forest Type	**DTW initiation threshold**	**Adjusted R^2**	**DTW p-value**	**Harvesting p-value**	**Interaction p-value**
CDOM	12 ha	0.096	0.001	0.001	0.008
MIX	8 ha	0.106	0.001	0.001	0.014
DDOM	16 ha	0.107	0.001	0.001	0.001

3.7 Figures



Wetter sites

Figure 3.1: Species richness in conifer-dominated stands for all harvesting treatments plotted against the natural log of depth-to-water (DTW) values based on the 1 ha initiation threshold, which was significant (Table 3.1). Lower DTW values represent wetter sites. Symbols represent plots, with their shape representing harvesting treatment. The regression line from the results of the mixed effects model analysis is shown

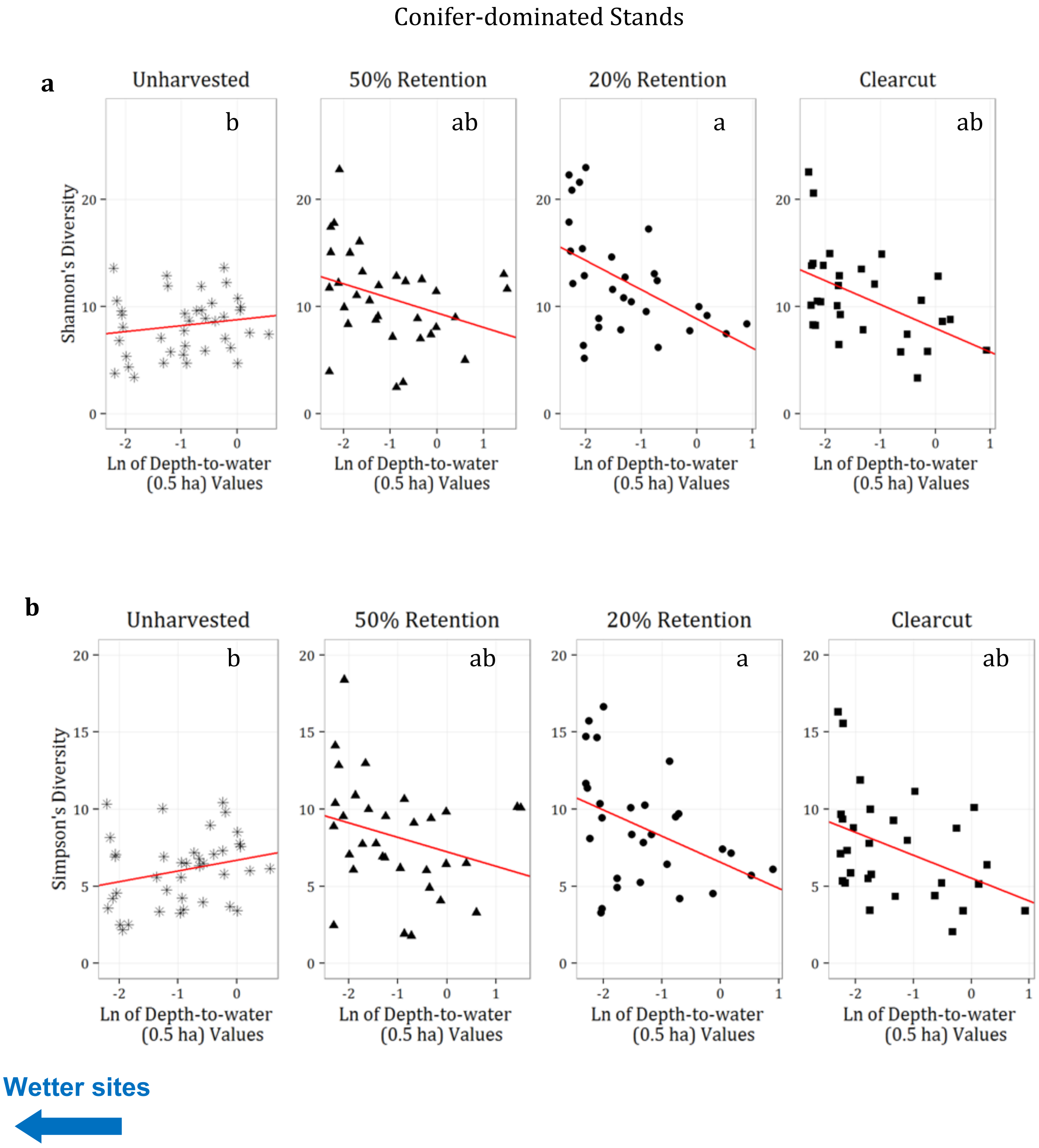


Figure 3.2: Shannon's diversity (**a**) and Simpson's diversity (**b**) in conifer-dominated stands as a function of the natural log of depth-to-water (DTW) values based on the 0.5 ha initiation threshold. Lower DTW values represent wetter sites. The regression line from the results of the mixed effects model analysis is shown. For both response variables, DTW, harvesting treatment and their interaction were significant (α = 0.05). Significantly different slopes, based on post-hoc analyses, are indicated with letters (see also Table 3.1).

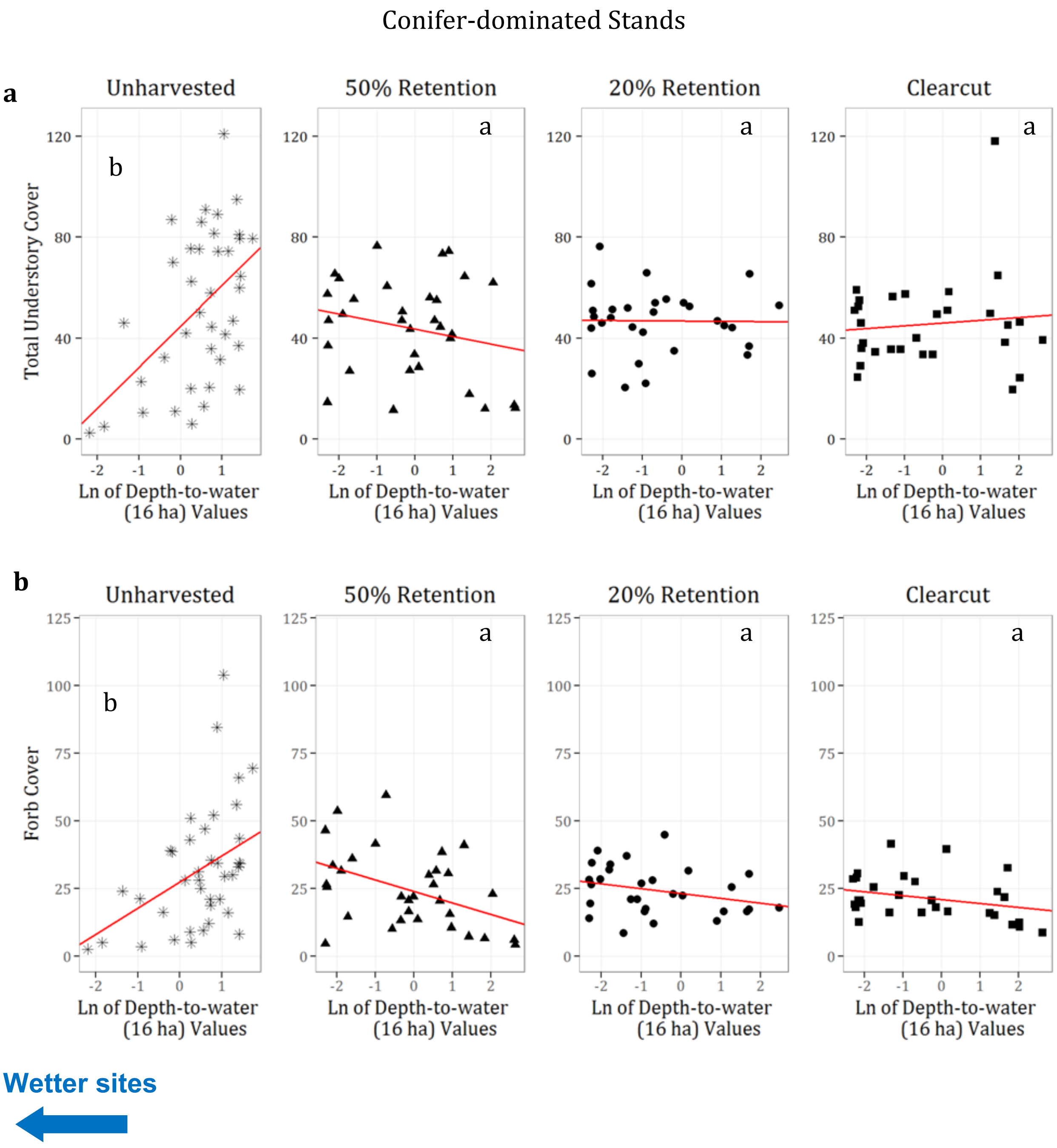


Figure 3.3: Total understory cover (**a**) and forb cover (**b**) in conifer-dominated stands as a function of the natural log of depth-to-water (DTW) values based on the 16 ha initiation threshold. Lower DTW values represent wetter sites. The regression line from the results of the mixed effects model analysis is shown. For both response variables, the harvesting by depth-to-water interaction was significant (α = 0.05). Significantly different slopes, based on post-hoc analyses, are indicated with letters (see also Table 3.1).

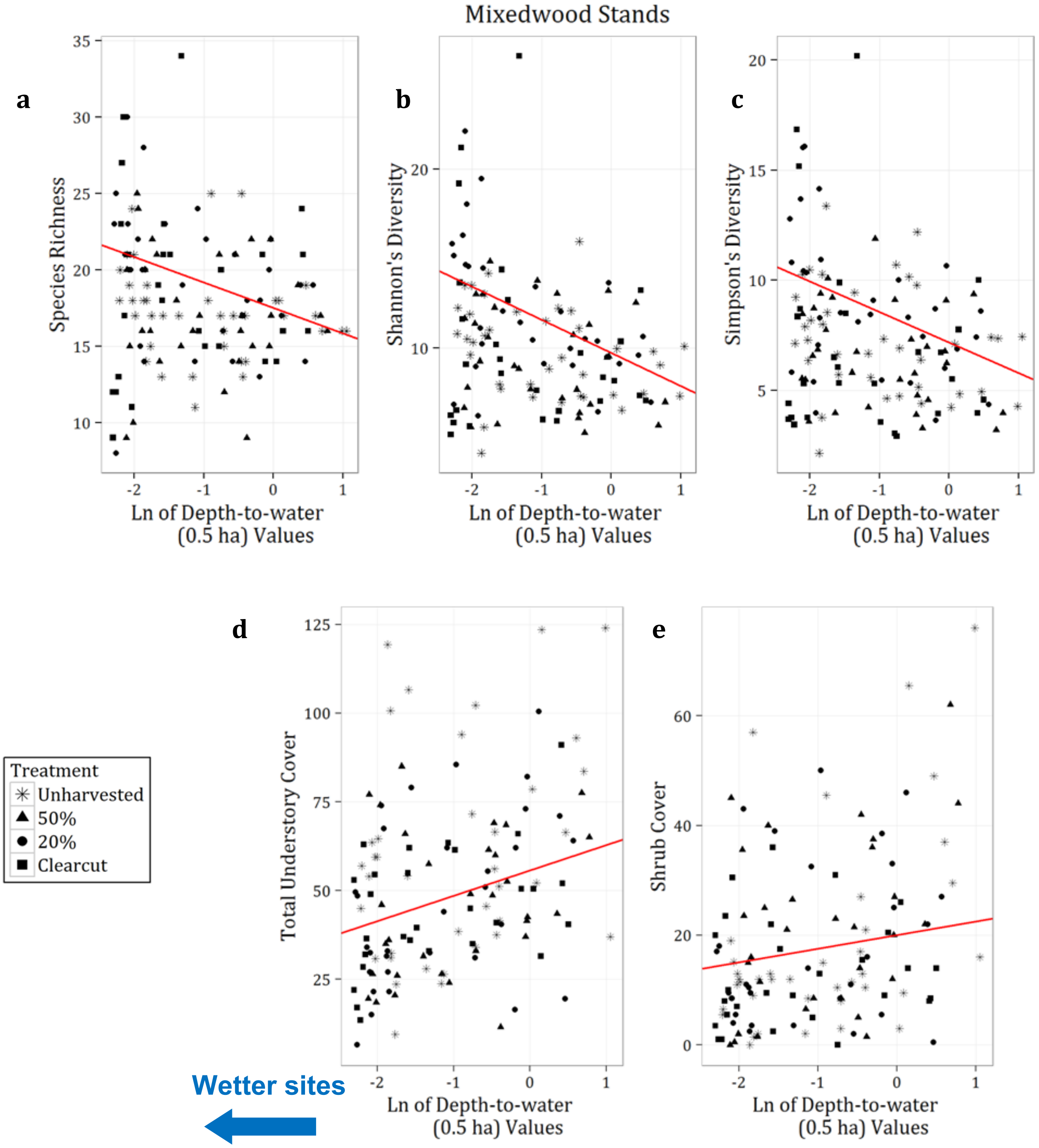


Figure 3.4: Species richness (**a**), Shannon's diversity (**b**), Simpson's diversity (**c**), total understory cover (**d**), and shrub cover (**e**) in mixedwood stands as a function of the natural log of depth-to-water (DTW) values based on the 0.5 ha initiation threshold. Lower DTW values represent wetter sites. The regression line from the results of the mixed effects model analysis is shown. For all response variables, depth-to-water was the only significant predictor variable (α = 0.05) (see also Table 3.1).

Mixedwood Stands

Figure 3.5: Forb cover in mixedwood stands as a function of the natural log of depth-to-water (DTW) values based on the 0.5 ha initiation threshold. Lower DTW values represent wetter sites. The regression line from the results of the mixed effects model analysis is shown. Harvesting treatment and depth-to-water values were significant (α = 0.05) (see also Table 3.1).

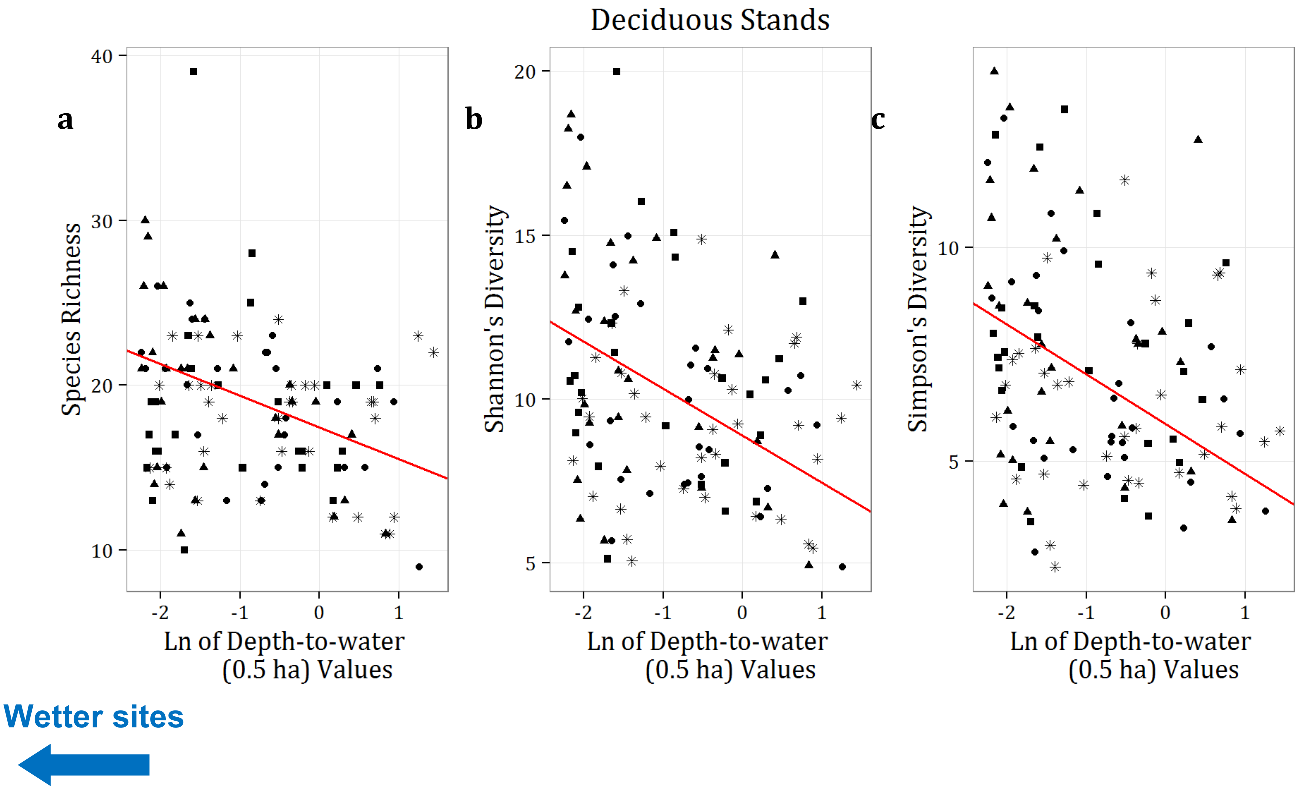


Figure 3.6: Species richness (**a**), Shannon's diversity (**b**), and Simpson's diversity (**c**) in deciduous stands as a function of the natural log of depth-to-water (DTW) values based on the 0.5 ha initiation threshold. Lower DTW values represent wetter sites. Symbols represent plots, with their shape representing harvesting treatment. The regression line from the results of the mixed effects model analysis is shown. Depth-to-water index was the only significant predictor variable ($\alpha = 0.05$) (Table 3.1).

Deciduous-dominated Stands

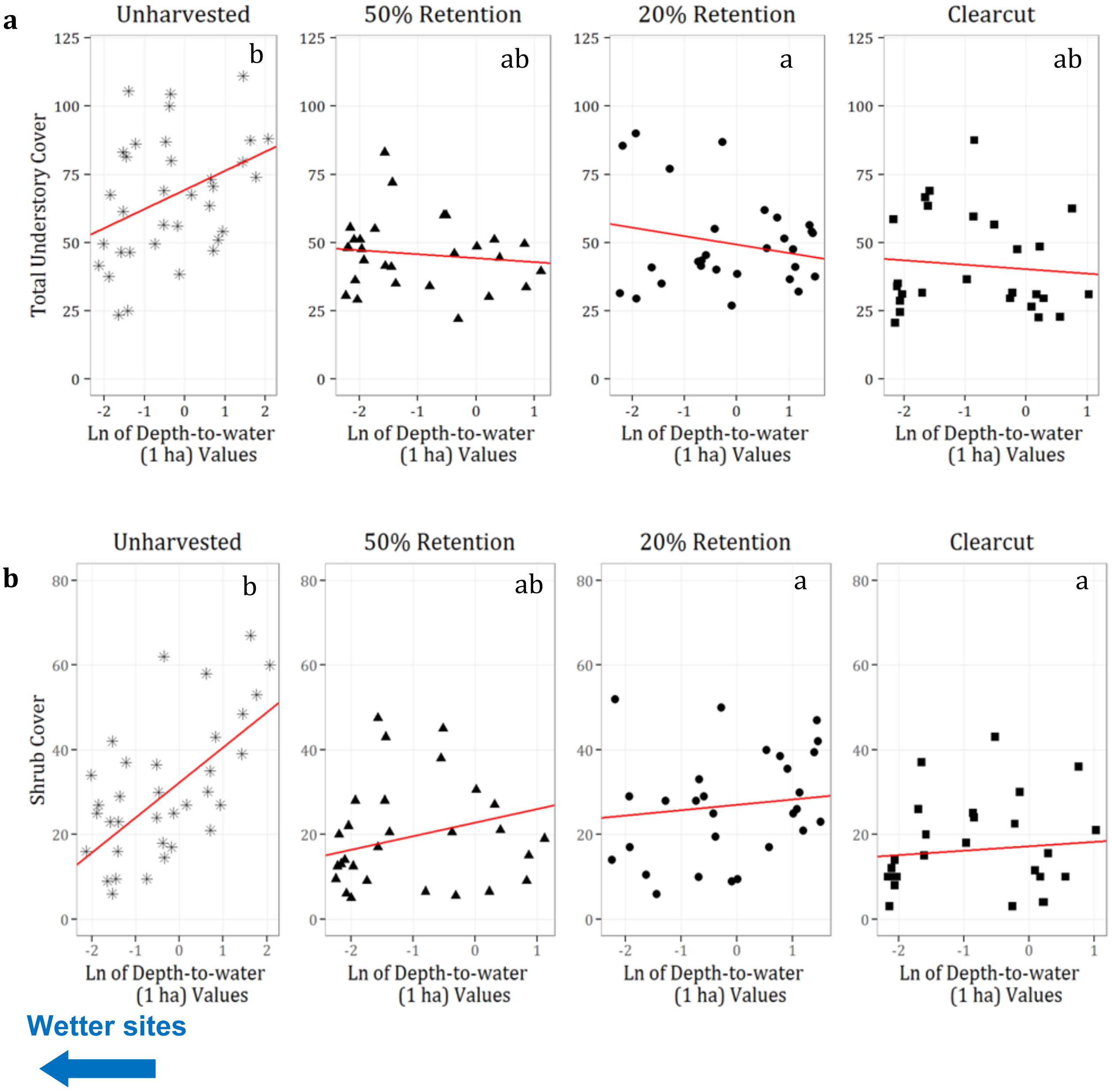


Figure 3.7: Total understory cover (**a**) and shrub cover (**b**) in deciduous-dominated stands as a function of the natural log of depth-to-water (DTW) values based on the 1 ha initiation threshold. Lower DTW values represent wetter sites. The regression line from the results of the mixed effects model analysis is shown. For both response variables, the harvesting by depth-to-water interaction was significant (α = 0.05). Harvesting was also significant for forb cover, while the depth-to-water index was significant for shrub cover. Significantly different slopes, based on post-hoc analyses, are indicated with letters (see also Table 3.1).

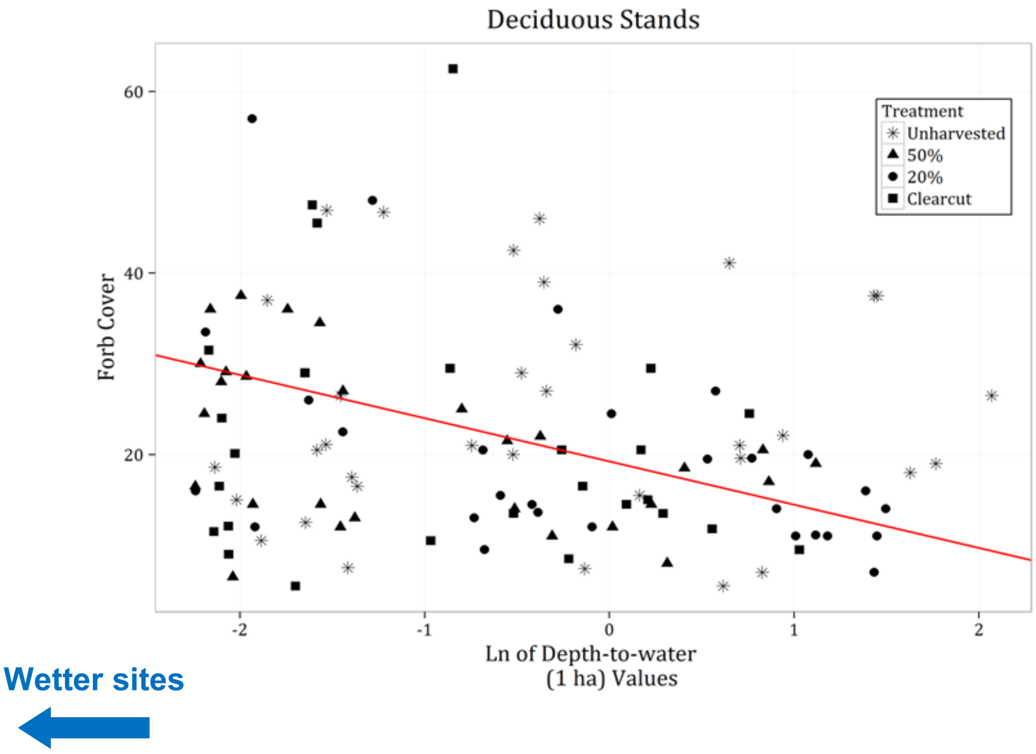


Figure 3.8: Forb cover in deciduous-dominated stands for all treatment levels plotted against the natural log of depth-to-water (DTW) values based on the 1 ha initiation threshold, which was significant (see also Table 3.1). Lower DTW values represent wetter sites. Symbols represent plots, with their shape representing harvesting treatment. The regression line from the results of the mixed effects model analysis is shown.

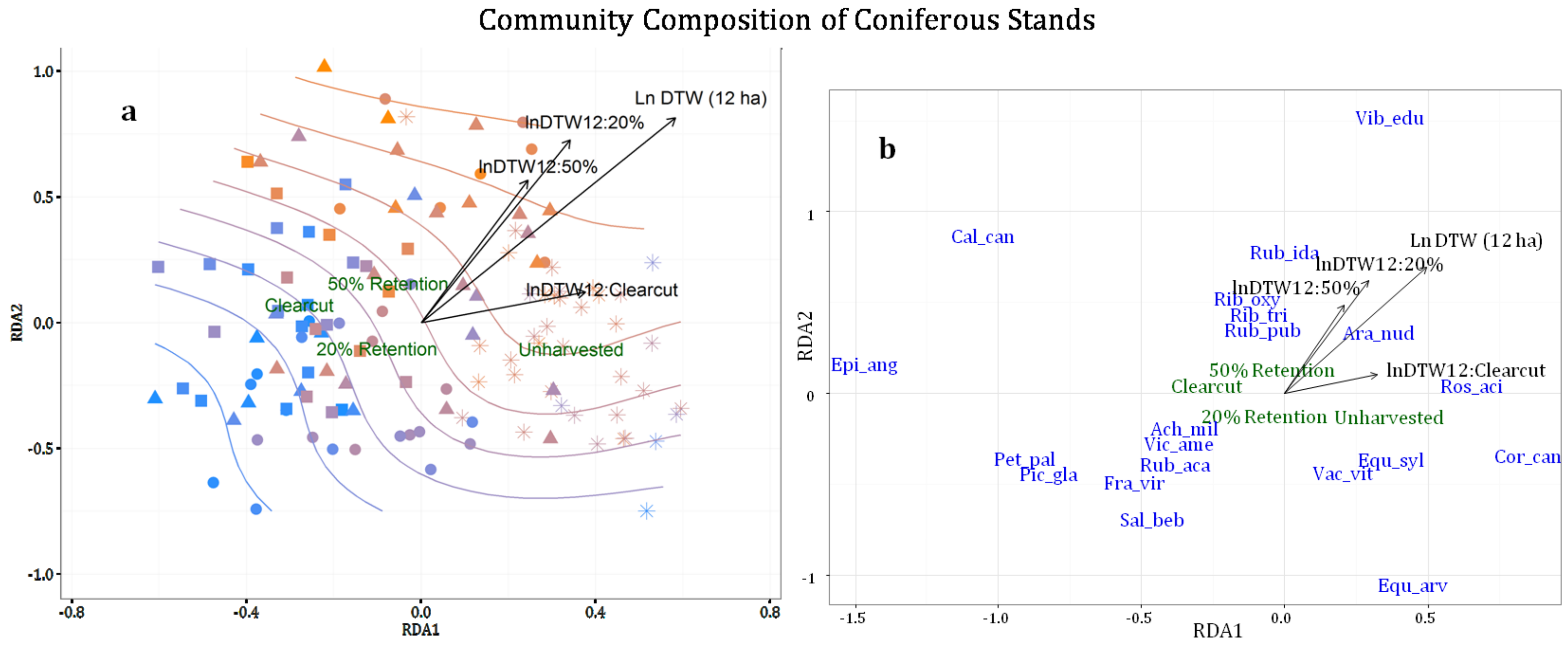


Figure 3.9: (a) Results from constrained ordination (redundancy analysis with a hellinger transformation applied to species abundances) examining the relationship of community composition of vascular understory vegetation with depth-to-water (DTW) values (based on a 12-ha initiation threshold), harvesting treatment, and their interaction in conifer-dominated stands (adjusted R^2 = 0.096). Arrows indicate the vector for DTW (12 ha), DTW (12 ha) for 50% retention stands, DTW (12 ha) for 20% retention stands, and DTW (12 ha) for clearcut stands values. Lower DTW values represent wetter sites. Symbols represent plots, with the shape representing the harvesting treatment and the color representing the DTW (12 ha) value for that plot. The centroids for each harvesting treatment are represented by the treatment name in green. Contour lines represent the DTW (12 ha) value along the ordination plane and were fitted using the vegan package in R (Oksanen et al. 2016). **(b)** Understory species which had an important contribution to the ordination analysis (species with vectors longer than the equilibrium contribution circle based on Borcard et al. (2011)) are represented by six letter codes (first three letters of genus and species epithet; see Appendix F).

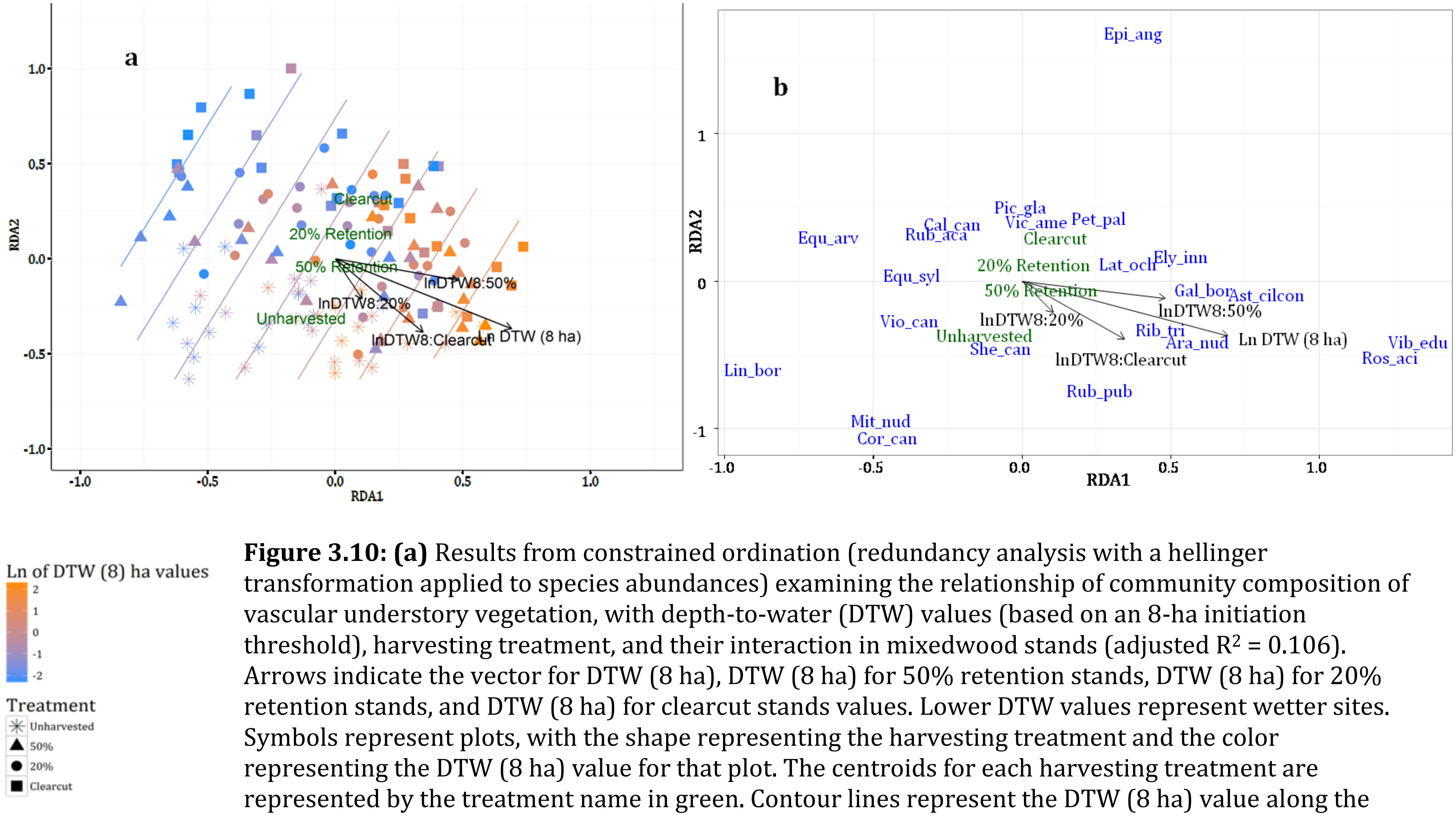


Figure 3.10: (a) Results from constrained ordination (redundancy analysis with a hellinger transformation applied to species abundances) examining the relationship of community composition of vascular understory vegetation, with depth-to-water (DTW) values (based on an 8-ha initiation threshold), harvesting treatment, and their interaction in mixedwood stands (adjusted $R^2 = 0.106$). Arrows indicate the vector for DTW (8 ha), DTW (8 ha) for 50% retention stands, DTW (8 ha) for 20% retention stands, and DTW (8 ha) for clearcut stands values. Lower DTW values represent wetter sites. Symbols represent plots, with the shape representing the harvesting treatment and the color representing the DTW (8 ha) value for that plot. The centroids for each harvesting treatment are represented by the treatment name in green. Contour lines represent the DTW (8 ha) value along the ordination plane and were fitted using the vegan package in R (Oksanen et al. 2016). **(b)** Understory species which had an important contribution to the ordination analysis (species with vectors longer than the equilibrium contribution circle based on Borcard et al. (2011)) are represented by six letter codes (first three letters of genus and species epithet; see Appendix F).

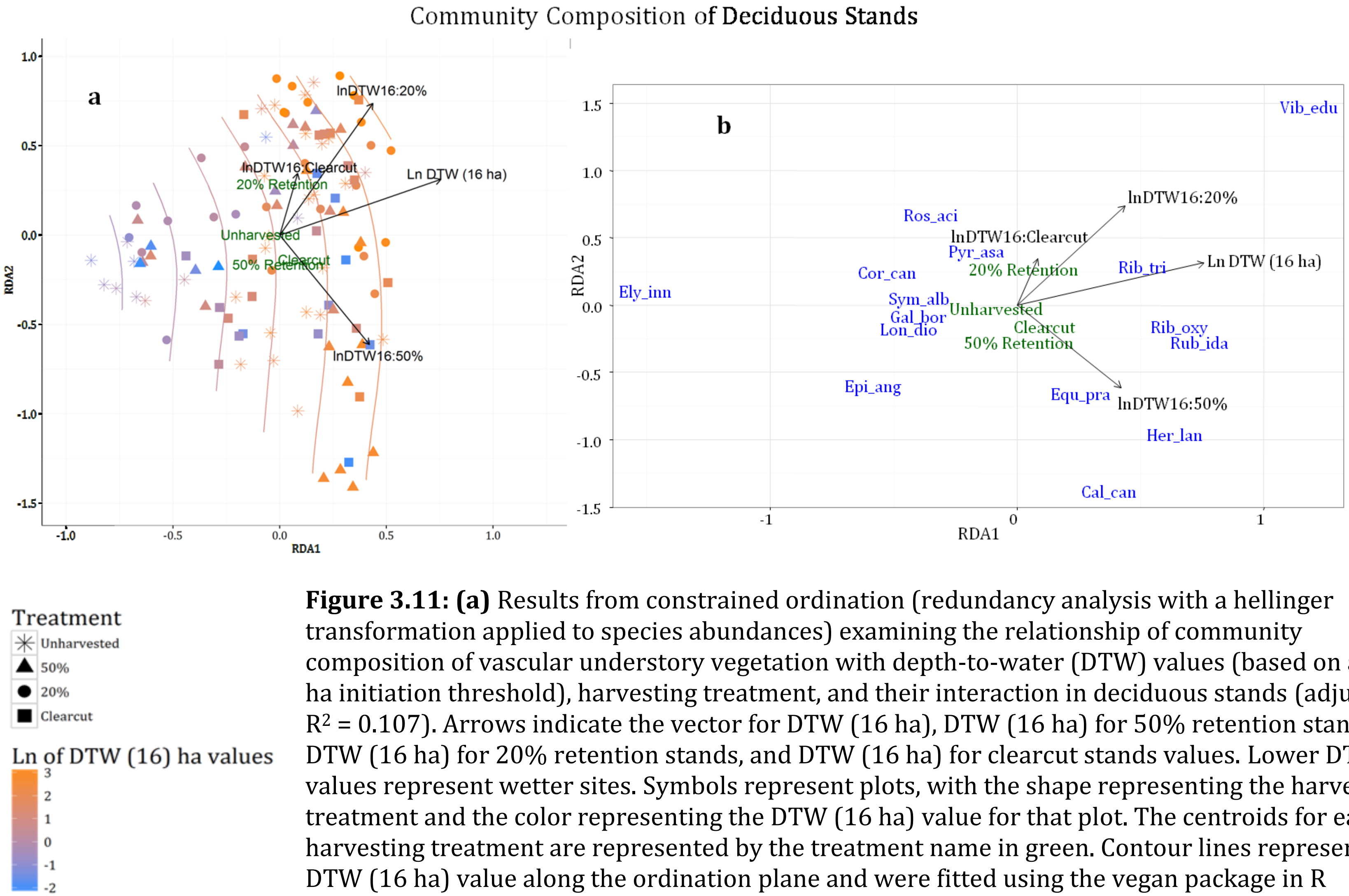


Figure 3.11: (a) Results from constrained ordination (redundancy analysis with a hellinger transformation applied to species abundances) examining the relationship of community composition of vascular understory vegetation with depth-to-water (DTW) values (based on a 16-ha initiation threshold), harvesting treatment, and their interaction in deciduous stands (adjusted $R^2 = 0.107$). Arrows indicate the vector for DTW (16 ha), DTW (16 ha) for 50% retention stands, DTW (16 ha) for 20% retention stands, and DTW (16 ha) for clearcut stands values. Lower DTW values represent wetter sites. Symbols represent plots, with the shape representing the harvesting treatment and the color representing the DTW (16 ha) value for that plot. The centroids for each harvesting treatment are represented by the treatment name in green. Contour lines represent the DTW (16 ha) value along the ordination plane and were fitted using the vegan package in R (Oksanen et al. 2016). **(b)** Understory species which had an important contribution to the ordination analysis (species with vectors longer than the equilibrium contribution circle based on Borcard et al. (2011)) are represented by six letter codes (first three letters of genus and species epithet; see Appendix F).

Chapter 4: General Conclusions

4.1 Conclusions

In this study, we found that topographic moisture is related to understory vascular plant diversity, abundance, and assemblage in boreal mixedwood forests, with the relationship between understory and moisture differing among forest types. In addition, we found that harvesting affected these relationships and that the effects of harvesting on the understory varied along the depth-to-water gradient. In accordance with previous studies, we found harvesting effects differed between the different forest types (Macdonald and Fenniak 2007, Pinzon et al. 2012). Lastly, we have shown the depth-to-water index is a useful tool for guiding the placement of retention patches in order to mitigate understory biodiversity losses in the managed forests of northwestern Alberta.

The conifer-dominated forest type was the most responsive to the depth-to-water (DTW) gradient; moreover it was also the forest type least resilient to harvesting. In unharvested conifer-dominated stands, diversity, abundance and composition were related to DTW, with higher diversity and abundance on drier sites. Excess water and limited nitrogen availability may be limiting the establishment of some plant species on wetter sites, hence the decrease in abundance and diversity. In addition, wetter sites might also be more heavily dominated by bryophytes. The relationships between the understory and DTW were sensitive to harvesting; only the relationship between species richness and DTW was unaffected by harvesting. In harvested stands, the relationships of understory attributes with DTW were either lost or changed in direction. For example, unlike the unharvested stands, harvested stands had higher diversity on wetter sites. Our results also showed that in coniferous stands, wetter areas were less resilient than drier areas. For example, wet areas in harvested stands had higher diversity than wet areas in unharvested stands, while drier areas had relatively similar diversity values for both unharvested and harvested stands. This increase in diversity on the wetter sites of harvested stands may be due to the establishment of early-successional species, as evident in the community composition analysis. Lastly, harvesting changed the optimal initiation threshold for calculation of DTW in terms of the relationship with understory attributes. While the 16 ha initiation threshold was optimal for diversity in unharvested stands, the best models for diversity in harvested stands included DTW based on the 0.5 ha initiation threshold.

In contrast to the conifer-dominated forest type, the mixedwood forest type was not as responsive to the DTW moisture gradient; it was, however, the most resilient forest type. In unharvested mixedwood stands, abundance and composition were related to the DTW gradient, with higher abundance on drier sites. Almost all of the relationships between understory attributes and DTW were unaffected by harvesting. Only the relationship of understory composition to DTW was affected by harvesting, with wetter sites appearing to be more resilient than drier areas. In addition, lower initiation thresholds were optimal for both unharvested and harvested mixedwood stands. The resilience of mixedwoods highlights the importance of maintaining mixedwood stands in the boreal mixedwood forest region.

Similar to mixedwood stands, deciduous stands also showed that only abundance and composition were related to the DTW gradient in unharvested stands; these relationships were changed by harvesting. In unharvested stands, we found higher abundance on drier sites. However, harvesting led to the loss or weakening of the relationship between abundance and the DTW gradient. In contrast to the other two forest types, in deciduous stands drier sites were less resilient than wetter sites. This trend could be attributed to aspen regeneration out-competing shrubs on drier sites. Much like mixedwoods, in the deciduous forest type the lower initiation thresholds were optimal for both unharvested and harvested stands.

In general, harvesting intensity did not strongly influence how DTW-understory relationships were changed by harvesting. However, differences in how the understory composition changed along the DTW gradient were evident between treatments. For example, in deciduous stands, the compositional changes along the DTW gradient in the 50% treatment differed from that of the 20% and clearcut treatments. It is possible that differences due to harvesting intensity may be stronger shortly after harvesting, but may have weakened as the forest regenerated.

While our results show that understory attributes are significantly related to DTW, we cannot speak to the predictive abilities of DTW due to our limited sampling size. Future studies can expand on these results by developing predictive models for understory vegetation. Studies can also build on these results by exploring the relationship of DTW with specific species of interest, such as invasive species or rare species. Our results showed the effects of harvesting on DTW-understory relationships and how resilience to harvesting changed along a moisture gradient. Future research can examine whether and how the effects of natural disturbances, such as wildfire, vary along a moisture gradient. We can ask if resilience along a moisture gradient is similar between a natural and anthropogenic disturbance and determine if the effects of retention harvesting emulate those of a natural disturbance.

4.2 Management implications

While the selection of areas to be retained is currently based on field surveys, our study shows we can use the depth-to-water index to capture areas with environmental differences that may not be obvious to field surveyors. Although we were unable to develop predictive models for understory vegetation diversity, we were able to show that differences in DTW values are related to differences in understory diversity, abundance, and composition. Thus, we can use the DTW index to identify areas for retention that we know are likely to support different understory diversity, abundance, and assemblages. In this way, we can maximize the environmental heterogeneity of retained areas and ensure we have maintained a variety of habitats for the understory vegetation (Bartels and Chen 2010).

Resilience can also be taken into account when placing retention patches. We have shown how the stand types vary in resilience, from the least resilient coniferous stand type to the most resilient mixedwood stands. In addition, we have identified how resilience might vary along a moisture gradient within these stands. Thus, harvesting intensity can be varied between these forest types and along the DTW gradient to reflect their differences in resilience. At a finer scale, we can identify which sites should be targeted for retention patches due to a higher sensitivity to harvesting. For example, we would suggest that wet areas in conifer-dominated and mixedwood stands be especially targeted for retention, since these areas have shown to be particularly sensitive to the effects of harvesting. In summary, this study shows that the depth-to-water index can be a useful tool for guiding retention harvesting to mitigate losses in the understory diversity.

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Appendices

Appendix A: Results of mixed effects models examining the relationship of understory vascular plant species richness, Shannon's diversity, Simpson's diversity, total understory cover, forb cover, and shrub cover with depth-to-water (DTW) values derived with different flow initiation threshold values, forest type, and their interaction, in conifer-dominated stands (CDOM), mixedwood stands (MIX), and deciduous-dominated stands (DDOM). Hill's numbers were used for the diversity indices, with the exponent of Shannon's entropy used for Shannon's diversity and the inverse of the Gini-Simpson index used for Simpson's diversity (Hill 1973, Jost 2006). The natural ln of DTW values were used for all initiation thresholds. Significant p-values are in bold (α = 0.05).

Response variable	DTW initiation threshold	DTW p-value	Forest type p-value	Interaction p-value
Species Richness	0.5 ha	0.188	0.260	0.980
	1 ha	0.343	0.290	0.679
	2 ha	0.408	0.286	0.764
	4 ha	0.667	0.304	0.756
	8 ha	0.329	0.056	**<0.006**
	12 ha	0.290	0.062	**<0.001**
	16 ha	0.086	0.064	**<0.001**
Shannon's Diversity	0.5 ha	0.562	0.239	0.151
	1 ha	0.411	0.211	0.191
	2 ha	0.976	0.256	0.432
	4 ha	0.297	0.296	0.428
	8 ha	0.135	0.330	**0.018**
	12 ha	0.118	0.386	**0.005**
	16 ha	0.134	0.412	**0.013**
Simpson's Diversity	0.5 ha	0.756	0.246	0.088
	1 ha	0.541	0.235	0.138
	2 ha	0.621	0.282	0.372
	4 ha	0.160	0.293	0.400
	8 ha	0.107	0.388	**0.041**

Response variable	**DTW initiation threshold**	**DTW p-value**	**Forest type p-value**	**Interaction p-value**
Simpson's Diversity	12 ha	**0.047**	0.382	**0.027**
	16 ha	0.080	0.364	0.103
Total Understory Cover	0.5 ha	0.073	0.735	0.668
	1 ha	**0.017**	0.748	0.708
	2 ha	0.061	0.752	0.500
	4 ha	0.423	0.727	0.63
	8 ha	0.678	0.692	0.978
	12 ha	0.952	0.675	0.866
	16 ha	0.417	0.681	0.444
Forb Cover	0.5 ha	0.692	0.474	0.320
	1 ha	0.551	0.484	0.340
	2 ha	0.271	0.489	0.462
	4 ha	0.062	0.514	0.922
	8 ha	0.070	0.646	0.992
	12 ha	0.256	0.607	0.931
	16 ha	0.681	0.176	**0.007**
Shrub Cover	0.5 ha	**<0.001**	0.425	0.394
	1 ha	**<0.001**	0.401	0.579
	2 ha	**<0.001**	0.402	0.617
	4 ha	**<0.001**	0.428	0.510
	8 ha	**<0.001**	0.285	0.534
	12 ha	**<0.001**	0.440	0.580
	16 ha	**<0.001**	0.501	0.673

Appendix B: Results of mixed effects models examining the relationship of species richness, Shannon's diversity, Simpson's diversity, total understory cover, forb cover, and shrub cover with depth-to-water (DTW) values in conifer-dominated stands (CDOM), mixedwood stands (MIX) and deciduous-dominated stands (DDOM). Hill's numbers were used for the diversity indices, with the exponent of Shannon's entropy used for Shannon's diversity and the inverse of the Gini-Simpson index used for Simpson's diversity (Hill 1973, Jost 2006). The natural log of DTW value was used for all analyses. Shown are the results comparing models with DTW calculated based on different initiation thresholds (i.e. 16 ha). The optimal model for each response variable in each forest type was determined by comparing the Akaike Information Criterion (AIC) values. The AIC values for the optimal models are in bold and later presented in Table 2.1.

		Model AIC values for each initiation threshold						
Forest Type	**Response Variable**	**0.5 ha**	**1 ha**	**2 ha**	**4 ha**	**8 ha**	**12 ha**	**16 ha**
CDOM	Species Richness	234.7	235.1	235.1	235.1	230.8	229.4	**225.6**
	Shannon's Diversity	195.0	195.3	195.3	194.8	188.0	**185.5**	187.8
	Simpson's Diversity	179.1	179.8	179.8	179.7	174.8	**172.3**	176.0
	Total Understory Cover	366.5	366.5	366.5	366.4	366.3	365.9	**363.5**
	Forb Cover	343.1	343.0	343.0	343.7	343.1	343.6	**342.5**
	Shrub Cover	309.2	305.5	**305.4**	306.4	308.7	307.8	308.5
MIX	Species Richness	198.6	**197.6**	198.5	199.2	199.6	198.8	199.5
	Shannon's Diversity	**182.2**	182.3	184.7	184.6	184.3	183.9	183.6
	Simpson's Diversity	**179.8**	180.3	182.1	181.2	181.2	180.3	180.2
	Total Understory Cover	**346.4**	346.8	348.4	348.7	348.6	348.6	348.6
	Forb Cover	316.7	317.2	317.3	**316.0**	316.1	316.6	316.7
	Shrub Cover	309.6	**307.4**	308.0	310.0	310.7	309.7	310.0
DDOM	Species Richness	**192.2**	193.2	193.3	193.2	192.6	192.4	192.8
	Shannon's Diversity	**163.1**	163.1	163.1	163.4	163.3	163.8	163.7
	Simpson's Diversity	**153.4**	153.4	153.5	153.6	153.5	153.7	153.7
	Total Understory Cover	304.6	**302.5**	302.6	306.2	306.5	307.0	307.2
	Forb Cover	267.0	267.3	267.4	266.2	**264.1**	266.5	266.8
	Shrub Cover	273.1	263.5	**262.9**	266.4	272.8	279.6	277.9

Appendix C: Species found in all sample plots with their corresponding codes as shown in the RDAs (Figures 2.3b, 2.4b, 2.5b). Nomenclature follows Moss (1983).

Abbreviation	**Latin Binomial**	**Abbreviation**	**Latin Binomial**
Ach_mil	*Achillea millefolium*	Lat_och	*Lathyrus ochroleucus*
Act_rub	*Actaea rubra*	Lat_ven	*Lathyrus venosus*
Ado_mos	*Adoxa moschatellini*	Led_gro	*Ledum groenlandicum*
Agr_tra	*Agropyron trachycaulum*	Lin_bor	*Linnaea borealis*
Aln_cri	*Alnus crispa*	Lon_dio	*Lonicera dioica*
Aln_rug	*Alnus rugosa*	Lyc_ann	*Lycopodium annotinum*
Ame_aln	*Amelanchier alnifolia*	Mai_can	*Maianthemum canadense*
Aqu_bre	*Aquilegia brevistyla*	Mer_pan	*Mertensia paniculata*
Ara_nud	*Aralia nudicaulis*	Mit_nud	*Mitella nuda*
Are_lat	*Arenaria laterifolia*	Mon_uni	*Moneses uniflora*
Arn_cor	*Arnica cordifolia*	Osm_dep	*Osmorhiza depauperata*
Ast_ame	*Astragalus americanus*	Pet_pal	*Petasites palmatus*
Ast_cilcon	*Aster ciliolatus* and *Aster conspicuus*	Pet_sag	*Petasites sagittatus*
Bet_pum	*Betula pumila*	Pic_gla	*Picea glauca*
Cal_can	*Calamagrostis canadensis*	Pol_aci	*Polemonium acutiflorum*
Cal_rub	*Calamagrostis rubescens*	Pop_bal	*Populus balsamifera*
Car_bru	*Carex brunnescens*	Pop_tre	*Populus tremuloides*
Car_dew	*Carex deweyana*	Pyr_asa	*Pyrola asarifolia*
Car_dis	*Carex disperma*	Pyr_min	*Pyrola minor*
Car_lol	*Carex loliaceae*	Pyr_sec	*Pyrola secunda*
Car_vag	*Carex vaginata*	Pyr_vir	*Pyrola virens*
Carex_sp	*Carex sp.*	Rib_gla	*Ribes glandulosum*
Chr_sp.	*Chrysosplenium sp.*	Rib_hud	*Ribes hudsonianum*
Cin_lat	*Cinna latifolia*	Rib_lac	*Ribes lacustre*
Cir_alp	*Circaea alpina*	Rib_oxy	*Ribes oxyacanthoides*
Cor_can	*Cornus canadensis*	Rib_tri	*Ribes triste*
Cor_mac_str	*Corallorhiza maculata* and *Corallorhiza striata*	Ros_aci	*Rosa acicularis*
Cor_tri	*Corallorhiza trifida*	Rub_aca	*Rubus acaulis*
Del_gla	*Delphinium glauca*	Rub_ida	*Rubus idaeus*
Dry_aus	*Dryopteris austriaca*	Rub_pub	*Rubus pubescens*
Ely_inn	*Elymus innovatus*	Sal_arb	*Salix arbusculoides*

Epi_ang	*Epilobium angustifolium*	Sal_beb	*Salix bebbiana*
Epi_gla	*Epilobium glandulosum*	Sal_myr	*Salix myrtillifolia*
Equ_arv	*Equisetum arvense*	Sal_pseudomyr	*Salix pseudomyrsinites*
Equ_pra	*Equisetum pratense*	Sch_pur	*Schizachne purpurascens*
Equ_sci	*Equisetum scirpoides*	Sen_pau	*Senecio pauperculus*
Equ_syl	*Equisetum sylvaticum*	She_can	*Shepherdia canadensis*
Fra_ves	*Fragaria vesca*	Smi_tri	*Smilacina trifolia*
Fra_vir	*Fragaria virginiana*	Ste_longifolia	*Stellaria longifolia*
Gal_bor	*Galium boreale*	Sym_alb	*Symphoricarpos albus*
Gal_trifidum	*Galium trifidum*	Tar_off	*Taraxacum officinale*
Gal_triflorum	*Galium triflorum*	Tha_sp.	*Thalictrum sp.*
Geo_liv	*Geocaulon lividum*	Tri_sp.	*Trientalis sp.*
Geu_mac	*Geum macrophyllum*	Urt_dio	*Urtica dioica*
Goo_rep	*Goodyera repens*	Vac_cae	*Vaccinium caespitosum*
Grass_sp	*Grass sp.*	Vac_vit	*Vaccinium vitis-idaea*
Hab_hyp	*Habenaria hyperborean*	Ver_ame	*Veronica americana*
Hab_obt	*Habenaria obtusata*	Vib_edu	*Viburnum edule*
Hab_orb	*Habenaria orbiculata*	Vic_ame	*Vicia americana*
Her_lan	*Heracleum lanatum*	Vio_can	*Viola canadensis*
Hie_umb	*Hieracium umbellatum*	Vio_ren	*Viola renifolia*

Appendix D: Average depth-to-water values for each forest type, by initiation threshold.

Initiation threshold	Coniferous Mean	Mixedwood Mean	Deciduous Mean
0.5 ha	0.42	0.52	0.89
1 ha	0.57	0.74	1.37
2 ha	0.57	1.06	1.49
4 ha	0.62	1.53	1.76
8 ha	1.89	1.61	3.02
12 ha	1.93	1.71	6.14
16 ha	2.05	1.79	7.38

Appendix E: Results of mixed effects models examining the relationship of understory vascular plant species richness, Shannon's diversity, Simpson's diversity, total understory cover, forb cover, and shrub cover with depth-to-water (DTW) values, harvesting treatment, and their interaction in conifer-dominated stands (CDOM), mixedwood stands (MIX), and deciduous-dominated stands (DDOM). Hill's numbers were used for the diversity indices, with the exponent of Shannon's entropy used for Shannon's diversity and the inverse of the Gini-Simpson index used for Simpson's diversity (Hill 1973, Jost 2006). The natural log of DTW value was used for all analyses. Shown are the results comparing models with DTW calculated based on different initiation thresholds (i.e. 16 ha). The optimal model for each response variable in each forest type was determined by comparing the Akaike Information Criterion (AIC) values. The optimal models are in bold and later presented in Table 3.1.

		Model AIC values for each initiation threshold						
Forest Type	**Response Variable**	**0.5 ha**	**1 ha**	**2 ha**	**4 ha**	**8 ha**	**12 ha**	**16 ha**
CDOM	Species Richness	784.6	**783.9**	786.2	789.9	790.3	789.7	788.7
	Shannon's Diversity	**713.5**	714.5	716.6	719.2	722.5	723.3	722.3
	Simpson's Diversity	**663.9**	665.4	667.0	668.8	672.4	672.9	671.6
	Total Understory Cover	1132.5	1133.0	1133.0	1133.2	1132.9	1131.7	**1126.2**
	Forb Cover	1037.4	1036.5	1036.7	1038.6	1038.6	1039.4	**1034.6**
	Shrub Cover	990.1	**985.9**	985.9	986.9	989.1	988.2	987.5
MIX	Species Richness	**727.9**	730.5	731.4	733.4	733.9	734.1	734.6
	Shannon's Diversity	**182.2**	182.3	184.7	184.6	184.3	183.9	183.6
	Simpson's Diversity	**179.8**	180.3	182.1	181.2	181.2	180.3	180.2
	Total Understory Cover	**1110.6**	1115.0	1116.9	1116.0	1117.3	1116.3	1116.3
	Forb Cover	**985.2**	989.1	990.0	990.0	990.7	991.6	991.9
	Shrub Cover	**995.7**	997.7	998.1	998.7	1000.5	1001.0	1001.3
DDOM	Species Richness	**676.6**	685.2	688.5	688.6	680.3	686.1	685.1
	Shannon's Diversity	**591.4**	595.3	598.0	599.1	598.8	600.9	598.8
	Simpson's Diversity	**546.7**	547.7	548.5	548.8	552.3	554.1	552.8
	Total Understory Cover	981.4	**977.7**	978.7	984.4	983.9	987.2	986.7
	Forb Cover	882.8	**879.4**	882.1	879.7	881.7	886.5	890.7
	Shrub Cover	884.1	**871.6**	872.8	877.9	890.6	897.6	894.9

Appendix F: Species found in all the sample plots with their corresponding codes (see Figure 3.9, 3.10, 3.11). Nomenclature follows Moss (1983).

Abbreviation	**Latin Binomial**	**Abbreviation**	**Latin Binomial**	**Abbreviation**	**Latin Binomial**
Abi_bal	*Abies balsamea*	Epi_lep	*Epilboium leptophyllum*	Pop_bal	*Populus balsamifera*
Ach_mil	*Achillea millefolium*	Epi_pal	*Epilobium palustre*	Pop_tre	*Populus tremuloides*
Ach_sib	*Achillea sibirica*	Equ_arv	*Equisetum arvense*	Pot_nor	*Potentilla norvegica*
Act_rub	*Actaea rubra*	Equ_pra	*Equisetum pratense*	Pot_pal	*Potentilla palustris*
Ado_mos	*Adoxa moschatellini*	Equ_sci	*Equisetum scirpoides*	Pyr_asa	*Pyrola asarifolia*
Agr_sca	*Agrostis scabra*	Equ_syl	*Equisetum sylvaticum*	Pyr_min	*Pyrola minor*
Agr_tra	*Agropyron trachycaulum*	Fra_ves	*Fragaria vesca*	Pyr_sec	*Pyrola secunda*
Aln_cri	*Alnus crispa*	Fra_vir	*Fragaria virginiana*	Pyr_vir	*Pyrola virens*
Aln_rug	*Alnus rugosa*	Gal_bor	*Galium boreale*	Ran_abo	*Ranunculus abortivus*
Ame_aln	*Amelanchier alnifolia*	Gal_tet	*Galeopsis tetrahit*	Ran_mac	*Ranunculus macounii*
Aqu_bre	*Aquilegia brevistyla*	Gal_trifidum	*Galium trifidum*	Rhi_bor	*Rhinanthus borealis*
Ara_nud	*Aralia nudicaulis*	Gal_triflorum	*Galium triflorum*	Rib_gla	*Ribes glandulosum*
Arc_uva	*Arctostaphylos uva-ursi*	Gen_ama	*Gentiana amarelle*	Rib_hud	*Ribes hudsonianum*
Are_lat	*Arenaria laterifolia*	Geo_liv	*Geocaulon lividum*	Rib_lac	*Ribes lacustre*
Arn_cha	*Arnica chamissonis*	Geu_ale	*Geum aleppicum*	Rib_oxy	*Ribes oxyacanthoides*
Arn_cor	*Arnica cordifolia*	Geu_mac	*Geum macrophyllum*	Rib_tri	*Ribes triste*
Ast_ame	*Astragalus americanus*	Goo_rep	*Goodyera repens*	Ros_aci	*Rosa acicularis*
Ast_cilcon	*Aster ciliolatus* and *Aster conspicuus*	Grass_sp	*Grass sp.*	Rub_aca	*Rubus acaulis*
Ast_pun	*Aster puniceus*	Gym_dry	*Gymnocarpium dryopteris*	Rub_ida	*Rubus idaeus*
Bet_pap	*Betula papyrifera*	Hab_hyp	*Habenaria hyperborea*	Rub_pub	*Rubus pubescens*

Abbreviation	**Latin Binomial**	**Abbreviation**	**Latin Binomial**	**Abbreviation**	**Latin Binomial**
Bet_pum	*Betula pumila*	Hab_obt	*Habenaria obtusata*	Sal_arb	*Salix arbusculoides*
Bot_vir	*Botyrichum virginianum*	Hab_orb	*Habenaria orbiculata*	Sal_beb	*Salix bebbiana*
Bro_cil	*Bromus ciliatus*	Hal_def	*Halenia deflexa*	Sal_dis	*Salix discolor*
Cal_bul	*Calypso bulbosa*	Her_lan	*Heracleum lanata*	Sal_mac	*Salix maccalliana*
Cal_can	*Calamagrostis canadensis*	Hie_umb	*Hieracium umbellatum*	Sal_myr	*Salix myrtillifolia*
Cal_rub	*Calamagrostis rubescens*	Juncus_sp.	*Juncus sp.*	Sal_pla	*Salix planifolia*
Car_aqu	*Carex aquatilis*	Koe_mac	*Koelaria macrantha*	Sal_pseudomon	*Salix pseudomonticola*
Car_aur	*Carex aurea*	Lar_lar	*Larix laricina*	Sal_pseudomyr	*Salix pseudomyrsinites*
Car_bru	*Carex brunnescens*	Lat_och	*Lathyrus ochroleucus*	Sal_pyr	*Salix pyrifolia*
Car_can	*Carex canescens*	Lat_ven	*Lathyrus venosus*	Salix_sp.	*Salix sp.*
Car_def	*Carex deflexa*	Led_gro	*Ledum groenlandicum*	Sch_pur	*Schizachne purpurascens*
Car_dew	*Carex deweyana*	Lem_min	*Lemna minor*	Sen_pau	*Senecio pauperculus*
Car_dis	*Carex disperma*	Lin_bor	*Linnaea borealis*	She_can	*Shepherdia canadensis*
Car_gyn	*Carex gynocrates*	Lis_bor	*Listera borealis*	Smi_tri	*Smilacina trifolia*
Car_lol	*Carex loliaceae*	Lis_cor	*Listera cordata*	Sol_can	*Solidago canadensis*
Car_nor	*Carex norvegica*	Lon_dio	*Lonicera dioica*	Spi_rom	*Spiranthes romanzoffiana*
Car_pec	*Carex peckii*	Luz_mul	*Luzula multiflora*	Ste_cal	*Stellaria calycantha*
Car_pen	*Cardamine pensylvanica*	Luz_par	*Luzula parviflora*	Ste_longifolia	*Stellaria longifolia*
Car_pra	*Carex praticola*	Lyc_ann	*Lycopodium annotinum*	Ste_longipes	*Stellaria longipes*
Car_ray	*Carex raymondii*	Mai_can	*Maianthemum canadense*	Stellaria_sp.	*Stellaria sp.*

Abbreviation	Latin Binomial	Abbreviation	Latin Binomial	Abbreviation	Latin Binomial
Car_sic	*Carex siccata*	Mal_mon	*Malaxis monophylla*	Sym_alb	*Symphoricarpos albus*
Car_vag	*Carex vaginata*	Mer_pan	*Mertensia paniculata*	Tar_off	*Taraxacum offinicale*
Carex_sp	*Carex sp.*	Mit_nud	*Mitella nuda*	Tha_sp.	*Thalictrum sp.*
Chr_sp.	*Chrysosplenium sp.*	Mon_uni	*Moneses uniflora*	Tri_hyb	*Trifolium hybridum*
Cin_lat	*Cinna latifolia*	Osm_dep	*Osmorhiza depauperata*	Tri_sp.	*Trientalis sp.*
Cir_alp	*Circaea alpina*	Par_pal	*Parnassia palustris*	Urt_dio	*Urtica dioica*
Cir_arv	*Cirsium arvense*	Ped_lab	*Pedicularis labradorica*	Vac_cae	*Vaccinium caespitosum*
Cor_can	*Cornus canadensis*	Pet_pal	*Petasites palmatus*	Vac_vit	*Vaccinium vitis-idaea*
Cor_mac_str	*Corallorhiza maculata* and *Corallorhiza striata*	Pet_sag	*Petasites sagittatus*	Ver_ame	*Veronica americana*
Cor_sto	*Cornus stolonifera*	Phl_pra	*Phleum pretense*	Vib_edu	*Viburnum edule*
Cor_tri	*Corallorhiza trifida*	Pic_gla	*Picea glauca*	Vic_ame	*Vicia americana*
Del_gla	*Delphinium glauca*	Pic_mar	*Picea mariana*	Vio_can	*Viola canadensis*
Dry_aus	*Dryopteris austriaca*	Pin_con	*Pinus contorta*	Vio_nep	*Viola nephrophylla*
Ely_inn	*Elymus innovatus*	Poa_pal	*Poa palustris*	Vio_ren	*Viola renifolia*
Epi_ang	*Epilobium angustifolium*	Poa_pra	*Poa pratensis*		
Epi_gla	*Epilobium glandulosum*	Pol_aci	*Polemonium acutiflorum*		

Appendix G: Results of linear mixed models describing the relationship of understory vascular plant species richness, Shannon's diversity, Simpson's diversity, total understory cover, forb cover, and shrub cover with depth-to-water (DTW) values (natural log transformed for analysis), harvesting treatment, and their interaction, in conifer-dominated (CDOM), mixedwood (MIX), deciduous-dominated (DDOM) stands. The models included are the best models for each response variable in each forest type, based on the Akaike Information Criterion (AIC) value (see Appendix E). The initiation threshold used, coefficient for the influence of DTW, the standard error for the DTW coefficient, degrees of freedom and F-values for DTW, harvesting treatment and their interaction are included. DTW coefficients in bold indicate DTW was significant (α = 0.05).

Forest type	**Response Variable**	**DTW initiation threshold**	**DTW coefficient**	**Standard Error**	**DTW df**	**DTW F-Value**	**Treatment df**	**Treatment F-value**	**Interaction df**	**Interaction F-value**
CDOM	Species Richness	1 ha	**-3.638**	0.943	113	25.17	8	3.64	113	2.06
CDOM	Shannon Diversity	0.5 ha	**-2.721**	0.784	113	20.42	8	5.29	113	3.51
CDOM	Simpson Diversity	0.5 ha	**-1.688**	0.638	113	10.93	8	4.21	113	3.00
CDOM	Total Cover	16 ha	-0.112	2.707	113	2.63	8	0.78	113	6.75
CDOM	Forb Cover	16 ha	-1.817	2.000	113	0.134	8	2.57	113	5.72
CDOM	Shrub Cover	1 ha	2.220	2.184	113	3.08	8	0.47	113	1.18
MIX	Species Richness	0.5 ha	**-1.672**	0.778	112	6.19	8	0.40	112	0.43
MIX	Shannon Diversity	0.5 ha	**-1.846**	0.632	112	13.40	8	0.61	112	0.85
MIX	Simpson Diversity	0.5 ha	**-1.389**	0.551	112	11.36	8	0.75	112	0.50

Forest type	**Response Variable**	**DTW initiation threshold**	**DTW coefficient**	**Standard Error**	**DTW df**	**DTW F-Value**	**Treatment df**	**Treatment F-value**	**Interaction df**	**Interaction F-value**
MIX	Total Cover	0.5 ha	**7.178**	3.799	112	10.77	8	0.62	112	0.06
MIX	Forb Cover	0.5 ha	**5.176**	2.325	112	4.97	8	5.85	112	1.15
MIX	Shrub Cover	0.5 ha	**2.480**	2.353	112	15.67	8	0.21	112	2.14
DDOM	Species Richness	0.5 ha	**-1.930**	0.877	100	9.50	8	0.20	100	1.73
DDOM	Shannon Diversity	0.5 ha	**-1.435**	0.592	100	10.69	8	0.99	100	1.27
DDOM	Simpson Diversity	0.5 ha	**-1.168**	0.481	100	7.39	8	0.83	100	1.08
DDOM	Total Cover	1 ha	-3.075	2.89	100	1.47	8	5.91	100	2.98
DDOM	Forb Cover	1 ha	**-4.769**	1.809	100	5.57	8	0.99	100	1.71
DDOM	Shrub Cover	1 ha	**1.254**	1.764	100	23.22	8	0.778	100	4.47