

THE UTAH FOREST DYNAMICS PLOT: LONG-TERM FOREST MONITORING
AND THEORETICAL ECOLOGY IN A HIGH-ELEVATION
SUBALPINE ENVIRONMENT

by

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ABSTRACT

The Utah Forest Dynamics Plot: Long-Term Ecological Monitoring and Theoretical
Ecology in a High-Elevation Subalpine Environment

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The Unified Neutral Theory of Biodiversity has been advanced as a universal theory for species coexistence in forests worldwide, but few studies have examined its relevance to high-elevation, stressful environments. I established the Utah Forest Dynamics Plot (UFDP) in a heterogeneous subalpine forest at 3,091 m elevation on the Colorado Plateau to examine three underlying assumptions of neutral theory (functional equivalence, ecological equivalence, and habitat generality) and one prediction (the species abundance distribution). The UFDP comprises 27,845 stems ≥ 1 cm diameter at breast height of 17 species, 10 genera, and 6 families over 13.6 ha. The neutral model was a poor fit to the observed species abundance distribution, but I did not find the alternative lognormal model to provide a better fit. Using spatial pattern analyses of tree data, topography, and soil type, I found some limited support for the neutral theory assumptions of functional and ecological equivalency, with notable exceptions. *Populus tremuloides*, *Pinus flexilis*, and *Pinus longaeva* were characterized by non-neutral

recruitment processes, and *Abies bifolia* and *Populus tremuloides* exhibited asymmetric competitive and facilitative interactions. The assumption of habitat generality was strongly contradicted, with all ten abundant species in the UFDP having habitat preference. In this subalpine temperate forest, species diversity and community structure are influenced more by habitat heterogeneity, species differences, and niche selection, with neutral processes playing a lesser role.

(92 pages)

PUBLIC ABSTRACT

The Utah Forest Dynamics Plot: Long-Term Ecological Monitoring and Theoretical
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In an era of global change, large-scale permanent plots contribute greatly to our ability to monitor global forest dynamics and advance universal ecological theory. The development of long-term data sets allows scientists to directly measure changes in forest ecosystems and to monitor the response of these systems to the full range of complex drivers and feedbacks we observe in nature. Furthermore, global permanent plot networks provide a framework through which researchers can conduct studies across a wide range of forest types, and can facilitate global collaborations. While this approach to forest ecology has spawned numerous ecological theories and contributed to the advancement of others, subalpine forests are underrepresented in global permanent plot networks, and the relevance of global ecological theory to these ecosystems is often overlooked.

The primary objective of this study is to establish a permanent monitoring plot, the Utah Forest Dynamics Plot, in a subalpine forest on the Colorado Plateau, implementing methods shared by the Smithsonian ForestGEO global plot network. The Utah Forest Dynamics Plot (UFDP) is located at 3,000 m elevation in a mixed-conifer/aspen subalpine forest, more than 1,000 m above the next highest plot in the ForestGEO network, contributing the unique perspective of subalpine forest ecosystems to this global research endeavor. Research at the UFDP will contribute to modern forest science by increasing the breadth of our inferences about global forest dynamics in the

context of permanent plot networks, and by capturing forest response to climate-mediated change in a subalpine forest ecosystem. Through observing recruitment and mortality dynamics in the UFDP, I aim to identify patterns in forest change and response to climate variability, improving our ability to understand and predict the effects of future climate scenarios on western forest ecosystems.

This study was motivated by two purposes: (1) establish a long-term data set that will lay the foundation for future studies of forest change in response to inter-annual climate variability and disturbance in subalpine forests in the Rocky Mountains; and (2) contribute to global forest monitoring and ecological theory by introducing a novel forest type to a global network of permanent research plots.

*I dedicate this thesis to all those who advocate for, protect, and manage
our public lands. May we continue to work together to conserve
these beautiful lands for future generations.*

ACKNOWLEDGMENTS

This thesis represents the collective efforts of a number of people to whom I owe a great deal of gratitude. First and foremost, I would like to thank my advisor Jim Lutz for his mentorship, support, vision, and friendship through the years. Jim has invested a huge amount of time and effort into this project in the lab and in the field; it would never have started, and it certainly would not have finished without him. I am forever grateful for the opportunity to study with him, as I have experienced a great deal of intellectual and personal growth over the past few years. I would also like to thank Andrew Larson for his mentorship over the past seven summers, and for his thoughtful feedback that helped me through the maze of spatial statistics and greatly improved this final thesis. I also thank Geno Schupp for his feedback on this thesis, and for all he does to make the local community a fantastic place to live.

I owe a huge amount of thanks to my lab mates Sara Germain, Kendall Becker, and Erika Blomdahl who have invested huge amounts of time and effort into field work in the UFDP in the past three summers. They stuck with the project no matter how challenging the work became: surveying in hail storms, tediously mapping thousands of trees, and working weekends to get the project done. Thank you for your hard work, positive attitudes, and dedication to the Big Plot dream. I cannot imagine a more fun, supportive, and intelligent lab; I am incredibly grateful to all of you.

The installation of the UFDP required a massive amount of field work, roughly 7,000 hours over the course of three summers. Thank you to the hard working field crews and volunteers: Maya Akpinar, Matt Bishop, Alex Chacon, Joseph Cooper, Katie Hogan, Drew Foster, James Freund, Will George, Martin Holdrege, Drew Jensen, Gillian

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Lastly, thank you to my family Phil, Bev, and Kinsey. You have given me unwavering love and support for the past 27 years; there is no way I can fully express my immense love and gratitude for you. You instilled a love of the natural world in me at a young age, you stoked my passion for science, and you gave me the means and ambition to pursue my education; you are the reason I am here, and I am forever grateful.

Tucker J. Furniss

CONTENTS

	Page
ABSTRACT	iii
PUBLIC ABSTRACT	v
DEDICATION	vii
ACKNOWLEDGMENTS	viii
LIST OF TABLES	xii
LIST OF FIGURES	xiii
INTRODUCTION	1
STUDY AREA	5
Site Description.....	5
Geology and Soils.....	5
Climate.....	7
Flora	8
Disturbance History	10
Human Use.....	11
METHODS	13
Plot Establishment	13
Surveying	13
Field Sampling of Trees, Shrubs, Snags	14
Analyses	15
Species Abundance Distribution.....	15
Functional Equivalence.....	16
Ecological Equivalence.....	18
Species-Habitat Associations.....	19
Spatial Patterns.....	23

	xi
RESULTS	27
Structure, Composition, and Spatial Patterns	27
Neutral Theory in a Temperate Forest	30
Species Abundance Distribution.....	30
Functional Equivalence.....	30
Ecological Equivalence.....	33
Species-Habitat Associations.....	35
DISCUSSION.....	38
Species Abundance Distribution.....	38
Functional Equivalence.....	39
Ecological Equivalence.....	42
Species-Habitat Associations.....	43
CONCLUSIONS.....	47
REFERENCES	50
APPENDICES	68
Appendix: Supplemental Figures and Tables	69

LIST OF TABLES

Table		Page
1	Trees and shrubs ≥ 1 cm dbh, snags ≥ 1 cm dbh, and live <i>Pinus</i> spp. seedlings < 1 cm dbh and ≥ 2 years old in the Utah Forest Dynamics Plot.....	29
2	Demographic rates for species within the Utah Forest Dynamics Plot	32
3	Species-habitat associations within the Utah Forest Dynamics Plot	36
A1	Habitat types within the Utah Forest Dynamics Plot.....	78

LIST OF FIGURES

Figure	Page
1	6
2	8
3	21
4	28
5	31
5	33
6	34
7	37
A1	70
A2	71
A3	72
A4	73
A5	74

		xiv
A6	Stem locations of principal tree species ≥ 1 cm dbh in the Utah Forest Dynamics Plot.....	75
A7	Survey monuments, control loops, and grid corners in the Utah Forest Dynamics Plot.	76
A8	Examples of the markers used for permanent survey monuments in the Utah Forest Dynamics Plot.	77

INTRODUCTION

One of the most notable ecological theories advanced in recent years is the Unified Neutral Theory of Biodiversity, which posits ecological equivalence between trophically similar species and assumes neutrality as a first approximation for investigating ecological processes (Hubbell 2001, 2005). The idea of equivalence between species stands in stark contrast to niche theory which relies on species differences and stabilizing mechanisms to maintain diversity (Grime 1977, Tilman 1985, Chesson 2000). Despite its radical approach, neutral theory has performed surprisingly well in its ability to model observed patterns in relative species abundance (Volkov et al. 2005), species-area relationships (Rosindell and Cornell 2009), and species coexistence (Hubbell 2006) in tropical forests. Much has been written in both support and opposition of neutral theory (McGill 2003*a*, Volkov et al. 2005, Ricklefs and Renner 2012), but the implementation of neutral models has proven to be revealing whether the underlying phenomena are found to be neutral or not (Chave et al. 2002, McGill et al. 2006, Rosindell et al. 2012).

Recent theoretical advancements have begun to reconcile the opposing concepts of niche and neutral theories by considering them as two ends of a continuum rather than as mutually exclusive paradigms (Chave 2004, Gravel et al. 2006, Adler et al. 2007). This niche-neutrality gradient hypothesis has enabled researchers to quantify the relative importance of niche and neutral processes in different ecosystems rather than simply refuting one theory or the other, advancing our understanding of global patterns in diversity (Condit et al. 2006, Weiher et al. 2011, Myers et al. 2013, Kubota et al. 2016).

Despite the prevalence of investigations of neutral theory in tropical systems, there have been very few tests in temperate forests. While studies in temperate grasslands (Adler 2004, Fargione et al. 2003, Harpole and Tilman 2006) and temperate forest understories (Gilbert and Lechowicz 2004, Kern et al. 2012) have found support for the dominance of niche processes, the few studies that consider temperate forest tree diversity have found contradictory results (Shibata et al. 2010, Wang et al. 2011, Myers et al. 2013, Masaki et al. 2015, Qiao et al. 2015). To elucidate the relevance of niche and neutral processes in temperate forests and to begin to unify the inconsistent results of previous studies, I address neutral theory in the extreme environment of a high-elevation subalpine forest. By assessing the relative importance of niche and neutral processes in a forest at the local elevational limit of forest cover, this study contributes to the developing body of work aimed at identifying which environmental characteristics determine the relative importance of niche and neutral processes, a necessary step in the synthesis of community ecology theory (Weiher et al. 2011, Kubota et al. 2016).

In this study, I take a robust approach to assessing the relevance of neutral theory in temperate forests by not only testing a prediction but also examining the underlying assumptions of neutral theory. Testing a neutral theory prediction makes this study directly comparable with previous studies, while addressing the underlying assumptions will yield insight into the relative strengths of niche and neutral processes.

Perhaps the most frequently tested prediction of neutral theory is the fit of a neutral model to observed species abundance distributions (Hubbell 2001, 2006, Chave et al. 2002, Volkov et al. 2003, 2005, McGill 2003a, summarized by McGill et al. [2006] and Chave [2004]). This previous work has posited the form of the species abundance

curve to be either a neutral zero-sum multinomial distribution (ZSM) or a non-neutral lognormal distribution, but these models have not been compared in a species-limited subalpine forest. In contrast to species abundance distributions, the underlying assumptions of neutral theory are rarely tested directly (sensu Fargione et al. 2003, Chave 2004, Harpole and Tilman 2006). I therefore developed tests for three fundamental assumptions of neutral theory:

- 1) Species are *functionally equivalent* in terms of recruitment rate, mortality rate, and dispersal ability (Hubbell 2005).

- 2) Species are *ecologically equivalent*. Ecological equivalence implies that interspecific interactions should be symmetric, and species identity of neighboring stems has no effect on competitive interactions (Chave 2004, Hubbell 2006). In tropical systems, interspecific interactions are often considered to be primarily competitive, but as facilitative interactions have been found to be important in subalpine ecosystems (Callaway 1998, Holmgren and Scheffer 2010), ecological equivalence should extend to positive as well as negative interactions.

- 3) Species are *habitat generalists*. Neutral theory posits that if species are functionally and ecologically equivalent, species will show no preference for one habitat type over another. A strength of this hypothesis is its ability to explain the high number of species that have converged on shade-tolerant life history strategies (e.g., Memiaghe et al. 2016) and occupy essentially the same functional group in tropical forests (Hubbell 2005). Neutral theory suggests competitive exclusion is prevented due to strong dispersal and recruitment limitation, allowing functionally similar species to coexist indefinitely (Hubbell et al. 1999, Hubbell 2006). Niche theory, in contrast, relies on habitat

heterogeneity and niche partitioning to explain species coexistence (Tilman 2004), which leads to the expectation that most species will be habitat specialists, and species diversity should be distributed equally across niche space.

To determine the relative importance of niche and neutral processes in structuring subalpine forest diversity, I established the Utah Forest Dynamics Plot (UFDP), a 13.64-ha permanent forest research plot located at 3,091 m on the Colorado Plateau, and within the plot quantified composition, structure, spatial patterns, and habitat associations of every woody stem ≥ 1 cm diameter at breast height (1.37 m; dbh). I implemented protocols and database standards consistent with the Smithsonian ForestGEO global plot network (pioneered at Barro Colorado Island, Panama, Hubbell and Foster 1983, 1986) to permit comparisons with other forest types and to extend our findings at the UFDP to ecological theory in a global context (Condit et al. 2014, Anderson-Teixeira et al. 2015, sensu Rees et al. 2001, Lutz 2015).

STUDY AREA

Site Description

The UFDP is located on the Markagunt Plateau in southwestern Utah, on the western edge of the Colorado Plateau bioregion (Fig. 1A), in a mixed-conifer/aspen forest on the north rim of Cedar Breaks National Monument (Fig. 1B). The plot is 13.6 hectares in size, with elevations ranging from 3020 m to 3169 m for a vertical relief of 149 m (North American Vertical Datum of 1988). Slopes range from 0° to 54°, with a mean of 19°. The plot is centered at 37.661 N 112.852 W (North American Datum of 1983 [NAD83]), with dimensions of 460 m east to west and 360 m north to south, aligned to the north-south lines of the Universal Transverse Mercator grid. The north edge of the plot is constrained by the boundary between Dixie National Forest and Cedar Breaks National Monument, and the south and east edges of the plot are constrained by the steep cliffs of the Cedar Breaks amphitheater. This research was performed under National Park Service research permits CEBR-2014-SCI-0001, CEBR-2015-SCI-0001, and CEBR-2016-SCI-0001.

Geology and Soils

Markagunt Plateau geology is a layered patchwork of sedimentary and volcanic deposits, shaped by plate tectonics, landslides, and erosion to create a heterogeneous and conspicuously scenic landscape. The most prominent geologic layer in the UFDP is the Claron Formation, derived from sedimentary material deposited in the late Paleocene and Eocene eras (56 – 36 million YBP). The Claron Formation is composed of fluvial,

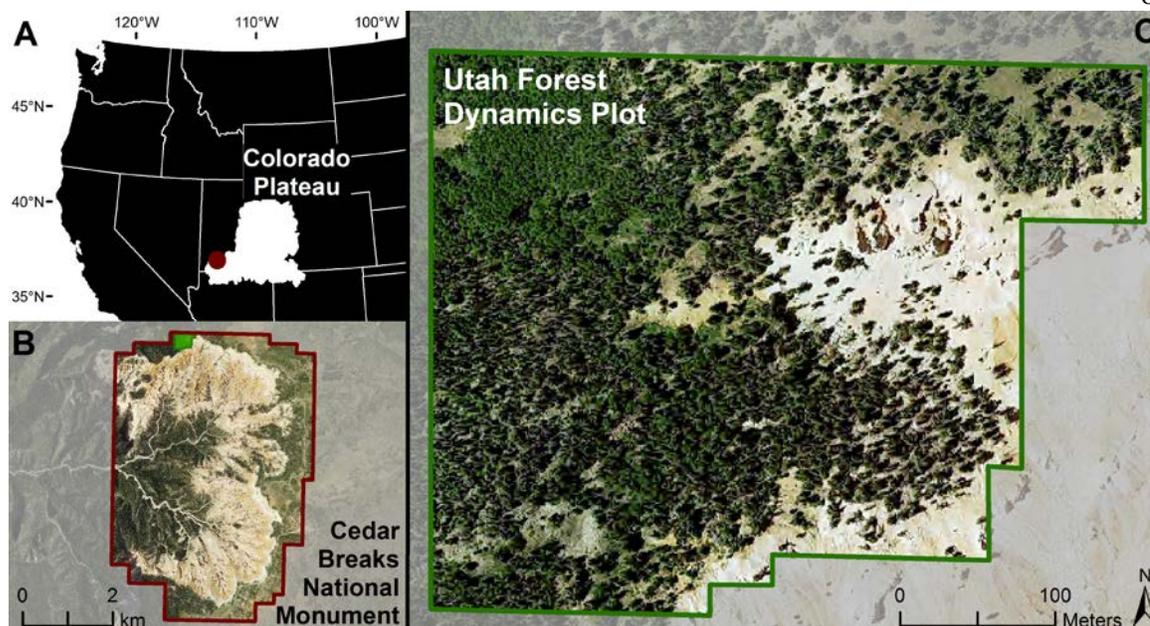


FIG. 1. Location of the Utah Forest Dynamics Plot (UFDP). The UFDP is located on the Colorado Plateau in the state of Utah (A) in Cedar Breaks National Monument (B) on the north side of the Cedar Breaks amphitheater (C). The UFDP comprises 13.6 ha of late-successional aspen/mixed-conifer subalpine forest, and is bounded on the southeast by the cliffs of the Cedar Breaks amphitheater. Orthoquad from National Agricultural Imagery Program (NAIP; USDA Farm Service Agency 2014).

floodplain, and lacustrine calcareous deposits of mudstone, siltstone, sandstone and limestone that have eroded into the colorful canyons and hoodoos of Cedar Breaks National Monument (Goldstrand 1994, Rowley et al. 2013). The remainder of the UFDP is characterized by more recent Pleistocene and Holocene landslide deposits. These pre-historic, historic, and recent landslides result in talus slopes and colluvial accumulations of Claron Formation and volcanically-derived Brian Head Formation parent material.

Soils in the UFDP exhibit the same degree of complexity and heterogeneity as does the geology. There are 12 distinct soil families representing four soil orders: Mollisols, Alfisols, Inceptisols, and Entisols. The soils are predominantly superactive and well drained, and with depths ranging from shallow to very deep. Parent materials are

mostly sedimentary, with lesser amounts of volcanic rocks and basalt; frequent landslides result in most soils forming in colluvium, residuum, or slope alluvium (US Forest Service 1996, Tendick et al. 2011).

Climate

Climate in the UFDP is characterized by short, cool summer growing seasons and long, cold winters. Weather patterns for most of the year originate over the Pacific Ocean, but July and August often experience a spike in precipitation due to the North American monsoon which brings in masses of moist air from the eastern Pacific Ocean, Gulf of California, and Gulf of Mexico (Mock 1996, Adams and Comrie 1997; Fig. 2A). Climate normals for the UFDP between 1981 and 2010 reflect temperature ranges from -11.2°C to -0.6°C in January and from 6.9°C to 20.5°C in July (PRISM 2016, 800 m grid; Fig. 2A). Mean annual precipitation is 84.9 cm, with 54% falling during winter months as snow (Fig. 2B). Thornthwaite-type water-balance models (Thornthwaite and Mather 1955, sensu Lutz et al. 2010) show low levels of annual climatic water deficit (Deficit; 81 mm; Fig. 2B), that have, however, been increasing over the 30-year period from 1981 to 2010 (Fig. 2C).

Climate influences disturbance regimes in Colorado Plateau subalpine forests (Swetnam and Betancourt 1998, Schoennagel et al. 2004). Recent warming temperatures in subalpine forests in the western US have increased duration and intensity of drought (Breshears et al. 2005, Williams et al. 2010), frequency and extent of fire (Bessie and Johnson 1995, Schoennagel et al. 2004, 2007, Littell et al. 2009), and magnitude of bark beetle outbreaks (Bentz et al. 2010, DeRose et al. 2013, O'Connor et al. 2015).

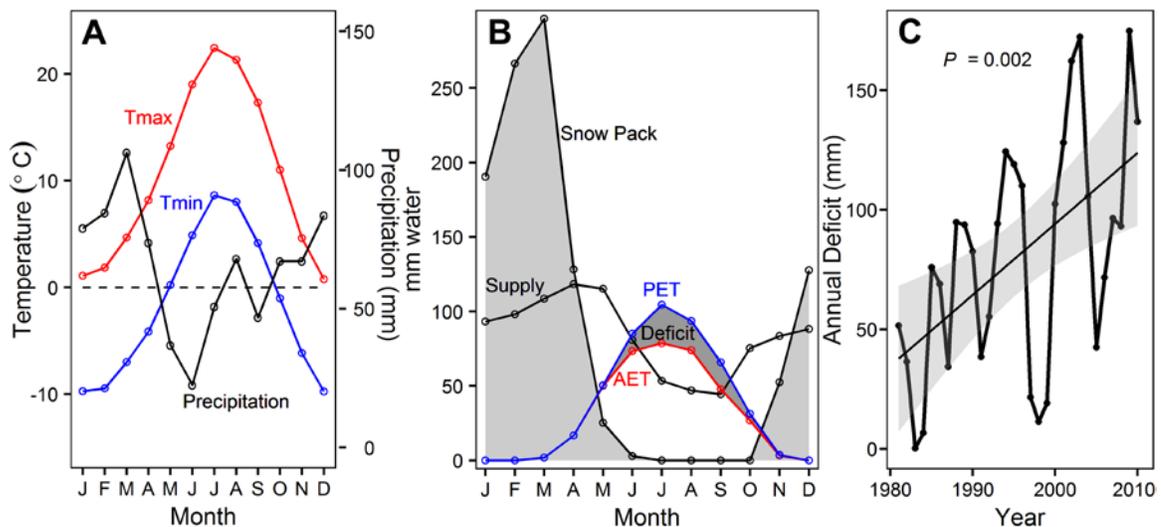


FIG. 2. Climate, water balance, and increasing climatic water deficit for the Utah Forest Dynamics Plot (UFDP) calculated from PRISM climate normals (800 m grid; PRISM 2016). Thirty-year climate averages for the UFDP from 1981 to 2010 calculated using monthly PRISM data (4 km grid; PRISM 2016). Precipitation falls mostly as snow during winter months, but the North American monsoon creates a spike in precipitation during July and August. Thornthwaite-type water balance models show that potential evapotranspiration exceeds actual evapotranspiration from June through September, but a deep snowpack and mid-summer monsoonal precipitation contribute to water supply in summer months and make for a relatively mild summer drought (B), which has been increasing between 1981 and 2010 (C).

Flora

Vegetation in the UFDP includes forest types from the Rocky Mountain Subalpine-High Montane Conifer Forest Macrogroup (US National Vegetation Classification System 2016 [USNVC]). Vegetation on gentle slopes in the highest elevation portion of the UFDP is characterized by a mosaic of open meadow and dense patches of *Abies lasiocarpa*-*Picea engelmannii*/*Ribes montigenum* (subalpine fir-Engelmann spruce/mountain gooseberry) forest. Vegetation on steep, rocky slopes and near the cliff edges is dominated by *Pinus flexilis*-*Pinus longaeva* (limber pine-Great Basin bristlecone pine) Intermountain Basins Subalpine Woodland Group and *Pinus*

longaeva Woodland. North-facing aspects and gentler slopes are characterized by *Populus tremuloides/Thalictrum fendleri* (quaking aspen/Fendler's meadowrue) Forest, *Populus tremuloides-Abies lasiocarpa*/Tall Forbs Forest, *Populus tremuloides-Abies lasiocarpa/Juniperus communis* (common juniper) Forest, and *Abies lasiocarpa-Picea engelmannii/Juniperus communis* Woodland (Jennings et al. 2009, Tendick et al. 2011). Vegetation types were identified based on the National Park Service Vegetation Classification and Mapping Project (Tendick et al. 2011) and field observations, and classified according to the USNVC. Hereafter, nomenclature follows Flora of North America (1993+), most notably considering interior subalpine fir as *Abies bifolia* rather than *Abies lasiocarpa*.

Vegetation in the UFDP is characteristic of the surrounding areas to the north and east. Areas to the south and west, however, rapidly decrease in elevation and are characterized by distinctly different vegetation types including *Pinus ponderosa-Pseudotsuga menziesii* Woodland, *Abies concolor-Arctostaphylos patula* Forest, and *Cercocarpus ledifolius* Woodland (Tendick et al. 2011). Given the proximity to a lower elevation species pool, propagules from this warmer habitat are dispersed by wind or birds into the UFDP on a presumably regular basis.

Few studies have reported demographic rates for subalpine forests on the Colorado Plateau. Rebertus et al. (1992) found mortality rates of 0.1% for *Picea engelmannii* and 0.4% for *Abies bifolia*. Stephenson and van Mantgem (2005) synthesized existing research for a wide range of forest types and elevations and established an average turnover rate of 0.8% for forests at 3,000 m (their Fig. 3).

Disturbance History

The UFDP and surrounding region are characterized by infrequent, high-severity fires with a fire return interval of approximately 350 years (Baker and Veblen 1990, Veblen et al. 1994, Schoennagel et al. 2004, Morris et al. 2013), but past fires on the Markagunt Plateau were patchy across the landscape (DeRose and Long 2012), likely with high proportions of unburned forest (Kolden et al. 2012, 2015). Due to the patchiness of historic disturbances on the Markagunt Plateau, it is likely that no single historic disturbance caused homogenous stand-initiation across the UFDP, resulting in an uneven-aged forest. Veblen (2000) and Kulakowski and Veblen (2006) provide evidence for uneven aged stands in similar forest types. Extremely old *Pinus flexilis* and *Pinus longaeva* are found near the cliff edge and on open talus slopes. These landscape positions feature low tree density and almost no surface fuels, which would buffer these trees from fire (excepting lightning strikes, evidenced by fire scars on some *Pinus* individuals). The maximum age of *Pinus flexilis* and *Pinus longaeva* in the UFDP is currently unknown, but *Pinus longaeva* in other parts of Cedar Breaks National Monument are over 1,600 years old (Schulman 1956, Ferguson and Graybill 1985). Parts of the plot with dense *Abies bifolia*-*Picea engelmannii* forest are much more susceptible to wildfire, and may have been initiated by a stand replacing fire about 250 year ago (based on data from DeRose and Long 2012; the full range of stand ages for their 11 study sites on the Markagunt Plateau was 200-350 years).

Historic beetle disturbance in this region has been characterized by non-stand-replacing levels of endemic bark beetle activity, with localized outbreaks that can cause high levels of mortality for the host species. The most important bark beetle species in the

UFDP are *Dendroctonus rufipennis* (spruce beetle), *Dryocoetes confusus* (western balsam bark beetle), and *Dendroctonus ponderosae* (mountain pine beetle), affecting *Picea engelmannii*, *Abies bifolia*, and *Pinus flexilis*, respectively. Prior to 1990, there was little evidence of stand-replacing beetle outbreaks on the Markagunt Plateau; most stands were established after fire, and beetle activity was not found to be a major antecedent disturbance (DeRose and Long 2007, DeRose and Long 2012). However, severe spruce beetle outbreak from 1986 to 1998 (Dymerski et al. 2001) resulted in *Picea engelmannii* mortality as high as 98% of stems >5 cm dbh (DeRose and Long 2007).

Human Use

There is archeological evidence of Native American presence on the Markagunt Plateau since the Archaic period (8,000 to 1,500 YBP; Fowler and Madsen 1986, Canaday et al. 1999). The Markagunt Plateau was primarily used seasonally for hunting, fishing, and chert collection (from Brian Head peak, 3 km northeast of the UFDP). The colorful landscape of Cedar Breaks was also considered a place of spiritual significance for some Southern Paiute tribes (Canaday 2001, Tendick et al. 2011). As this area was not permanently inhabited, pre-historic human impact in the UFDP would have been minimal.

European settlement in the region began when Mormon settlers colonized Cedar City and Parowan in the 1850s and began exploring the Markagunt Plateau area for resources (Canaday 2001). By 1900, herds of cattle and sheep were common atop the plateau during summer months, and numerous small sawmills milled timber in the high country for construction in Parowan and Cedar City (Canaday 2001).

Federal management of the area around the UFDP began in the 1890s with the General Revision Act of 1891 and the Organic Act of 1897 creating the National Forest Reserves. The Dixie National Forest, encompassing Cedar Breaks and much of the Markagunt Plateau, was created in 1905 by the General Land Office. This changed land use on the plateau, imposing federal regulations on mining, grazing, and logging (Canaday 2001). Franklin Delano Roosevelt designated Cedar Breaks National Monument on Aug. 22, 1933 (Proclamation No. 2054), and the UFDP has been free from grazing and logging since that time (Tendick et al. 2011).

METHODS

Plot Establishment

The installation of the UFDP required a great deal of effort over the course of three years. I estimate the combined efforts of the 24 people who worked in the field total 2,300 hours of land survey, 4,080 hours of tagging and mapping stems, 530 hours of recruitment and mortality census, and 560 hours of data entry.

Surveying

We conducted a land survey using Total Stations with accuracy of 3-5 seconds of arc (Topcon OS105, Topcon GTS312) to establish a sampling grid for mapping stem locations. To reference this grid to a global datum, we installed seven permanent survey monuments (Berntsen A130 30" Aluminum Survey Monument) distributed across the plot using static global navigation satellite system (GNSS) receivers (Topcon HiPer SR) mounted on survey tripods logging positional data for a minimum of four hours. From these monuments, we surveyed 16 control loops throughout the plot which we used to install permanent quadrat markers on a 20 m grid. The GNSS data for our seven survey-grade monuments was post-processed using base station data from the nearest Continuously Operating Reference Stations (CORS; base station IDs: P009, SGU1, FRED, NVPI; 80 to 130 km from the UFDP) using the Online Positioning User Service (NOAA 2014), only fixing final coordinates for monuments that met our desired level of accuracy. Raw Total Station data was combined with the processed GNSS baselines, and post-processed using a Star*net least-squares adjustment (MicroSurvey Software Inc.). In addition to our land survey methods, we used Real Time Kinematic methods with a pair

of GNSS receivers (Topcon HiPer SR) to install 21 grid points. Mean standard deviations of the error ellipses for the final positions to the datum were: 5 mm horizontal and 11 mm vertical for survey monuments; 10 mm horizontal and 12 mm vertical for control loops; and 14 mm horizontal and 14 mm vertical for grid corners (see also Knox and Lutz 2015).

Field sampling of trees, shrubs, and snags

In the summers of 2014, 2015, and 2016 we tagged and mapped all live and dead trees and shrubs ≥ 1 cm dbh (1.37 m). We followed methods of Condit (1998), with some alterations to maintain consistency with companion plots in Yosemite, CA (Yosemite Forest Dynamics Plot; Lutz et al. 2012) and Wind River, WA (Wind River Forest Dynamics Plot; Lutz et al. 2013). We nailed conifers at the point of measurement when possible using 3" ring shank nails (Simpson Strong Tie S10ABN), and wired trees that were too small to accept a nail using (Malin MS20995-C). All tags, nails, and wire were 304 stainless steel which does not contain bioavailable micronutrients and withstands fire. All trees that were not nailed at the point of measurement were marked with permanent marker (Sharpie) and paint stick (Markal B Paintstik 80227) at the point of measurement. Trees near the public trail that runs through the plot were nailed on the opposite side of the bole and near the ground to reduce visibility. *Populus tremuloides* were tagged at 0.37 m to avoid inaccurate subsequent measurements due to swelling at the nail. Shrubs, fir-skirts, and multi-leader *Pinus longaeva* were given one tag per ground ramet and the number of additional branches was recorded. We measured diameter, height, snag decomposition class, snag top diameter, and species for all snags ≥ 1 cm dbh. We tagged and mapped all live *Pinus* seedlings (>1 year old), burying tags in

surrounding soil or rocks to reduce elevated heat conductance associated with the metal of the tag.

Trees were mapped using handheld lasers (Laser Technologies Inc., Impulse 200 LR), mirror compasses, and transect tapes stretched between quadrat corners. We recorded distance along the transect tape and perpendicular distance to the rooting location of each stem. Tree positions were calculated by adjusting perpendicular distance measurements for tree diameter (assuming vertical and cylindrical boles) and slope-adjusting transect distance using the 3-dimensional coordinates of each quadrat marker.

Analyses

Species Abundance Distribution

I tested the prediction of neutral theory that the species abundance distribution follows a zero-sum multinomial distribution (Hubbell 2001, Volkov et al. 2003). I compared this model with a common alternative, the lognormal distribution (Chave et al. 2002, McGill 2003*a*), to determine which distribution provided the best fit. I used all live stems ≥ 1 cm dbh within the UFDP for a total of 17 species. I ranked species according to decreasing abundance and plotted log-transformed abundance for each species as the response variable (sensu McGill 2003*a*, Hubbell 2006). I used observed species abundance to parameterize both models, then calculated AIC, χ^2 , and Kolmogorov-Smirnov goodness-of-fit metrics of each curve (sensu Matthews and Whittaker 2014). I also generated a species abundance distribution using log-transformed abundance as the predictor variable and number of species as the response (sensu McGill 2003*a*, Volkov et

al. 2003, 2005, Chave 2004). All analyses were performed in R version 3.1.2 (R Core Team 2014) and the abundance distribution used the ‘sads’ package (Prado et al. 2016).

Functional Equivalence

Demographic Rates

I tested the assumption of functional equivalence by calculating demographic rates for all principal tree species (density ≥ 10 stems ha^{-1}). In the summer of 2016, we conducted a mortality and recruitment survey for those stems originally mapped in 2014 and 2015, and I used these data to calculate annually compounded recruitment and mortality based on a two-year interval for quadrats that were first censused in 2014, and on a one-year interval for quadrats first censused in 2015. I compared demographic rates by calculating mortality and recruitment rates per species for individual hectares within the UFDP, and comparing these rates for each species to overall rates for all other stems with Welch’s two-sample *t*-tests. I assessed significance at $\alpha = 0.004$ (Bonferroni adjusted $\alpha = 0.05$ for 12 tests).

Dispersal Processes

I further examined the functional equivalence assumption by assessing the net effects of dispersal and recruitment processes on the spatial patterns of adult and juvenile individuals for each species. Based on the descriptions of diameters at reproductive maturity for each species (*Abies lasiocarpa*, Alexander et al. 1990; *Picea engelmannii*, Alexander and Shepperd 1990; *Picea pungens*, Fechner 1990; *Populus tremuloides*, Perala 1990; *Pinus flexilis*, Steele 1990) and a preliminary analysis of the diameter distribution in the UFDP, adults were defined as individuals ≥ 20 cm dbh and juveniles

were defined as individuals <5 cm dbh. Although this approach does not permit isolation of specific mechanisms influencing dispersal and recruitment, it allows me to compare the cumulative effects of dispersal and recruitment processes on resulting spatial patterns.

For each species, I used the univariate pair-correlation function (PCF; see Spatial Patterns below) to summarize the spatial patterns of juveniles and compared this to a simulation envelope generated according to a random labelling null model to determine if recruitment of juveniles is more aggregated than the overall pattern of all stems. I used the bivariate form of the PCF to summarize the relationship between juveniles and adults, and compared the observed patterns to null models generated according to independence and random labelling null models. By comparing the bivariate patterns to an independence null model, I investigated whether the patterns of juveniles are dependent on the patterns of adults. If the patterns are not independent, we can infer dispersal and recruitment processes have *a priori* effects on the spatial patterns of juveniles. I then compared the bivariate patterns to random labelling null models, allowing me to infer whether proximity to adults has *a posteriori* effects on the spatial pattern of juveniles via density-dependent mortality processes (see Null Models, below).

Under the null hypothesis of neutrality, I expect these spatial patterns to be consistent among all species. For any species that shows a different pattern of recruitment, I must reject the null hypothesis, indicating some dispersal or recruitment processes is species-specific. I performed a sensitivity analysis on specific diameter cutoff values throughout a $\pm 50\%$ range of diameter thresholds (e.g., defining juveniles as <2 cm dbh to <10 cm dbh and defining adults as ≥ 10 cm dbh to ≥ 30 cm dbh). For genus *Pinus*, I repeated this analysis with adult trees ≥ 20 cm dbh and seedlings >1 years old and

<1 cm dbh. This is a novel application of point pattern analysis, and among the first studies of neutral theory to use spatial patterns to test the assumption of functional equivalence

Ecological Equivalence

I assessed competitive equivalence by comparing the patterns of mortality with the null hypothesis of random mortality (sensu Kenkel 1988). I used random labelling techniques to control for the overall pattern of each species. This technique allowed me to determine whether the probability of mortality for an individual of one species was affected by the presence of live individuals of another species, thus assessing competitive equivalence for each species pair while controlling for the overall degree of segregation or attraction between the spatial patterns of two species. Although this method does not enable me to evaluate the strength of competition between species, my objective was to determine the net result of competitive interactions on mortality for each species. Neutrality may be maintained as long as each species that is influenced by the presence of another has a symmetric effect on that other species; neutrality will be rejected for every species pair that demonstrates asymmetric competition or facilitation. The attraction between live and dead stems may arise in two ways: first, the presence of a live stem of species A may increase the probability of mortality for species B (competition-related mortality); second, the presence of a dead stem of species B may increase the probability of recruitment for species A (dead-wood facilitation sensu Maher et al. 2015). My methods do not permit me to clearly distinguish between these two processes, but isolating specific mechanisms is not necessary to simply evaluate the degree of symmetry between species pairs. I included all tree species with >50 stems in my analyses of

functional equivalence and ecological equivalence because point pattern analysis requires a sufficient number of points to detect significant patterns. This minimum sample size was chosen based on cutoff values used in other studies (70 stems, Wiegand et al. 2007a; 50 stems, Wang et al. 2010; 50 stems, PUNCHI-MANAGE et al. 2015).

Species-Habitat Associations

I identified habitat types for each quadrat according to parent soil type and aspect (considering four neighboring cells, following methods of Horn [1981]). I classified aspect into two categories to avoid over-parsing habitat types. Aspects between 135° and 225° that receive the most direct solar incident radiation were considered “south-facing”, while aspects >225° and <135° were grouped together considering the reduced amount of sun exposure at these sites. As temperature and direct solar radiation may be of equal or greater importance than water availability in structuring high-elevation vegetation communities (Körner and Paulsen 2004), I grouped aspects according to solar incident radiation (greatest at 180°) rather than heat load (greatest at ~225°, McCune and Keon 2002).

Parent soil type was derived from the geologic map of the Brian Head Quadrangle (Rowley et al. 2013). The map was first georeferenced using ArcGIS version 10 (ESRI 2011), then parent soil type was assigned to each quadrat based on geologic layer underlying the center of each quadrat. There are five distinct parent soil types: three sedimentary layers and two types of landslide deposits. In order of descending geologic layer (and increasing geologic age), the three sedimentary layers were: Tcwt – the uppermost mudstone, siltstone, and sandstone unit of the white member of the Claron formation; Tcwu – the upper limestone unit of the white member of the Claron formation;

and Tcwm – the middle mudstone, siltstone, and sandstone unit of the white member of the Claron formation. The two landslide deposit layers were Qms1 and Qms2; Qms1 rests beneath the Brian Head formation sedimentary layer and the Tcwm layer of the Claron formation, while Qms2 is positioned beneath the Tcwm and Tcwu layers of the Claron formation. Both landslide layers were Pleistocene to Holocene-age accumulations of colluvium and talus, but their spatial segregation on the geologic map indicates that the two layers may differ in parent material and time since landslide activity. I classified habitat types according to these five parent soil types and two aspect categories for a total of 10 possible habitats. Habitats that covered less than 0.2 ha were categorized based only on parent soil type, resulting in a total of eight distinct habitat types (Fig. 3, Fig. A1).

Species-habitat associations were assessed for all species with densities >1 stem ha^{-1} , and significant associations were determined using χ^2 tests and torus-translation tests (sensu Harms et al. 2001). As previous studies have found that these two methods vary in their ability to detect habitat associations, based on the unique characteristics of species' distributions and shapes of habitat types (Harms et al. 2001, Plotkin et al. 2000, Wiegand and Moloney 2013), I implemented both methods to ensure these results were not subject to the sensitivities of a single test. This also allows me to compare the results of these two tests, providing insight into the relative strengths and weaknesses of both methods.

To investigate the effect of habitat type on forest structure, I calculated density, basal area (BA), and α -diversity for each habitat type and each individual $20 \text{ m} \times 20 \text{ m}$ quadrat. For species with abundance ≥ 10 stems ha^{-1} that showed habitat associations, I compared BA per stem of the focal species within their associated habitat to BA per stem outside of the associated habitat. This allowed me to determine if habitat associations

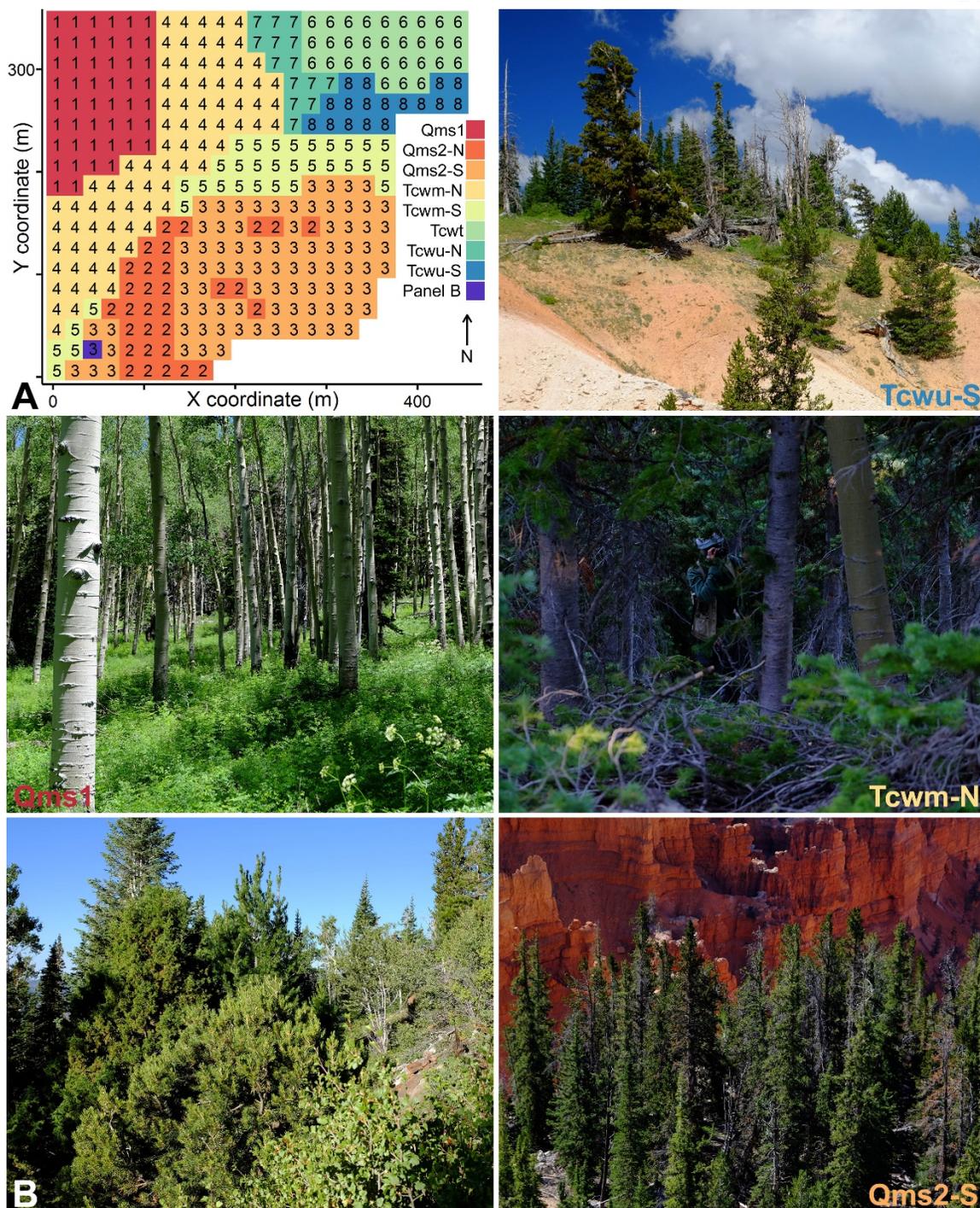


FIG. 3. Vegetation in identified habitat types classified according to geologic parent material and slope aspect within the Utah Forest Dynamics Plot (A). Numbers correspond to Map Class column in Table A1. Images depict distinct vegetation communities associated with four habitat types. Image (B) shows an open, south-facing slope with high α -diversity due to immigration of lower-elevation species.

influenced not only the abundance of certain species, but also the performance of individual stems within habitat types. Significant differences in density, BA, and BA per stem were determined using Wilcoxon rank-sum tests ($\alpha = 0.05$). To account for multiple tests, I used a Bonferroni correction. Adjusted $\alpha = 0.00625$ for density, BA, and α -diversity of each habitat type ($n = 8$ habitat types), and adjusted $\alpha = 0.00833$ for BA per stem ($n = 6$ species-habitat associations for abundant species).

Chi-squared tests

I performed χ^2 tests by comparing observed abundance of each species in each habitat type to expected values under the null model of even distribution throughout the plot. Expected values for each unique species–habitat combination were calculated according to the equation $E_{i,j} = \frac{(n_i \times n_j)}{N}$, where n_i is the number of stems of the focal species i in all habitats, n_j is the number of stems of all species within the focal habitat j , and the total number of all stems in all habitats is N . I conducted χ^2 goodness-of-fit tests for each species-habitat combination at $\alpha = 0.05$, and used the conservative critical value $\chi^2_{k=7} = 14.07$ to account for all eight habitats.

Torus-translation tests

Torus-translations were conducted following the methods of Harms et al. (2001; see also Gunatilleke et al. 2006). This test quantifies observed abundance of each species in each habitat type, and compares these observed values to abundance values calculated for a set of simulated habitat maps. These simulated maps were generated by systematically shifting the entire map of habitat types according to a two-dimensional torus pattern while keeping the spatial locations of all stems constant. Each 20 m

increment of the toroidal shift created a unique distribution of habitat types across the plot, but maintained the same relative cover of each habitat type. I conducted all possible 20 m torus translations resulting in 414 simulated habitat maps, and compared the observed abundance of each species per habitat type to the abundance values generated for the simulated habitat maps. Positive (negative) habitat associations were considered significant at $\alpha = 0.05$ (two-tailed) if observed abundance was higher (lower) than simulated abundance in $>97.5\%$ of the torus-translation maps. Species-habitat associations implemented code from Harms et al. (2001) and used the R raster package version 2.4-18 (Hijmans 2015).

Spatial Patterns

Summary Statistics, Heterogeneity, and Simulation Envelopes

I quantified spatial patterns using univariate and bivariate forms of the pair correlation function (PCF), $g(r)$, a spatial statistic closely related to the derivative of Ripley's K function (Wiegand and Moloney 2004). The PCF counts the number of points within radius r of each point in an observed pattern, and compares this count to the theoretical value under various null models (e.g., complete spatial randomness [CSR]). The $g(r)$ function is a second-order summary statistic that describes spatial structure of a point pattern in terms of aggregation and dispersion where r is inter-tree distance, σ^2 is the variance of the Gaussian distribution, and ρ is the intensity of the point pattern:

$$g(r, \sigma, \rho) = 1 + \frac{\exp(-r^2/4\sigma^2)}{4\pi\sigma^2\rho}$$

I used two strategies to control for the first-order effects of environmental heterogeneity within the UFDP and isolate the second-order effects of plant-plant interactions on observed patterns. First, I used the inhomogeneous form of the PCF (Baddeley et al. 2000) which uses a variable estimate of first-order intensity λ to compensate for heterogeneity in observed abundance. In addition, I limited the scale of spatial analyses to 20 m, an estimate of the maximum scale of second-order interactions (Wiegand et al. 2007b), yet smaller than the scale of variability in first-order habitat associations (Harms et al. 2001, John et al. 2007).

I used the univariate form of the PCF to analyze point patterns of live stems for each of the six most abundant species, all species pooled, and all dead stems as of the 2016 census. For the functional equivalency analysis, I used the univariate PCF to summarize the spatial pattern of juveniles of each species, and the bivariate PCF $g(r)_{i,j}$ to test for attraction or repulsion between juveniles and adults. For the ecological equivalency analysis, I used the bivariate PCF $g(r)_{i,j}$ to test for competitive symmetry between species pairs.

Null Models

I compared the observed spatial patterns of live stems for the six principal tree species, all species pooled, and all dead stems to the null model of CSR. Under CSR, $g(r)$ has a value of 1, values >1 indicate aggregation, and values <1 indicate hyper-dispersion. To assess the univariate patterns of juveniles, bivariate interactions between juveniles and adults, and bivariate interactions between species pairs, I used independence and random labelling null models (sensu Wiegand and Moloney 2004). Independence null models are appropriate for bivariate point patterns where the location of each type of points may

result from *a priori* independent spatial processes (Goreaud and Pélissier 2003). I compared the bivariate interactions between juveniles and adults to the null model of independence to assess the role of dispersal and recruitment processes on the spatial pattern of recruitment for each species. Random labelling null models are fundamentally different from the null model of independence; random labelling is used to assess process that act *a posteriori* upon an established pattern rather than the processes that generated the pattern itself. I compared the bivariate interactions between juveniles and adults to random mortality null models to assess the effects of adults on survival of juveniles after effective dispersal and establishment. I also used random labelling null models to assess competitive interactions between species.

Independence null model simulations were generated by maintaining the location of adult stems while randomly shifting the entire pattern of juvenile stems by a random vector. To account for the heterogeneity of observed abundance and irregular shape of the UFDP, I shifted the pattern of juveniles by 20 m and clipped any points that fell outside of the study area. I chose the scale of 20 m because it is large enough to allow me to test for independence at intertree distances 0 to 10 m without generating simulated patterns of juveniles in starkly different habitats within the plot. I repeated the simulation process with shift distances of 40 m and 60 m and found no significant difference in the results.

Random labelling simulations were generated by holding the location of each point fixed while randomly assigning 'marks' to each point where 'mark' refers to a characteristic of a tree, such as size class or live/dead status. Marks were assigned in proportion to their observed abundance. For the competitive interaction analysis, I conducted two tests for each species pair. One test used observed live stems of species A

and randomly labelled dead status for species B, and a second test used the live stems of species B and randomly labelled dead status for species A. Dead stems included snags present at plot establishment and stems that were newly dead in the 2016 census.

For all spatial analyses, I generated 999 simulations according to the relevant null model, and calculated $g(r)$ for each simulated point pattern. Monte Carlo simulation envelopes were generated using the 25th largest (97.5th percentile) and smallest (2.5th percentile) values of $g(r)$ for all 999 simulations, and the theoretical value of $g(r)$ was calculated as the mean of all 1,000 patterns (999 simulations + 1 observed). The resulting null model may be interpreted as the amount of variation in $g(r)$ we would expect if the ecological processes determining the patterns were random.

As dispersal, recruitment, and competitive interactions have been found to be strongest at small-scales (Kenkel 1988, Wiegand et al. 2007*b*, Das et al. 2011, Lutz et al. 2014, Larson et al. 2015), I restricted the scale of the dispersal and competitive interaction analysis to inter-tree distances up to 10 m. All spatial analyses used the spatstat package version 1.46-1 (Baddeley et al. 2015).

RESULTS

Composition, Structure, and Spatial Patterns

In the 13.6 ha of the UFDP, there were 23,177 live stems ≥ 1 cm dbh, with a live tree BA of $33.5 \text{ m}^2 \text{ ha}^{-1}$ (Table 1, Fig. 4). There were 12 tree and five shrub species, representing 10 genera and six plant families. The largest tree was a *Pinus longaeva* of 132 cm dbh (Fig. 4C). All species were native, but I also found *Pinus ponderosa*, *Pinus edulis*, *Abies concolor*, *Juniperus scopulorum*, and *Cercocarpus ledifolius* in the UFDP, above their expected elevation ranges (Oliver and Ryker 1990, Ronco 1990, Noble 1990, Laacke 1990, Gucker 2006). There were 4,425 snags ≥ 1 cm dbh, with a BA of $11.6 \text{ m}^2 \text{ ha}^{-1}$. Individual 400 m^2 quadrat densities ranged from 0 to 8,375 stems ha^{-1} , with a mean density of 1,717 stems ha^{-1} (standard deviation 1,429 stems ha^{-1} ; Fig. 4A). Quadrat BA ranged from 0 to $132.5 \text{ m}^2 \text{ ha}^{-1}$ with a mean of $33.5 \text{ m}^2 \text{ ha}^{-1}$ (standard deviation $20.5 \text{ m}^2 \text{ ha}^{-1}$; Fig. 4B). *Picea engelmannii* was the third most abundant species, though dead BA of *Picea engelmannii* was 1.4 times greater than live BA, presumably due to high mortality rates of mature *Picea engelmannii* during the 1990s spruce beetle outbreak.

Quadrats with the highest density ($>90^{\text{th}}$ percentile of stems per quadrat) were mostly dominated in both abundance and BA by *Abies bifolia*. Quadrats with the highest BA ($>90^{\text{th}}$ percentile of BA) were dominated in BA by *Pinus longaeva*, *Pinus flexilis*, *Populus tremuloides*, and *Picea pungens*. For many of these quadrats, *Abies bifolia* was the most abundant species by density, but it was rarely the dominant contributor to BA. Basal area per quadrat peaked at a density of 500 stems ha^{-1} .

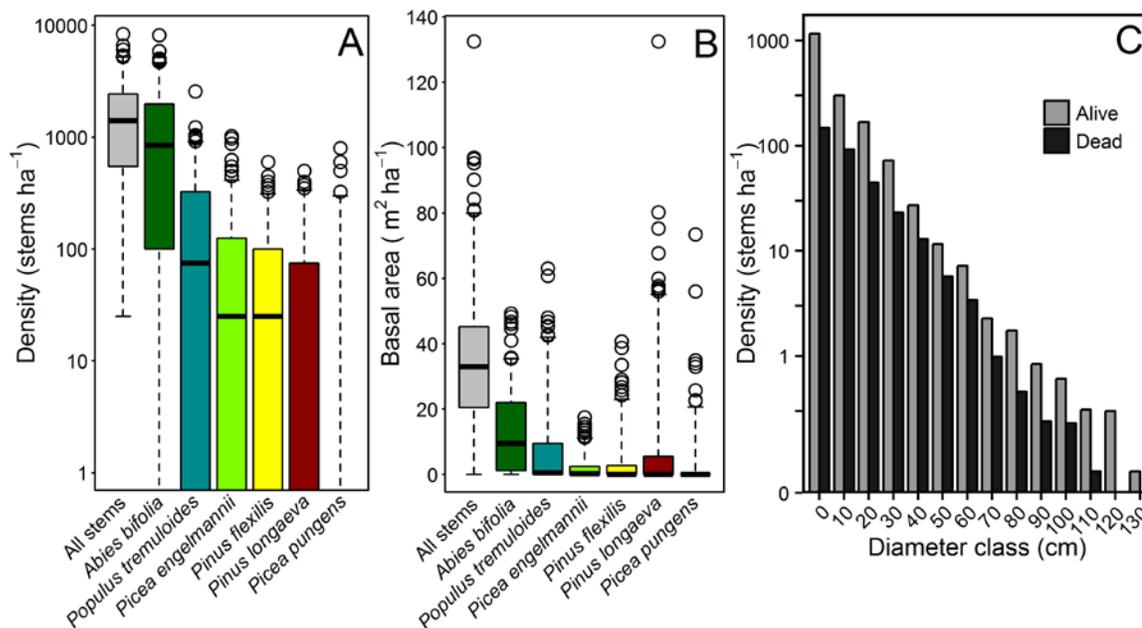


FIG. 4. Density, basal area, and diameter distribution of principal tree species within the Utah Forest Dynamics Plot (UFDP). Each boxplot represents density (A) or basal area (B) by species for all 341 20×20 m quadrats in the UFDP. Boxes indicate the 25th percentile, median, and 75th percentile; whiskers indicate the 2.5th and 97.5th percentiles. The y-axis for the density boxplot is log-transformed. Diameter distribution includes all trees and shrubs ≥ 1 cm diameter at breast height (dbh; 1.37 m) (C); the y-axis is log-transformed stem density and the x-axis is dbh binned into 10 cm classes.

All principal tree species in the UFDP showed clustering at small to intermediate spatial scales (Fig. A2A). *Abies bifolia*, *Populus tremuloides*, *Pinus flexilis*, and *Pinus longaeva* were all strongly aggregated at all distances 0 – 20 m (Fig. A2C, D, G, H), while the patterns of *Picea engelmannii* and *Picea pungens* became random as inter-tree distance approached 20 m (Fig. A2E, F). The test of the random mortality hypothesis found that dead trees were more strongly aggregated than live trees from 0 – 6 m (Fig. A2B).

TABLE 1. Trees and shrubs ≥ 1 cm dbh, snags ≥ 1 cm dbh, and live *Pinus* spp. seedlings < 1 cm dbh and ≥ 2 years old in the Utah Forest Dynamics Plot. Stems were considered live or dead based on their status at establishment.

Species	Family	Density (stems ha ⁻¹)	Basal Area (m ² ha ⁻¹)	Stems ≥ 1 cm dbh	Stems ≥ 10 cm	Stems ≥ 100 cm
Live trees						
<i>Abies bifolia</i>	Pinaceae	1260.19	12.52	17189	4128	-
<i>Populus tremuloides</i>	Salicaceae	201.03	6.88	2742	1983	-
<i>Picea engelmannii</i>	Pinaceae	87.02	1.83	1187	450	-
<i>Pinus flexilis</i>	Pinaceae	62.39	3.03	851	437	1
<i>Pinus longaeva</i>	Pinaceae	53.67	6.86	732	533	15
<i>Picea pungens</i>	Pinaceae	30.21	2.16	412	259	1
<i>Pseudotsuga menziesii</i>	Pinaceae	2.20	0.14	30	14	-
<i>Abies concolor</i>	Pinaceae	1.03	0.04	14	6	-
<i>Cercocarpus ledifolius</i>	Rosaceae	0.66	t	9	3	-
<i>Pinus edulis</i>	Pinaceae	0.51	t	7	-	-
<i>Juniperus scopulorum</i>	Cupressaceae	0.22	0.01	3	2	-
<i>Pinus ponderosa</i>	Pinaceae	0.07	0.01	1	1	-
Live tree total	4 families	1699.2	33.48	23177	7816	17
Live shrubs						
<i>Juniperus communis</i>	Cupressaceae	12.68	t	173	-	-
<i>Ribes cereum</i>	Grossulariaceae	4.77	t	65	-	-
<i>Sambucus racemosa</i>	Adoxaceae	0.22	t	3	-	-
<i>Amelanchier alnifolia</i>	Rosaceae	0.07	t	1	-	-
<i>Ribes montigenum</i>	Grossulariaceae	0.07	t	1	-	-
Live shrub total	4 families	17.8	t	243	-	-
Snags						
<i>Abies bifolia</i>		188.9	3.60	2576	1068	-
<i>Populus tremuloides</i>		75.5	1.47	1030	717	-
<i>Picea engelmannii</i>		27.6	2.68	376	295	-
<i>Pinus longaeva</i>		15.8	2.06	216	203	3
<i>Pinus flexilis</i>		9.9	1.39	135	117	2
<i>Picea pungens</i>		3.4	0.16	47	28	-
<i>Juniperus communis</i>		0.4	t	5	-	-
<i>Pseudotsuga menziesii</i>		0.4	0.04	5	3	-
<i>Abies concolor</i>		0.3	t	4	-	-
Unknown		0.4	0.01	5	5	-
Unknown <i>Picea</i>		0.1	0.01	1	1	-
Unknown <i>Pinus</i>		1.8	0.22	25	24	-
Dead total		324.4	11.62	4425	2461	5
<u><1cm dbh</u>						
Live seedlings						
<i>Pinus flexilis</i>		70.3	-	959	-	-
<i>Pinus longaeva</i>		29.6	-	404	-	-
<i>Pinus edulis</i>		0.4	-	5	-	-
<i>Pinus ponderosa</i>		0.2	-	3	-	-
Live seedling total		100.5	-	1371	-	-

t - trace; density less than one tree per 10 ha; basal area less than 0.01 m²/ha

Species Abundance Distributions

The ZSM and lognormal models performed similarly in their approximation of my observed data (Fig. 5). The ZSM model was a marginally better fit, with ΔAIC of 6.6 when compared to the lognormal model. However, it would be remiss to claim this as definitive support for neutral theory. The empirical species abundance distribution was not differentiated from either the lognormal or the ZSM model according to Kolmogorov-Smirnov tests ($P > 0.1$). Conversely, the empirical data were clearly differentiated from *both* distributions by χ^2 tests ($P < 0.001$). Visual examination of the data supports these findings; both models are roughly equivalent in their fit of the data, but *neither* model may be considered an excellent fit. Fig. 5B displays the same species abundance data according to \log_2 -transformed abundance classes (sensu Hubbell 2001, McGill 2003a, Volkov et al. 2003, 2005). This figure exposes unconformities in the data not readily apparent in the rank-abundance plot above (Fig. 5A). Although abundance-class species abundance distributions for other data sets generally show a bell shape that conforms nicely to both lognormal and ZSM models (Volkov et al. 2005, McGill 2003a), the species abundance curve within the UFDP is mostly flat (Fig. 5B).

Functional Equivalence

Demographic Rates

The short-term annual mortality rate for all stems within the UFDP was 0.8%, the recruitment rate 0.9%, and the turnover rate 0.85% (Table 2). *Pinus longaeva*, *Pinus flexilis*, *Picea engelmannii*, and *Picea pungens* had significantly lower mortality rates,

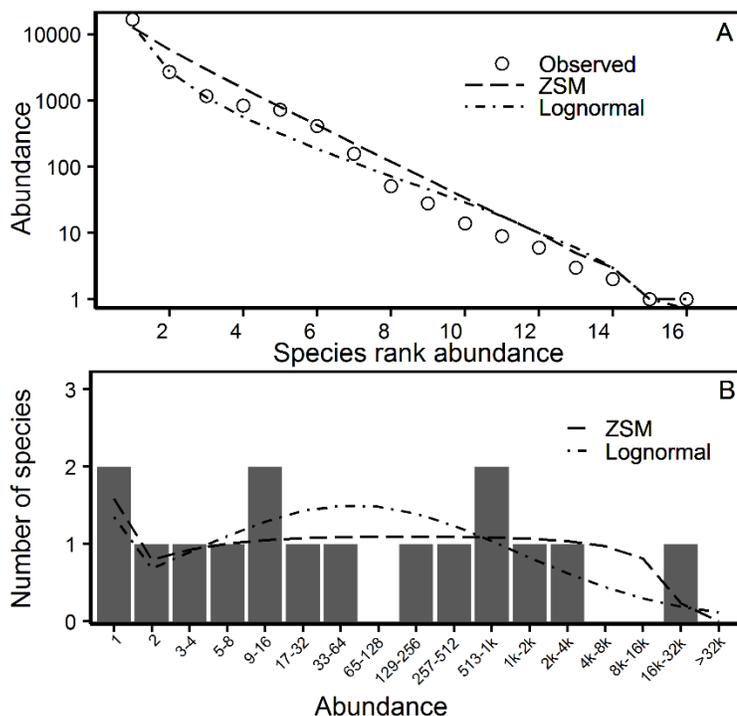


FIG. 5. Species abundance distribution for the Utah Forest Dynamics Plot. A) A standard rank-abundance plot of the observed species abundance approximated by a neutral zero-sum multinomial distribution and a non-neutral lognormal distribution. B) The same species abundance data displayed as a binned histogram with abundance classes plotted on a \log_2 scale.

while mortality rates of *Abies bifolia* and *Populus tremuloides* were consistent with the overall rate. *Pinus longaeva* and *Pinus flexilis* also had significantly lower recruitment rates, but all other species were consistent in recruitment rate (Table 2).

Dispersal Processes

Univariate spatial patterns of juveniles for *Abies bifolia* were more aggregated than the overall pattern of all *Abies bifolia* from 0 to 1 m (Fig. A3A), while adult *Abies bifolia* showed no significant trend. Univariate patterns of juvenile and adult *Picea engelmannii*, *Pinus flexilis*, *Pinus longaeva*, and *Picea pungens* were not different from

TABLE 2. Demographic rates for species within the Utah Forest Dynamics Plot. Values are annually compounding recruitment and mortality rates for all stems ≥ 1 cm dbh.

Species	Mortality rate (%)	Ingrowth rate (%)	Turnover rate (%)
<i>Abies bifolia</i>	0.89	0.85	0.87
<i>Populus tremuloides</i>	0.92	1.37	1.15
<i>Picea engelmannii</i>	0.26 [†]	1.57	0.92
<i>Pinus flexilis</i>	0.24 [†]	0.00 [†]	0.12
<i>Pinus longaeva</i>	0.28 [†]	0.00 [†]	0.14
<i>Picea pungens</i>	0.00 [†]	1.49	0.75
All stems	0.81	0.89	0.85

[†] - Indicates significant deviation from baseline demographic rates calculated for all other species at $\alpha = 0.004$ (Bonferroni adjustment for $n = 12$ tests at $\alpha = 0.05$).

the overall pattern of each species (Fig. A3C-F, I-L). *Populus tremuloides* was distinctly different; juveniles were strongly aggregated from 0 to 8 m (Fig. A3B), while adults were hyper-dispersed from 0 to 2 m (Fig. A3H).

I rejected the null model of independence for the bivariate spatial patterns of *Abies bifolia*, *Picea engelmannii*, and *Picea pungens* (Fig. 6A, C, F). *Pinus flexilis* and *Pinus longaeva* both showed a trend of association between juveniles and adults, but the observed spatial patterns did not exceed the simulation envelopes for the null model of independence. Bivariate patterns for juvenile and adult *Populus tremuloides* were also found to be independent, but there was a trend of segregation rather than association between the two types of points. I did not reject the null model of random labelling for *Abies bifolia*, *Picea engelmannii*, *Pinus flexilis*, *Pinus longaeva*, or *Picea pungens* (Fig. 6G, I-L). However, I rejected the null model of random labelling for the bivariate interaction between juvenile and adult *Populus tremuloides* for intertree distances from 0 to 10 m (Fig. 6H).

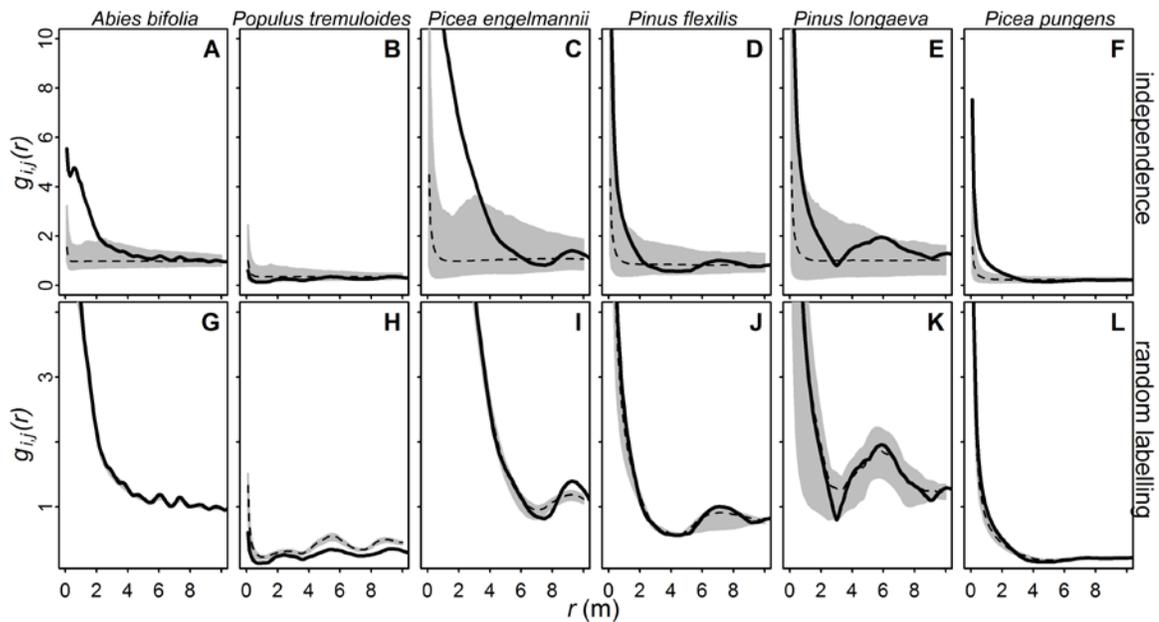


FIG. 6. Bivariate spatial patterns between juvenile and adult trees in the Utah Forest Dynamics Plot. Black lines indicate observed values of the pair correlation function (PCF), gray area represents simulation envelopes based on the 2.5th and 97.5th percentile values of 999 simulated point patterns generated according to the null models of independence (A-F) and random labelling (G-L). Deviations of the observed pattern above the simulation envelope indicate attraction between juvenile and adult point patterns, while deviations below the simulation envelope indicate the repulsion between juvenile and adult point patterns.

Pinus flexilis and *Pinus longaeva* seedlings were aggregated from 0 to 2 m and 0 to 3 m, respectively (Fig. A4A, B). However, I failed to reject the null model of independence between *Pinus* seedlings (<1 cm dbh) and *Pinus* adults. Results were not sensitive to the specific choices of diameter definitions for adults (20 cm dbh) and juveniles (5 cm dbh), nor were results sensitive to the distance chosen to shift the point pattern of juveniles (20 m) for the independence simulations.

Ecological Equivalence

For most species pairs, plant-plant interactions were roughly symmetric (Fig. 7, all data shown in Fig. A5). The bivariate interactions for 14 out of 15 species pairs were

within the simulation envelopes, indicating mortality for most species was not strongly influenced by the presence of any one other species. Brief deviations from the simulation envelopes appeared to be due to stochastic variability in the data. The bivariate interactions between *Abies bifolia* and *Pinus longaeva* typify the patterns I observed for most species; the observed spatial patterns between live and dead for both species were within the simulation envelopes, suggesting the presence of live individuals of one species does not increase probability of mortality for the other species (Fig. 7A, D). The pattern between *Abies bifolia* and *Picea pungens* were also within the simulation envelopes, but I observed a subtle amount of repulsion between live and dead stems for both species (Fig. 7B, E). This decreased likelihood of mortality for both species in the presence of the other species may indicate facilitative effects between *Abies bifolia* and *Picea pungens*, or possibly a lesser degree of competition as compared to other possible

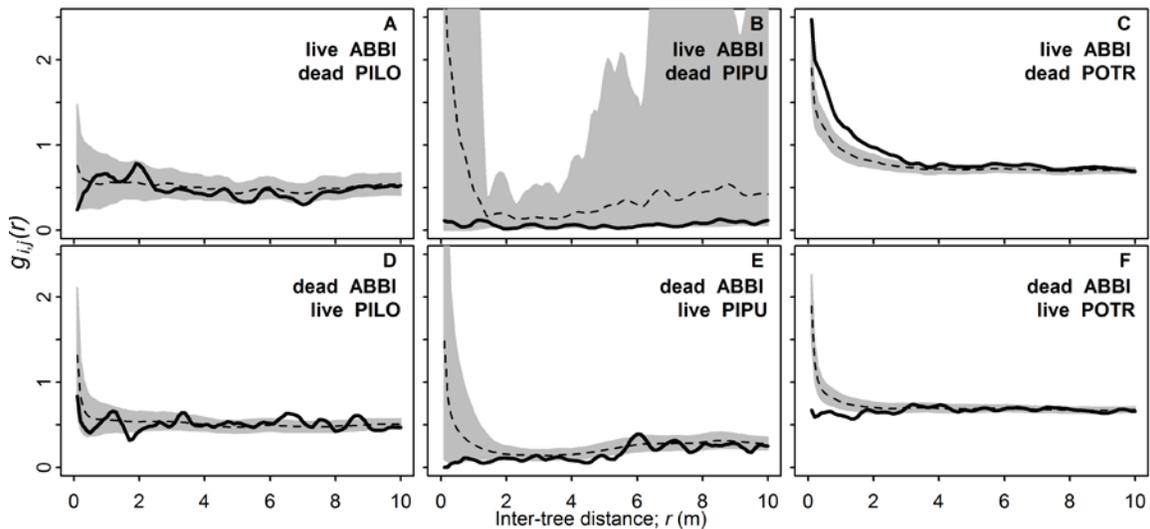


FIG. 7. Bivariate spatial patterns between *Abies bifolia* (ABBI) and *Pinus longaeva* (PILO; A and D), *Abies bifolia* and *Picea pungens* (PIPU; B and E), and *Abies bifolia* and *Populus tremuloides* (POTR; C and F). Grey area represents confidence envelopes derived using the 25th highest and lowest values of $g(r)$ from 999 simulations generated according to the null model of random mortality. All pairwise comparisons are displayed in Fig. A5.

neighbors. However, this interaction not only appears to be weak, it is also symmetric. The interaction between *Populus tremuloides* and *Abies bifolia*, however, was distinctly different. I found attraction between live *Abies bifolia* and dead *Populus tremuloides*, and repulsion between live *Populus tremuloides* and dead *Abies bifolia*. In other words, probability of mortality for *Populus tremuloides* was higher in the presence of live *Abies bifolia*, while probability of mortality for *Abies bifolia* was lower in the presence of live *Populus tremuloides* (Fig. 7C, F).

Species-Habitat Associations

All species with densities >1 stem ha^{-1} exhibited habitat associations (Table 3). All species showed a positive association with at least one habitat type, and species with densities ≥ 10 stems ha^{-1} also showed a negative association with at least one habitat type. The torus-translation tests identified eight positive species-habitat associations and two negative associations, compared with 15 positive associations and 21 negative associations identified by the χ^2 tests. Considering significant associations identified by either test, I found a total of 19 distinct positive associations and 21 negative associations, for a total of 40 out of 80 possible unique species-habitat combinations (10 species \times 8 habitat types). All habitat types had at least one significant species-habitat association. These quantitatively-determined habitat types matched the observed variation in the UFDP (Fig. 3, Fig. A1).

Each habitat type was characterized by a unique combination of positive and negative species associates (Table 3). Geologic classification was an important driver of these differences, but I also observed a great deal of variability between N and S habitats within the same geologic layer. *Pinus longaeva* was positively associated with both

TABLE 3. Species-habitat associations within the Utah Forest Dynamics Plot. Positive associations are indicated by a plus sign (+), negative associations are indicated by a minus sign (-). Letters represent significant results of the torus-translation tests (t) and χ^2 test (x) for each species-habitat pair.

Species	Habitat Type							
	Qms1	Qms2-N	Qms2-S	Tcwm-N	Tcwm-S	Tcwt	Tcwu-N	Tcwu-S
<i>Abies bifolia</i>				+ (t)	- (x)	+ (x)	- (x)	- (x)
<i>Populus tremuloides</i>	+ (x,t)		- (x)	+ (x)		- (x)	- (x)	- (x)
<i>Picea engelmannii</i>				- (x)	- (x,t)	+ (x,t)	+ (x)	
<i>Pinus flexilis</i>	- (x)				+ (x)	- (x)	+ (x,t)	+ (x)
<i>Pinus longaeva</i>	- (x,t)	- (x)	+ (x,t)	- (x)	+ (x)	- (x)	+ (x)	+ (x)
<i>Picea pungens</i>	- (x)		+ (x)	- (x)	+ (x)	- (x)	- (x)	
<i>Juniperus communis</i>	- (x)			+ (t)		- (x)		
<i>Ribes cereum</i>					+ (x)			
<i>Pseudotsuga menziesii</i>				+ (t)				
<i>Abies concolor</i>							+ (t)	

Qms2-S and Tcwm-S, but negatively associated with Qms2-N and Tcwm-N. Aspect effect was particularly strong on Tcwm habitats; *Pinus longaeva*, and *Picea pungens* had positive associations with Tcwm-S and negative associations with Tcwm-N, while *Abies bifolia* showed the opposite trend. Conversely, aspect effect on Tcwu habitats appeared to be less important, as *Pinus flexilis* and *Pinus longaeva* were positively associated with both north and south aspects, while *Abies bifolia* and *Populus tremuloides* were negatively associated with both aspects.

Structure and Spatial Pattern by Habitat

Stand structure varied across the eight habitat types within the UFDP, though density and BA varied independently (Table A1, Fig. 8A). Qms1 habitat had the highest BA (42.7 m² ha⁻¹) and second highest density, while Qms2-S had the second highest BA but below average density. Tcwm-N habitat had the highest density (2575 stems ha⁻¹), but BA was average. Mean quadrat diversity was highest in Tcwm-N habitat (5 species)

and lowest in Tcwu-S (2 species).

In addition to having elevated abundance, *Abies bifolia*, *Populus tremuloides*, *Pinus longaeva*, *Pinus flexilis*, and *Picea pungens* had greater BA per stem within their associated habitat types compared to all other habitats (Table A1). *Picea engelmannii* showed the opposite trend, likely due to the high, spatially aggregated mortality rates of large-diameter *Picea engelmannii* during the spruce-beetle during the 1990s.

Spatial patterns for all habitat types exhibited aggregation at small scales and dispersion at larger scales, but I observed variability in the transition point from aggregation to dispersion (Fig. 8B). Qms2-N, Tcwt, and Tcwm-S showed aggregation at intertree distances <4 m, while all other habitat types became dispersed at greater scales. Tcwm-N habitat showed the largest cluster size, becoming dispersed at about 16 m.

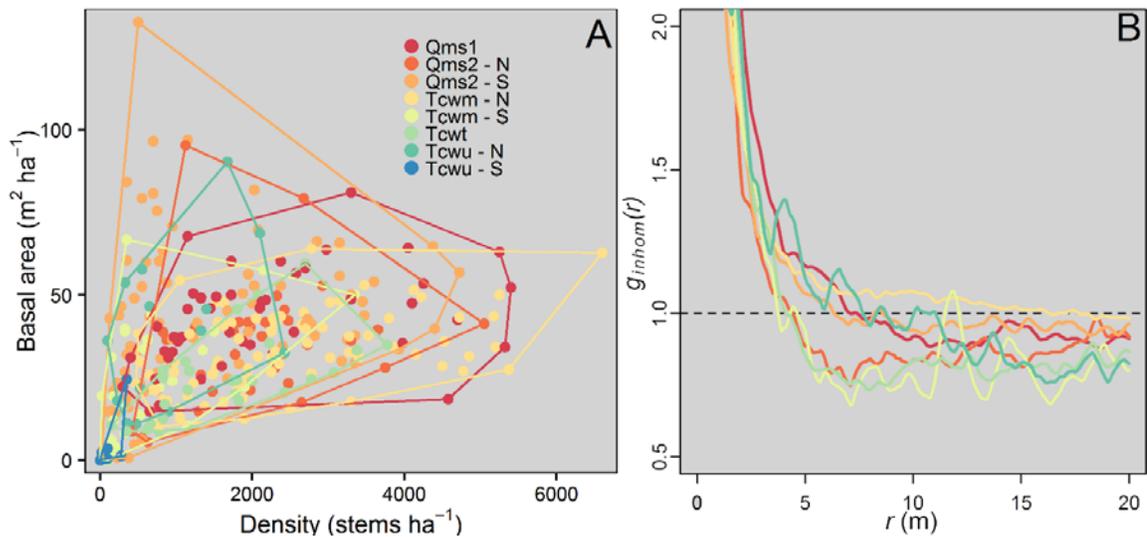


FIG. 8. Structure (A) and spatial patterns (B) of trees classified according to the eight distinct habitat types within the Utah Forest Dynamics Plot. Colors indicate habitat types delineated according to geologic parent material and slope aspect and match the map of habitat types in Fig. 3A. Points represent individual quadrats; lines indicate the outer bounds of the point cloud for all quadrats within each habitat (A). Spatial patterns of trees within each habitat type summarized by the pair-correlation function, $g(r)$. Values of $g(r)$ above the dashed line indicate aggregation, values below represent dispersion (B).

DISCUSSION

The Unified Neutral Theory of Biodiversity it is often regarded as a ‘universal’ theory (Hubbell 2001, McGill et al. 2006, Rosindell et al. 2011), but much of the theoretical debate in the literature has focused on whether this theory is suggestive of an underlying law of nature or merely a coincidental fit to observed patterns in tropical forests (McGill 2003*b*, Volkov et al. 2003, Rosindell et al. 2010, Rosindell et al. 2012, Ricklefs and Renner 2012). While recent work has begun to resolve this debate by considering neutral theory and niche theory as two ends of a spectrum (Gravel et al. 2006), we lack a synthesized framework for understanding what determines the relative importance of these contrasting processes in different ecosystems (Weiher et al. 2011). A few studies have attempted to determine possible drivers of this continuum (Chisholm and Pacala 2011, Myers et al. 2013, Qiao et al. 2015), but there remains a considerable lack of clarity when synthesizing the findings of these studies into a unified framework which could be used to identify drivers of the niche-neutrality gradient (Kubota et al. 2016). In this study, I found neutral theory did not perform well with the limited species diversity and extreme climatic environment of the UFDP.

Species Abundance Distribution

The neutral ZSM model did not fit the observed species abundance distribution better than the alternative lognormal model. Although the AIC of the ZSM was slightly lower than that of the lognormal model, this is most likely due to subtle differences in the fit of each model and stochastic characteristics of the data set, and does not provide strong support for this prediction of neutral theory. I used multiple goodness-of-fit

metrics as advocated for by Matthews and Whittaker (2014), and found the ZSM and lognormal models performed the same in Kolmogorov-Smirnov and χ^2 tests. Neither model was rejected using the Kolmogorov-Smirnov test, but both models were rejected by more rigorous χ^2 tests. This is a surprising result, considering many other studies have found both ZSM and lognormal models predict tropical species abundance distributions well (McGill 2003a, Volkov et al. 2003, Volkov et al. 2005, Hubbell 2006). In the subalpine UFDP, this discrepancy is probably a consequence of the relatively low species diversity and the prevalence of rare species (41% of species <1 tree ha^{-1}), causing the species abundance distribution to be strongly influenced by slight variation in the abundance of a single species (Fig. 5B). It is also possible that, due to the abiotic characteristics of the UFDP (e.g., highly heterogeneous habitat and close proximity to lower elevation species pools), the observed species abundance distribution is not reflective of relative abundance on the broader landscape. Although I reject both the neutral and lognormal models for species abundance distributions within the UFDP, I note that further investigation will be required to determine if this finding is dependent on the specific site or scale of the UFDP, or if it is a phenomenon that may apply in a broader context to subalpine forests.

Functional Equivalence

Demographic Rates

Our one- and two-year mortality and recruitment rates cannot be considered representative of the longer-term rates for the UFDP. However, the difference in rates among species for this time period shows that, irrespective of the applicability of neutral

theory to long-term vital rates, species are not functionally equivalent in the short term. Mortality rates for *Pinus longaeva* (0.28%), *Pinus flexilis* (0.24%), *Picea engelmannii* (0.26%) and *Picea pungens* (0%) were below the average mortality rate of 0.81% (Table 2). Most species were equivalent in their recruitment rates, but recruitment of *Pinus longaeva* (0%) and *Pinus flexilis* (0%) was lower than overall rates. Although these deviations from baseline demographic rates may be due to stochasticity and temporal fluctuation in environmental conditions, it appears species within the same genera parallel each other in their demographic fluctuations, suggesting species identity is an important factor influencing recruitment and mortality. Overall turnover rates of 0.85% were consistent with the turnover-productivity relationship reported by Stephenson and van Mantgem (2005), and with long-term demographic rates in other subalpine conifer forests (Larson and Franklin 2010, Larson et al. 2015).

Although I did observe a high abundance of *Picea engelmannii* snags, the number of live, mature *Picea engelmannii* suggests bark beetle-mediated mortality rates in the UFDP were lower than in the study sites of DeRose and Long (2007). The lower proportion of *Picea engelmannii* in the pre-1990s UFDP (i.e., trees plus snags; Table 1) supports DeRose and Long's (2007) finding that stands with higher diversity (diversity in the UFDP is relatively high compared to the dense *Abies bifolia*-*Picea engelmannii* forest that dominates much of the rest of the Markagunt Plateau) had lower levels of mortality and greater resilience to the bark beetle disturbance.

Dispersal Processes

The net effect of dispersal and recruitment processes within the UFDP appear to act uniquely upon the spatial patterns of each species. Univariate patterns of juveniles

show clustered recruitment for *Abies bifolia* from 0 to 1 m, and for *Populus tremuloides* from 0 to 8 m (Fig. A3A, B), while juveniles of all other species were not differentiated from the overall patterns. *Populus tremuloides* was the only species to exhibit a significant trend in the univariate pattern of adults, which were hyper-dispersed from 0 to 2 m.

I compared the bivariate interactions between adults and juveniles against the null model of independence to assess the net effects of *a priori* processes on spatial patterns of recruitment, and found attraction between juveniles and adults of *Abies bifolia*, *Picea engelmannii*, and *Picea pungens* (Fig. 6A, C, F). This indicates dispersal and establishment limitations may be important factors influencing recruitment of these species. In contrast, bivariate patterns of juvenile and adult *Populus tremuloides* were found to be independent (Fig. 6B), suggesting dispersal limitation may be less important for this species. Spatial patterns of *Pinus flexilis* and *Pinus longaeva* also showed independence between juveniles and adults (Fig. 6D, E), possibly be due high rates of vertebrate dispersal which is an important dispersal mechanism for both *Pinus* species (most notably *Nucifraga columbiana*, Clark's nutcracker; Lanner and Vander Wall 1980, Lanner 1988, Torick et al. 1996). Univariate and bivariate spatial patterns of *Pinus* seedlings corroborate this result; seedlings were aggregated at small spatial scales (Fig. A4C, D), but were independent of the spatial pattern of adults (Fig. A4A, B), as would be expected if seeds were dispersed and cached by vertebrates.

I also compared the bivariate patterns for each species to random labelling null models to assess the net effects of *a posteriori* processes on recruitment. For *Abies bifolia*, *Picea engelmannii*, *Pinus flexilis*, *Pinus longaeva*, and *Picea pungens*, proximity

to adults did not have significant effects on recruitment (Fig. 6G, I-L). *Populus tremuloides*, however, showed repulsion between live juveniles and live adults from 0 to 10 m (Fig. 6H). In other words, recruits of *Populus tremuloides* were more likely to survive if they were not within 10 m of an adult, suggesting negative density-dependent processes (i.e., intraspecific competition with or without Janzen-Connell effects) structure *Populus tremuloides* recruitment.

While dispersal and recruitment processes appeared to act uniformly upon the spatial patterns of some species, I found species identity was important for four out of six species. *Populus tremuloides* stands out as the most notable exception in every intraspecific spatial analyses. This is likely due to the clonal reproduction of *Populus tremuloides*, as well as life-history traits that enable a strong recruitment response to disturbance. These results suggest that recruitment processes, dispersal, and intraspecific competition in *Populus tremuloides* may be characteristically different than intraspecific competition in non-clonal species.

Ecological Equivalence

Fourteen out of 15 species pairs were symmetric in their competitive interactions. Observed spatial patterns for most species pairs did not fall outside of simulation envelopes, suggesting the species identity of nearby stems does not increase the probability of mortality for most species (Fig. A5). Some species pairs did show subtle deviations from the null model, but the direction of deviation was generally symmetric. As with the dispersal analyses, *Populus tremuloides* was a notable exception to my findings. The *Populus tremuloides* – *Abies bifolia* species pair showed a strong, asymmetrical pattern (Fig. 7C, F). These results demonstrate that *Populus tremuloides*

facilitates recruitment of *Abies bifolia*, while the presence of *Abies bifolia* increases the likelihood of *Populus tremuloides* mortality. This asymmetric interaction is consistent with the current understanding of *Populus tremuloides* – *Abies bifolia* competitive dynamics (Rogers 2002, Kulakowski et al. 2013), and also supports the work of Calder and St. Clair (2012) that identified facilitation of *Abies bifolia* by *Populus tremuloides* as an important driver of conifer forest succession. This single species pair is the only exception to the neutral theory assumption of ecological equivalence in the UFDP, but *Populus tremuloides* and *Abies bifolia* together comprise over 80% of all stems (Table 1).

Species-Habitat Associations

All common species (>1 tree ha^{-1}) had preferred habitat types delineated according to geologic parent material and aspect. While other studies have found relatively high proportions of habitat specialization (79% in Sinharaja, Sri Lanka, Gunatilleke et al. 2006; 63% in Korup, Cameroon, Chuyong et al. 2011), no other study to my knowledge has found habitat preference for 100% of species with densities >1 tree ha^{-1} . This demonstrates habitat type is a dominant driver of forest composition and species coexistence in subalpine forests. This finding is in stark contrast to studies in tropical forest ecosystems that have found most species to be habitat generalists (Barro Colorado Island, Panama, Hubbell and Foster 1986, Harms et al. 2001, Hubbell 2005; La Planada, Colombia and Yasuni, Ecuador, John et al. 2007). The prevalence of habitat associations in the UFDP may be simply due to high levels of local habitat heterogeneity, and perhaps we would see more habitat specialization in tropical forests with greater habitat heterogeneity. This raises the question of scale; if the scale of observation includes little heterogeneity compared to the surrounding landscape, we might expect

most species to appear to be generalists. As we broaden the scale of observation, and consequently increase heterogeneity, the species that once appeared to be generalists may be found to actually be specialists on the habitat that encompassed the smaller scale of observation. In tropical forests, perhaps the scale of observation required to observe a high degree of habitat specialization is much larger than any single study site, while in heterogeneous temperate forests, specialization is detectable at smaller scales (i.e., the scale of this study).

Many species had positive, negative, and neutral associations with multiple habitat types (Table 3). *Pinus longaeva*, however, had four positive, four negative, and no neutral associations. This extreme case of habitat specificity is likely associated with specific soil conditions (Hiebert and Hamrick 1984, Fryer 2004). This may have important implications for management of high-elevation species in the context of recent climate trends. My results show that in addition to broad-scale climate limitations, soil characteristics and microclimate variability are determinants of species' realized ranges. Any future studies that seek to model species range shifts in response to changing climate should consider these variables as additional factors affecting habitat suitability. This finding may be particularly useful to land managers that bear the challenge of preserving scientifically and culturally important species such as *Pinus longaeva* in the face of increasing climate variability.

In addition to species associations with each habitat, stand density, BA, and diversity varied by habitat type (Fig. 8, Table A1). Each habitat type was characterized by a unique range of stand structural conditions, likely driven by variability in composition due to species associations (Table A1, Fig. 8A). Spatial patterns also varied

by habitat type (Fig. 8B), further supporting the conclusion that habitat heterogeneity can also drive forest structure and spatial patterns.

Our study corroborated the conclusion from Harms et al. (2001) that torus-translation tests are more conservative than the χ^2 tests. However, my findings differed in that the results of the torus-translation tests were not a subset of the results from the χ^2 tests, as four out of ten torus-translation associations were not identified by the χ^2 tests. Although these two tests vary in their sensitivity and exhibit different results, the lack of significance with one test does not prove that there is no species-habitat association, and does not diminish the validity of significant associations identified by another test. Rather, the discrepancies between the two tests arose from different sensitivities to specific characteristics of each species' distribution across the plot. For example, the χ^2 test did not identify a positive association for *Abies bifolia* on the Tcwm-N habitat, despite having a strong association as identified by visual assessment of stem maps (Fig. A6), the torus translation test, and field observations. Conversely, the torus-translation tests failed to identify the association between *Picea pungens* and the Qms2-S habitat. This association was identified by the χ^2 test, and stem maps (Fig. A6) reveal this association may even be stronger than the *Pinus longaeva* – Qms2-S association identified by the torus-translation test, and is perhaps the strongest species-habitat association for any of the six principal species.

Interestingly, while both tests missed some strong habitat associations, neither test identified a positive association that was contradicted by a negative association from the other test, and neither test identified any association that was not corroborated by my field observations. To generalize the behavior of each test, the χ^2 tests were more

sensitive to negative associations and species with high abundance, while the torus-translation tests were more sensitive to positive associations and species with low abundance. I note that the development of methods that maintain consistency across a wide range of observed abundance, while reducing the sensitivity to coincidental shapes of habitat zones or characteristics of species' distributions, is a priority for future research considering habitat specificity.

The prevalence of habitat associations in the UFDP suggests soil characteristics and aspect-influenced microclimate variability are important factors structuring subalpine forest species diversity. I therefore reject the assumption of neutral theory that most species are habitat generalists. In subalpine forests, niche differentiation is likely a more important mechanism fostering species coexistence and landscape-level tree diversity.

CONCLUSIONS

Although the relative species abundance did not conform to the neutral model, I found limited evidence for the functional equivalence of species, and most species pairs exhibited competitive equivalence. However, I found demographic differences for most species, and competitive differences for the two most abundant species, suggesting these assumptions of neutral theory are not appropriate for the majority of stems nor the majority of species in the UFDP. Habitat specificity was perhaps the greatest objection to neutral theory, as I found all species with densities >1 stem ha^{-1} were habitat specialists.

I therefore conclude that neutral processes play a limited role in structuring the diversity and composition within subalpine forests. There are three possible explanations for this: 1) the spatial scale of this study was not sufficient to capture the true neutral nature of subalpine forest systems; 2) past disturbance has shifted this forest out of a neutral state, but it would eventually conform to neutral models given enough time; and 3) neutral theory is not relevant in subalpine forest ecosystems.

If we consider niche and neutral theories as two ends of a spectrum, all three of these explanations may contain an element of truth. The first two points consider spatial and temporal scale as important factors determining the relative importance of neutral and alternative models (Chave et al. 2002, McGill et al. 2006, Rosindell and Cornell 2007). While it appears non-neutral processes play a dominant role at the spatial and temporal scales of this study, perhaps we would find support for neutral theory if we were to consider a larger scale. Other studies have suggested spatial scale to be an important driver of the niche-neutrality gradient (Wang et al. 2011, Masaki et al. 2015), but I

suggest scale should be considered in the context of heterogeneity rather than as absolute spatial scales.

The third point reflects on the universality of neutral theory. This study suggests neutral theory is less relevant in subalpine forests, which is consistent with other studies that have found temperature and latitude to be important drivers of the relative importance of niche and neutral processes (Myers et al. 2013, Qiao et al. 2015). However, while climate may be an important driver, it alone does not explain observed patterns of the niche-neutrality gradient on a global scale (Kubota et al. 2016). Perhaps the dominance of niche processes is due to having much lower species diversity as compared to tropical forests. This reflects the findings of Chisholm and Pacala (2011) that show neutral processes are less relevant in low-diversity ecosystems. However, phylogenetic diversity may actually be higher in temperate forests due to the prevalence of basal gymnosperms (e.g., Cupressaceae and Pinaceae; Erickson et al. 2014), providing greater potential for niche differentiation and divergent evolution of functional traits. If this is the case, phylogenetic diversity may be an additional driver of the niche-neutrality gradient that operates independently of species diversity.

As with many theoretical models, neutral theory aims to predict attributes of ecological communities as they approach an equilibrium state, generally requiring the absence of major disturbance. This is a hypothetical state for most temperate forests, as biotic disturbances, fire, and climate variability maintain a state of constant flux (Veblen et al. 1994, Swetnam and Betancourt 1998, Morris et al. 2013). If wide-spread disturbance and climate bottlenecks were absent in a subalpine forest for thousands of years, perhaps we would observe more support for the predictions and underlying

assumptions of neutral theory. Given the improbability of attaining long-term stability in a subalpine forest, however, the relevance of any universal theory that does not explicitly consider the role of disturbance is called into question.

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APPENDICES

APPENDIX: SUPPLEMENTAL FIGURES AND TABLES



FIG. A1. Vegetation in identified habitat types within the Utah Forest Dynamics Plot (UFDP). Habitats were classified according to geologic parent material and slope aspect for each of the 341 quadrats within the UFDP (Fig. 3A). Images depict vegetation communities associated with the four habitat types not included in Fig. 3.

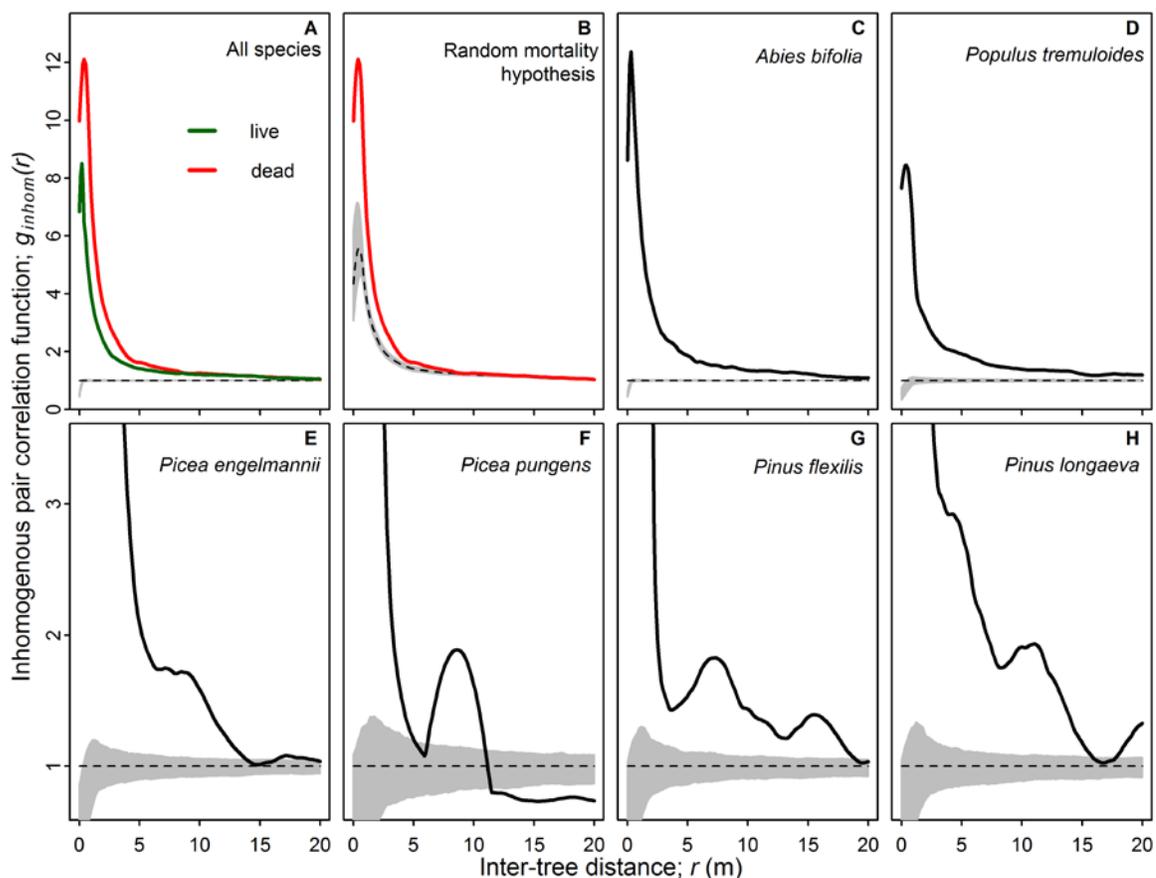


FIG. A2. Univariate spatial patterns of principal species of the Utah Forest Dynamics Plot. Lines indicate the $g(r)$ statistic derived from the univariate pair correlation function for observed patterns at inter-tree distance r . Horizontal dotted lines represent expected values under complete spatial randomness (CSR), grey areas represent simulation envelopes generated from 999 simulations of CSR. Values above the 97.5th percentile of simulation envelopes indicate aggregation, values below the 2.5th percentile indicate dispersion. The green line indicates the pattern of live stems, the red lines indicate the pattern of dead stems. For the random mortality hypothesis panel, dotted line indicates the mean value of $g(r)$ expected for dead stems if mortality were a random process.

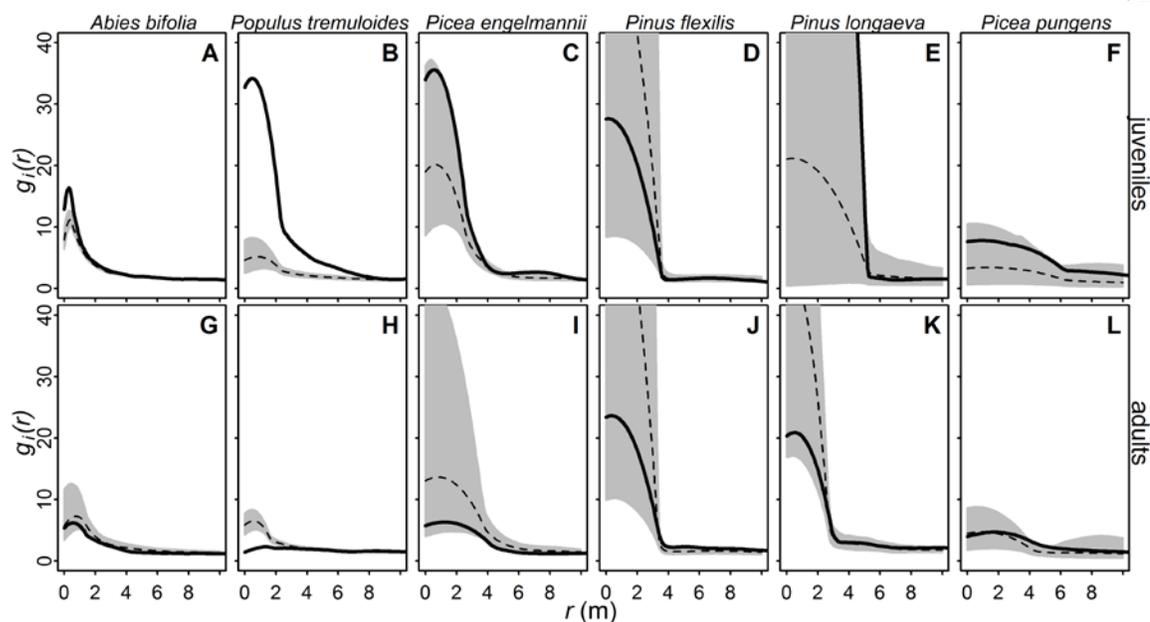


FIG. A3. Univariate spatial patterns of juvenile (A-F) and adult (G-L) trees in the Utah Forest Dynamics Plot. Black lines indicate observed values of the pair correlation function, $g(r)$, gray area represents simulation envelopes based on the 2.5th and 97.5th percentile values of 999 simulated point patterns generated by randomly assigning age class to each point. Deviations of the observed pattern above the simulation envelope indicate the pattern is more aggregated than stems of all sizes, while deviations below the simulation envelope indicate the pattern is hyper-dispersed compared to all stems of all sizes.

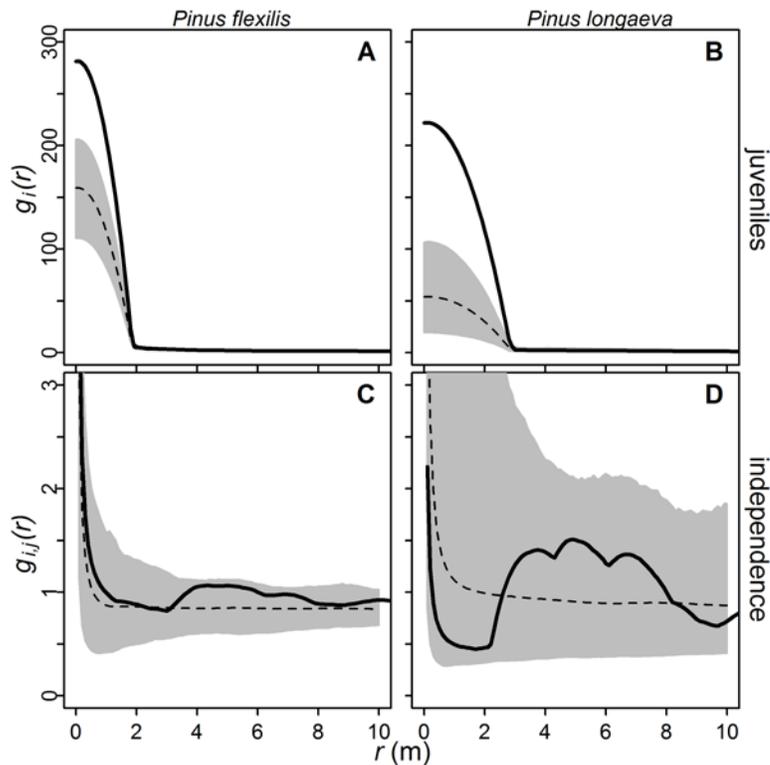


FIG. A4. Spatial patterns of *Pinus flexilis* and *Pinus longaeva* seedlings in the Utah Forest Dynamics Plot. Lines represent observed values of the univariate pair correlation function, $g_i(r)$ (PCF; A, B), and bivariate PCF, $g_{i,j}(r)$ (C, D). Gray area represents simulation envelopes based on the 2.5th and 97.5th percentile values of 999 simulated point patterns. The univariate patterns of seedlings were compared to the null model of random labelling (A, B). Bivariate spatial patterns between seedlings and adult *Pinus flexilis* and *Pinus longaeva* were compared to the null model of independence (C, D).

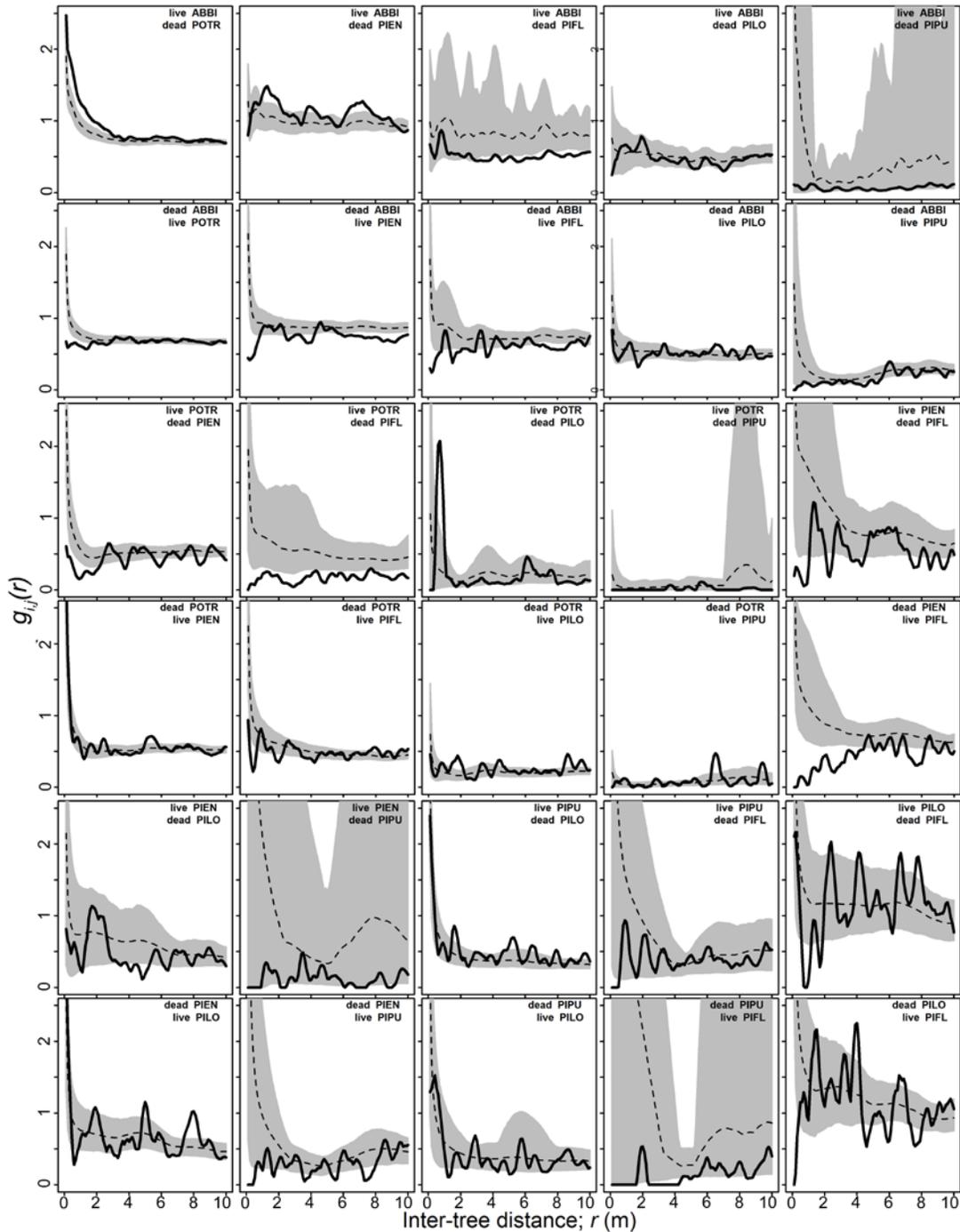


FIG. A5. Pair-wise bivariate spatial patterns between live and dead stems for *Abies bifolia* (ABBI), *Populus tremuloides* (POTR), *Picea engelmannii* (PIEN), *Pinus flexilis* (PIFL), *Pinus longaeva* (PILO), and *Picea pungens* (PIPU) within the Utah Forest Dynamics Plot. Lines are observed values of $g_{i,j}(r)$, grey area represents the 2.5th and 97.5th percentile of values of 999 simulations generated according to the null model of random mortality. Deviations of the observed pattern above the simulation envelope indicate attraction between the two types of points, while deviations below the simulation envelope repulsion between the two types of points.

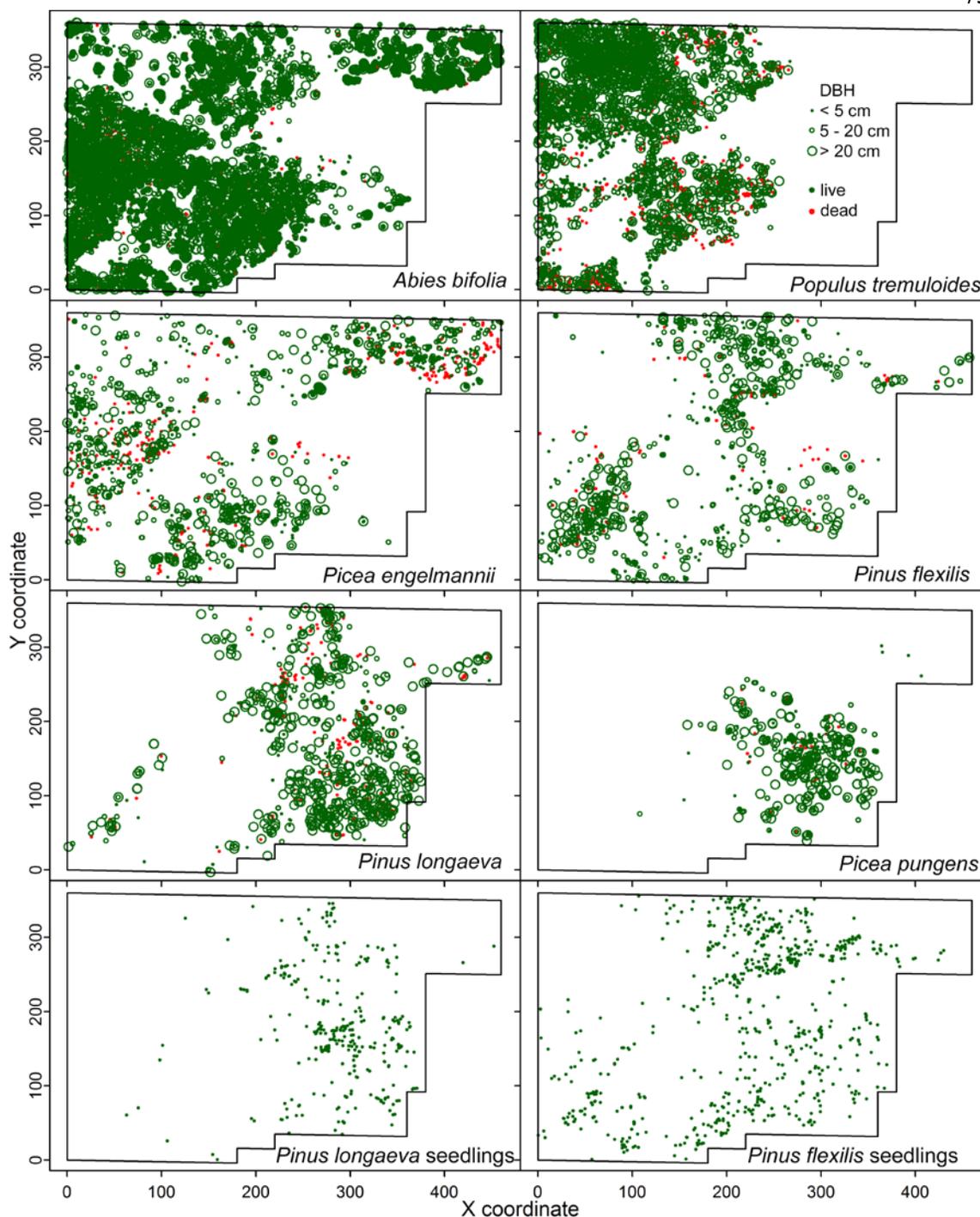


FIG. A6. Stem locations of principal tree species ≥ 1 cm dbh in the Utah Forest Dynamics Plot. Green indicates live stems, red indicates snags. Point size indicates diameter at breast height (1.37 m) for live stems. Seedlings are all stems < 1 cm dbh and ≥ 2 years old.

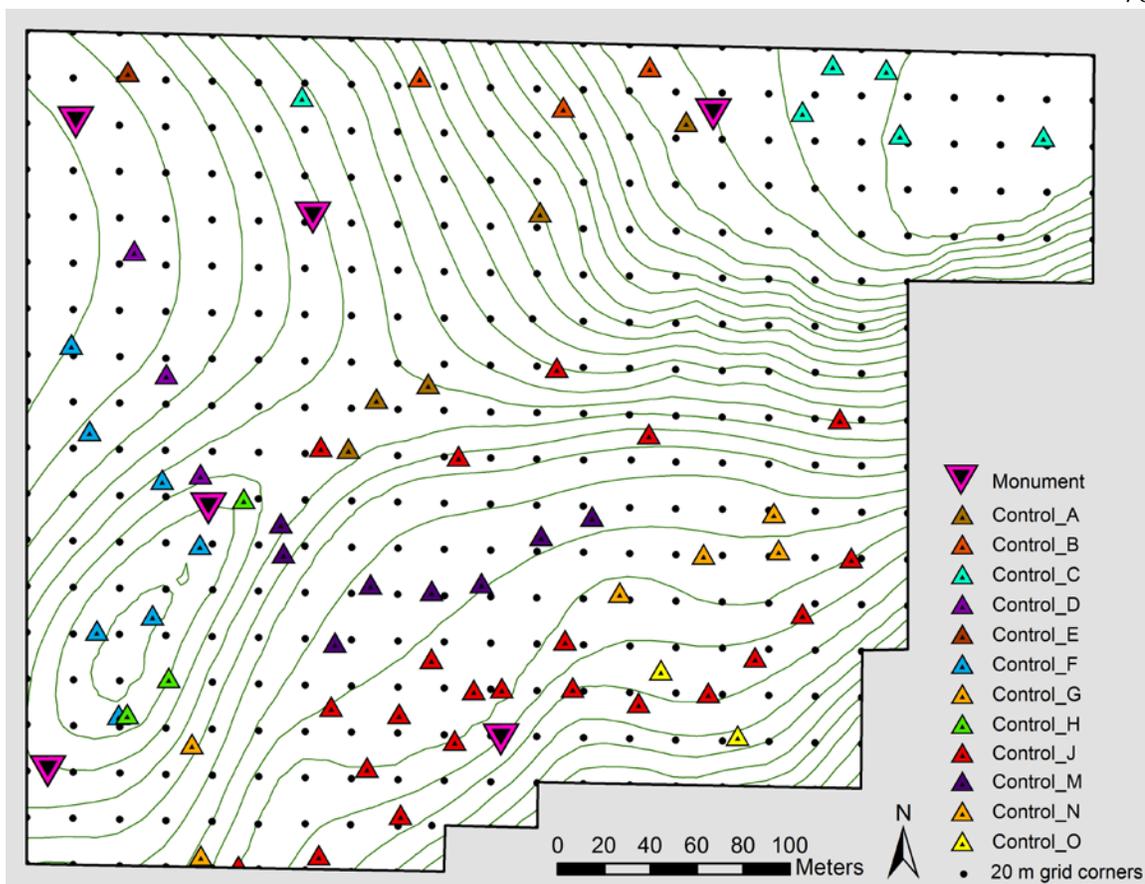


FIG. A7. Survey monuments, control loops, and grid corners in the Utah Forest Dynamics Plot.



FIG. A8. Examples of the markers used for permanent survey monuments in the Utah Forest Dynamics Plot.

TABLE A1. Habitat types within the Utah Forest Dynamics Plot. Map class corresponds to the numbers in Fig. 3. Habitat category indicates 8 total habitat types classified according to geologic parent material and slope aspect. Abbreviations are: Tcwt - uppermost mudstone, siltstone, and sandstone unit of the white member of the Claron formation (Tcw); Tcwu – upper limestone unit of the Tcw; Tcwm – middle mudstone, siltstone, and sandstone unit of the Tcw; Qms1 – landslide deposits that rest beneath Brian Head formation material and the Tcwm layer; and Qms2 – landslide deposits beneath the Tcwm and Tcwu layers. South aspects (S) range from southeast (135°) to southwest (225°), north aspects (N) are all other azimuths. Density and basal area represent mean values for quadrats within each habitat type; α -diversity represents the mean quadrat diversity of woody species ≥ 1 cm dbh within each habitat. Significance was determined using Wilcoxon rank-sum tests. Species associates are positive species-habitat associations as determined by χ^2 tests and torus-translation tests.

Map Class	Habitat category	Area (ha)	Density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	α -diversity	Species associates
1	Qms1	1.9	2190 [†]	42.7 [†]	3 [‡]	<i>Populus tremuloides</i> [†]
2	Qms2-N	1.2	2147 [†]	35.7	4 [†]	-
3	Qms2-S	3.4	1565 [‡]	40.7 [†]	4 [†]	<i>Pinus longaeva</i> [†] ; <i>Picea pungens</i> [†] ;
4	Tcwm-N	3.2	2575 [†]	33.3	5 [†]	<i>Abies bifolia</i> [†] ; <i>Juniperus communis</i> ; <i>Pseudotsuga menziesii</i> ; <i>Populus tremuloides</i> [†]
5	Tcwm-S	1.3	655 [‡]	19.5 [‡]	3 [‡]	<i>Pinus longaeva</i> [†] ; <i>Pinus flexilis</i> [†] ; <i>Picea pungens</i> [†] ; <i>Pinus edulis</i> ; <i>Ribes cereum</i>
6	Tcwt	1.2	2109	27.7 [‡]	3 [‡]	<i>Abies bifolia</i> [†] ; <i>Picea engelmannii</i> [‡]
7	Tcwu-N	0.6	1255 [‡]	38.4	4	<i>Pinus longaeva</i> [†] ; <i>Pinus flexilis</i> [†] ; <i>Picea engelmannii</i> [‡] ;
8	Tcwu-S	0.7	310 [‡]	5.1 [‡]	2 [‡]	<i>Abies concolor</i> <i>Pinus longaeva</i> [†] ; <i>Pinus flexilis</i> [†]

Note: Bold indicates significance at $\alpha = 0.00625$ (Bonferroni adjustment for $n = 8$ tests at $\alpha = 0.05$). Plain type plus annotation indicates marginal significance at $\alpha = 0.05$.

† - Indicates this value is *greater* within this habitat than the mean for all other habitats.

‡ - Indicates this value is *lower* within this habitat than the mean for all other habitats.