Reconciling niches and neutrality in a subalpine temperate forest

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Abstract. The Unified Neutral Theory of Biodiversity has been put forth to explain species coexistence in forests worldwide, but its assumption of species equivalence has been met with much debate. Theoretical advancements have reconciled the opposing concepts of neutral and niche theories as two ends of a continuum, improving our understanding of global patterns in diversity and community assembly. However, the relative importance of niche and neutral processes remains understudied in temperate forests. To determine the balance of niche and neutral processes in climatically limited subalpine temperate forests, we established the Utah Forest Dynamics Plot, a 13.64-ha plot comprising 27,845 stems ≥1 cm diameter at breast height (1.37 m) representing 17 species at 3100 m elevation on the Colorado Plateau. We examined the fit of niche- and neutral-based models to the species abundance distribution (SAD), and tested three underlying assumptions of neutral theory. The neutral model was a poor fit to the SAD, but we did not find the alternative model to provide a better fit. Using spatial analyses, we tested the neutral assumptions of functional equivalence, ecological equivalence, and habitat generality. Half of species analyzed were characterized by non-neutral recruitment processes, and the two most abundant species exhibited asymmetric competitive and facilitative interactions with each other. The assumption of habitat generality was strongly contradicted, with all common species having habitat preferences. We conclude niche-based processes play the dominant role in structuring subalpine forest communities, and we suggest possible explanations for variation in the relative importance of niche vs. neutral processes along ecological gradients.

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INTRODUCTION

One of the most notable contemporary ecological theories 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). 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. Recent advancements have begun to reconcile the opposing concepts of niche and neutral theories as two ends of a continuum rather than as mutually exclusive paradigms (Chave 2004, Gravel et al. 2006, Adler et al. 2007, Vellend 2010). 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 few tests in temperate forests. While studies in temperate grasslands (Fargione et al. 2003, Adler 2004, 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, studies that consider temperate forests have found contradictory results (Shibata et al. 2010, Wang et al. 2011, Myers et al. 2013, Masaki et al. 2015, Qiao et al. 2015). This lack of clarity may be partially explained by the absence of studies that directly address the niche–neutrality gradient in climatically extreme temperate environments where the contrast between temperate and tropical forests is most evident. Indeed, at least one study has found the relative importance of neutral processes decreases with increasing environmental stress (Qiao et al. 2015), suggesting the most informative comparison of neutral processes between tropical and temperate forests would involve sites located in extreme temperate environments. Therefore, we assess the relative importance of niche and neutral processes in temperate forests by testing a prediction and three fundamental assumptions of neutral theory in a high-elevation subalpine ecosystem near the altitudinal limit of forest cover at an extreme end of the temperate–tropical ecological gradient.

We tested the prediction of neutral theory that the species abundance distribution (SAD) should follow a zero-sum multinomial distribution (ZSM; Hubbell 2001) to allow direct comparisons with other forest types (e.g., McGill 2003, Volkov et al. 2005, Qiao et al. 2015). Previous work has posited an alternative form of the SAD to be the non-neutral lognormal distribution (McGill 2003), but these models have not been directly compared in a subalpine forest with comparatively low woody species diversity. We also developed tests to examine three underlying assumptions of neutral theory:

1. *Species are functionally equivalent* in terms of demographic rates and dispersal ability

(Hubbell 2001). For example, two species with different mortality (or recruitment) rates would be considered functionally different.

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 between species of the same trophic level, 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 occupy essentially the same shade-tolerant functional niche in tropical forests (Hubbell 2006). Neutral theory suggests competitive exclusion is prevented due to strong dispersal and recruitment limitations, 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.

Study site

We established the Utah Forest Dynamics Plot (UFDP), a 13.64-ha forest research plot located on the Colorado Plateau, and within the plot quantified composition, structure, spatial patterns, and habitat associations of every live and dead woody stem ≥1 cm diameter at breast height (dbh; 1.37 m along the main stem) and all *Pinus* seedlings >1 yr old. The UFDP is located in a mixed-conifer/aspen forest on the north rim of Cedar Breaks National Monument in southwestern Utah, USA (Fig. 1). Climate in the UFDP is characterized by cool, short summers and snowy, cold winters. Most
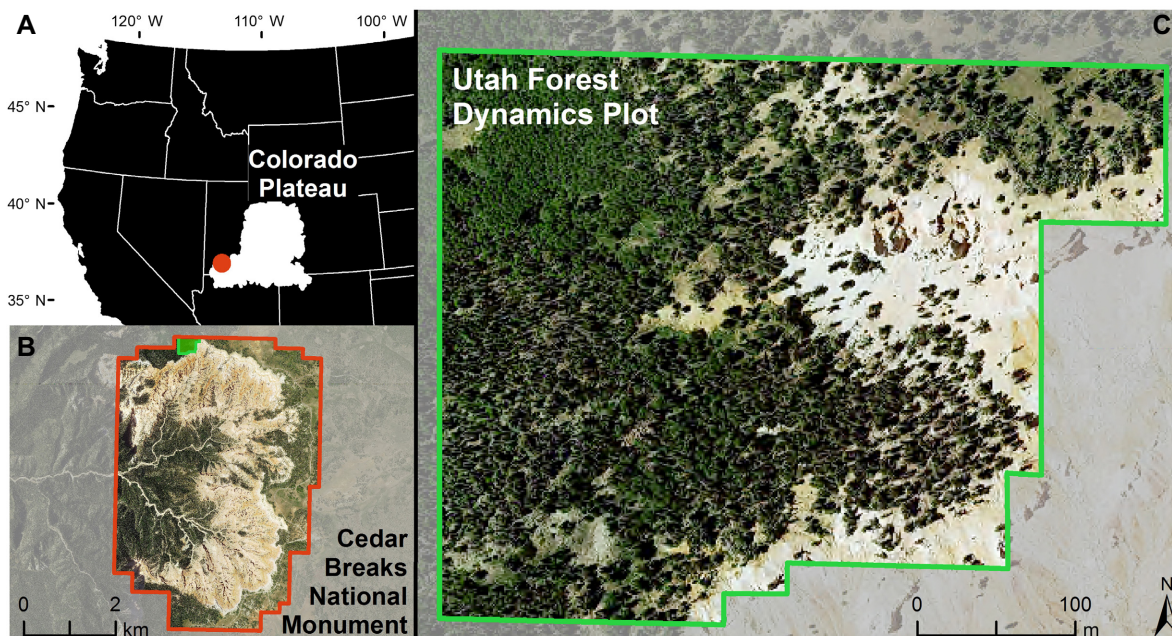
Fig. 1. Location of the Utah Forest Dynamics Plot (UFDP). The UFDP is located on the Colorado Plateau in the state of Utah (A) in Cedar Breaks National Monument (B) on the north side of the Cedar Breaks amphitheater (C). The UFDP comprises 13.64 ha of late-successional aspen/mixed-conifer subalpine forest. The UFDP is bounded on the southeast by the 600-m cliffs of the Cedar Breaks amphitheater. Imagery from National Agricultural Imagery Program (USDA Farm Service Agency 2014).

precipitation falls during the winter as snow, but the North American Monsoon creates a spike in precipitation in July and August (Appendix S1: Fig. S1; Adams and Comrie 1997). Elevations range from 3020 to 3169 m for a vertical relief of 149 m, and slopes range from 0° to 54° with a mean of 19°. The plot is centered at 37.661 N 112.852 W, with dimensions of 460 m east to west and 360 m north to south. Details about geology, climate, vegetation, disturbance history, anthropogenic influence, and detailed plot establishment methods are outlined in Furniss (2016). Within the UFDP, we mapped all stems relative to a 20 × 20 m grid of permanent survey-grade quadrat markers covering the entire plot (mean standard deviation of error ellipses 14 mm). Methods followed those of the Smithsonian ForestGEO global plot network (Anderson-Teixeira et al. 2015) as modified for temperate forests (Lutz et al. 2012, 2013, Lutz 2015). This research was performed under National Park Service research permits CEBR-2014-SCI-0001, CEBR-2015-SCI-0001, and CEBR-2016-SCI-0001.

METHODS

Species abundance distribution

We compared the fit of a ZSM distribution and a lognormal distribution to the observed SAD for all 17 woody species ≥1 cm dbh within the UFDP. We used observed species abundance to parameterize both models, then calculated Akaike's information criterion (AIC), χ^2, and Kolmogorov-Smirnov goodness-of-fit metrics of each curve (sensu Matthews and Whittaker 2014). We plotted the SAD using log-transformed abundance as the predictor variable and the number of species as the response (sensu McGill 2003, Chave 2004, Volkov et al. 2005). All analyses were performed in R version 3.1.2 (R Core Team 2016), and the models were fit using the "sads" package (Prado et al. 2016).

Functional equivalence

We tested the assumption of functional equivalence by calculating demographic rates for all species with densities ≥10 stems/ha. In the

summer of 2016, we conducted a mortality and recruitment survey and used these data to calculate annually compounded recruitment and mortality based on a two-year interval for the portion of the UFDP that was first censused in 2014, and on a one-year interval for the portion first censused in 2015. As demographic rates in high-elevation ecosystems are generally low (Stephenson and van Mantgem 2005), our rates based on one- and two-year time spans do not allow us to assess long-term demographic rates with confidence and we therefore restrict the scope of our inferences from this analysis to short temporal scales. We 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 species with Welch's two-sample t-tests. We assessed significance at $\alpha = 0.05$ and performed a Bonferroni correction for 12 tests (modified $\alpha = 0.0042$).

We further examined functional equivalence by assessing the net effects of dispersal and recruitment processes on the spatial patterns of adult and juvenile individuals for each species. We used the bivariate pair correlation function (PCF), $g_{i,j}(r)$, to summarize the spatial relationship between conspecific adults and juveniles for each species, and we compared the observed patterns to independence and random labeling null models (sensu Wiegand and Moloney 2004). This analysis allowed us to quantify both a priori and a posteriori effects of adult stems on spatial patterns of juveniles. We used the independence null models to infer a priori effects of dispersal and recruitment processes, and the random labeling null models to infer a posteriori effects of density-dependent mortality processes. Under the null hypothesis of neutrality, we expect these spatial patterns to be consistent among all species. For any species that showed a different bivariate spatial relationship between adults and juveniles, we rejected the null hypothesis, indicating some dispersal or recruitment processes is species specific. Full details about the PCF and null model selection are found in Wiegand and Moloney (2004), and on appropriate use of independence and random labeling null models in Goreaud and Pélissier (2003). Adults were defined as individuals ≥ 20 cm dbh, and juveniles were defined as individuals <5 cm dbh. Our objective in choosing

these diameter thresholds was to identify adults as those trees that are the primary contributors to recruitment while identifying juveniles as recent recruits that contribute minimally to reproduction. Diameter thresholds were chosen to maximize our confidence in isolating populations of adults and juveniles while retaining the minimum number of stems required for point pattern analysis. We excluded intermediate stems ≥ 5 and <20 cm from this analysis as their reproductive status is difficult to infer from size alone. We performed a sensitivity analysis on specific diameter cutoff values throughout a $\pm 50\%$ range of diameter thresholds (e.g., cutoff values of <2.5 to <7.5 cm dbh for juveniles and ≥ 10 to ≥ 30 cm dbh for adults). For genus *Pinus*, we repeated this analysis with adult trees ≥ 20 cm dbh and seedlings >1 yr old and <1 cm dbh. We also used the univariate form of the PCF, $g_i(r)$, to compare the pattern of *Pinus* seedlings to a random labeling null model to determine whether the pattern of seedlings was more aggregated than the pattern of all *Pinus* stems.

Ecological equivalence

We assessed competitive equivalence by comparing the patterns of mortality with the null hypothesis of random mortality (sensu Kenkel 1988). We used random labeling techniques to determine whether the probability of mortality for an individual of one species was affected by the presence of live individuals of another species at small spatial scales (<10 m), thus assessing competitive equivalence for each species pair while controlling for the overall degree of segregation or overlap between the spatial patterns of two species at larger spatial scales. This approach implicitly controls for variability in mortality rates across the study site by using the inhomogeneous PCF (details below), and also by only considering small spatial scales (0–10 m) that are much smaller than the scale of habitat variability observed in the UFDP. For example, species A could have a high mortality rate in part of the UFDP and a low mortality rate in another part of the UFDP and still be found to be "ecologically equivalent" to species B if mortality of species A was constant at distance 0–10 m from species B. Neutrality was maintained as long as each species that was influenced by the presence of another had a symmetric effect on

that other species; neutrality was rejected for every species pair that demonstrated 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. Our methods do not permit us to distinguish between these two processes, but isolating specific mechanisms was not necessary to simply evaluate the degree of symmetry between species pairs.

Regarding functional and ecological equivalence analyses

For all point pattern analyses, we limited our analysis to tree species with ≥50 stems because point pattern statistics require a sufficient number of points to detect patterns. This minimum sample size was chosen based on cutoff values between 50 and 70 stems used in other studies (Wiegand et al. 2007, Wang et al. 2010, Punchi-Manage et al. 2015). We controlled for observed habitat heterogeneity by using the inhomogeneous form of the PCF (Baddeley et al. 2000), which uses a variable estimate of first-order intensity (density of stems) to compensate for heterogeneity in the abundance of each species. In the case of the ecological equivalency analysis, the inhomogeneous PCF controls for variability in mortality rates by using a variable estimate of the expected number of dead stems based on variation in the observed number of dead stems across the UFDP. In this cold and dry ecosystem, the long residence time of dead stems (Brown et al. 1998, Kueppers et al. 2004) allows us to infer that the relative patterns of living and dead stems accurately represent recent mortality.

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 up to 20 m. We chose a distance of 20 m because it was large enough to test for independence at intertree distances 0–10 m without generating simulated patterns of juveniles in starkly different habitats within the plot. We conducted a sensitivity analysis by repeating the simulation process with shift distances of 40 and 60 m. Random labeling simulations were generated by holding the location of each point fixed while randomly assigning "marks" to each point ("mark" refers to juvenile/adult status for the functional equivalence analysis and live/dead status for the ecological equivalence analysis) in proportion to observed abundance of each type of mark. Dead stems included all stems that were dead in the 2016 census.

For all spatial analyses, we generated 999 simulations according to the relevant null model, and calculated $g_{i,j}(r)$ 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 $g_{i,j}(r)$ for all 999 simulations, and the theoretical value of $g_{i,j}(r)$ was calculated as the mean of all 1000 patterns (999 simulations + 1 observed). The resulting null model may be interpreted as the amount of variation in $g_{i,j}(r)$ we would expect if the ecological processes determining the patterns were random. All spatial analyses used the spatstat package version 1.46-1 (Baddeley et al. 2015).

Species–habitat associations

We identified habitat types for each quadrat according to parent soil type and aspect (considering four neighboring cells, following the methods of Horn [1981]). Aspects between 135° and 225° that receive the most direct solar 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), we 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) and was assigned to each quadrat based on the map polygon beneath the center of each quadrat. We classified habitat types according to the five parent soil types within the UFDP and two aspect categories for a total of 10 possible habitats. The five parent soil types included three sedimentary layers (all from the white member of the Claron Formation) and two types of landslide deposits (descriptions included in Appendix S1:

Table S1; further details in Furniss 2016 and Rowley et al. 2013). 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. 2). Species–habitat associations were assessed for all species with densities >1 stem/ha, 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 (Plotkin et al. 2000, Harms et al. 2001), we implemented both methods to ensure that our results were not subject to the sensitivities of a single test.

We performed χ^2 tests by comparing observed abundance of each species in each habitat type to values expected if abundance was even throughout the UFDP. Expected values for each unique species–habitat combination were calculated according to the equation:

$$E_{i,j} = (n_i \times n_j)/N$$

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 N is the total number of all stems in all habitats. We 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 translations were conducted following the methods of Harms et al. (2001). 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 generated by systematically shifting the entire map of habitat types according to a two-dimensional torus pattern while keeping the locations of stems constant. Each 20-m increment of the toroidal shift created a unique distribution of habitat types across the plot while maintaining the same relative cover of each habitat type. Torus translations resulted in 414 simulated habitat maps which we compared to the observed abundance of each species per habitat type. 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 simulated maps. Species–habitat associations implemented
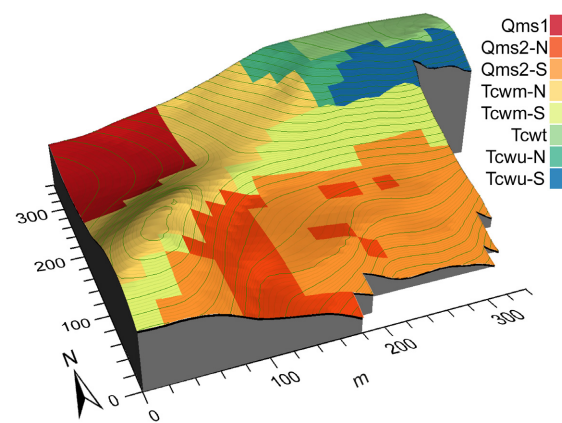

Fig. 2. Habitat types within the Utah Forest Dynamics Plot classified according to geologic parent material and aspect. Colors delineate distinct habitats labeled according to geologic layer. Geologic codes are defined as follows: Qms1—landslide deposits that rest beneath Brian Head Formation material and the Tcwm layer; Qms2—landslide deposits beneath the Tcwm and Tcwu layers; Tcwt—uppermost mudstone, siltstone, and sandstone unit of the white member of the Claron Formation; Tcwu—upper limestone unit of the white member of the Claron Formation; Tcwm—middle mudstone, siltstone, and sandstone unit of white member of the Claron Formation. "N" and "S" following geologic code indicate north- or south-facing habitats. Contour lines represent five-meter increments in elevation.

code from Harms et al. (Harms et al. 2001) and the raster package version 2.4-18 (Hijmans 2016).

Results

In the UFDP, there were 12 tree and five shrub species, representing 10 genera and six plant families. Including all species, there were 23,177 live trees, 4425 snags, and 243 shrubs for a total of 27,845 stems ≥1 cm dbh and 1371 *Pinus* seedlings <1 cm dbh (Appendix S1: Table S2). Stem densities ranged from 0 to 8375 stems/ha with a mean of 1717 stems/ha, and quadrat basal area ranged from 0 to 132.5 m²/ha (Fig. 3).

Species abundance distributions

The ZSM and lognormal models performed similarly in their approximation of the observed data (Fig. 4). The ZSM model was a marginally better fit, with ΔAIC of 6.6 when compared to the lognormal model. Neither model was
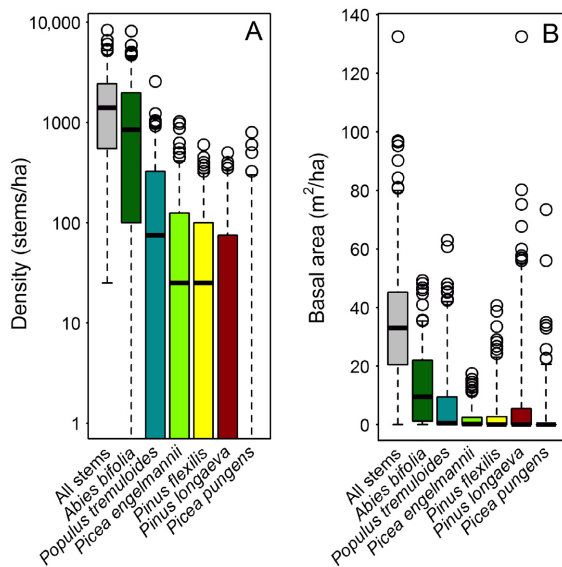
Fig. 3. Density and basal area of principal tree species within the Utah Forest Dynamics Plot (UFDP). Each boxplot represents density (A) or basal area (B) by species for all 341 20 × 20 m quadrats in the UFDP. Boxes indicate the 25th percentile, median, and 75th percentile; whiskers indicate the 2.5th and 97.5th percentiles. The *y*-axis for (A) is log-transformed.

rejected according to Kolmogorov-Smirnov tests ($P > 0.1$; Fig. 4), yet both models were rejected by χ^2 tests ($P < 0.001$).

Functional equivalence

The short-term mortality rate for all stems within the UFDP was 0.8% per yr, the recruitment
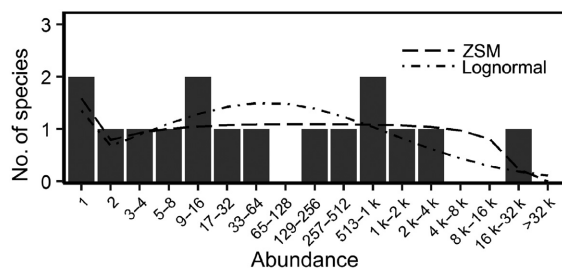

Fig. 4. Species abundance distribution (SAD) for the Utah Forest Dynamics Plot. A standard rank–abundance plot of the observed SAD approximated by a neutral zero-sum multinomial (ZSM) distribution and a non-neutral lognormal distribution displayed as a binned histogram with abundance classes (*x*-axis) plotted on a $\log_2$ scale.

rate 0.9% per yr, and the turnover rate 0.85% per yr (Fig. 5). *Pinus longaeva*, *Pinus flexilis*, *Picea engelmannii*, and *Picea pungens* had lower mortality rates, while mortality rates of *Abies bifolia* and *Populus tremuloides* were consistent with the overall rate. *Pinus longaeva* and *P. flexilis* had lower recruitment rates, but all other species were consistent in recruitment rate.

We found attraction between the spatial patterns of adult and juvenile *A. bifolia*, *P. engelmannii*, and *P. pungens* (Fig. 6A). Spatial patterns of juvenile *P. flexilis*, *P. longaeva*, and *P. tremuloides*, however, were found to be independent of adults (Fig. 6B; all species shown in Appendix S1: Fig. S2). *Pinus flexilis* and *P. longaeva* seedlings (<1 cm dbh) were aggregated with respect to each other from 0 to 2 m and 0 to 3 m, respectively, but the spatial patterns of *Pinus* seedlings were independent of *Pinus* adults (Appendix S1: Fig. S3). We compared the spatial patterns of juveniles to random labeling null models and found proximity to adults did not increase the probability of mortality for juvenile *A. bifolia*, *P. engelmannii*, *P. flexilis*, *P. longaeva*, or *P. pungens* (Fig. 6D, F). However, we found mortality of juvenile *P. tremuloides* was higher in the presence of adult *P. tremuloides* at distances from 0 to 10 m (Fig. 6E). Results were not sensitive to the specific choices
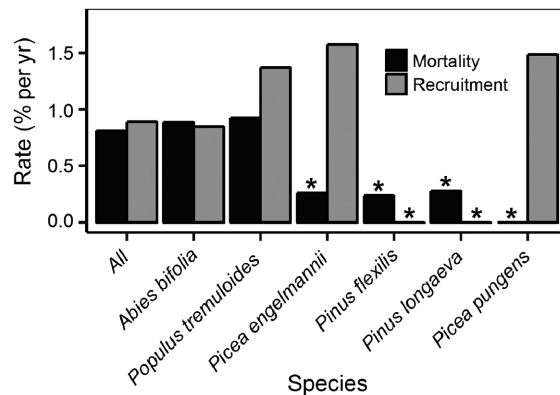

Fig. 5. Demographic rates for species within the Utah Forest Dynamics Plot. The *y*-axis represents annually compounding recruitment and mortality rates calculated based on one- and two-year intervals for all stems ≥1 cm dbh. Asterisks indicate significant deviation from baseline mortality or recruitment rates calculated for all other species at α = 0.05 with a Bonferroni correction for 12 tests (adjusted α = 0.0042).
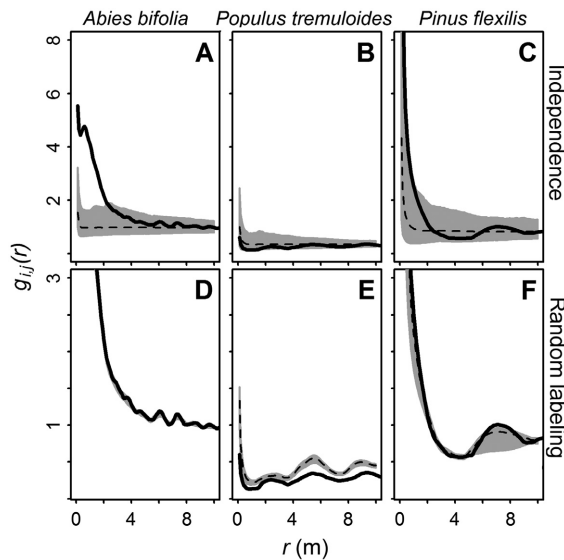
Fig. 6. Bivariate spatial patterns between juvenile (<5 cm dbh) and adult (≥20 cm dbh) *Abies bifolia* (A, D), *Populus tremuloides* (B,E), and *Pinus flexilis* (C,F). Black lines indicate observed values of the bivariate pair correlation function, $g_{i,j}(r)$; gray area represents simulation envelopes based on the 2.5th and 97.5th percentile values of 999 simulated point patterns generated according to the null models of independence (A–C) and random labeling (D–F). For the independence null model, values of $g_{i,j}(r)$ above the simulation envelope indicate dependence of juveniles on the pattern of adults, while values of $g_{i,j}(r)$ within the simulation envelope indicate independence between the patterns of adults and juveniles. For the random labeling null model, values above (below) the simulation envelope indicate juveniles are more (less) likely to be alive at distance r from adults.

of diameter definitions for adults and juveniles (Appendix S1: Fig. S4), nor were results sensitive to the distance chosen to shift the point pattern of juveniles (20 m) for the independence simulations.

Ecological equivalence

For 14 out of 15 species pairs, plant–plant interactions were roughly symmetric, indicating mortality for most species was not strongly influenced by the presence of any one other species. However, we found attraction between live *A. bifolia* and dead *P. tremuloides* (Fig. 7A), and repulsion between live *P. tremuloides* and dead

A. bifolia (Fig. 7B). In other words, probability of mortality for *P. tremuloides* was higher in the presence of live *A. bifolia*, while probability of mortality for *A. bifolia* was lower in the presence of live *P. tremuloides* (all species pairs in Appendix S1: Fig. S5).

Species–habitat associations

All species with densities ≥1 stem/ha exhibited habitat associations with at least one out of eight distinct habitat types classified according to geology and aspect (Fig. 2; Appendix S1: Table S3). All species showed a positive association with at least one habitat, and species with densities ≥10 stems/ha also showed a negative association with at least one habitat. We 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 × 8 habitats). These quantitatively determined habitat types matched the observed variation in the UFDP (Fig. 8; Appendix S1: Fig. S6).
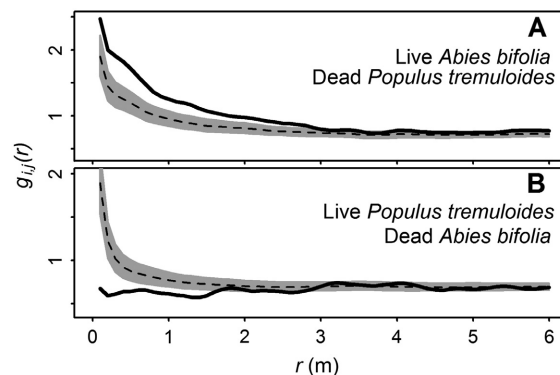

Fig. 7. Bivariate spatial patterns between *Abies bifolia* and *Populus tremuloides*. Black lines indicate observed values of the bivariate pair correlation function, $g_{i,j}(r)$; gray area represents confidence envelopes derived using the 2.5th and 97.5th percentile values $g_{i,j}(r)$ from 999 simulations generated according to the null model of random mortality using the observed live stems of one species while randomly assigning a status of dead to stems of the other species. Values of $g_{i,j}(r)$ above the simulation envelope indicate mortality of *P. tremuloides* is more likely in the presence of *Abies bifolia* (A), while values below the simulation envelope indicate mortality of *A. bifolia* is lower in the presence of *P. tremuloides* (B).

Fig. 8. Vegetation communities associated with eight distinct habitat types within the Utah Forest Dynamics Plot. Text matches habitat codes and map colors in Fig. 2. Definitions of each habitat type are included in Appendix S1: Table S1 and Fig. 2. Photo credits: T. Furniss.

While geology was an important driver of forest composition, we observed a great deal of variability between northerly and southerly aspects within the same geologic layer. Aspect effect appeared particularly strong in Tcwm habitats; *P. longaeva* and *P. pungens* both had positive associations with south-facing slopes on Tcwm, but negative associations with north-facing slopes, while *Abies bifolia* showed the opposite trend (Appendix S1: Table S3). Conversely, aspect effect on Tcwu habitats appeared to be less important, as *P. flexilis* and *P. longaeva* were positively associated with both north and south aspects, while *A. bifolia* and *P. tremuloides* were negatively associated with both aspects (Appendix S1: Table S3).

DISCUSSION

Neutral theory did not perform well in this subalpine forest. Both the neutral ZSM model and the alternative lognormal model were a poor fit to the observed SAD in the UFDP, a surprising result considering many other studies have found both ZSM and lognormal models predict tropical SADs well (McGill 2003, Volkov et al. 2005, Hubbell 2006). The poor fit of the neutral model to this temperate forest SAD is likely a consequence of the relatively low woody plant species diversity of subalpine forests, and the high number of rare species (41% of species had abundance <1 tree/ha).

We tested the assumption of functional equivalence and found species within the same genera paralleled each other in their demographic rates in the short term (Fig. 5). While these rates were calculated based on a relatively short time span, 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). We further explored species' functional equivalency by assessing the net effect of dispersal and recruitment processes on spatial patterns for each species. We found intraspecific attraction between juveniles and adults for *Abies bifolia, Picea engelmannii,* and *Picea pungens* (Appendix S1: Fig. S2), indicating dispersal and establishment limitations may be important demographic processes for these species.

In contrast, dispersal limitation appeared less important for *Pinus flexilis*, *Pinus longaeva*, and *Populus tremuloides* (Fig. 6B; Appendix S1: Fig. S2). This conclusion was further supported by the spatial patterns of *Pinus* seedlings which were independent of adults and were aggregated at small scales (Appendix S1: Fig. S3). This clustered pattern of seedlings is consistent with our understanding of *Pinus* seed dispersal strategies which include primary dispersal by wind, primary dispersal by vertebrates, and secondary dispersal by vertebrates (Vander Wall 2003). Previous studies have found vertebrate dispersal (primarily Clark's nutcracker) to be a particularly common dispersal mechanism for both *P. longaeva* and *P. flexilis* at high-elevation sites (Lanner and Vander Wall 1980, Lanner 1988), likely giving rise to the clustering we observed in *Pinus* seedlings. We also found higher rates of mortality for juvenile *P. tremuloides* within 10 m of conspecific adults, suggesting negative density-dependent processes may influence recruitment for this species. While dispersal and recruitment processes appeared to act similarly upon species within the same genera, we rejected the assumption of functional equivalence for non-congeners.

The *P. tremuloides–A. bifolia* species pair showed a strong non-neutral pattern (Fig. 7). Live *P. tremuloides* decreased the probability of mortality for *A. bifolia*, while live *A. bifolia* increased mortality of *P. tremuloides*. This asymmetric interaction is consistent with the current understanding of *P. tremuloides–A. bifolia* competitive dynamics (Rogers 2002, Kulakowski et al. 2013), and also supports the work of Calder and St. Clair (2012) that identified facilitation of *A. bifolia* by *P. tremuloides* as an important driver of conifer forest succession. This single-species pair was the only exception to the neutral theory assumption of ecological equivalence in the UFDP, but *P. tremuloides* and *A. bifolia* together comprise over 80% of all stems in this forest (Appendix S1: Table S2).

The habitat specificity of all tree species ≥1 tree/ha constituted the greatest departure from neutral theory. 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 of forests

has found habitat preference for 100% of woody species with densities ≥1 tree/ha. 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], La Planada, Colombia, and Yasuni, Ecuador [John et al. 2007]). The prevalence of habitat associations in the UFDP may be due to high levels of local habitat heterogeneity, which may not have been present in the tropical forest studies (Hubbell and Foster 1986, Harms et al. 2001, Gunatilleke et al. 2006, John et al. 2007, Chuyong et al. 2011). If this is the case, future studies of the niche–neutrality gradient should explicitly consider spatial scale and the degree of local habitat variability, as these may be important ecosystem characteristics that influence the strength of niche-based processes (Wang et al. 2011, Masaki et al. 2015). This finding may partially explain the inconsistency in results of other neutral theory studies in temperate forests. For example, a temperate forest on a very heterogeneous landscape may be dominated by niche processes, while a climatically identical forest on a homogeneous landscape may be found to be dominated by neutral processes.

The prevalence of habitat associations in the UFDP suggests habitat variability is an important factor structuring subalpine forest species diversity, and we thereby reject the habitat generality assumption of neutral theory. Niche differentiation is a more important mechanism fostering species coexistence and landscape-level tree diversity in this heterogeneous subalpine forest.

Conclusions

We propose three possible explanations for the lack of support of neutral theory in our study: (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 a practical model for subalpine forest ecosystems. The first two points consider spatial and temporal scale as important factors determining the relative importance of niche and neutral processes. While it appears non-neutral processes play a

dominant role at the spatial and temporal scales of this study, there may be support for neutral theory at larger or smaller scales (Chave et al. 2002, McGill et al. 2006). 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 our habitat specificity results indicate the degree of local habitat heterogeneity should be considered in addition to absolute spatial scales.

The third point reflects on the universality of neutral theory. This study suggests neutral theory is less relevant in subalpine forests, especially one near the altitudinal limits of closed-canopy forest, 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). This hypothesis may help explain the lack of consistent results from other temperate forest neutral theory studies, as most assessments of neutral theory in temperate forests have been in less-limiting climates. However, while climate may be important, it alone does not explain observed patterns of the niche–neutrality gradient on a global scale (Kubota et al. 2016). It is likely that other ecosystem characteristics are also influencing the relevance of neutral theory, such as climate-related stress, disturbance history, and scale of observation (Weiher et al. 2011).

Perhaps the dominance of niche processes in temperate forests is due to the lower γ-diversity compared to tropical forests. Indeed, Chisholm and Pacala (2011) showed that neutral processes were 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.

It appears that no one environmental characteristic is the sole driver of the niche–neutrality gradient. Scale, habitat heterogeneity, climate, and diversity likely each play a role in determining the relevance of niche and neutral processes, and these drivers may act in opposing ways. To disentangle the effects of each of these drivers

and develop a framework for better understanding the importance of neutral processes in a global context, future studies need to continue to test neutral theory in novel ecosystems using a range of methodologies. Assessing the underlying assumptions of neutral theory, as we have done in this study, enables researchers not only to assess whether an ecosystem is "neutral," but to determine which elements of neutral theory may be relevant and which elements are not.

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, but generally unattainable 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, DeRose and Long 2012). If widespread disturbance and climate bottlenecks were long absent in a subalpine forest, perhaps we would observe more support for the predictions and underlying assumptions of neutral theory. Given the improbability of attaining long-term stability in many forests, however, the relevance of any universal theory that does not explicitly consider the role of disturbance is questionable.

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