Resource use efficiency as a function of species richness and stand composition in upper montane conifer forests of the Sierra Nevada

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Abstract
Questions: 1. Does resource use efficiency increase with increased species richness in conifer forests? 2. Do patterns found in resource use support niche differentiation/complementarity between species, or is any increase indicative of a selection effect?

Location: All data were collected from upper montane (2200-2600 m a.s.l) conifer forests of the Desolation Wilderness in the central California Sierra Nevada, USA.

Methods: We established 281 plots of varying levels of conifer richness throughout the wilderness area. Within each plot we used hemispherical photos to measure canopy closure and LAI, total soil carbon and nitrogen from the A-horizon, and stand basal area. We used linear regression and ANOVA to analyse the relationship between stand species richness and resource availability.

Results: We found no correlation of either soil nitrogen or carbon with stand biomass. Nor did soil nitrogen and carbon levels change with species richness. Canopy closure increased with species richness but also varied significantly between pure stands of different species. Pure Pinus monticola stands had the lowest canopy closure, Tsuga mertensiana stands the highest. Composition explained more canopy cover variation than did species richness. We found evidence supporting both the sampling effect and niche differentiation models at different stages of stand development.

Conclusions: During initial stages of stand development, the interaction between the shade-intolerant Pinus species and shade-tolerant Abies magnifica and T. mertensiana followed the niche differentiation model, but switched to the sampling effect model during the competitive-exclusion stage. In contrast, interaction between A. magnifica and T. mertensiana followed the niche differentiation model.

Keywords: Biodiversity; Complementarity effect; Ecosystem function; Pinus contorta; Pinus monticola; Abies magnifica; Sampling effect; Selection effect; Tsuga mertensiana.

Introduction

There has been an increasingly urgent call for ecologists to focus on the role of species richness in the functioning of ecosystems (Mooney 2002). Natural ecosystems provide important services to human societies. Clean drinking water, soil stabilization, buffering of vector-transmitted disease outbreaks, and pollination are ecosystem services that, in most cases, are irreplaceable or prohibitively expensive to replicate (Costanza et al. 1997; Daily 1997; Huber 1999; Sala 2001). One particular function thought to increase with increasing species richness is resource-use efficiency (Tilman 1982, 1994; Tilman et al. 2002; Gastine et al. 2003). Research on the role of species richness and ecosystem functioning is based on the idea that as species richness increases, so does the number of niches (Trenbath 1976; Vandermeer 1989; Swift & Anderson 1993). It follows that niche differentiation should increase with species richness, leading to more efficient capture of limited resources.

The increased resource-use efficiency of species-rich systems is often presented as the mechanism driving diversity/productivity relationships (McNaughton 1993; Swift & Anderson 1993; Naeem et al. 1994,1995; Tilman et al. 1996). In a field study in Costa Rica, Ewel et al. (1991) found that areas planted with many species retained higher soil fertility than those planted to monocultures. These results were the first evidence supporting the diversity/nutrient retention hypothesis. Hooper & Vitousek (1997, 1998) were able to replicate this result in California grasslands. In a four-year experiment at Cedar Creek, Minnesota, Tilman et al. (2001) found that decreasing soil nitrate concentrations were significantly related to increasing plant diversity. The diversity/nutrient retention hypothesis has frequently been tested in laboratory conditions and natural experiments in forests such as Hubbard Brook (Likens et al. 1970) with many applications such as riparian buffer strips (Tufekcioglu et al. 2003).
There is also evidence that increased tree diversity can increase light-use efficiency and productivity in forest systems (Smith 1986; Chen et al. 2003), however it has rarely been tested in unmanaged communities dominated by long-lived plants.

In this study, we use upper-montane conifer forest stands to first explore the hypothesis that resource use efficiency for soil nitrogen and intercepted light increases with conifer richness. Upper-montane conifer forests (Barbour & Christiansen 1993) contain stands with every possible combination of Pinus contorta ssp. murrayana, P. monticola, Abies magnifica and Tsuga mertensiana. The principle resources for which these species compete are water, light, and soil nutrients. We measured the canopy closure, percent total soil nitrogen, and percent total soil carbon of forest stands in order to test the hypothesis that species-rich stands use resources more efficiently than those with few species.

Secondly, we explore whether patterns in resource use followed assumptions either of the sampling effect or the niche differentiation models. The sampling effect model assumes that the most competitive species are also the most productive ones (Tilman 1982). When all species are assumed to be competing for a single resource, the species with the lowest resource requirement ($R^*$ per Tilman 1982) for that resource will displace all other species at equilibrium. Thus, the sampling effect model predicts that communities become dominated by the most competitive species at the expense of less competitive species (Tilman & Lehman 2001); it further predicts that the average level of unconsumed resource, and its variance, will decline as species number increases and that the resource level is drawn down by the most competitive species (Tilman & Lehman 2001). Finally, the sampling effect model predicts that, as species are added to the mixture, the probability of containing a productive species in the species assemblage increases, hence the names ‘sampling effect’ or ‘selection effect’ model.

The niche differentiation model (Tilman et al. 1997; Loreau 1998; Tilman 1999; Lehman & Tilman 2000) predicts long-term co-existence of species via interspecific differentiation in response to exploitative competition for environmentally limiting factors. Two or more species can co-exist as long as they are competing for multiple resources and that those resource levels are spatially heterogenous. The niche differentiation model has a different resource-use signature than the sampling effect model. Concentrations of unused resources are predicted to be a decreasing function of species richness, where single species stands are unable to use resources as completely as species-rich stands. If this is the case, each added level of species-richness should further decrease the resource level. In contrast the sampling effect model predicts that resource levels are a function of the single most efficient species where the resource level remains low so long as the most efficient species is found in the stand. Therefore, with niche differentiation models, the lower bounds of resource curves are a decreasing function of diversity and not flat lines, as in the sampling effect model (Tilman et al. 2001; Tilman & Lehman 2001).

**Methods**

We sampled 281 forest stands in the Desolation Wilderness in El Dorado County, CA, from August through October in 2002 and 2003. All stands were located within the wilderness boundary with the exception of 15 western Pinus monticola stands located 66 km north in the Babbitt Peak Research Natural Area (Sawyer & Keeler-Wolf 1995). We sampled a minimum of ten stands for every possible combination of P. contorta, P. monticola, A. magnifica and T. mertensiana (Hickman 1993).

It is well recognized that plant communities change along elevational and environmental gradients in the Sierra Nevada. To limit environmental variability and to focus our sampling on sites suitable to the growth of all four species, we constrained the location of potential stands with a GIS model limiting the environmental parameters suitable for stand selection. The GIS model used the Sierra Nevada Ecosystem Project database (http://ceres.ca.gov/snep/) to homogenize environmental variation by identifying stands located on slopes < 20°, between 1900-2500 m elevation, and having only conifer cover classes. We further limited environmental and stand variability in the field by only including stands with ≤ 1% bedrock visible on the soil surface, a minimum of 65% canopy closure, and a minimum tree age of 120 years to avoid sampling stands in the increase phase of growth (Bell et al. 1990; Burns et al. 1990). We avoided wet sites indicated by the presence of Salix, or Vaccinium and dry sites indicated by Arctostaphylos or Quercus shrubs. Our minimum canopy closure requirement also facilitated in avoiding sites that were overly dry. We field-tested the model and found that it accurately located suitable sample sites within the potential niches of all four species.

We measured stand basal area as an indicator of biomass. Biomass has a 1:1 relationship with net ecosystem productivity and forest ecologists use it as an indicator of cumulative productivity (Peet 1992). Although basal area does not permit defining size class distributions, or measuring stand volume, it permitted us to estimate stand biomass of a large number of plots within a large roadless geographic region. Forest stands...
rapidly accumulate biomass during early stages of stand development, eventually levelling off where gross photosynthetic gain just exceeds loss to respiration (Bell & Dilworth 1990; Burns & Honkala 1990; Peet 1992; Pallardy et al. 1995). All sampled stands were ≥ 120 years of age. Upper montane forests are relatively closed with only two canopy layers: an overstorey canopy layer, and an understory of scattered shrubs and herbs (Barbour & Woodward 1985). We only sampled stands where conifer biomass was the overwhelming source of productivity with minor contributions (< 1%) from herbs and shrubs. We used variable plot sampling with a 20 basal area factor prism and standard forestry sampling protocols to measure stand basal area (Bell & Dilworth 1990). We recorded the location of each stand with an Etrex 12 channel hand-held GPS (WGS 84 Map Datum). Elevation was recorded using a wrist altimeter.

A soil sample from the A-horizon was collected from each stand centre. We dried and sieved the soils with a 2-mm sieve, then measured total nitrogen and carbon levels using 0.05-mg subsamples burned in a Carlo-Erba gas analyzer (Carlo-Erba Instruments, Milan – described in Schepers et al. 1989). Soil carbon was used as a surrogate for soil organic matter, and to calculate C:N ratios.

We measured canopy cover by taking a hemispherical digital photo from the stand centre with a Nikon Coolpix digital camera with a fisheye lens. To calculate the percent canopy openness and leaf area index (LAI) of each stand, we used Gap Light Analyzer 2.0 (http://www.ecostudies.org/gla/). We used percent canopy closure as a measure of competition for light, and the inverse, percent canopy openness as a measure of unused light levels.

Data were analysed with JMP statistical software. Multiple regression analysis and ANOVA were used to test correlations and difference between conifer diversity, composition, biomass, nitrogen and carbon levels, and canopy openness.

**Results**

Our GIS model and field criteria for selecting suitable plot sites successfully reduced site effects on stand composition and productivity. A founding principle of vegetation science since the time of von Humboldt (1814-1829) and Whittaker (1960) is that community composition changes with environmental gradients. Autecological work describing the potential and preferred niches of the four species used in this study is available; for example, *Tsuga mertensiana* prefers moist sites on north facing slopes at higher elevations (Dahms & Franklin 1965), whereas *Pinus monticola* is more tolerant of dry south facing slopes (Graham 1990). However, vegetation scientists recognize that there are regions within environmental gradients with abundant species overlap and co-existence. We made every effort to limit our study to sites where environmental variables do not limit species composition. We measured our success in achieving this goal by testing the relationship between environmental variables (elevation, slope and aspect) and community response variables (species proportion, basal area and canopy closure). As shown in Table 1, correlations between the proportions of each species are not significant. There is a weak relationship between elevation and the proportion of *Tsuga mertensiana* and *Abies magnifica* in the stands, where *Tsuga mertensiana* is more prevalent at higher elevations, and *A. magnifica* more prevalent at lower. However the correlation coefficient for both is quite low. Since pure stands of *P. monticola* are non-existent throughout most of California having been lost to white pine blister rust, we were limited to sampling pure stands in their nearest known location, the Babbitt Peak Natural Reserve Area 60 km north of the Desolation Wilderness. This limitation caused *P. monticola* to be highly correlated to all site variables measured, therefore regression coefficients in Table 1 exclude pure stands of *P. monticola* from the analysis.

There is no significant relationship between basal area and site variables, and there is only a very weak negative relationship between canopy closure and elevation (Table 1). Canopy closure increases with elevation, which is opposite expected trends in the upper montane. We explain this trend with the increased probability of sampling a pure mountain hemlock stand at higher elevation.

Mean total soil carbon and nitrogen values and ranges were typical for the northern Sierra Nevada (Dahlgren et al. 1997; Johnson et al. 1997). The mean total soil carbon was 5.6% with a range from 0.4 to 25.3, mean

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**Table 1.** Relationship between environmental variables (elevation, slope and aspect) and community variables - proportion of each species in a stand (%), basal area (m²) and canopy closure (%). Note that because pure stands of *Pinus monticola* were only found in one location (Babbitt Peak RNA) they were excluded from the analysis. Inclusion of pure stands causes the proportion of *P. monticola* to be significantly correlated with all environmental variables measured.

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<th>Elevation (m)</th>
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<tr>
<td></td>
<td>R²</td>
<td>p</td>
<td>R²</td>
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<tr>
<td><em>Tsuga mertensiana</em></td>
<td>0.039</td>
<td>0.023</td>
<td>0.006</td>
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<td><em>Abies magnifica</em></td>
<td>0.015</td>
<td>0.084</td>
<td>0.017</td>
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<tr>
<td><em>Pinus contorta</em></td>
<td>0.005</td>
<td>0.307</td>
<td>0.003</td>
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<tr>
<td><em>Pinus monticola</em></td>
<td>0.006</td>
<td>0.307</td>
<td>0.006</td>
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<td>Basal area (m²/ha)</td>
<td>0.003</td>
<td>0.341</td>
<td>0.007</td>
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<td>Canopy closure (%)</td>
<td>0.052</td>
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total nitrogen was 0.19% with a range from 0.03 to 1.03. Both carbon and nitrogen were highly correlated ($r^2 = 0.91; p = 0.0001$) and skewed to lower percentages. The C:N ratio was 28.6 ± 2.8. Neither total carbon nor total nitrogen was correlated to stand species richness. Total carbon and nitrogen decreased insignificantly with species richness ($r^2 = 0.00; p = 0.48$; Fig. 1a) and stand basal area ($r^2 = 0.01; p = 0.1841$; Fig. 1b). There was no correlation of C:N ratio with species richness ($r^2 = 0.005; p = 0.316$), basal area ($r^2 = 0.006; p = 0.267$), nor composition ($r^2 = 0.082; p = 0.246$). Total carbon and nitrogen differed with composition with slightly higher nitrogen and carbon content in stands containing Pinus contorta. This may be indicative of higher nitrogen levels during early stages of stand development. However, there is no strong indication that soil nitrogen and carbon play important roles determining stand productivity or composition.

Mean canopy closure (CC) was 78.6% for the 250 stands where photographs were taken. The lowest mean canopy closure was found in pure stands of white pine (75% CC) and the highest in red fir-mountain hemlock mixtures (88% CC). Canopy closure exhibited small but significant increases with increasing species richness ($F_{1,249} = 9.147; r^2 = 0.04; p = 0.0028$; Fig. 1c) and was significantly correlated with stand basal area ($F_{1,249} = 37.56; r^2 = 0.13; p = 0.0001$) that also increased significantly with species richness (Fig. 1d). When species richness was used as the independent variable in an ANOVA on canopy closure, the one- (76% CC) and four-species stands (80% CC) were significantly different whereas the two- and three-species stands were not significantly different from one another (78% CC). LAI ranged between 0.8 and 2.3 with a mean value of 1.59. Since LAI was highly correlated with canopy closure ($r^2 = 0.90; p = 0.0001$), we refer only to canopy closure below.

Fig. 1. Relationship of species richness with total soil nitrogen (a), of stand basal area with total soil nitrogen (b), and of canopy openness (c) and stand basal area (d) with species richness. Since soil carbon and nitrogen are auto-correlated, the results in Fig. 1a, b also apply to soil carbon. None of the relationships were significant indicating that total soil nitrogen and carbon levels did not change with species richness or basal area. On the left, the diagonal line represents the linear relationship between canopy openness and species richness whereas the horizontal dotted lower line indicates the lower bounds of canopy openness. This flat line is diagnostic of the sampling effect model whereas a downward sloping line would be indicative of the niche differentiation model. On the right, the lower diagonal line represents the linear relationship between species richness and basal area. The upper diagonal represents the upper bounds of the diversity species richness relationship. The increasing upper bound is representative of the complimentary effect whereas a flat line would be indicative of the sampling effect.
There were significant differences between canopy closures of single-species stands ($r^2 = 0.35; p = 0.0021$; Fig. 2a). Canopy closure was highest in *Tsuga mertensiana* stands (82% CC), but not significantly different from *Abies magnifica* stands (79% CC), and *A. magnifica* stands were not significantly different from *P. contorta* stands (76% CC). *P. monticola* stands had the lowest mean canopy closure (73% CC) but they were not significantly different from *P. contorta* stands.

The sampling effect model predicts that the average level and variance of unconsumed resource will decline with increasing species richness (Tilman & Lehman 2001). We found that canopy openness (the inverse of canopy closure and a measure of unused light) declined significantly with increasing species richness (Fig. 1c). We also found that the variance in CC declined with increasing species richness, further supporting predictions of the sampling effect model. The lower bound of the canopy openness by species richness relationship was flat rather than a decreasing function of species richness, also supporting the sampling effect model (Fig. 1c). In contrast, variance in soil nitrogen and carbon did not change with increasing species richness.

**Fig. 2.** Canopy closure ranked by composition (a) and stand basal area ranked by composition (b). Stand composition is indicated by L = *Pinus contorta*, W = *P. monticola*, H = *T. mertensiana* and R = *A. magnifica*; the overall mean is indicated by the line running horizontally through the figure. Although the lower axis represents composition, the ranking from low canopy cover to high canopy, and from low basal area to high basal area cover follows accepted forest succession trends of upper montane forests. The composition axis can be visualized as a time axis, each section had been labeled 1, 2, or 3 matching stand dynamics stages described in the Discussion. Note the stair step pattern of increasing canopy closure and that the composition ranking is slightly different in both figures.
Discussion

Our results indicate that light interception in Sierra Nevada upper montane conifer forests follows trends predicted by biodiversity and ecosystem function theory. Soil nitrogen and carbon on the other hand, appear to have little to no effect on interspecific dynamics. Light acquisition increased with increased species richness as predicted by both the sampling effect and the niche differentiation model. Canopy openness, the inverse of canopy closure and a measure of unused light, has a flat lower bound (Fig. 1c) supporting the sampling effect model. The sampling effect model predicts that the species that can tolerate the lowest resource levels in pure stands (typically the most productive species) should dominate in mixed stands at equilibrium. In contrast, the niche differentiation model predicts co-existence at equilibrium. Both models consider the ecological traits of the member species. The results therefore require an understanding of the autecological differences among the four conifer species.

Tree shade tolerance, drought tolerance, potential height, and productivity are the important autecological traits that exert control over forest development in the Sierra Nevada (Barbour & Minnich 2000; Royce & Barbour 2001a, b). These traits differ significantly among the four conifer species in the study. Our analysis of canopy closure of pure stands clearly demonstrated that *P. monticola* stands had the lowest canopy closure, followed by *P. contorta* stands, while *A. magnifica* stands had moderate canopy closures and *T. mertensiana* stands had the highest canopy closure (Fig. 2a). These findings can be interpreted by referring to standard forestry models of shade tolerance: species with low canopy closures are classified as shade-intolerant, and those with high canopy closures are classified as shade-tolerant (Graham 1990). Based on the shade-tolerance of the species, there are two mechanisms of competitive exclusion possible. First, species that are intolerant of shade typically are competitively excluded from low-light environments, although exclusion may require decades to centuries. Second, the effect of competitive exclusion is exhibited in the inability of seedlings of shade-intolerant species to establish themselves in low-light environments beneath the canopy of the shade-tolerant species (Graham 1990; Lotan & Critchfield 1990; Barbour et al. 1998). Throughout the remainder of this paper we refer to the *Pinus* species as drought-tolerant, and *A. magnifica* and *T. mertensiana* as drought-intolerant. It should be noted, however, that once any individuals of the four species have become established, they all survive numerous droughts of various intensity and duration. *T. mertensiana* and *A. magnifica* often have life spans of > 500 a, a period of time long enough to include numerous droughts and the cumulative effect of recent global warming. Like shade-tolerance, the effects of drought-tolerance or intolerance are most notable during the seedling stage, before the plant has a well-established taproot (Laacke 1990). *P. monticola* seedlings can experience high mortality during drought years in shaded conditions when root penetration is slow and unable to keep pace with receding soil moisture (Graham 1990). *A. magnifica* and *T. mertensiana* seedling survival can be facilitated on dry sites by the presence of mature overstory pine canopy cover (Dahms & Franklin 1965). In addition to calculating the mean drought resistance of each species, we converted annual basal area growth by species. *A. magnifica* is the most productive (19.69 cm².a⁻¹), followed by *P. contorta* (18.79 cm².a⁻¹), whereas *P. monticola* (9.36 cm².a⁻¹) and *T. mertensiana* (8.26 cm².a⁻¹) were the least productive.

The last species traits of importance to either the sampling effect model or the niche differentiation model are tree height and life span. The height and the life span of the four species differ. *P. contorta* is the shortest-statured and lived of the four, attaining heights of only 15-20 m and ages of > 200 a (Rundel et al. 1988; Lotan & Critchfield 1990). *P. monticola* can reach heights of 70+ m and ages of 300-400 a. *A. magnifica* trees can be 70 m tall, and > 500 a in age. *T. mertensiana* trees can reach heights of only 40 m, but ages of > 800 a.

The most commonly accepted model for upper montane forests in the northern Sierra Nevada postulates that *P. contorta* or *P. monticola* seedlings are the first to colonize open sites. *A. magnifica* and *T. mertensiana* seedlings perform well under shaded conditions, often requiring the shade of pine trees for germination, establishment, and growth (Dahms & Franklin 1965; Barbour & Woodward 1985; Laacke 1990; Barbour et al. 1998). Thus, the interaction among the four species can be described by a three-stage stand dynamics model: (1) stand initiation, (2) understory establishment, and
(3) old growth. Each stage of development has different structural and compositional characteristics and each can exhibit signs of either sampling effect or niche differentiation models.

During the establishment stage in the upper montane, *P. contorta* is the first conifer to become established following a stand-initiating disturbance. At this stage in development of the stand, light, space, and soil resources are abundant. From our study, canopy openness, soil nitrogen, and soil carbon were highest in pure or mixed stands of *Pinus*. Exposure and moisture stress induced by an open canopy are both quite high, but *P. contorta* and *P. monticola* are the most resistant of the four conifers to low moisture levels (Graham 1990; Lotan & Critchfield 1990; De Clerck 2004).

During the understory establishment stage, *A. magnifica* and *T. mertensiana* seedlings germinate and become established in the understory. The pines decrease the moisture stress below their canopies thereby facilitating the establishment of *A. magnifica* and *T. mertensiana* seedlings that are shade-tolerant but not drought-resistant. At this time, the two assumptions of the niche differentiation model are met. According to theoretical models, for two species to co-exist when competing for resources, there must first be an interspecific trade-off for at least two resources, one species being better at competing for one resource while the second species being the better competitor for the second resource (Volterra 1926; Tilman 1982, 1988). Second, the two resources must be spatially heterogenous in their supply rates (Tilman et al. 1997). The *Pinus* species are better competitors for low water levels, but are poor competitors in low light levels; the inverse is true of *A. magnifica* and *T. mertensiana*.

Forest are three-dimensional systems, where resources vary along both the horizontal and the vertical axes or through the canopy. During the understory establishment stage of growth, moisture stress is high in the high-light environment of the upper canopy dominated by the *Pinus* species because exposure is 100%, but light is reduced to 25% of full sun (Fig. 2a) beneath the canopy of pines where *A. magnifica* and *T. mertensiana* seedlings are becoming established. Canopy closure values increase (Fig. 2a) to the point where light is limiting to *P. contorta* trees whose crowns cannot overtop those of *A. magnifica* or *T. mertensiana*. During this phase, *P. contorta* are competitively excluded, or the seedlings of both *P. contorta* and *P. monticola* are unable to germinate and develop in the low light conditions (Graham 1990; Lotan & Critchfield 1990). This observation is supported by our canopy cover by composition analysis where all three-species stands comprised of both *Pinus* species fall below the mean canopy closure; the highest mean canopy closure was found in pure *T. mertensiana* or mixed *T. mertensiana/A. magnifica* stands (Fig. 2a). The competitive exclusion of *Pinus* by *A. magnifica* and *T. mertensiana* through competition for light, suggests evidence for the sampling effect model in old-growth stands.

Although our interpretation of the interactions between pines and shade-tolerant species supports the sampling effect model, they do not explain how highest canopy cover and biomass occurs in mixed *A. magnifica* and *T. mertensiana* stands rather than in pure stands of *T. mertensiana*. Sampling effect models predict the exclusion of *A. magnifica* by *T. mertensiana* through
competitive exclusion for light during the old-growth stage. *T. mertensiana*, the competitive dominant, cannot attain the height of *A. magnifica*, therefore both species remain niche-differentiated, with *A. magnifica* remaining in the high-light environment of the overstorey and *T. mertensiana* in the low-light environment of the understory. Indeed, in ten of twelve plots containing both *A. magnifica* and *T. mertensiana* where the DBH of all individuals was collected, the mean diameter of *A. magnifica* was significantly larger than mean *T. mertensiana* diameters. Since tree diameter and height are highly correlated we can infer that *A. magnifica* was typically taller than *T. mertensiana* in these plots. On average, *A. magnifica* diameters were 20 cm larger than those of *T. mertensiana*. We conclude that depending on the species in question, the old-growth stage suggests evidence of both the sampling effect and niche differentiation models. Predictions of the sampling effect model are met with the competitive exclusion of *Pinus* by reduced available light, whereas predictions of the niche differentiation model are found through the co-existence of *A. magnifica* and *T. mertensiana*, where added height growth is the mechanism differentiating the two species and permitting co-existence.

Debate on the sampling effect has centred on the idea that the presence of a highly productive species in a plot or stand drives overyielding, rather than a positive interaction between species. This concept however, is born from grassland studies where species interactions are re-initiated on an annual basis each spring following a period of winter/summer dormancy or mortality. Our results indicate that the mechanism might be quite different in long-lived systems where sampling effects are not driven by the most productive species, but rather are driven by the species that can tolerate the lowest resource level. In our case, mountain hemlock is the most shade tolerant and as a consequence should have the greatest biomass per unit area at equilibrium. However it is also the least productive species, supporting the notion that in long-lived systems the rule may be that ‘slow and steady wins the race’ rather than the sampling effect being determined by the most productive species. This is not a new concept to plant ecology with origins in Grime’s (1979) stress tolerator life history. It has been pointed out that Grime’s stress tolerator is the equivalent of Tilman’s competitor or the species that can tolerate the lowest resource level (Crawley 1997). However, the emphasis on grassland systems in biodiversity ecosystem function studies has led to a focus on productivity rather than long-term effects and dynamics of interspecific interactions. The concept of slow growing species, rather than the most productive species, driving community biomass, and the addition of non-grassland ecosystems to biodiversity and ecosystem function studies merit further attention.

While we find the same diversity/productivity and resource use efficiency patterns found in experimental grassland studies, we emphasize different mechanisms and outcomes. We observe seemingly opposing mechanisms between different pairs of species: interactions between *Pinus* and *Abies* or *Tsuga* support sampling effects, whereas interactions between *Tsuga* and *Abies* may support complementary effects. This suggests that biodiversity-ecosystem function studies need to focus on the species-specific interactions rather than on absolute numbers of species or functional richness. Secondly, our observations demonstrate that the nature of the interaction between groups of species can change over time through biologically driven changes in resource availability: whereas the interaction between *Pinus* and *Abies* or *Tsuga* may initially be one of facilitation and complementarity, it changes to one of competitive exclusion and sampling effects with successional time. These are observations that could not be made in experimental grassland systems where species composition may change on an annual basis due to climate heterogeneity. We also note that although resource use efficiency may increase with species richness, partitioning the variance found in species richness by composition suggests that changes in species composition driven by successional trajectories are more important for explaining both productivity and resource use efficiency in forest systems than absolute species richness. Our high diversity four-species had the maximum canopy closure and basal area, however this level of species richness is an unstable transition point rather than an equilibrium state found in *Tsuga/Abies* stands that may be more stable, more productive, and more efficient. These results highlight the importance of testing theories on biodiversity and ecosystem functioning in natural systems, where observations can complement advances made in experimental studies while suggesting alternative mechanisms and processes driving the relationship between biodiversity and ecosystem function that should be tested experimentally.

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