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Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality

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Abstract

The objective of this study was to determine the relationship, or lack thereof, between growth and diversity of tree species and size in conifer stands of western North America. Growth was measured by net basal area growth and its components: survivor growth, recruitment, and mortality. The analysis used inventory data from permanent plots in the Douglas-fir/western hemlock forest type in Oregon and Washington, and in the mixed-conifer forest type in California. The methods consisted of generalized least square regression with spatial autocorrelation, controlling for the effect of other stand characteristics. Other things being equal, in the two forest types under study there was a strong positive relationship between net basal area growth and tree-species diversity. This effect was associated with higher recruitment in stands of higher tree-species diversity. Neither mortality nor growth of survivors was related to tree-species diversity. The relationship between growth and tree-size diversity was less clear. For Douglas-fir/western hemlock, net basal area growth was negatively correlated with tree-size diversity, essentially because recruitment was lower on plots of high tree-size diversity. For mixed conifers, net basal area growth tended also to be lower in plots of high tree-size diversity, but this was mostly because mortality was higher in plots of higher tree-size diversity.

Keywords: Species diversity; Size diversity; Forest growth; Recruitment; Mortality; Spatial autocorrelation

1. Introduction

Does plant diversity increase ecosystem productivity? This question has attracted wide attention, both for theoretical and managerial reasons. Lately, positive correlations have been observed between vegetation productivity and species diversity in various terrestrial ecosystems, but the relationship may be transient and it varies across species assemblages and spatial scales (Schulze and Mooney, 1993; Huston, 1997; Chapin et al., 2000; Loreau et al., 2003).

Some grassland experiments suggest that diversity effects are neither transient nor explained solely by a few productive species. Tilman, among others, has noted that even the best-chosen monocultures cannot achieve greater productivity than higher-diversity sites (Tilman et al., 1996; Hector et al., 1999; Tilman et al., 2001). However, it remains unclear whether these results hold true at the landscape level, and across ecosystem types (Loreau et al., 2001; Cardinale et al., 2004).

In the case of forest ecosystems, there are still few studies of the relationship between forest productivity and tree diversity, due in part to the complexity and long life cycle of forest ecosystems (Caspersen and Pacala, 2001; Monserud, 2002; Vilà et al., 2003). The traditional view in forestry was that the clearcutting system with artificial regeneration (an even-aged monoculture) maximized volume productivity (e.g., Assmann, 1970; Gulden and Baker, 1988). However, Hasse and Ek (1981) and Haight and Monserud (1990) found that this maxim does not generalize. Using simulation with a widely-used forest management model (viz., Wykoff et al., 1982), Haight and Monserud (1990) compared long-term optimal forest stand productivity between a monoculture of western white pine (*Pinus monticola*) and a multi-age mixed-species management strategy that relied on periodic thinnings and natural regeneration (an uneven-aged shelterwood). The mixed-species stands had much higher species and size diversity, yet the optimal long-term productivity ($m^3\ ha^{-1}\ year^{-1}$) of the two

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contrasting stands was essentially identical (Haight and Monserud, 1990).

The diversity of a forest stand may not be sufficiently described by tree species diversity alone. Structural diversity, resulting from recruitment of trees of different sizes into multi-layered canopies, should also be taken into account. This characteristic, which can be approximated by the diversity of tree size, affects the amount of light and precipitation received by subordinate trees and understory plants (Anderson et al., 1969), and may thus influence the productivity of forest ecosystems. In addition, silvicultural treatments are often defined by target stand states defined by the distribution of tree by size class (Smith et al., 1997). Thus manipulating tree-size diversity is a practical tool for forest managers who strive for greater biodiversity and/or greater productivity (Varga et al., 2005).

Studies dealing with tree-size diversity include Oren et al. (1987), and Lusk and Ortega (2003). Liang et al. (2005) consider the effects of both tree-species diversity and tree-size diversity on individual tree growth, mortality, and recruitment. However, most previous studies have dealt with tree-species diversity only. Insignificant or negative productivity–diversity relationships (Sterba and Monserud, 1995; Chen and Klinka, 2003; Vilà et al., 2003) are as common as positive ones (Kelty, 1989; Caspersen and Pacala, 2001; Liang et al., 2005). Much still needs to be learned on the effects of species and size diversity on forest growth.

The literature on diversity in ecology is vast (Dennis et al., 1979). Three measures of diversity are prominent. Species richness, a simple count of the number of species, is straightforward but it ignores species frequency. Shannon's (or Shannon–Wiener's) index of diversity was originally a measure of entropy (Boltzmann, 1872), later applied to information theory (Shannon, 1948; Shannon and Weaver, 1949). The Simpson (1949) (or Gini–Simpson) index of ecological diversity had in fact been used earlier to measure economic inequality (Gini, 1912). All three indices are closely related and they can be derived from the same one-parameter family of diversity indices (Patil and Taillie, 1979; Keylock, 2005). Both Shannon's and Simpson's indices have stood the test of time "and are still generally regarded as the premier measures of ecological diversity" (Gorelick, 2006). We chose Shannon's index because it reflects both evenness and richness of species (Magurran, 1988, p. 34), without favoring either dominant or rare species. Simpson's index gives more weight to dominant species. We also found that with our data the explanatory power of Shannon's index was superior to the species count.

In the present study we examined the effects of diversity of tree species and size on the net basal area growth of forest stands. We also investigated diversity effects on the components of net basal area growth, namely, survivor growth, recruitment, and mortality. The data were from forests in the U.S. west coast region, which stretch over a vast area from northern Washington to southern California, and cover several ecoregions (Omernik and Gallant, 1986).

To check the consistency of the diversity effects in different ecosystems, we examined two forest types: the Douglas-fir/western hemlock type, and the mixed conifer type in California. The Douglas-fir/western hemlock (*Pseudotsuga menziesii/Tsuga heterophylla*) forests are among the most productive in North America. They thrive in the moist temperate rainforest west of the crest of the Cascade Mountains in Oregon and Washington. These forests are mostly in seral stages but there are still areas of old-growth with massive Douglas-fir (*P. menziesii*) and western hemlock (*T. heterophylla*). Although Douglas-fir and western hemlock are most abundant, they coexist with many other tree species in natural stands, in particular *Alnus rubra*, *Thuja plicata*, and *Acer macrophyllum* (Franklin and Dyrness, 1988).

Farther south along the Pacific coast, mixed-conifer forests cover 13% of California's land area. The dominant tree species are *Pinus ponderosa*, *Pinus jeffreyi*, *Pinus lambertiana*, *P. menziesii*, *Abies concolor* and *Libocedrus decurrens* (Barbour and Major, 1977).

2. Data and methods

Data were obtained from 2.5 ha circular forest plots in the PNW-FIA Integrated Database (IDB 2.0, Hiserote and Waddell, 2005). This is the most complete database to date for the Douglas-fir/western hemlock and the mixed-conifer forest types. The plots covered a large area from northern Washington, along the Cascades, the Klamath Mountains and the Sierra Nevada, down to southern California (Fig. 1). The database assembles past inventories from the USFS National Forest System (R5, R6), Bureau of Land Management, and Forest Inventory and Analysis,

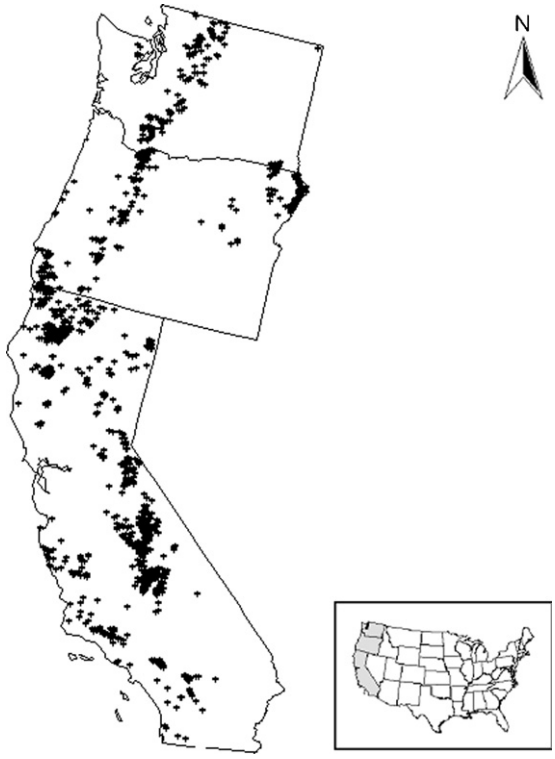

Fig. 1. Geographic distribution of the 1160 FIA plots and location of the study regions in the United States (dark shaded area of the inset at lower right). All the plots were reserved from human interference. In Washington and Oregon (two states to the north), all the plots belonged to Douglas-fir/western hemlock type. In California, all the plots were in mixed conifer type.

covering the period 1988–2000. To minimize the effects of human interference, we only used the data from the reserved plots, where forest growth was protected from artificial alteration. There were 1160 such plots, 373 Douglas-fir/western hemlock in Oregon and Washington, and 787 for mixed conifers in California. More than 99% of the plots were in National Forests.

All plots had been measured twice at a 10-year interval between 1988 and 2000. From these successive measurements on each plot we calculated the mean net annual growth, g, the mean annual survivor growth, u, the mean annual recruitment, r, and the mean annual mortality, m, all expressed in basal area (the sum of the cross-section of the trees of at least 7.6 cm in diameter at breast height).

Survivor growth was the change in basal area of the trees that were alive at the first and second inventory. The recruitment was based on trees that passed the 7.6 cm threshold between successive inventories. The mean net annual growth is related to survivor growth, recruitment and mortality by the relation: $g = u + r - m$ (Table 1).

Shannon's index (Shannon, 1948) based on basal area was used to measure tree-species diversity, H_s, and tree-size diversity, H_d, on each plot:

$$H_s = -\sum_{i=1}^{n_s} \frac{B_i}{B} \ln\left(\frac{B_i}{B}\right),$$

and

$$H_d = -\sum_{j=1}^{n_d} \frac{B_j}{B} \ln\left(\frac{B_j}{B}\right),$$

where B, B_i, and B_j were, respectively, the total stand basal area, the basal area of trees of species i, and the basal area of trees of diameter class j; and n_s and n_d were the number of tree species and the number of diameter classes, respectively. As 37 species (Table 2) and 19 two-inch diameter classes were used to classify the trees on the plots, the theoretical range of H_s was between 0 and $\ln(37) = 3.61$, while H_d was between 0 and $\ln(19) = 2.94$. There was little correlation between H_s and H_d (0.18 within the Douglas-fir/western hemlock forest type, and 0.17 within the mixed conifer type), thus tree-species diversity and tree-size diversity were distinct dimensions of the explanatory space.

Shannon's index increases with the number of species or diameter classes (richness of species or tree sizes), and with the evenness of the distribution of basal area by species or diameter class. This index has been used effectively to measure forest stand diversity in previous work (Buongiorno et al., 1994; Holland et al., 1994; Wills et al., 1997; Varga et al., 2005; Liang et al., 2005, 2006). We also explored an even simpler measure of species diversity, the total number of tree species (Tilman et al., 1996, 1997; Vilà et al., 2003). But, with our data, Shannon's H_s had more explanatory power than the total number of species. This is presumably because Shannon's index takes into account both evenness and species richness (Magurran, 1988, p. 34). The index is also sensitive to changes in rare species (Pielou, 1966), which may make significant contributions to ecosystem functioning (Lyons et al., 2005). As shown by the standard deviations in Table 1, there was substantial variation across plots in their growth rates, their diversity of tree species and size, and other plot characteristics. The variables used to control for the effects of other stand characteristics, besides tree diversity, on stand growth are also summarized in Table 1. The effect of total stand basal area, B, on tree growth, mortality, and recruitment is well documented for these forest types (see for example Liang et al., 2005). Stand age was not available for the plots used in this study, most of which had an uneven-aged structure. Regardless, tree size more

Table 1
Definition, mean, and standard deviation (S.D.) of plot variables used in the analysis

Variables	Description	Unit	Douglas-fir/western hemlock		Mixed conifer	
			Mean	(S.D.)	Mean	(S.D.)
Dependent variables						
n	Net annual growth	$m^2\ ha^{-1}\ year^{-1}$	0.35	(0.71)	0.35	(0.36)
s	Annual survivor growth	$m^2\ ha^{-1}\ year^{-1}$	0.47	(0.30)	0.41	(0.31)
r	Recruitment, basal area of trees passing the 7.62 cm threshold	$m^2\ ha^{-1}\ year^{-1}$	0.07	(0.12)	0.04	(0.08)
m	Mortality, basal area of trees that died each year	$m^2\ ha^{-1}\ year^{-1}$	0.19	(0.40)	0.10	(0.21)
Stand diversity variables						
H_d	Size diversity (Shannon's index)		2.22	(0.43)	1.69	(0.57)
H_s	Species diversity (Shannon's index)		0.89	(0.44)	0.64	(0.45)
Control variables						
B	Stand basal area in the first inventory	$m^2\ ha^{-1}$	43.38	(28.02)	32.26	(27.86)
C	Site productivity	$m^3\ ha^{-1}\ year^{-1}$	6.65	(3.82)	5.90	(4.56)
D	Mean diameter of all live trees at the first inventory	cm	13.19	(5.44)	14.72	(7.67)
S	Average percent slope		–	–	40.12	(21.29)
A	Aspect, the absolute angle between the south and the direction to which a slope faces	degree	–	–	92.46	(55.06)
E	Elevation	m	107.20	(50.04)	1830.89	(678.89)
x	Easting of plot UTM coordinates	10^5 m	5.47	(0.75)	4.43	(1.41)
y	Northing of plot UTM coordinates	10^5 m	50.43	(1.91)	42.10	(2.73)

Table 2
Frequency of tree species in all sample plots, by forest type

Common name	Scientific name	Frequency (%)	
		Douglas-fir/western hemlock	Mixed conifer
Douglas-fir	*Pseudotsuga menziesii*	39.77	14.59
Western hemlock	*Tsuga heterophylla*	13.06	0.03
Western redcedar	*Thuja plicata*	4.18	0.00
Port Orford cedar	*Chamaecyparis lawsoniana*	0.26	0.12
Noble fir	*Abies procera*	1.02	0.00
Bigleaf maple	*Acer macrophyllum*	1.21	0.42
Redwood	*Sequoia sempervirens*	0.01	3.43
Jeffrey pine	*Pinus jeffreyi*	0.08	7.27
Sitka spruce	*Picea sitchensis*	0.59	0.04
Pacific silver fir	*Abies amabilis*	6.08	0.00
White fir	*Abies concolor*	3.57	16.75
Sugar pine	*Pinus lambertiana*	0.57	3.45
Subalpine fir	*Abies lasiocarpa*	1.62	0.00
Red alder	*Alnus rubra*	3.34	0.29
Pacific yew	*Taxus brevifolia*	0.12	0.02
Incense cedar	*Calocedrus decurrens*	0.96	6.98
Grand fir	*Abies grandis*	2.01	0.08
Black cottonwood	*Populus balsamifera* ssp. *trichocarpa*	0.21	0.04
Engelmann spruce	*Picea engelmannii*	0.87	0.00
Western juniper	*Juniperus occidentalis*	0.28	1.77
Pacific madrone	*Arbutus menzeisii*	0.64	1.70
Oregon ash	*Fraxinus latifolia*	0.08	0.02
Mountain hemlock	*Tsuga mertensiana*	4.15	0.72
Alaska cedar	*Chamaecyparis nootkatensis*	0.35	0.00
Western white pine	*Pinus monticola*	0.53	1.21
Ponderosa pine	*Pinus ponderosa*	7.15	9.55
Lodgepole pine	*Pinus contorta*	4.02	4.23
Western larch	*Larix occidentalis*	0.33	0.00
Quaking aspen	*Populus tremuloides*	0.07	0.16
Oregon white oak	*Quercus garryana*	0.22	0.77
California black oak	*Quercus kelloggii*	0.14	5.01
California red fir	*Abies magnifica*	0.00	7.34
Canyon live oak	*Quercus chrysolepis*	0.17	5.41
Golden chinkapin	*Castanopsis chrysophylla*	0.20	0.08
Shasta red fir	*Abies magnifica* var. *shastensis*	0.93	0.11
Tanoak	*Lithocarpus densiflorus*	0.60	3.18
Others		0.62	5.22
All species		100.00	100.00

directly influences tree growth and stand productivity than age (Gower et al., 1996).

Site characteristics also influence stand growth. Lacking data on soil characteristics, we used maximum mean annual increment ($m^3\ ha^{-1}\ year^{-1}$) as a measure of site productivity based on site index. Additional control variables for the site consisted of elevation, E, aspect, A, and slope, S, which determine the solar radiation and temperature (Stathers et al., 1990). Plot Universal Transverse Mercator (UTM) coordinates (Snyder, 1987), x for easting distance and y for northing distance from the UTM origin, were used to test for spatial autocorrelation effects across plots, as well as for large-scale spatial effects, using semivariograms (Gooevaerts, 1997; Webster and Oliver, 2001).

The effects of species and size diversity on net annual growth, survivor growth, recruitment, and mortality were tested in the same way, with nested models. For example, in the case of net annual growth, the most general model used cubic polynomials in H_s and H_d to allow for non-linearity, in addition to the control variables:

$$g_i = \alpha_0 + \alpha_s H_{s,i} + \alpha_d H_{d,i} + \alpha_{sd} H_{s,i} H_{d,i} + \alpha_{s2} H_{s,i}^2 + \alpha_{d2} H_{d,i}^2 + \alpha_{sd2} H_{s,i} H_{d,i}^2 + \alpha_{s2d} H_{s,i}^2 H_{d,i} + \alpha_{s3} H_{s,i}^3 + \alpha_{d3} H_{d,i}^3 + \alpha_B B_i + \alpha_C C_i + \alpha_D D_i + \alpha_{sl} S_i + \alpha_a A_i + \alpha_e E_i + e(x,y)_i, \quad i = 1, ..., N, \tag{1}$$

where g_i was the average annual net growth of basal area of plot i between the two inventories ($m^2\ ha^{-1}\ year^{-1}$), and the independent variables were levels at the time of the first inventory. The α's were coefficients estimated from the plot data. The residuals $e(x, y)$ were assumed to have an isotropic and spherical spatial autocorrelation (Cressie, 1993).

The parameters were estimated by generalized least squares (GLS) to account for spatial autocorrelation and heteroskedasticity (unequal variance) of the residual, which was present especially in the equations for recruitment and mortality. The

analysis was conducted with geoR (Ribeiro and Diggle, 2004) in R (R Development Core Team, 2006).

The most sweeping hypothesis was that species and size diversity had no effect on net growth: $H_0^1 : \alpha_s = \alpha_d = \alpha_{sd} = \alpha_{s2} = \alpha_{d2} = \alpha_{sd2} = \alpha_{s2d} = \alpha_{s3} = \alpha_{d3} = 0$. This used a χ^2-test comparing the log-likelihood in (1) with a restricted model, without any term in H_s or H_d:

$$g_i = \alpha_0 + \alpha_C C_i + \alpha_D D_i + \alpha_{sl} S_i + \alpha_a A_i + \alpha_e E_i + e(x,y)_i \quad (2)$$

If H_0^1 was rejected, we next hypothesized that species diversity alone had an effect on net growth: $H_0^2 : \alpha_d = \alpha_{sd} = \alpha_{d2} = \alpha_{sd2} = \alpha_{s2d} = \alpha_{d3} = 0$ was tested by comparing the log-likelihood in the full model (1) with a restricted model without terms in H_d:

$$g_i = \alpha_0 + \alpha_s H_{si} + \alpha_{s2} H_{si}^2 + \alpha_{s3} H_{si}^3 + \alpha_B B_i + \alpha_C C_i + \alpha_D D_i + \alpha_{sl} S_i + \alpha_a A_i + \alpha_e E_i + e(x,y)_i \quad (3)$$

If H_0^2 was rejected, we then hypothesized that size diversity alone had an effect on net growth: $H_0^3 : \alpha_s = \alpha_{sd} = \alpha_{s2} = \alpha_{sd2} = \alpha_{s2d} = \alpha_{s3} = 0$ was tested by comparing the log-likelihood in the full model (1) with a restricted model without terms in H_s:

$$g_i = \alpha_0 + \alpha_d H_{di} + \alpha_{d2} H_{di}^2 + \alpha_{d3} H_{di}^3 + \alpha_B B_i + \alpha_C C_i + \alpha_D D_i + \alpha_{sl} S_i + \alpha_a A_i + \alpha_e E_i + e(x,y)_i \quad (4)$$

If H_0^3 was rejected, size and species diversity were both likely to affect net growth. In this case, and in the case where H_0^1, H_0^2 or H_0^3 could not be rejected, more efficient and parsimonious versions of models (1), (2), (3), or (4) were sought, with only statistically significant explanatory variables and with minimum collinearity. To this end, the insignificant term with the highest P-value was removed and the model re-estimated. This was repeated until the Akaike information criterion (AIC) (Akaike, 1973) and Bayesian information criterion (BIC) (Schwarz, 1978) could not be lowered, or the coefficients of all explanatory terms were significant at the 0.05 level (MacNally, 2000). The last model obtained in this way was re-estimated assuming a random error, to assess the significance of the spatial autocorrelation of the residuals.

Based on the final models, effects of species and size diversity on net basal area growth, survivor growth, recruitment, and mortality, were computed by varying them within the range of their mean ± 2S.D., while holding other factors fixed at their sample mean. By doing this we could assess the biological importance of species and size diversity in addition to their statistical significance.

3. Results and discussion

3.1. Statistical tests of diversity effects

The hypothesis H_0^1, that neither species diversity nor size diversity had an effect, was rejected at the $\alpha = 0.05$ level for all but one component of growth in both forest types (Table 3). The only exception was for survivor growth of Douglas-fir/western hemlock. Thus, there was evidence that either species diversity, size diversity, or both affected at least one component of stand growth.

Table 3
Tests of significance of overall effects of species diversity and size diversity

	Douglas-fir/western hemlock		Mixed conifer	
	Hypothesis[a]	P-Value	Hypothesis[a]	P-Value
Net growth	1	0.002	1	0.001
	2	0.000	2	<0.001
	3	0.000	3	0.040
Survivor growth	1	0.077	1	0.000
	2	n.a.	2	0.000
	3	n.a.	3	0.429
Recruitment	1	0.000	1	<0.001
	2	0.000	2	0.036
	3	0.000	3	0.004
Mortality	1	0.014	1	<0.001
	2	0.017	2	0.013
	3	0.106	3	0.001

n.a., not applicable because hypothesis 1 could not be rejected.

[a] Hypothesis 1, species and size diversity had no effect: $H_0^1 : \alpha_s = \alpha_d = \alpha_{sd} = \alpha_{s2} = \alpha_{d2} = \alpha_{sd2} = \alpha_{s2d} = \alpha_{s3} = \alpha_{d3} = 0$; hypothesis 2, species diversity alone had an effect: $H_0^2 : \alpha_d = \alpha_{sd} = \alpha_{d2} = \alpha_{sd2} = \alpha_{s2d} = \alpha_{d3} = 0$; hypothesis 3, size diversity alone had an effect: $H_0^3 : \alpha_s = \alpha_{sd} = \alpha_{s2} = \alpha_{sd2} = \alpha_{s2d} = \alpha_{s3} = 0$.

For net growth and recruitment, hypothesis H_0^2 and H_0^3 were also rejected at the 0.05 level, suggesting that both species and size diversity affected net growth and recruitment, in both forest types.

The results were less general, across forest type, for survivor growth and mortality. While there was no evidence of an effect of either type of diversity on the survivor growth of Douglas-fir/western hemlock, size diversity had an effect on the survivor growth of mixed conifers. And, while the mortality of mixed conifers was significantly affected (in a statistical sense) by both species and size diversity, the mortality of Douglas-fir/western hemlock was affected by species diversity alone.

3.2. Growth models with diversity effects

The models (a) in Tables 4 and 5 are truncated versions of the general model (1), consistent with the results of Table 3. For example, as we could not reject the hypothesis that both species and size diversity influenced the net growth of Douglas-fir/western hemlock (Table 3), the corresponding model (a) in Table 4 contains all the terms in H_s and H_d. And, as we could not reject the hypothesis that tree-species diversity alone affected mortality of Douglas-fir/western hemlock (Table 3), the corresponding model (a) in Table 4 contains only terms in H_d.

The P-values of the tests comparing the likelihood ratios of model (a) and model (b) showed that, in all but one case, backward elimination applied to model (a) increased significantly the likelihood ratio, at the 0.05 significance level. The only exception was net growth of Douglas-fir/western hemlock, for which the likelihood ratio of (b) was not significantly different from that of (a). In model (b) for the mortality of mixed conifers, the terms in H_s and H_d were not significant individually at the 0.05 level, but they were significant as a group, in agreement with Table 2.

Table 4
Regression models to predict net growth and its components in Douglas-fir/western hemlock forests in Oregon and Washington

Model	AIC	BIC	L	P-Value
Net growth ($m^2\ ha^{-1}\ year^{-1}$)				
(a) $1.87 + 0.0001B + 0.02C - 0.0001E - 0.02D^{*} - 2.40H_s - 0.51H_d + 0.42H_s^2 - 0.34H_d^2 + 0.18H_s^3 + 0.13H_d^3 + 1.87H_sH_d - 0.27H_s^2H_d - 0.38H_sH_d^2$	816.1	882.1	−391.0	
(b) $0.15 + 0.04C^{**} - 0.02D^{*} + 0.41H_sH_d^{*} - 0.15H_sH_d^{2*}$	807.7	839.0	−395.9	0.38[a]
(c) $0.15 + 0.04C^{**} - 0.02D^{*} + 0.41H_sH_d^{*} - 0.15H_sH_d^{2*}$	803.7	827.1	−395.9	1.00[b]
Survivor growth ($m^2\ ha^{-1}\ year^{-1}$)				
(a) $0.39 + 0.005B^{**} + 0.03C^{**} - 0.0004E - 0.02D^{**}$	29.5	60.7	−6.7	
(b) $0.33 + 0.005B^{**} + 0.03C^{**} - 0.02D^{**}$	15.3	42.6	−0.7	<0.01
(c) $0.33 + 0.005B^{**} + 0.03C^{**} - 0.02D^{**}$	15.8	35.3	−2.9	0.11
Recruitment ($m^2\ ha^{-1}\ year^{-1}$)				
(a) $1.26^{**} + 0.003B^{*} - 0.002C - 0.001E^{**} - 0.01D^{**} - 0.30H_s - 1.31H_d^{**} - 0.07H_s^2 + 0.40H_d^{2**} - 0.09H_s^3 - 0.01H_d^3 + 0.60H_sH_d^{**} + 0.18H_s^2H_d^{**} - 0.26H_sH_d^{2**}$	−629.5	−563.5	331.8	
(b) $1.22^{**} - 0.0005E^{**} - 0.01D^{**} - 0.36H_s - 1.23H_d^{**} + 0.35H_d^{2**} - 0.11H_s^{3*} + 0.61H_sH_d^{**} + 0.16H_s^2H_d^{**} - 0.26H_sH_d^{2**}$	−666.8	−616.2	346.4	<0.01
(c) $1.22^{**} - 0.0005E^{**} - 0.01D^{**} - 0.36H_s - 1.23H_d^{**} + 0.35H_d^{2**} - 0.11H_s^{3*} + 0.61H_sH_d^{**} + 0.16H_s^2H_d^{**} - 0.26H_sH_d^{2**}$	−670.8	−628.0	346.4	1.00
Mortality ($m^2\ ha^{-1}\ year^{-1}$)				
(a) $-0.06 + 0.004B^{**} - 0.001C + 0.001E^{*} - 0.01D - 0.23H_d + 0.23H_d^2 - 0.06H_d^3$	404.7	447.6	−191.4	
(b) $-0.16 + 0.004B^{**} + 0.001E^{*} - 0.005D + 0.09H_d^{2*} - 0.03H_d^{3*}$	393.1	428.2	−187.5	<0.01
(c) $-0.16 + 0.004B^{**} + 0.001E^{*} - 0.005D + 0.09H_d^{2*} - 0.03H_d^{3*}$	389.1	416.4	−187.5	1.00

H_s and H_d, tree-species diversity and tree-size diversity. Other variables defined in Table 2. $^{*}P < 0.05$; $^{**}P < 0.01$ for test of significant difference of parameter value from 0. (a): Model consistent with the results of Table 1, with spatial autocorrelation; (b): parsimonious version of model (a), with spatial autocorrelation; (c) model (b), without spatial autocorrelation. AIC: Akaike information criterion (smaller is better); BIC: Bayesian information criterion (smaller is better); L: log-likelihood ratio.

[a] P-value for the test of the increase in L from model (a) to model (b).

[b] P-value for the test of spatial autocorrelation.

Table 5
Regression models to predict net growth and its components in California mixed conifer forests

Model	AIC	BIC	L	P-Value
Net growth ($m^2\ ha^{-1}\ year^{-1}$)				
(a) $0.18 + 0.004B^{**} + 0.02C^{**} - 0.001S^{*} + 0.00003E + 0.0003A - 0.02D^{*} - 0.40H_s + 0.52H_d^{**} + 0.14H_s^{2*} - 0.32H_d^2 - 0.04H_s^3 + 0.06H_d^3 + 0.59H_sH_d^{**} - 0.06H_s^2H_d - 0.16H_sH_d^{2*}$	490.8	579.1	−226.4	
(b) $0.19^{**} + 0.004B^{**} + 0.02C^{**} - 0.002S^{**} - 0.02D^{*} - 0.25H_s^{*} + 0.30H_d^{**} - 0.08H_d^{2*} + 0.42H_sH_d^{*} - 0.13H_sH_d^{2*}$	439.3	499.8	−206.6	<0.01[a]
(c) $0.19^{**} + 0.004B^{**} + 0.02C^{**} - 0.002S^{**} - 0.02D^{**} - 0.25H_s^{*} + 0.30H_d^{**} - 0.08H_d^{2*} + 0.42H_sH_d^{*} - 0.13H_sH_d^{2*}$	435.3	486.5	−206.6	1.00[b]
Survivor growth ($m^2\ ha^{-1}\ year^{-1}$)				
(a) $-0.04 + 0.01B^{**} + 0.02C^{**} - 0.001S^{**} + 0.0001E^{**} + 0.0004A^{**} - 0.02D^{**} + 0.34H_d^{**} - 0.05H_d^2 - 0.01H_d^3$	−94.7	−43.7	58.4	
(b) $-0.05 + 0.01B^{**} + 0.02C^{**} - 0.001S^{**} + 0.0001E^{**} + 0.0004A^{**} - 0.02D^{**} - 0.38H_d^{**} - 0.08H_d^{2**}$	−102.0	−55.7	61.0	0.02
(c) $-0.05 + 0.01B^{**} + 0.02C^{**} - 0.001S^{**} + 0.0001E^{**} + 0.0004A^{**} - 0.02D^{**} - 0.38H_d^{**} - 0.08H_d^{2**}$	−103.0	−55.9	61.0	1.00
Recruitment ($m^2\ ha^{-1}\ year^{-1}$)				
(a) $0.09^{**} + 0.0004B^{**} + 0.001C - 0.0004S^{**} + 0.000004E - 0.0001A - 0.004D^{**} - 0.05H_s + 0.06H_d + 0.01H_s^2 - 0.09H_d^{2*} + 0.01H_s^3 + 0.02H_d^{3**} + 0.13H_sH_d^{**} - 0.02H_s^2H_d - 0.04H_sH_d^{2**}$	−1741	−1653	889.7	
(b) $0.10^{**} + 0.0005B^{**} - 0.0004S^{**} - 0.004D^{**} - 0.03H_s^{2*} + 0.01H_s^{3*} + 0.12H_sH_d^{**} - 0.04H_s^2H_d^{**}$	−1832	−1781	927.1	<0.01
(c) $0.10^{**} + 0.0005B^{**} - 0.0004S^{**} - 0.004D^{**} - 0.03H_s^{2*} + 0.01H_s^{3*} + 0.12H_sH_d^{**} - 0.04H_s^2H_d^{**}$	−1836	−1794	927.1	1.00
Mortality ($m^2\ ha^{-1}\ year^{-1}$)				
(a) $-0.04 + 0.003B^{**} - 0.001C + 0.00002S + 0.00003E^{*} + 0.00002A - 0.004D^{**} - 0.04H_s - 0.003H_d - 0.04H_s^2 - 0.01H_d^2 + 0.01H_s^3 + 0.01H_d^3 + 0.03H_sH_d + 0.03H_s^2H_d - 0.04H_sH_d^2$	−159.0	−70.7	98.5	
(b) $-0.04 + 0.003B^{**} + 0.00003E^{**} - 0.004D^{**} + 0.02H_s + 0.01H_d - 0.04H_s^2 - 0.02H_d^2 + 0.003H_s^3 + 0.02H_d^3 + 0.05H_sH_d + 0.02H_s^2H_d - 0.03H_sH_d^2$	−203.0	−128.5	117.5	<0.01
(c) $-0.04 + 0.003B^{**} + 0.00003E^{**} - 0.004D^{**} + 0.05H_s + 0.02H_d - 0.09H_s^2 - 0.03H_d^2 + 0.009H_s^3 + 0.02H_d^3 + 0.04H_sH_d + 0.03H_s^2H_d - 0.04H_sH_d^2$	−204.0	−138.9	116.0	0.23

H_s and H_d, tree-species diversity and tree-size diversity. Other variables defined in Table 1. $^{*}P < 0.05$; $^{**}P < 0.01$ for test of significant difference of parameter value from 0. (a): Model consistent with the results of Table 2, with spatial autocorrelation; (b): parsimonious version of model (a), with spatial autocorrelation; (c) model (b), without spatial autocorrelation. AIC: Akaike information criterion (smaller is better); BIC: Bayesian information criterion (smaller is better); L: log-likelihood ratio.

[a] P-value for the test of the increase in L from model (a) to model (b).

[b] P-value for the test of spatial autocorrelation.

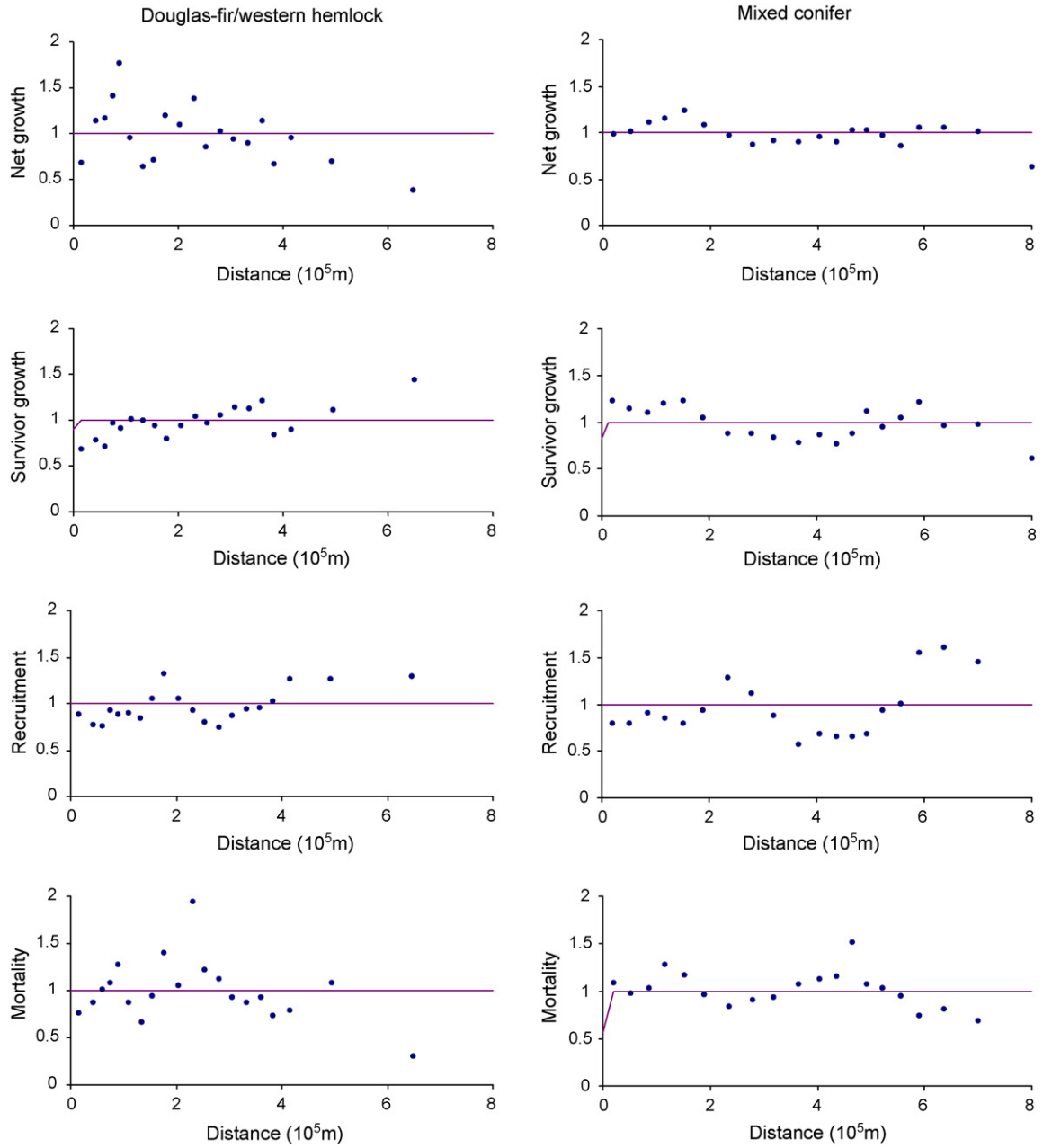

Fig. 2. Semivariograms of the standardized residuals from the reduced models predicting net growth, survival growth, recruitment, and mortality.

Comparison of the likelihood ratios of models (b) and (c) showed that there was no significant spatial autocorrelation, at the 0.05 level. This was confirmed by the semivariograms of the standardized residuals from the reduced models with respect to distance between plots (Fig. 2). Therefore, the non-spatial linear models (model (c) in Tables 4 and 5) estimated by GLS were used to study the effects of changes in species and size diversity on net basal area growth, survivor growth, recruitment, and mortality.

3.3. Biological significance of diversity effects

Figs. 3 and 4 show the effects on the various growth components of changes in species diversity or size diversity, within the range of the data, while other stand characteristics were being held constant at their mean observed value.

3.3.1. Tree-species diversity and stand growth

As tree-species diversity increased, net basal area growth increased substantially and linearly for both forest types (Fig. 3A and B). For Douglas-fir/western hemlock forests, a doubling of tree-species diversity corresponded to a 38% increase in annual net basal area growth. For mixed conifers it corresponded to a 21% increase.

The survivor growth of both Douglas-fir/western hemlock and mixed conifer forests did not vary with tree-species diversity (Fig. 3C and D). Similarly, there was no significant relationship between mortality and species diversity in either forest type (Fig. 3G and H).

Recruitment in Douglas-fir/western hemlock forests and in mixed conifers was substantially higher in stands of higher species diversity (Fig. 3E and F). The relationship was linear for

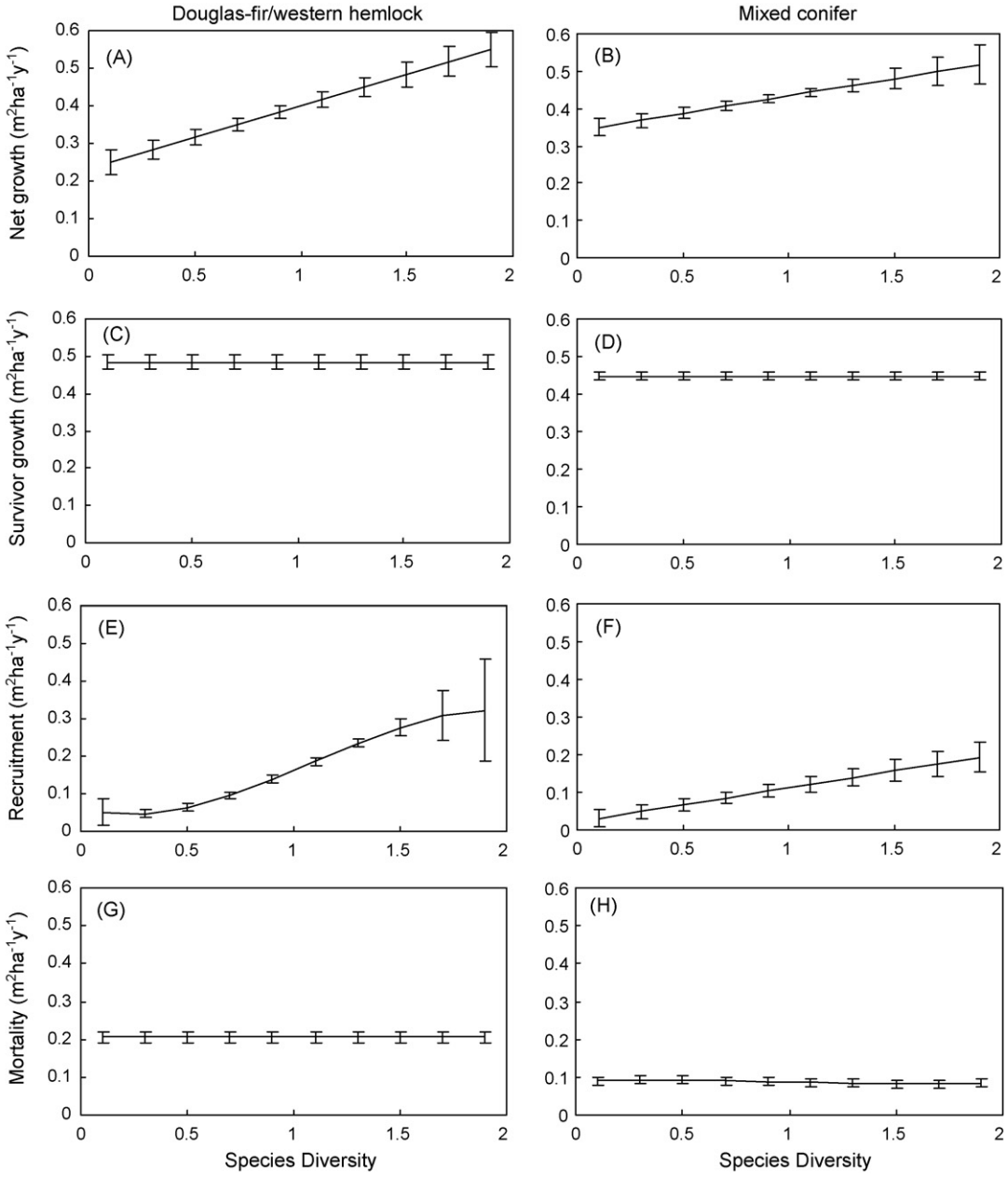

Fig. 3. The expected effects of tree-species diversity (Shannon's index) on net growth (A and B), survivor growth (C and D), recruitment (E and F), and mortality (G and H). Vertical bars show 1S.D. of the prediction. Species diversity varies within ±2S.D. around the mean, while other variables are held constant at their mean.

mixed conifers, and somewhat sigmoid (but with large standard errors at high diversity levels) for Douglas-fir/western hemlock. If one ignores this non-linearity, the relationship between recruitment and species diversity appears to parallel that between net growth and species diversity. Thus, the entire effect of species diversity on net growth could be traced to effects of species diversity on recruitment, with no effect due to survivor growth and mortality.

3.3.2. *Tree-size diversity and stand growth*

The relationship between net growth and tree-size diversity was curvilinear for both vegetation types (Fig. 4A and B). For Douglas-fir/western hemlock, net growth was highest at very low levels of tree-size diversity, and it decreased rapidly as size diversity increased. For mixed conifers, net growth increased slightly at first with increasing size diversity, reaching a maximum when size diversity was average (Shannon index = 1.69, Table 2), and decreasing thereafter. At the highest tree-size diversity, net growth was similar for mixed conifers and for Douglas-fir/western hemlock.

The survivor growth of Douglas-fir/western hemlock was unrelated to tree-size diversity, while survivor growth tended to increased slightly with size diversity for mixed conifers (Fig. 4C and D). Recruitment of Douglas-fir/western hemlock tended to decrease with tree-size diversity, while that of mixed conifers was unaffected by tree-size diversity (Fig. 4E and F).

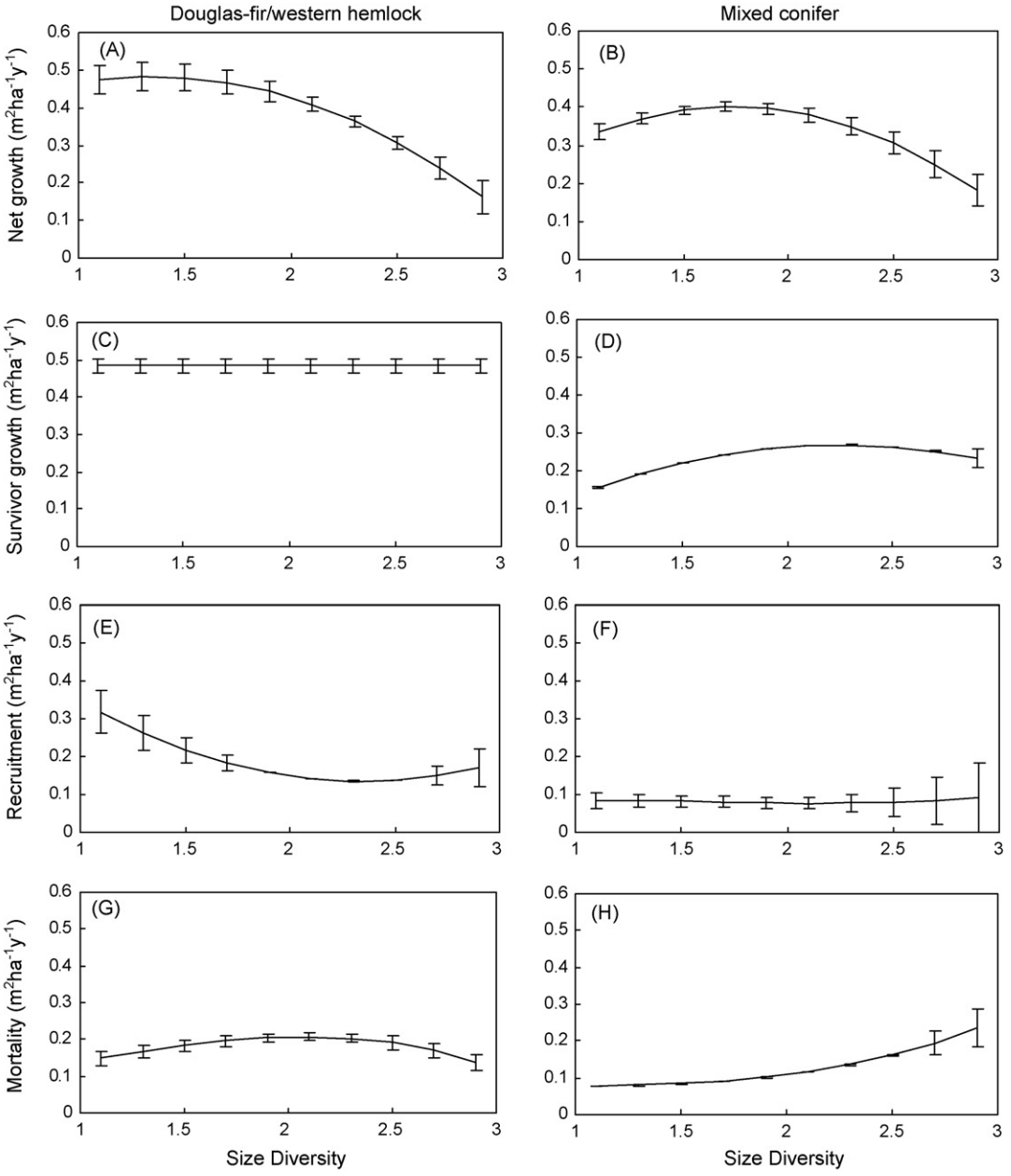

Fig. 4. The expected effects of tree-size diversity (Shannon's index) on net growth (A and B), survivor growth (C and D), recruitment (E and F), and mortality (G and H). Vertical bars show 1S.D. of the prediction. Size diversity varies within ±2S.D. around the mean, while other variables are held constant at their mean.

Mortality was higher in mixed conifer stands of high tree-size diversity, while there was a weak quadratic trend in the relation between mortality of Douglas-fir/western hemlock and tree-size diversity (Fig. 4G and H).

The overall conclusion from Fig. 4 is that the lower net growth of stands of high tree-size diversity is related to lower recruitment in the case of Douglas-fir/western hemlock, and to higher mortality in the case of mixed conifers.

Taken as a whole, our findings indicate that there is a strong positive relationship between net growth and tree-species diversity, in both Douglas-fir/western hemlock and mixed conifer stands. The increase in net growth stemmed essentially from higher recruitment in stands of higher tree-species diversity. Meanwhile, mortality and survivor growth were unaffected by tree-species diversity.

To determine how much tree diversity contributed to the goodness-of-fit of the dependent variables measured by log likelihood, hierarchical portioning (Chevan and Sutherland, 1991) was applied to model (c) in Tables 4 and 5. Diversity terms were a substantial part of the total explanatory power of Douglas-fir/western hemlock recruitment and mixed conifer mortality, while other models were determined largely by the control variables (Table 6). Nevertheless, the expected effect of a change in H_s or H_d alone, other things being equal, could be substantial.

That increasing tree-species diversity had a positive effect on net timber productivity, and mostly through recruitment, is

Table 6
Independent contribution of tree diversity variables to the goodness-of-fit measured by log likelihood

Model	Douglas-fir/western hemlock type	Mixed conifer type
Net basal area growth	0.24[a]	0.27
Survival growth	0.00	0.14
Recruitment	0.76	0.26
Mortality	0.11	0.59

[a] A value of 1 indicates that the goodness-of-fit is solely determined by the diversity variables, H_s and H_d. A value of 0 indicates that the goodness-of-fit is solely determined by the other variables.

in agreement with the theory that marked differences in species life histories lead to complementarity and niche differentiation (Fridley, 2003) or facilitation (Tilman et al., 2001; Jonsson and Malmqvist, 2003; Bauhus et al., 2004). These effects can enhance ecosystem productivity (Lusk and Ortega, 2003), especially when herbivory and decomposition are considered (Jonsson and Malmqvist, 2003). This finding also agrees with the forest studies by Kelty (1989), Caspersen and Pacala (2001), and Liang et al. (2005). One possible explanation of the strong positive effect of tree species diversity on recruitment is that high species diversity led to an increase in regeneration niches, or, owing to the diversity of propagules, an increase in the likelihood that existing niches would be exploited. Another possibility is that, especially during periodic stress such as protracted droughts, the overall growth and survival of smaller trees (potential recruits) was facilitated by species diversity. Mulder et al. (2001) found that increases in plant species diversity result in increased productivity through decreased overall mortality during drought. As younger trees are often most vulnerable to drought (e.g., Barden, 1988; Lawson et al., 1999), they might benefit most from such stress-dependent facilitation.

The results were less general across forest types for the effects of tree-size diversity. The strongest finding was that net basal area growth was lower in stands of highest tree-size diversity, in both forest types. This finding is in agreement with the observations of Sterba and Monserud (1995), Edgar and Burk (2001), and Liang et al. (2005, 2006).

In contrast with results for tree-species diversity, relationships between components of net growth and tree-size diversity differed by forest type. For Douglas-fir/western hemlock, the lower net growth at high tree-size diversity could be traced mostly to lower recruitment rates at high tree-size diversity (Fig. 4E). For mixed conifers, instead, it stemmed from higher mortality at high tree-size diversity (Fig. 4H).

The observed trends are subject to the usual caveats due to the use of non-experimental data. On the positive side, we found no spatial autocorrelation in any model formulation. On the other hand, multicollinearity is a pervasive problem with such data. Multicollinearity does not lead to biased parameters, but it may lead to difficulty in measuring the partial effect of each variable (Goldberber, 1991, p. 248). The hypothesis tests in Table 1 are unaffected by multicollinearity, but the partial effects of each variable (Figs. 3 and 4), may be more uncertain. Nevertheless, multicollinearity was not excessive in the present case. The highest partial correlation was of 0.59 between H_s and H_d in mixed conifers. Furthermore, the final parsimonious models of maximum likelihood (models (c) in Tables 4 and 5) did generally have parameters with low standard errors.

The question remains as to why diversity with respect to species but not size would have a positive influence on basal area growth. If we assume that tree-size diversity is positively associated with canopy depth and leaf area index, this would suggest higher efficiency of light capture by stands of high tree-size diversity. However, this gain is necessarily accompanied by the loss of light transmittance to lower canopy strata and understory vegetation (Grace, 1999). In the two forest types under study it appears that the benefit of increased light capture for the productivity of tree crowns in the mid- and upper-canopy strata was more than offset by consequent decreases in establishment or increases in mortality of trees beneath them.

A contribution of this study is that it differentiated the partial effects of the diversity of tree species from the diversity of tree size (stand structure). Our findings suggest that maintaining species diversity is an important means to obtain high growth rate in forest management. In contrast, the finding that size diversity was negatively associated with net basal area growth suggests that multi-layered forests were not better in growth rate than even-sized forests. For the purpose of optimizing growth, forest managers should focus on tree species rather than size. Further studies should explore whether keystone species exist, those with functional impacts on ecosystem disproportional to their abundance (Power et al., 1996), which should be kept as a high priority by forest managers.

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