

## SPECIES RICHNESS AND STAND STABILITY IN CONIFER FORESTS OF THE SIERRA NEVADA

FABRICE A. J. DECLERCK,<sup>1,4</sup> MICHAEL G. BARBOUR,<sup>2</sup> AND JOHN O. SAWYER<sup>3</sup>

<sup>1</sup>*Geography Graduate Group, University of California Davis, 1 Shields Avenue, Davis, California 95616*

<sup>2</sup>*Department of Plant Sciences, University of California Davis, 1 Shields Avenue, Davis, California 95616*

<sup>3</sup>*Biological Sciences, Humboldt State University, 1 Harpst Street, Arcata, California 95521*

**Abstract.** Theoretical and empirical studies have long suggested that stability and complexity are intimately related, but evidence from long-lived systems at large scales is lacking. Stability can either be driven by complex species interactions, or it can be driven by the presence/absence and abundance of a species best able to perform a specific ecosystem function. We use 64 years of stand productivity measures in forest systems composed of four dominant conifer tree species to contrast the effect of species richness and abundance on three stability measures. To perform this contrast, we measured the annual growth increments of >900 trees in mixed and pure forest stands to test three hypotheses: increased species richness will (1) decrease stand variance, (2) increase stand resistance to drought events, and (3) increase stand resilience to drought events. In each case, the alternate hypothesis was that species richness had no effect, but that species composition and abundance within a stand drove variance, resistance, and resilience. In pure stands, the four species demonstrated significant differences in productivity, and in their resistance and resilience to drought events. The two pine species were the most drought resistant and resilient, whereas mountain hemlock was the least resistant and resilient, and red fir was intermediate. For community measures we found a moderately significant ( $P = 0.08$ ) increase in the community coefficient of variation and a significant ( $P = 0.03$ ) increase in resilience with increased species richness, but no significant relationship between species richness and community resistance, though the variance in community resistance to drought decreased with species richness. Community resistance to drought was significantly ( $P = 0.001$ ) correlated to the relative abundance of lodgepole pine, the most resistant species. We propose that resistance is driven by competition for a single limiting resource, with negative diversity effects. In contrast resilience measures the capacity of communities to partition resources in the absence of a single limiting resource, demonstrating positive diversity effects.

**Key words:** biodiversity; coefficient of variation; compensatory growth; conifers; ecosystem function; portfolio effect; resilience; resistance; Sierra Nevada, California, USA; species diversity; statistical averaging; variance.

### INTRODUCTION

With global rates of species extinction remaining high, how biodiversity loss impacts ecosystem properties has been the subject of much attention (McCann 2000, Hooper et al. 2005). During the 1990s, ecologists struggled to understand the role biodiversity plays in the maintenance of ecosystem functions and the provisioning of goods and services. One issue of particular interest is the relationship between biodiversity and ecosystem stability, a topic that has been intensely studied for over a century. In the 1950s, ecologists formalized the view that diversity begets ecosystem stability (Odum 1952, MacArthur 1955, Elton

1958), but their arguments were based on theory and observation and lacked experimental support. This conventional wisdom was seriously challenged by theorists in the 1970s (Gardner and Ashby 1970, Levins 1970, May 1972, 1973), who showed through mathematical models that more complex systems were less likely to be stable.

Loreau et al. (2002b) proposed a new look at the relationship between diversity and stability, stating that the formalism of autonomous, deterministic, dynamical systems inherently excludes a number of phenomena that characterize biological and ecological systems. In particular, the formalisms of the local-stability approach do not allow for the fact that biological systems are subject to continuous environmental changes at various temporal scales and have the ability to react to these changes through asynchronous population fluctuations, species replacement, phenotypic plasticity, and evolutionary changes. By ignoring these features, most of the theory on complexity and stability of ecological systems

Manuscript received 29 July 2005; revised 7 April 2006; accepted 12 April 2006; final version received 10 May 2006.  
Corresponding Editor: T. J. Stohlgren.

<sup>4</sup> Present address: Department of Agriculture and Agroforestry, CATIE 7170, Turrialba, Costa Rica.  
E-mail: fadeclerck@mac.com

has focused on deterministic equilibria and ignored much of the potential for functional compensation, both within and between species. Functional compensation occurs when changes in the level of functioning contributed by one species or functional type are associated with opposite changes in the level of functioning contributed by another. This compensation is the basis for the stabilization of aggregate ecosystem properties (McNaughton 1977, Yachi and Loreau 1999, Loreau et al. 2002a) and serves as the theoretical framework for our study. In this manuscript we focus on three frequently used measures of stability, variance, and the resistance and resilience to drought events, to test three hypotheses: increased species richness will (1) decrease stand variance, (2) increase stand resistance to drought events, and (3) increase stand resilience to drought events. In each case, the alternate hypothesis was that species richness had no effect, but that stand species composition and abundance of the most resistant or resilient species drives stability.

Variance is defined as a measure of the magnitude of temporal change in a system property (Loreau et al. 2002a), often measured as the coefficient of variation (cv). We used variability in stand productivity to test the insurance hypothesis, or portfolio hypothesis (McNaughton 1977, Doak et al. 1998, Yachi and Loreau 1999), which proposes that biodiversity buffers ecosystem processes against environmental changes. Several alternative mechanisms have been proposed (see statistical averaging [Doak et al. 1998], the portfolio effect [Tilman et al. 1998], differential temporal optima [Yachi and Loreau 1999], compensatory growth [McNaughton 1977], or species redundancy [Naeem and Li 1997]). The biological rationale is that species' differential responses to temporal changes in the environment lead to functional compensation among species or phenotypes, and hence more predictable aggregate community or ecosystem properties (Patten 1975, McNaughton 1977, Naeem et al. 1998, Loreau and Hector 2001, Loreau et al. 2002a). Since different species respond differently to environmental fluctuations, the total variance in ecosystem function should decrease in systems with higher biodiversity so long as covariance is negative. Variance in annual productivity is measurable in conifer forests using annual growth in stem basal area. Our first hypothesis is that mixed forest stands will have less variance in annual productivity than pure stands and that the decreased variance is a function of compensatory growth in the face of fluctuations in resource abundance.

Resilience is a measure of the speed at which a system returns to its original state after being disturbed (Webster et al. 1975). It is generally measured as the return of community composition to an equilibrium state; however, it can also be applied to community properties, such as productivity, that return to nonequilibrium trajectories (Loreau et al. 2002a). In forest systems, resilience can be measured as the rate of return

to mean community productivity following a disturbance. Here we use drought year and postdrought productivity to test our second hypothesis: mixed forest stands will be more resilient to drought events than pure stands.

Resistance is a measure of the ability of a system to maintain its original state in the face of perturbation (Harrison 1979). It is similar to the concept of tolerance used by foresters and ecologists, who describe species as fire tolerant or drought tolerant. These qualitative terms describe the resistance of species to various forms of disturbance. We tested the resistance of mixed and pure stands to drought years of varying intensity and severity. We use predrought, drought, and postdrought productivity to test our third hypothesis: mixed forest stands will be more resistant to drought events than pure stands.

The alternate hypothesis is that the presence, absence, and abundance of one of the four species drive stand response to environmental fluctuations. In addition to testing the effects of species richness on resistance and resilience, we also tested the effect of the percentage of each species on stand stability. This concept has been heavily debated in ecology, particularly in regard to whether community productivity is driven by intraspecific interactions, which is known as the complementarity effect (Loreau 1998), or by the presence or absence of a dominant species, known as the sampling effect (Huston 1997).

To test the three hypotheses, we used annual stand productivity (basal area) of individuals with >10 cm diameter at breast height (dbh) as our measure of ecosystem function. Traditionally, studies of community or ecosystem stability have been based on fluctuations in species abundances or biomass; we use variation in community productivity ( $\text{cm}^2$  basal area/yr) of a fixed number of individuals. However, previous experiments (Tilman 1996, Pfisterer and Schmid 2002) and theory (Doak et al. 1998, Loreau et al. 2002a) regarding community stability predict reduced variance in ecosystem function, such as productivity, rather than biomass or abundance, in the face of environmental heterogeneity. Typically, reduced variance has been observed through changes in species abundances or composition. However, it can also arise through compensatory growth as measured through changes in productivity. We used stand productivity as our variable of interest and predicted that different species will be favored by, and will be more resistant to, different climatic conditions. Drawing on the insurance hypothesis (Yachi and Loreau 1999), the differential responses demonstrated by the four species should lead to reduced variance in mixed stands due to compensatory growth.

Most past studies of diversity and measures of stability have been conducted in microcosms, or in controlled field experiments using grasslands (Tilman and Elhaddi 1992, Naeem et al. 1994, Tilman and Downing 1994, Tilman 1996, Hector et al. 2002, Naeem

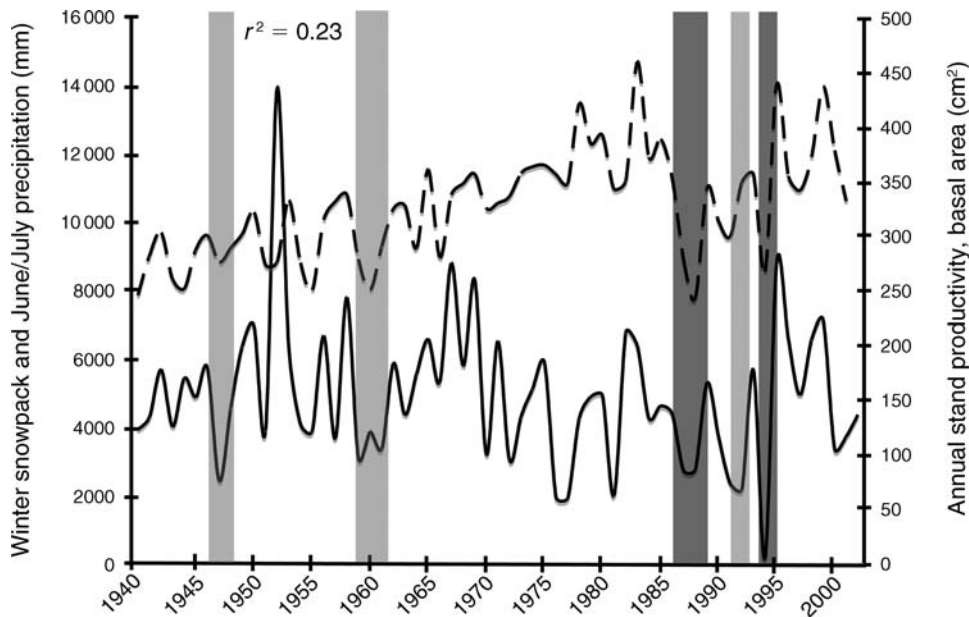


FIG. 1. Mean annual productivity of individual trees for all species from 1940 to 2004 (basal area; dashed line;  $n = 953$  cores) and the sum of the annual snowpack plus June and July precipitation (solid line). Light gray areas indicate periods of mild droughts where both the mean annual productivity of all individuals and the sum of the winter snowpack and June/July precipitation were  $>0.5$  sd and  $<1.0$  sd below the mean. Dark gray areas indicate severe drought events where mean annual productivity and precipitation were  $>1.0$  sd below the mean. The  $r^2$  value describes the fit of the climate model to the mean annual stand basal area.

2002), with an increasing call for studies that (1) test these same principles in other ecosystems (Mooney 2002), (2) test every possible combination of species to differentiate between the effects of composition and species richness (Aarssen 1997), and (3) use natural rather than artificial assemblages of species (Huston 1997). The difficulty is that in order to conduct biodiversity and ecosystem functioning studies, monocultural values of each species are needed. For natural experiments, this means being able to find pure stands for each species included in the study, as well as multiple iterations of two, three, or more species combinations. These conditions are rare in natural environments but can be found in the upper montane zone of the Sierra Nevada where four species of conifers are found in pure stands, and in every possible combination of two, three, and four species. While four species are low in comparison to most diversity and ecosystem function studies and constrain our results, the opportunity to observe principles of biodiversity and ecosystem functioning in natural, long-lived systems is unique and offers greater realism than manipulated grassland experiments that offer greater control (Diamond 1983). Through a combination of laboratory experiments, field experiments, and natural field experiments such as this, we can fully understand the relationship between biodiversity and ecosystem functioning.

#### METHODS

We used mixed and pure stands of conifers found in the upper montane zone (1500–3000 m) of the northern

Sierra Nevada, California, USA. Stands were comprised of various combinations of four conifers, including lodgepole pine (*Pinus contorta* ssp. *murrayana*), western white pine (*Pinus monticola*), red fir (*Abies magnifica*), and mountain hemlock (*Tsuga mertensiana*) (Hickman 1993). These conifer stands are comprised of long-lived individuals that have been subjected to several decades of environmental variation, including annual climatic heterogeneity and long-term trends of climate change (Fig. 1). Interannual variation in the climate is strong enough to influence primary productivity of the individuals, populations, and communities to test hypotheses related to species richness and stability.

We sampled 40 stands in the Desolation Wilderness in El Dorado County, California, from August through October in 2002 and 2003 (see Plate 1). All stands were located within the wilderness boundary with the exception of three western white pine stands located 66 km north in the Babbitt Peak Research Natural Area (RNA). We sampled at least three stands for every richness level among the four species.

We developed a Geographic Information System (GIS) model using the Sierra Nevada Ecosystem Project database (*available online*)<sup>5</sup> that restricted environmental variability to stands located on north-facing slopes of  $<20\%$  that are between 2100 and 2600 m elevation. We field-tested the model and found it to accurately locate suitable sites. This procedure effectively reduced the

<sup>5</sup> (<http://ceres.ca.gov/snep/>)

TABLE 1. Summary plot data.

Species richness	<i>n</i>	Density (stems/ha)		Basal area (m <sup>2</sup> /ha)		Shannon-Wiener index		Evenness	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
1	11	902	634–1698	141	84–230	0	0	0	0
2	14	1124	807–1480	126	63–220	0.26	0.13–0.60	0.38	0.20–0.86
3	11	1077	702–1840	151	78–235	0.83	0.34–1.03	0.76	0.31–0.94
4	4	1388	944–2247	183	84–284	1	0.71–1.21	0.72	0.51–0.87

Note: Number of plots is represented by *n*.

sampling area from 25 774 ha to 6500 ha, or 25% of the wilderness. The model also effectively reduced sampling error due to site conditions. We further limited environmental and stand variability in the field to sites with <5% exposed bedrock, >70% canopy closure, and >120 yr of age. Stands with any evidence of major disturbance, indicated by single-aged cohorts, or a high number of stumps or snags, were excluded from the study. Conifers dominated the stands, with little to no shrub, forb, or grass cover. 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 measured our success in achieving this goal by testing the relationship between environmental variables (elevation, slope, and aspect) and community response variables (species percentage, basal area, and canopy closure) and found that correlations between the percentages of each species are not significant (see DeClerck et al. 2005: Table 1). 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. Canopy closures increased with elevation, which is opposite expected trends in the upper montane. We explained this trend with the increased probability of sampling a pure mountain hemlock stand at higher elevations when site conditions are constrained as in our GIS model.

We used the single-species stands as the baseline for species response traits (productivity, biomass, and measures of stability); these are the equivalent of monocultural stands in combinatorial biodiversity studies. Since we prioritized our sampling for composition, we combined the three- and four-species richness levels to obtain an equal number of replicates for each species richness treatment. We did not control for density and abundance in our stand selection; therefore the population density and abundance varied within our replicates of composition and species richness. However, using the sum of individual productivity for all community analyses incorporates density effects, since dense stands have less productivity per individual than less-dense stands when site conditions are equal (Yoda et al. 1963). A description of the number of stands per treatment, stem density, basal area, productivity, diversity, and evenness is found in Table 1.

We sampled each stand with a 314-m<sup>2</sup> circular plot. Within each plot we identified and measured the diameter of each tree at breast height (dbh = 1.3 m above the ground). We took a single core from each individual >10 cm dbh within the plot to a depth of 21 cm or to the center of the stem, whichever occurred first. We cored 953 trees and measured over 86 000 annual growth increments in the 40 plots. All cores were mounted, dried, and sanded according to methods described by Fritts (1976). We measured the first 133 rings to the nearest 0.001 mm using Coore Recorder software and cross-dated each core with Cdendro software (Cybis [2003], Version 4.0, Saltsjöbaden, Sweden; [available online](http://www.cybis.se/)),<sup>6</sup> creating a master chronology for each species dating to 1870 (Fig. 1). In this standard procedure, individual cores are weighed against a master chronology consisting of numerous correlated cores. The correlation of cores considers both the greatest correlation coefficient and the number of years that the correlation is high between the master chronology and an individual core. We used cores that had a minimum correlation coefficient of 0.33 over 130 years. Cores with lower correlations, or higher correlation over <70 years were checked for missing rings and eliminated from the study if our confidence in the cross-dating of these cores remained low. We were careful not to eliminate cores simply because their rings were small.

In conifers, a common effect is an age-dependent autocorrelation between the age of the tree and ring widths with larger rings during the individual's early development. Therefore, annual ring width increment appears to be a decreasing function of age. We accounted for this phenomenon by converting annual ring width increments to basal area produced per year per individual:

$$\text{dbh}_t/2 = r_t \quad (1)$$

$$r_{t-1} = r_t - i_t \quad (2)$$

$$\pi r_t^2 - \pi r_{t-1}^2 = \text{BA}_t \quad (3)$$

where the dbh was used to derive the initial radius (Eq. 1), and successive subtraction of annual incremental growth (*i*) from the same year's radius determined the individual's radius for each successive year (*r<sub>t</sub>*, Eq. 2).

<sup>6</sup> [www.cybis.se/](http://www.cybis.se/)

Annual basal area produced is then simply the difference between the area of the stem at time  $t$  ( $\pi r_t^2$ ) and the area of the stem at time  $t - 1$  (Eq. 3). Stand or community basal area growth is calculated as the sum of basal area growth of individuals within that stand for each year and accounts for differences in community density. We use annual basal area produced as our measure of species, population, and community productivity, where population productivity is the sum of annual basal area produced by individuals of the same species, and community productivity is the sum of population basal areas within a stand. Throughout the remainder of the manuscript we refer to basal area ( $\text{cm}^2/\text{yr}$ ) as “productivity,” and stand productivity as “community productivity.”

We tested the insurance hypothesis by using the coefficient of variation for individuals, populations, and community productivity ( $\text{cv} = \log[100 \times 1 \text{ sd}/\text{mean}]$ ) for each stand across all years (Tilman 1996, Chapin et al. 1998, Hughes et al. 2002). The cv standardizes for the mean and therefore is less dependent on the mean than sd, and it provides an index of year-to-year variation in community biomass relative to the mean (Tilman 1996).

To study resilience and resistance, we used variation in precipitation in the form of drought events as external perturbations. We obtained long-term climate data from the National Oceanic and Atmospheric Administration (NOAA) database (*available online*)<sup>7</sup> for Tahoe City, California, situated directly between the Desolation Wilderness and the Babbitt RNA. Climatic values from Tahoe City (1900 m above mean sea level [amsl]) are not the same as those encountered in the upper montane (2400 m amsl); however, patterns in precipitation and temperature at Tahoe City are reflective of both research sites. Monthly and annual measures were precipitation, snowfall, snow depth, and minimum/maximum and mean temperatures. We conducted principal component analysis (PCA) and multiple regressions to derive a model best describing the growth variation exhibited by the conifers from the earliest available data in 1931 to the present. We limited the study to productivity and climate data from 1940 to 2004 in an effort to reduce error values due to changes in stand density and composition prior to 1940. Our PCA and multiple regressions with climate data indicated that no single climatic variable accounted for a variation in productivity. We derived a simple model where current growth ( $G_t$ ) was best explained by the sum of the winter snow pack ( $S$ ) and June/July precipitation ( $P_{jj}$ ) of the previous year (Eq. 4). Data from the previous year are critical since they represent the potential amount of energy available for the development of buds and leaf primordia that limit the productivity of the following year (Fritts 1976):

$$G_t = (S + P_{jj})_{t-1}. \quad (4)$$

A Pearson's correlation of our climate model (Eq. 4) on mean productivity for all individuals was statistically ( $P < 0.05$ ) and ecologically significant for all four species: lodgepole pine ( $r^2 = 0.44$ ), western white pine ( $r^2 = 0.36$ ), red fir ( $r^2 = 0.36$ ), mountain hemlock ( $r^2 = 0.56$ ), and all species ( $r^2 = 0.48$ ). This result suggests that productivity reflects variance in annual snow pack depth and June/July precipitation (Fig. 1).

We used both the mean annual productivity of all individuals and the climate record to define two levels of drought severity (Fig. 1). Mild drought years included those years where both the mean annual productivity of all individuals and the sum of the winter snowpack and June/July precipitation were  $>0.5 \text{ sd}$  and  $<1.0 \text{ sd}$  below the mean. We defined severe drought years in a similar manner, using years when mean annual productivity and precipitation were  $>1.0 \text{ sd}$  below the mean. This analysis identified three mild drought events (1948, 1960–1962, and 1992) and two severe drought events (1988–1989 and 1995). We used the mean values of the five drought events to calculate mean drought resistance and resilience.

To quantify drought resilience, we used Pimm's (1984) equation calculating the difference between the community productivity of a stand in a given postdrought year and its 10-yr predrought average. This value was then divided by the difference between the peak of the drought and the 10-yr predrought average to calculate “relative productivity deviation” ( $\text{RPD}_{\text{Pimm}}$ ):

$$\text{RPD}_{\text{Pimm}} = (\text{postdrought}_p - 10\text{-yr mean predrought}_p) / (\text{drought}_p - 10\text{-yr mean predrought}_p)$$

where  $p$  represents productivity. Pimm's equation creates data that cannot be log-transformed because they contain negative values; positive results indicate low resilience and postdrought productivity that has not surpassed equilibrium values, zero values indicate complete recovery and resilience, and negative values indicate that postdrought productivity has surpassed equilibrium values.

We modified Pimm's equation by calculating the relative biomass deviation for a given year as the ratio of the postdrought year to equilibrium value, which we calculated as the 10-yr predrought average. We called this metric  $\text{RPD}_2$ . When log-transformed,  $\text{RPD}_2$  resembled the well-studied log response ratio, whose properties include an approximately normal distribution (Hedges et al. 1999). Thus positive values indicate communities and individuals that are more resilient and have surpassed 10-yr predrought mean productivity levels, while negative values indicate the relative degree to which individuals or communities have not recovered. We present untransformed resilience measures as the percentage equilibrium growth recovered the year immediately following a drought to facilitate interpre-

<sup>7</sup> <http://www.ncdc.noaa.gov/oa.ncdc.html>

tation of the results. However, we did not use these untransformed values in our statistical analyses.

Standard measures of resistance calculate the ratio of productivity during a drought to the growth prior to a disturbance ( $\text{resistance} = \log [\text{productivity}_{\text{drt}}/\text{productivity}_{\text{pdr}}]$ ), where *drt* represents drought and *pdr* represents predrought. This specific rate of change in community productivity, called RGR, is a measure of drought resistance (Tilman and Downing 1994). Resistance stands have higher values, indicating that productivity was not greatly affected. During multiyear droughts, we used the productivity values from the lowest precipitation year (peak of the drought) as our drought value. Note that with trees, in contrast to annual species, the effect of weather is seen as an increase or decline in growth the following year; for example a drought in 1994 would be reflected by reduced growth in 1995. We calibrated both the resistance and resilience equations to reflect this offset.

We performed all analyses using JMP Version 5.0.1a (SAS Institute, 1989–2002) and fitted curves using least squares regression. Because apparent relationships between various measures of stability and species richness might be caused by factors that covaried with species richness, multiple regressions were used to control for such variables (e.g., community productivity, relative abundance, Shannon's diversity [Shannon and Weaver 1949], Hill's  $N_1$  [Hill 1973], evenness [Pielou 1975], and density). Climatic variables were not used because we lacked the stand-specific climate data; we assumed that all stands experienced similar broad climate patterns. As a further check on the possible role of species richness, we used backward, stepwise regression, only retaining those variables that contributed significantly ( $P \geq 0.05$ ). In backward elimination, the least significant variable is eliminated from a multiple regression, and a new multiple regression is performed, until all remaining variables are significant. Analyses of variance and multiple regression used the General Linear Models routines.

We performed a one-way ANOVA and each-pair means comparisons with Student's *t* test (0.05) to evaluate differences between single-species stands. This analysis quantified species-specific resilience, resistance, and cv, and permitted an evaluation of species-specific response traits.

## RESULTS

Throughout the results sections we refer to three different categories of measurements. First, we give the species-specific results derived from single-species stands or pure stands. Second, we give the results of individual species across diversity levels; for consistency we refer to these as changes in population responses to species richness. Finally, we give the results of the community that includes changes in all species with increasing species richness. All values are given as mean  $\pm$  SE. On average, our 40 stands contained  $27 \pm 2$  individuals

(Table 1). Individual trees had a mean dbh of  $47 \pm 0.75$  cm and added  $14.25 \pm 0.48$  cm<sup>2</sup> basal area annually ( $n = 951$ ; Fig. 1).

### Variance

Using mean annual productivity of individuals by species in pure stands, we found significant differences in growth rates between species from 1940 to 2004 (Fig. 2a;  $F_{3,248} = 433$ ;  $r^2 = 0.84$ ;  $P = 0.0001$ ). Basal area productivity (cm<sup>2</sup>/yr) was significantly highest for red fir ( $19.69 \pm 2.97$ ; all values mean  $\pm$  SE) and lodgepole pine ( $18.79 \pm 1.48$ ). These productivity levels were significantly greater than those of western white pine ( $9.36 \pm 0.91$ ) and mountain hemlock ( $8.26 \pm 0.76$ ). Mean annual stand productivity was  $1.04$  m<sup>2</sup>·ha<sup>-1</sup>·yr<sup>-1</sup> and increased significantly ( $P = 0.01$ ) with species richness from a mean of  $0.8$  m<sup>2</sup>·ha<sup>-1</sup>·yr<sup>-1</sup> in the single-species stands to  $1.2$  m<sup>2</sup>·ha<sup>-1</sup>·yr<sup>-1</sup> in three-species stands (Fig. 3a). The productivity of populations of hemlock and white pine increased significantly with species richness ( $P < 0.0001$  for white pine and hemlock), whereas it decreased significantly for lodgepole pine ( $P = 0.002$ ) and did not change for red fir ( $P = 0.62$ ). Pairwise correlations of mean annual productivity between species were positive and strong (Pearson correlation:  $r = 0.71$ – $0.81$ ;  $P = 0.0001$ ; Table 2).

The insurance hypothesis states that different species will respond differently to environmental variation, leading to functional compensation with environmental heterogeneity (Yachi and Loreau 1999, Loreau 2000, 2004). Complete functional compensation would occur if conditions that were poor for one species proved to be advantageous for a second and vice versa. We tested this hypothesis by conducting pairwise correlations of the basal area growth of all four species. When considering temporally heterogeneous resource availability, the hypothesis predicts that species that are perfectly differentiated in their resource use have negative correlations, whereas species belonging to same functional groups should have positive correlations. Our results did not find any indication of either complete or partial functional compensation; rather, all correlations were positive and highly correlated (Table 2). This result indicates that when productivity is the function of concern, all four species respond in a similar manner to climatic heterogeneity, i.e., that conditions that were favorable for the growth of a single conifer species were also favorable to the productivity of the remaining species.

We found significant differences in log cv values for each species in pure stands ( $F_{3,7} = 3.5$ ;  $R^2 = 0.60$ ;  $P = 0.07$ ; Fig. 2b), where red fir exhibited the lowest values ( $2.73 \pm 0.11$ ; all values mean  $\pm$  SE) with western white pine ( $2.76 \pm 0.08$ ), and mountain hemlock ( $3.06 \pm 0.11$ ) and lodgepole pine ( $3.07 \pm 0.09$ ) had the greatest values. Population log cv by species increased significantly with species richness for red fir ( $P < 0.0001$ ) but showed no change for the other three species ( $R^2 = 0.00$ ;  $P = 0.521$

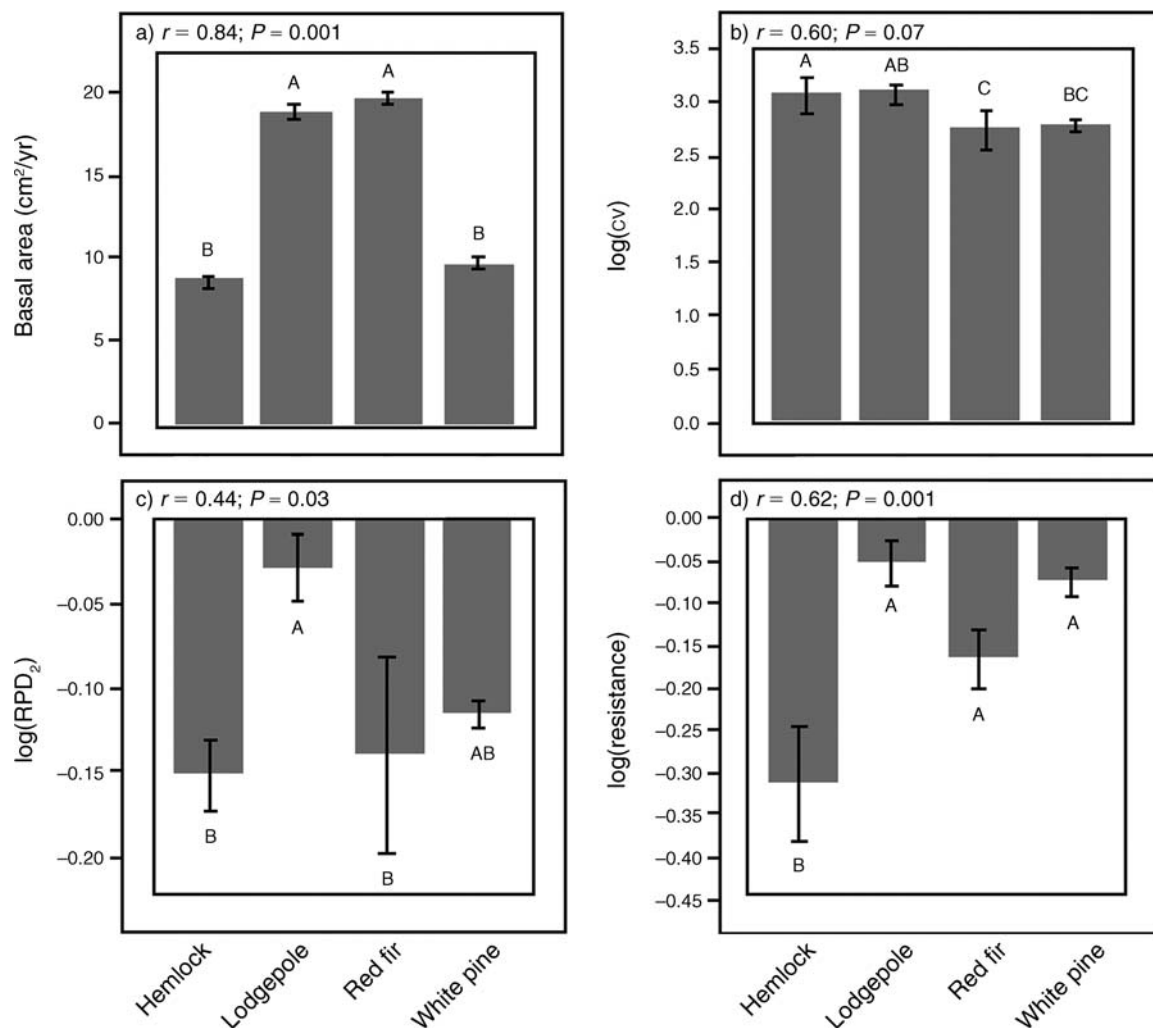


FIG. 2. Species values (mean  $\pm$  SE) derived from single-species stands for (a) productivity, (b) log cv, (c) log RPD<sub>2</sub>, and (d) log resistance. Comparisons of each pair with Student's *t* test were conducted; species that differ significantly at the 0.05 level are indicated by different uppercase letters.

for hemlock;  $P = 0.2855$  for lodgepole pine; and  $P = 0.154$  for white pine). Community log cv values increased marginally with species richness ( $R^2 = 0.07$ ;  $P = 0.084$ ; Fig. 3b). Multiple regressions and pairwise correlations indicate that mean productivity, species richness, and community log cv covary.

#### Resilience

Though response trends in resilience to drought events followed the same pattern regardless of drought severity, the significance of the response increased with drought severity. Therefore, we only describe the results from severe events here. We found significant differences in species RPD<sub>2</sub> to severe drought in single-species communities ( $F_{3,7} = 3.98$ ;  $r^2 = 0.44$ ;  $P = 0.026$ ; Fig. 2c). All values are given as mean  $\pm$  SE. Percentages represent the predrought growth rate that was recovered in the postdrought period. In single-species stands, lodgepole

pine ( $-0.03 \pm 0.024$ ; 94%) was the most resilient, followed by western white pine ( $-0.116 \pm 0.03$ ; 77%). Red fir ( $-0.140 \pm 0.03$ ; 74%) and mountain hemlock ( $-0.153 \pm 0.03$ ; 71%) were significantly less resilient than lodgepole pine. We obtained similar resilience results with RPD<sub>Pimm</sub>; species differences were moderately significant ( $F_{3,7} = 3.5$ ;  $R^2 = 0.60$ ;  $P = 0.078$ ). Lodgepole pine and red fir were the most resilient ( $-5.11 \pm 0.136$  and  $-0.812 \pm 1.66$ , respectively), whereas hemlock and white pine were the least resilient ( $0.099 \pm 1.66$  and  $0.304 \pm 1.175$ , respectively). Population RPD<sub>2</sub> also increased significantly with species richness for all species except lodgepole pine whose population RPD<sub>2</sub> decreased with species richness ( $P = 0.01$ , hemlock;  $P = 0.03$ , lodgepole pine;  $P < 0.0001$ , red fir; and  $P = 0.0008$ , white pine). Stepwise regression of community RPD<sub>Pimm</sub> indicated that species richness best explained increasing community resilience during severe droughts ( $F_{3,7} =$

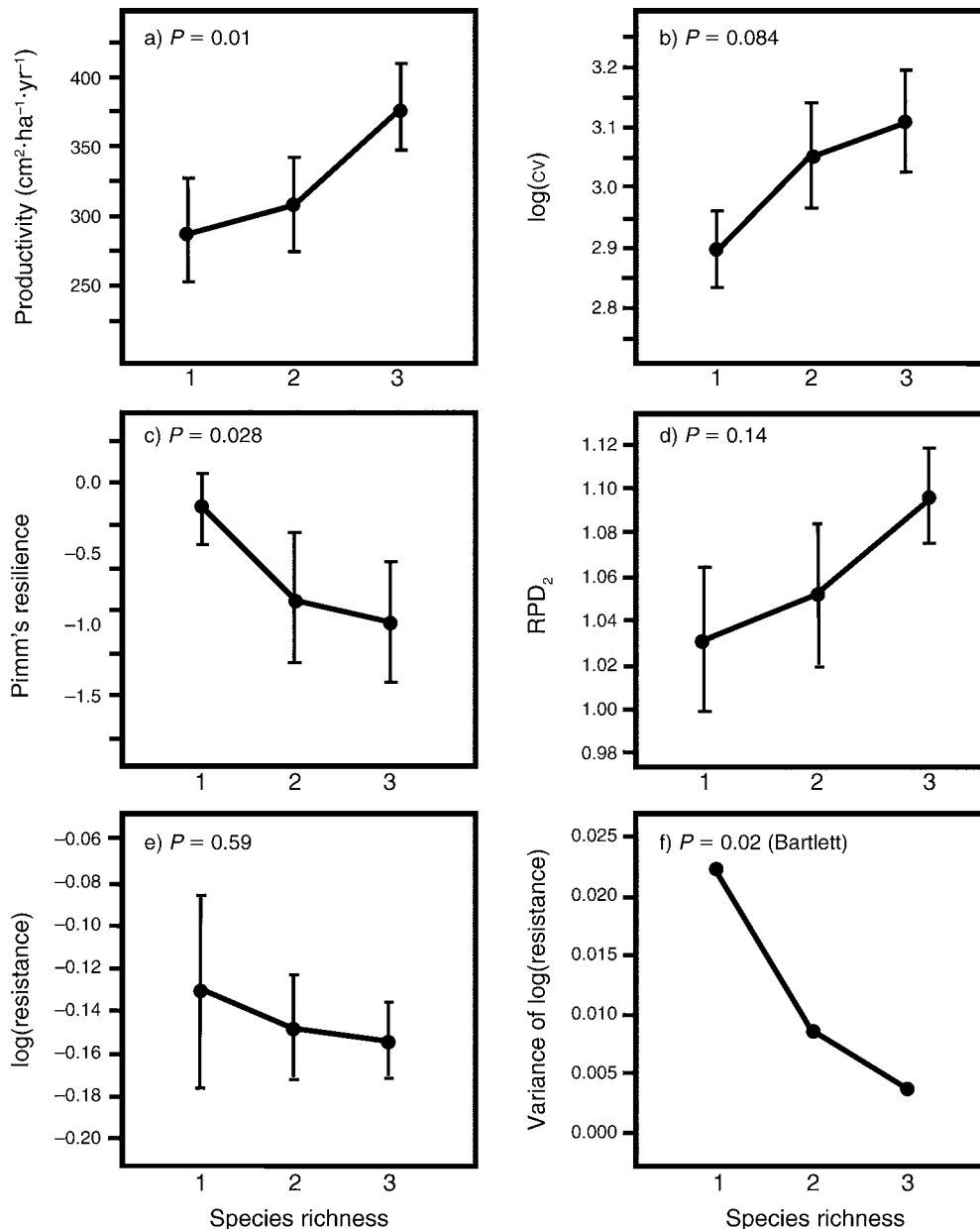


FIG. 3. Relationship between community values and species richness for (a) productivity, (b)  $\log \text{cv}$ , (c) Pimm's resilience, (d)  $\text{RPD}_2$ , and (e)  $\log \text{resistance}$ . (f) The variance  $\log \text{resistance}$  was obtained using Bartlett's test for homogeneity of variances. Richness is measured as the actual number of conifer species in the stand.

5.22;  $r^2 = 0.12$ ;  $P = 0.0280$ ; Table 3; Fig. 3c). We obtained similar results with  $\text{RPD}_2$ , though in addition to species richness, the percentage of lodgepole pine, the most resilient species, was also identified as significant ( $F_{2,37} = 6.13$ ;  $r^2 = 0.25$ ;  $P = 0.005$ ; Fig. 3d).

#### Resistance

The species trends for mean  $\log \text{resistance}$  for severe drought events followed a pattern similar to resilience, with significant differences between species ( $F_{3,15} = 9.16$ ;  $r^2 = 0.62$ ;  $P = 0.0001$ ; Fig. 2d). All values are given as

mean  $\pm$  SE. Percentages represent the predrought growth rate that was recovered in the postdrought period. Lodgepole pine ( $-0.05 \pm 0.03$ ; 91%) and western white pine ( $-0.08 \pm 0.04$ ; 84%) were the most resistant species. Red fir ( $-0.16 \pm 0.04$ ; 69%) was moderately resistant, and mountain hemlock ( $-0.32 \pm 0.05$ ; 50%) was significantly less resistant (Fig. 2d). Population resistance to severe drought did not change significantly with species richness, though the trend was of decreasing resistance with increasing species richness (lodgepole pine  $P = 0.62$ ; white pine  $P = 0.22$ ; red fir  $P = 0.44$ ;



TABLE 2. Pairwise correlation and covariance matrix of average annual productivity, by conifer species, across all levels of species richness and all years.

Species	White pine	Red fir	Lodgepole pine	Hemlock
a) Correlation, $r^2$				
Hemlock	0.74	0.81	0.71	1.00
Lodgepole pine	0.81	0.75	1.00	
Red fir	0.79	1.00		
White pine	1.00			
b) Covariance, cov				
Hemlock	4.19	6.43	2.13	4.30
Lodgepole pine	3.18	4.18	2.07	
Red fir	8.25	14.83		
White pine	7.41			

Note: All pairwise correlations were highly significant ( $P < 0.001$ ).

hemlock  $P = 0.69$ ). Community-level resistance to all levels of drought events decreased insignificantly with species richness (Fig. 3e). Community resistance was significantly lowest for severe drought events ( $-0.14 \pm 0.02$ ; 73%) with no species richness effect ( $P = 0.59$ ), in comparison to resistance to mild drought events ( $-0.06 \pm 0.004$ ; 87%) where resistance increased, though insignificantly, with species richness ( $P = 0.18$ ). Although resistance did not change significantly with species richness, the variance of the resistance to severe drought decreased significantly with increasing species richness (Bartlett's test for unequal variance:  $F_{2,37} = 3.9$ ;  $P = 0.019$ ; Fig. 3f).

Backward regression of resistance to severe drought on the six variables described in the *Methods* section retained the relative abundance of hemlock and red fir ( $P < 0.0001$  and  $P < 0.0064$ , respectively; Table 4). A model solely containing the relative abundance of lodgepole pine was also highly significant with log resistance to severe droughts increasing with the relative abundance of lodgepole pine ( $F_{1,38} = 11.82$ ;  $R^2 = 0.23$ ;  $P$

TABLE 3. Regression of relative productivity deviation after Pimm (1984;  $RPD_{Pimm}$ ) to all drought events on species richness.

A) ANOVA				
Source	df	MS	F	P
Model	1	0.2227	5.222	
Error	38	0.426		
Total	39			0.028
B) Regression parameter estimates				
Term	Estimate	SE	t	P
Intercept	0.588	0.291	36.15	0.0504
Species richness	-0.299	0.131	2.78	0.020

Notes: Summary of fit:  $R^2 = 0.12$ ; root mean square error (RMSE) = 0.65; mean of response =  $-0.03$ ; observations (or sum of weights) = 40. Forward and backward stepwise regression initially included six other variables that were all eliminated with a 0.250 limit to enter the model and a 0.100 limit to be eliminated from the model.

TABLE 4. Regression of resistance to severe drought events on species richness.

A) ANOVA				
Source	df	MS	F	P
Model	2	0.118	25.55	
Error	37	0.004		
Total	39			<0.0001
B) Regression parameter estimates				
Term	Estimate	SE	t	P
Intercept	-0.067	0.0165	-4.09	0.0002
Relative abundance (red fir)	-0.1021	0.0353	-2.89	0.0064
Relative abundance (hemlock)	-2.368	0.0334	-7.10	<0.0001

Notes: Summary of fit:  $R^2 = 0.58$ ; root mean square error (RMSE) = 0.068; mean of response =  $-0.14$ ; observations (or sum of weights) = 40. Backward stepwise regression initially included six variables that were all eliminated with a  $P > 0.100$  limit required for elimination from the model.

= 0.0014). Species richness was not identified as a significant model parameter.

We considered whether the resilience, resistance, or variance of a community might be better explained by using diversity indices that might account for species relative abundance within the mixed communities. We used Hill's  $N1$  (Hill 1973), and Shannon's index (Shannon and Weaver 1949) as measures of diversity, and Pielou's  $J'$  (Pielou 1975) as a measure of evenness. We found no significant relationship between these three measures and our measures of stability.

## DISCUSSION

The principal objective of this study was to test current theories of the relationship between diversity and stability and to determine whether the stability of long-lived conifers follows the same trends found in experimental grassland studies. Based on our results, we are unable to generalize that stability increased with species richness. Rather, we found a moderately significant increasing trend for log cv (if  $P < 0.1$  is used as moderately significant) and a decreasing but insignificant trend for resistance with increasing species richness. Only with community resilience was species richness identified as the most significant explanatory variable.

The cv values demonstrated a moderately significant increase with species richness rather than the expected decrease. Authors who have described statistical averaging and the portfolio effect have stated that the averaging effect occurs because of fluxes in population abundances (Doak et al. 1998). Although we do not measure population abundance, we expect to find the same effect with community productivity in systems comprised of perennial species. We fail to support the predictions made by the statistical averaging or portfolio hypotheses, although this is readily explained by the significant correlation in annual productivity in four

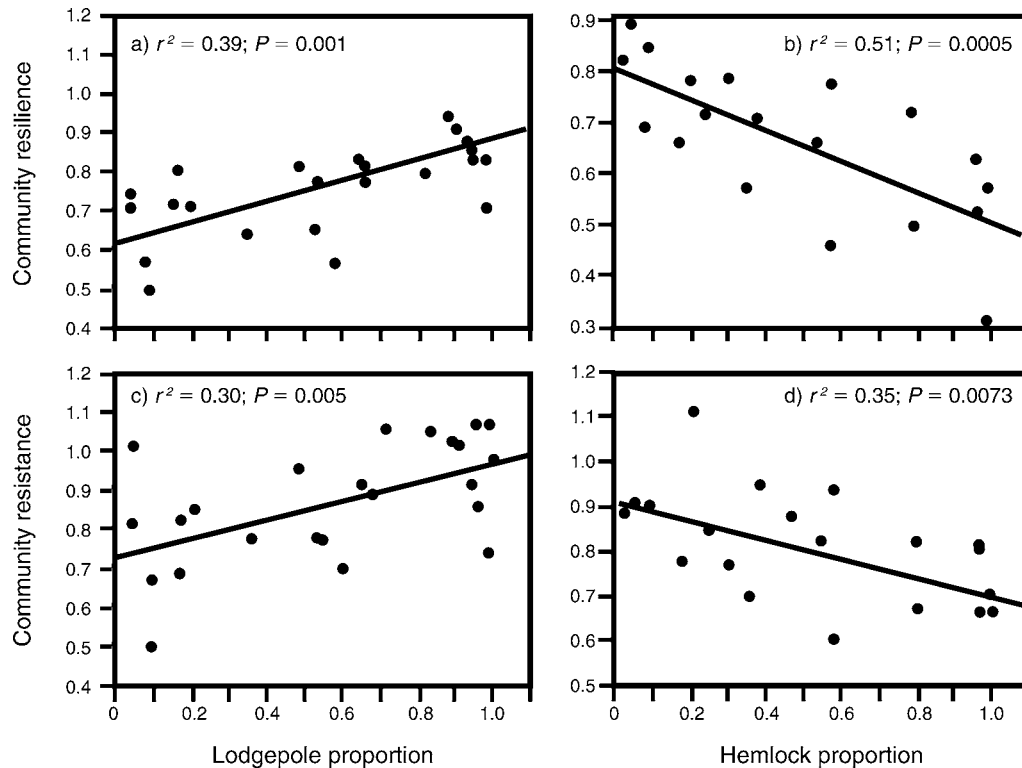


FIG. 4. Pearson's correlation between the percentage of lodgepole pine (left) and mountain hemlock (right) with community resilience (top) and resistance (bottom). Communities that did not contain lodgepole pine or hemlock are excluded from the respective analyses, although their presence did not alter the significance of the results.

species. Doak et al. (1998) have stated that if community biomass is the sum of the biomass values of many species, each varying through time, then adding more species together will result in more "averaging" of their fluctuations and hence less variation in total biomass. They note that this will be true whether the abundances of different species are positively or negatively correlated through time; as long as the species abundances are not perfectly, positively correlated with one another, greater species richness will lead to less variation. While it was assumed that this condition was rare, our results indicate that it may be common in coniferous forest communities when variance in productivity is measured.

The presence and abundance of lodgepole pine and mountain hemlock in the stand played a much more significant role in determining the resistance (Fig. 4). Stability measures of lodgepole pine and mountain hemlock in single-species communities have demonstrated that lodgepole pine is the most resistant and resilient, whereas mountain hemlock is the least resistant and resilient of the four species used in this study. These results point to a variation of the selection effect, where diverse stands are only more resistant if they contain a high percentage of the most resistant species and a low percentage of the least resistant species (Aarssen 1997, Huston 1997, Tilman and Lehman 2001).

Our results suggest that two different mechanisms are responsible for the trends found in the resistance and resilience analysis. Resistance to a drought measures the degree to which a community can sustain its predrought productivity when faced with an external perturbation. In the case of resistance, we assume that water is the single most limiting resource in the upper montane during the drought years (Hallgren and Helms 1988, Pavlik and Barbour 1991), and therefore theory relating to competition for a single limiting resource should describe the driving force. If several species compete for the same single limiting resource and there is no spatial or temporal heterogeneity, the single species that can tolerate the lowest resource level should displace all other species from the habitat (Tilman 1982). Our core analysis indicates that lodgepole pine is the most resistant species, capable of maintaining 91% of the predrought growth rates during severe drought events. This suggests that when soil moisture is the most limiting resource, lodgepole pine should outperform the remaining conifer species. Should drought conditions persist for an extended period of time, we predict that lodgepole pine would outcompete the three other conifer species (Fig. 5a). This also suggests that selection effect and competitive dominance are the mechanisms driving the negative trend between diversity and resistance in the upper montane conifer forests.

In contrast, community resilience measures the ability of a species or community to recover to predisturbance productivity levels in the years following a drought event. From a competition theory perspective, resilience potentially measures growth when water is no longer the sole limiting resource (Fig. 5b). All communities demonstrate increasing resilience with species richness. We hypothesize that as water becomes more abundant, secondary resources such as light or soil nutrients may come into play. Competition theory predicts that two species coexist if there are two or more limiting resources and if the two species are limited by different resources (Fig. 5b). Therefore, resilience can be driven by both the presence of a dominant species and complimentary resource partitioning.

Based on these results, we propose that resistance and resilience are driven by differing mechanisms. Resistance is driven by competition for a limiting resource predicting dominance by a single species and negative diversity effects; in contrast resilience is driven by resource partitioning, thereby permitting complementarity and positive diversity effects.

There are several possible explanations as to why our results differ from grassland studies. The first is that we were limited to 4 species rather than the 36 or more commonly used in grassland studies. Second, past studies have suggested that functional richness is more important than species richness, and that diversity effects are strongest when species are functionally dissimilar (Heemsbergen et al. 2004). It is quite possible that the four conifer species used are too functionally similar to demonstrate compensatory growth. The high positive correlation in the growth of the four species supports this hypothesis. The third possibility is that we failed to find significant differences in cv and resistance because we were unable to sufficiently eliminate inherent site-to-site variability. Finally, our results may differ from grassland studies because in the latter, most of the biomass is stored underground during dormancy; the timing and conditions at the onset of spring allow for greater intraspecific compensation than in forest systems, where large investments are put into aboveground biomass. In contrast, long-lived populations should be well adapted to withstanding climatic heterogeneity and do not exhibit the yearly changes in population abundance found in annual systems. We may find higher levels of complementarity in herbaceous systems where life history traits and community composition can respond much more quickly to environmental heterogeneity.

The idea that diversity begets stability makes intuitive sense, and it is also a very appealing concept, fitting the notion of “balance in nature.” However, we were unable to find convincing evidence in our four-species system that more-rich stands had less variance or were more resistant than single-species stands. Only resilience increased with increasing species richness. It appears that, hidden within the generality of species richness, the

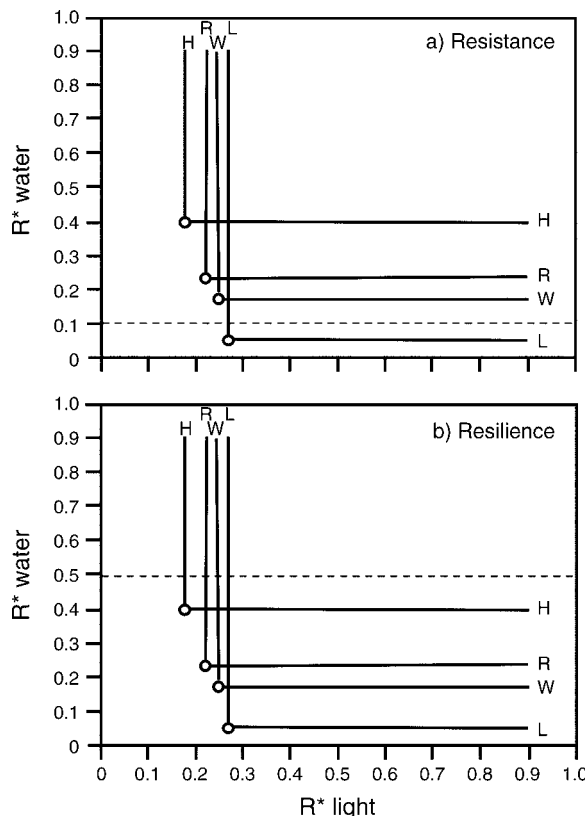


FIG. 5. Zero net growth isoclines based on each species' limitation for light and water, presenting a hypothesized explanation for the inverse relationship between resistance (panel a) and resilience (panel b). (a) During severe drought events, water becomes the most limiting resource, leading to reduced growth. Lodgepole pine, the most resistant species, would theoretically exclude all other species on dry sites or if drought conditions were to persist, and no richness effect is exhibited. (b) Since resilience measures growth following resource limitation, resource partitioning between species can occur, and positive species richness effects can be found. Water limitations are generalized using each species' resistance to severe drought events ( $1 - \text{resistance}$ ). Light limitations are derived from mean canopy openness for each species. Species codes are: L, lodgepole pine; W, white pine; R, red fir; and H, hemlock.  $R^*$  represents the environmental resource concentration required for the growth rate of a species to exactly balance its various sources of loss, or the lowest resource level that an individual species can tolerate (Tilman 1997).

specifics of composition are critical. Hughes et al. (2002) point out that competition may play a very indirect role in increasing stability, and that stability can be obtained in a high-diversity system without any strong interspecific interactions. If so, species–environment interactions may be more important for stability than interspecific interactions, and stability is influenced by the diversity of responses to environmental perturbations found in the composition, rather than by species diversity (Hughes et al. 2002). Thus an important question is whether diverse communities, by exhibiting a greater range of species responses to environmental fluctuations



PLATE 1. Morning light on a stand of upper montane conifers near Velma Lakes, Desolation Wilderness, Sierra Nevada of California (USA). Photo credit: F. DeClerck.

than depauperate communities, have a lower average correlation between species responses to environmental fluctuations. A significant amount of the variation in conifer productivity follows climatic patterns associated with winter snow and summer rain. Therefore, any stability derived from compensation should be due to species differing in their responses to environmental variability. However, correlations between the four species used in this study demonstrate that all four responded similarly to annual climatic variability, and therefore conifer productivity did not exhibit functional compensation.

#### ACKNOWLEDGMENTS

We particularly thank Allyson Carroll of Humboldt State University, who spent innumerable hours measuring and cross-dating over 400 of the cores collected. We also thank members of the Geography and Ecology Graduate Groups at the University of California–Davis, the Naem lab at Columbia University, and several anonymous reviewers whose comments have significantly improved the quality of this manuscript.

#### LITERATURE CITED

- Aarssen, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* **80**:183–184.
- Chapin, F. S., et al. 1998. Ecosystem consequences of changing biodiversity: experimental evidence and a research agenda for the future. *Bioscience* **48**:45–52.
- DeClerck, F. A. J., M. G. Barbour, and J. O. Sawyer. 2005. Resource use efficiency as a function of species richness and stand composition in upper montane conifer forests of the Sierra Nevada. *Journal of Vegetation Science* **16**:443–452.
- Diamond, J. M. 1983. Ecology: laboratory, field and natural experiments. *Nature* **304**:586–587.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability–diversity relationships in community ecology. *American Naturalist* **151**:264–276.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.
- Fritts, H. C. 1976. *Tree rings and climate*. Academic Press, New York, New York, USA.
- Gardner, M. R., and W. R. Ashby. 1970. Connectance of large (cybernetic) systems: critical values for stability. *Nature* **228**:784.
- Hallgren, S. W., and J. A. Helms. 1988. Control of height growth components in seedling of California red and white fir by seed source and water stress. *Canadian Journal of Forest Research* **18**:521–529.
- Harrison, G. W. 1979. Stability under environmental stress: resistance, resilience, persistence, and variability. *American Naturalist* **113**:659–669.
- Hector, A., M. Loreau, and B. Schmid, the BIODEPTH project. 2002. Biodiversity manipulation experiments: studies repli-

- cated at multiple sites. Page 294 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, UK.
- Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* **80**:1150–1156.
- Heemsbergen, D. A., M. P. Berg, M. Loreau, J. R. van Haj, J. H. Faber, and H. A. Verhoef. 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science* **306**:1019–1020.
- Hickman, J. C. 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley, California, USA.
- Hill, M. O. 1973. Diversity and evenness: a unifying notion and its consequences. *Ecology* **54**:427–432.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**:3–35.
- Hughes, J. B., A. R. Ives, and J. Norberg. 2002. Do species interactions buffer environmental variation (in theory)? Pages 92–101 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, UK.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**:449–460.
- Levins, R. 1970. Complex systems. Pages 73–88 in C. H. Waddington, editor. *Towards a theoretical biology*. Edinburgh University Press, Edinburgh, UK.
- Loreau, M. 1998. Separating sampling and other effects in biodiversity experiments. *Oikos* **82**:600–602.
- Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**:3–17.
- Loreau, M. 2004. Does functional redundancy exist? *Oikos* **104**:606–611.
- Loreau, M., J. A. Downing, M. Emmerson, A. Gonzalez, J. Hughes, P. Inchausti, J. Joshi, J. Norberg, and O. Sala. 2002a. A new look at the relationship between diversity and stability. Pages 294 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, UK.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**:72–76.
- Loreau, M., S. Naeem, and P. Inchausti, editors. 2002b. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, UK.
- MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* **36**:533–536.
- May, R. M. 1972. Will large and complex systems be stable? *Nature* **238**:413–414.
- May, R. M. 1973. *Stability and complexity in model ecosystems*. Second edition. Princeton University Press, Princeton, New Jersey, USA.
- McCann, K. S. 2000. The diversity–stability debate. *Nature* **405**:228–233.
- McNaughton, S. J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* **111**:515–525.
- Mooney, H. A. 2002. The debate on the role of biodiversity and ecosystem functioning. Page 294 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, UK.
- Naeem, S. 2002. Biodiversity: biodiversity equals instability? *Nature* **416**:23–24.
- Naeem, S., Z. Kawabata, and M. Loreau. 1998. Transcending boundaries in biodiversity research. *Trends in Ecology and Evolution* **13**:134–135.
- Naeem, S., and S. B. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* **390**:507–509.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**:734–737.
- Odum, E. P. 1952. *Fundamentals of ecology*. Saunders, Philadelphia, Pennsylvania, USA.
- Patten, B. C. 1975. Ecosystem linearization: evolutionary design problem. *American Naturalist* **126**:14–29.
- Pavlik, B. M., and M. G. Barbour. 1991. Seasonal patterns of growth, water potential and gas-exchange of red and white fir saplings across a montane ecotone. *American Midland Naturalist* **126**:14–29.
- Pfisterer, A. B., and B. Schmid. 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature* **416**:84–86.
- Pielou, E. C. 1975. *Ecological diversity*. Wiley, New York, New York, USA.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* **307**:321–326.
- SAS Institute. 1989–2002. *JMP Version 5.0.1a*. SAS Institute, Cary, North Carolina, USA.
- Shannon, C. E., and W. Weaver. 1949. *The mathematical theory of communication*. University of Illinois Press, Urbana, Illinois, USA.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**:350–363.
- Tilman, D. 1997. Mechanisms of plant competition. In M. J. Crawley, editor. *Plant ecology*. Second Edition. Blackwell Science, Oxford, UK.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* **367**:363–365.
- Tilman, D., and A. Elhaddi. 1992. Drought and biodiversity in grasslands. *Oecologia* **89**:257–264.
- Tilman, D., and C. Lehman. 2001. Biodiversity, composition, and ecosystem processes: theory and concepts. Page 365 in A. P. Kinzig, S. W. Pacala, and D. Tilman, editors. *The functional consequences of biodiversity*. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity–stability relationships: statistical inevitability or ecological consequence? *American Naturalist* **151**:277–282.
- Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient recycling and the stability of ecosystems. Pages 1–27 in F. G. Horwell, J. B. Gentry, and M. H. Smith, editors. *Mineral cycling in southeastern ecosystems*. National Technical Information Service, Springfield, Virginia, USA.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences (USA)* **96**:1463–1468.
- Yoda, K., T. Kira, H. Ogawa, and K. Kozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology* **14**:107–129.