# Beyond the tropics: forest structure in a temperate forest mapped plot

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## Abstract

**Question:** How do the diversity, size structure, and spatial pattern of woody species in a temperate (Mediterranean climate) forest compare to temperate and tropical forests?

**Location:** Mixed evergreen coastal forest in the Santa Cruz Mountains, California, USA.

**Methods:** We mapped, tagged, identified, and measured all woody stems ($\geq 1$ cm diameter) in a 6-ha forest plot, following Center for Tropical Forest Science protocols. We compared patterns to those found in 14 tropical and 12 temperate forest plots.

**Results:** The forest is dominated by Douglas-fir (*Pseudotsuga menziesii*) and three species of Fagaceae (*Quercus agrifolia, Q. parvula* var. *shrevei*, and *Lithocarpus densiflorus*), and includes 31 woody species and 8180 individuals. Much of the diversity was in small-diameter shrubs, treelets, and vines that have not been included in most other temperate forest plots because stems < 5-cm diameter had been excluded from study. The density of woody stems (1363 stems ha$^{-1}$) was lower than that in all but one tropical plot. The density of large trees (diameter $\geq 30$ cm) and basal area were higher than in any tropical plot. Stem density and basal area were similar to most other temperate plots, but were less than in low-diversity conifer forests. Rare species were strongly aggregated, with the degree of aggregation decreasing with abundance so that the most common species were significantly more regular than random.

**Conclusions:** The patterns raise questions about differences in structure and dynamics between tropical and temperate forests; these need to be confirmed with additional temperate zone mapped plots that include small-diameter individuals.

## Introduction

Most ecological theory and modern scientific methodologies have their origins in temperate regions. Plant community ecology, concerned with explaining the structure and dynamics of plant communities, is no exception. From the early biogeographic writings of von Humboldt and Bonpland (1814) and Wallace (1895), through foundational research on the structure (Fedorov 1966), dynamics (Webb et al. 1972), interactions (Janzen 1970), evolution (Dobzhansky 1950), and diversity (Terborgh 1985) of tropical forests, researchers have framed their questions and findings in the context of "normal" temperate systems, and used research approaches with long traditions among temperate zone researchers. Temperate system attributes are often normative; researchers seek to explain what generates or maintains "high" diversity in tropical systems – not why temperate systems are so species-poor. MacArthur (1969) began his classic paper on *Patterns of communities in the tropics* with "The wet tropical lowland environment is different from that in temperate regions, and in this tropical environment plant and animal communities exhibit various *extreme* patterns" (emphasis added).

One important development in plant ecology, however, arose in the tropics. Thirty years ago, the

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establishment of large, fully mapped plots in tropical forests (Hubbell 1979; Hubbell & Foster 1983) dispelled ingrained beliefs about the uniform dispersion and low density of tropical tree species that had been held since the time of Wallace (1895). Hubbell and Foster established a spatial census approach to understanding forest ecology, where they mapped, measured, and identified all woody stems larger than 1-cm diameter across large areas of forest. The 50-ha plot on Barro Colorado Island in Panama was the model for a network of Forest Dynamics Plots coordinated by the Center for Tropical Forest Science (CTFS) of the Smithsonian Tropical Research Institute. The CTFS network now includes 20 mapped plots across the tropics, where more than three million trees from over 6000 species are re-censused every 5 years (see synthesis of findings of the first 16 plots in Losos & Leigh Jr. 2004). The detailed size and spatial data from these tropical plots have provided excellent quantitative descriptions of forest structure, and have allowed fundamental advances in the theory of community ecology (Hubbell 2001; Volkov et al. 2007).

These spatial census plots have three important components. First, the censuses include a broad range of size classes from 1-cm diameter saplings through to the largest adults. Second, individuals are mapped to a resolution ($\leq 1$ m) that allows analysis of spatial patterns at ecologically important scales. Third, the area is large enough to include enough individuals of many woody species to permit meaningful population-level analyses of size distributions and temporal changes. While there are many existing temperate forest plots, none of them combine these three components, which are critical for studying community structure and dynamics.

Much of what we currently know about temperate forest structure and dynamics has come from forest inventories derived from small plots of $< 1$ ha, by sampling along transects, or sampling without spatial information (e.g., Jones 1945; Nakashizuka 1991; Frelich & Reich 1995; Busing 1998; Quigley & Platt 2003; Chapman et al. 2006; Tsujino et al. 2006; Wang et al. 2006; Drewa et al. 2008; Johnson et al. 2008). Those temperate plots that are large enough (1-12 ha, plus one at 32 ha) to permit analysis of temporal trends and size distributions at the population level include only larger diameter trees (4–10 cm minimum DBH) (Appendix 3SB and Masaki et al. 1992; Cain & Shelton 1995; Tanouchi & Yamamoto 1995; Chen & Bradshaw 1999; Miura et al. 2001; Busing & Fujimori 2002; Harcombe et al. 2002; North et al. 2004; Commarmot et al. 2005; Meyer 2005; Takyu et al. 2005; Wunder et al. 2007).

Together, this body of work has provided us with a great deal of information regarding the demography and community structure of well-established individuals and larger species. However, important processes associated with juveniles, as well as almost all the shrubs and treelets, have generally been excluded from study; in a few cases smaller stems were included in very small subplots within the larger plots (e.g., Cain & Shelton 1995; Busing & Fujimori 2002). However, we know of no published plot in the temperate zone that provides the combination of small size classes (i.e., DBH $\geq 1$ cm), fine-scale spatial resolution ($\leq 1$ m), and large sample size that provide the same kind of insights as Hubbell–Foster-style plots and allow for direct comparison to the CTFS network of tropical plots.

Furthermore, in the literature on temperate forests, Mediterranean climate forests are poorly represented (but see Busing & Fujimori 2002). Most mapped temperate plots are in wet (1200-2800 mm precipitation) climates with cold winters (Appendix S3C). In contrast, Mediterranean regions are characterized by hot, dry summers and low annual precipitation that falls mostly as winter rain. Drought and fire tolerance are key attributes for woody species in these regions (Kalin Arroyo et al. 1995; Rodà et al. 1999). Because of the long history of intensive human occupation of many Mediterranean climate regions, much of the ecological research in these areas has focused on forests where management practices are the dominant force shaping plant community structure and dynamics (Rodà et al. 1999; Hidalgo et al. 2008; Moya et al. 2009). In contrast, we know relatively little about the structure and dynamics of Mediterranean climate temperate forests that experience less anthropogenic manipulation. Given the ecological and conservation value of Mediterranean climate regions (e.g., Myers et al. 2000), the lack of large-scale, fine-resolution plots to study spatial patterns and dynamics is particularly notable.

We adopted the methodologies established for tropical spatial census forest plots to study the structure and dynamics of a temperate, Mediterranean climate forest. The University of California Santa Cruz-Forest Ecology Research Plot (UCSC-FERP) is a 6-ha mapped plot in the mixed-evergreen forest on the Central Coast of California, USA. We followed the CTFS methods (Condit 1998) to map all stems with a diameter $\geq 1$ cm. In this paper, we present the basic structural data of the UCSC-FERP, adopting key analytical approaches used for comparisons among the CTFS plots to examine "snapshot" data of forest diversity, size, and spatial

structure. As much as possible, we also place the UCSC-FERP plot into the context of what is known from other spatial census plots throughout tropical and temperate forests. Because comparable data and analyses are much more common from tropical forests, the tropical forests here become the norm against which to compare the FERP and other temperate plots.

This project fills several needs in forest ecology. First, it is the first large, mapped forest plot in a mixed species Mediterranean zone forest; such forests differ from most other temperate forests by the strong influence of an extended dry season and mild winters. Second, California mixed evergreen forests are under increasing pressure from growing human populations in coastal zones and are particularly vulnerable to changes in precipitation patterns associated with global climate change. Detailed data of the structure and dynamics of this type of forest provide opportunities for understanding the impact of such changes on an important, and currently little studied, ecosystem. Third, by embracing the size class, spatial resolution, and analytical approaches of the CTFS network of forest plots, we can begin the process of a truly global understanding of forest structure and dynamics that includes recent novel insights from the tropical forests. Some differences from tropical forests are easy to predict; for instance, we would be surprised to find anything other than lower species diversity and lower stem density than in most tropical forests, even though a Mediterranean mixed evergreen forest is likely to have greater diversity than temperate zone forests that are dominated by a small number of conifer species.

Other patterns are harder to predict a priori. For instance, tropical tree species are almost universally clumped in space, and the degree of clumping is greater for rarer species (Hubbell 1979; Condit et al. 2000). Nevertheless, that tropical species are *less* clumped than expected based on their seed dispersal patterns is also a widespread phenomenon, and thought to be a key factor in the maintenance of species diversity in tropical forests (Janzen 1970; Harms et al. 2000; Gilbert 2002). Temperate tree species also tend to be aggregated (e.g., Busing 1998; Aldrich et al. 2003). It is not, however, readily apparent whether to expect the degree or patterns of aggregation to be any different between temperate and tropical forests, and only a completely mapped plot, with size distributions comparable to those from tropical plots, will allow examination of these patterns. Similarly, it is not clear what to predict about size class distributions. Because a special feature of tropical forests is an

extensive "seedling bank" of extremely slow-growing juveniles in the dark tropical understory (Clark & Clark 1992; Condit et al. 1993; Metcalf et al. 2009), we might expect that the size distributions of individuals in our much lighter forest might be less strongly skewed towards small size classes. For example, Enquist & Niklas (2001) found that forests at higher latitudes tended to have lower densities of small stems.

Our goals here are to provide an overall description of the forest composition, diversity, and structure of the University of California Santa Cruz – Forest Ecology Research Plot, and to evaluate differences in patterns of diversity and structure between this plot, the tropical CTFS plots, and other temperate sites, using the detailed spatial census data that characterize them. The purpose here is not to test specific hypotheses about why the FERP forest differs from tropical or other temperate forests, nor to infer ecological process from snapshot pattern data. Instead, we begin by asking how the structure of this particular temperate forest deviates from "normal" reference tropical ecosystems, using the CTFS analytical framework. We hope these comparisons will stimulate future studies on ecological process, both in the UCSC-FERP and elsewhere. Specifically, we investigate (1) how woody plant species richness varies with stem diameter classes (Condit et al. 1996; Losos & Leigh Jr. 2004), (2) how stems and basal area are distributed across diameter classes (Losos & Leigh Jr. 2004), and (3) how spatial aggregation of woody species varies with species abundance (Condit et al. 2000) in the UCSC-FERP, and compare these results to those from 26 other large mapped plots in tropical and temperate forests.

## Methods

### Study site

#### Location

The UCSC Forest Ecology Research Plot (UCSC-FERP) is located in a mixed evergreen coastal forest in the hills above the town of Santa Cruz, California, USA. This forest is in the northern ("Upper Campus") part of the University of California, Santa Cruz, and is protected as part of the 160-ha Campus Natural Reserve (http://ucreserve.ucsc.edu/UCSCCNR) (UC Santa Cruz 2005), which is bordered by extensive contiguous protected forest lands.

The FERP measures 6 ha, extending 300 m north and 200 m east from its southwest corner at
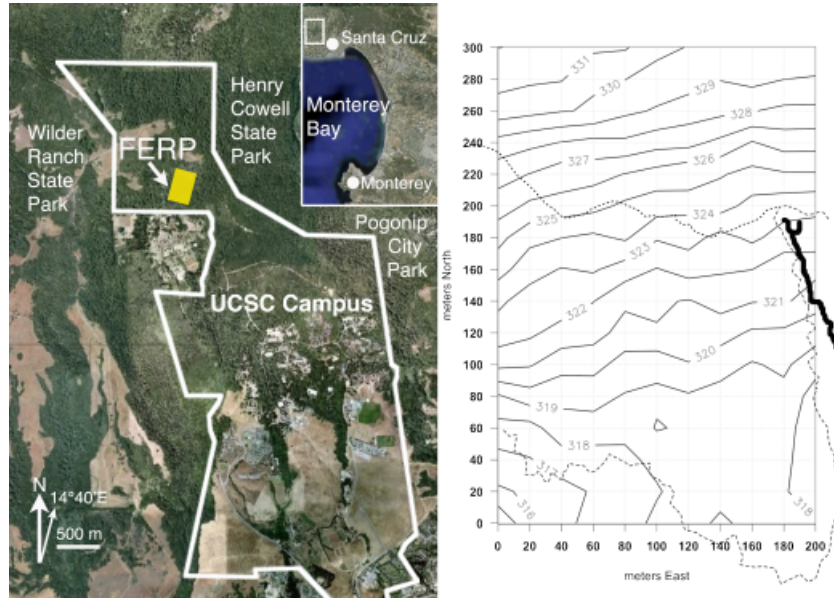
**Fig. 1.** Location of the UCSC Forest Ecology Research Plot (FERP) on the upper campus of the University of California, Santa Cruz. The plot is located in contiguous, protected forest including the UCSC Campus Natural Reserve and three state and city parks. Map at right shows the topography of the FERP, with contour lines in 1-m increments for meters above sea level, dashed and dotted lines for trails, and a thick line for a creek on the eastern border.

37°0.745′N, 122°4.490′W, 314 m a.s.l. The plot is oriented to magnetic north to facilitate orientation on the ground, with local declination of 14°40′ east. North, west (across two-lane Empire Grade Road), and east of the plot is protected forest habitat. A low-density housing area (Cave Gulch), dating to the mid-19th century, begins a few hundred meters to the south. A 1- to 2-m wide recreational trail with foot and some bicycle traffic crosses the southern part of the plot.

The FERP topography is nearly flat, sloping gently upward from 314 m .a.s.l. in the south to 332 m a.s.l. in the north (Fig. 1, Appendix S5). There is a semi-permanent creek with steeply cut banks (average 1.6-m deep and 2.5-m wide) on the eastern border, with significant flow only during the rainy season.

The FERP's single plot, 6-ha design has two purposes. As part of a research project on the epidemiology of tree diseases, the mapped forest plot required a scale large enough to model the spread of several generations of a fungal pathogen across a contiguous landscape. Second, the plot is intended to be a permanent resource for teaching and research on the UCSC Campus Natural Reserve. The FERP is a 25-min walk from the main science laboratories on campus, and has quickly become a standard resource for class projects and students theses. Ongoing monitoring includes tree phenology through a network of litter traps; micrometeorology

with a network of meteorological stations; relationships between the distribution and growth of plants and soil nutrient and moisture dynamics; the structure, diversity, and dynamics of ecological interactions ranging from fungal communities to pollination systems; and the population dynamics and habitat use patterns of small mammal communities. Many of these lines of inquiry are most easily accomplished within large contiguous areas, and sizeable populations of individual species that would not be possible in a smaller area, even if it captured nearly all the species. It is not larger than 6 ha primarily because of logistical and funding constraints of maintaining monitoring programs over the long term.

### Climate

The Mediterranean climate of Santa Cruz is characterized by highly seasonal precipitation and mild temperatures. It is classified as temperate, dry summer, warm summer (Csb) according to the updated Köppen-Geiger climate classification system (average temperature of hottest and coldest months, 17.11 and 9.71°C, respectively; precipitation in the driest summer and wettest winter months, 1.15 and 142.69 mm, respectively; 11 months with average temperature above 10°C) (Peel et al. 2007). Of the 776-mm annual rainfall, 96% falls during the rainy season from October to April (NOAA 2008) (Appendix S1). During the rainy season, average

daily maximum and minimum temperatures are 18.1°C and 5.8°C, respectively; 23.2°C and 10.2°C during the dry season. Freezing temperatures and snowfall are very rare and not persistent. Dense fog is frequent during the dry season.

### Geology and soils

Soil is primarily Watsonville series, a fine, montmorillonitic, thermic Xeric Argialbolls (Order Mollisols, Suborder Albolls in the USDA-NRCS classification system) (Beaudette & O'Geen 2008). This series is characterized as deep and somewhat poorly drained because of perched water tables, and was formed in an alluvium. Soil on the plot has an average sand:silt:clay composition of 69:21:10, organic matter 4.3%, and pH = 5.2 (G. Gilbert, unpubl. data). The soil primarily overlays weathered Miocene deposits of sedimentary Santa Margarita Sandstone and some inclusions of volcanic Ben Lomond Quartz Diorite (Cretaceous origin), which dominates the surrounding landscape (Stanley & Weber 2008). There are no obvious abiotically determined habitat types.

### Vegetation

The forest on the FERP is dominated by a mixture of conifer and oak species. The forest has a closed canopy of very uneven height (canopy openness = 13.32 ± 2.8%, mean ± SD, $n$ = 176; mature oaks generally range in height from 12 to 26 m, and conifers reach 30–49 m, G.S. Gilbert unpubl. data). Vegetation on the plot can be classified primarily into the Douglas Fir–Tanoak series, with a small patch of mature Woolyleaf Manzanita series chaparral in the southeastern corner of the plot (Sawyer & Keeler-Wolf 1995).

### Site history

Human occupation of the present UCSC campus lands dates to 4000 years or more before present, and archeological evidence indicates that native groups (Ohlone and their ancestors) participated in land-altering activities on campus lands that included hunting, gathering and processing plant foods, and grassland burning (Jones 2002; Anderson 2005; Haff & Hayes 2008). Beginning in the 1830s, logging, limestone quarries and kilns, and cattle ranching were active on Cowell Ranch, 8.1 km$^2$ of which later became the UCSC campus. Active ranch management ended in 1946. In 1961, construction began to create the campus of the University of California, Santa Cruz, of which 243 ha have been transformed into university infrastructure. The Upper Campus area remains undeveloped, and includes much of the Campus Natural Reserve (including the FERP site), which was established in 1988 to protect natural habitat for research and teaching use.

Given the long and varied human impacts on forests throughout the California Central Coast, it is likely that trees were selectively extracted from the forest on the UCSC-FERP at some time. However, there are no known archaeological resources, no clear records of timbering activities, no records of prescribed burning, and no evidence of fire scars on the plot itself; all of these disturbance indicators are present in forested areas elsewhere on campus, including a fire in large parts of Upper Campus in 1999. Coring of 16 of the largest trees on the plot (eight *Pseudotsuga menziesii*, five *Sequoia sempervirens*, one *Arbutus menziesii*, one *Lithocarpus densiflorus*, and one *Pinus ponderosa*), showed that most of the larger trees ranged from 70 to 80 years old, with one *Pseudotsuga* at 113 years (Russell 2008). Taken together, the data suggest that major disturbances to the plot date to before 1930, and that the history and structure of the forest in the FERP is typical of mixed evergreen coastal California forest. As is true in all fire-prone California coastal ecosystems, the FERP forest appears to be a forest in transition. Such forests, by their nature dynamic, have expected fire return frequencies of 5 to 261 years (Hunter & Parker 1993; Hunter 1997; Horton et al. 1999; Hunter & Barbour 2001). Disturbance-related species like *Arctostaphylos* spp. and *Arbutus* are noticeably dying in the shade of large *Pseudotsuga* and *Quercus*, as one would expect many decades into a fire cycle. The site is neither highly disturbed nor unusually undisturbed for a forest of this type. Additional information about the history and natural history of the UCSC campus is available in Haff et al. (2008), the UCSC Long-range Development Plan (UC Santa Cruz 2005), and the UCSC plants portal at http://envs.ucsc.edu/plants.

### Sampling

We mapped all woody stems larger than 1-cm diameter (DBH, measured at 1.3-m high), following the standards established for the CTFS network of tropical forest plots (Condit 1998). We established a permanent grid for the forest plot, placing PVC pipe markers at the corners of each 20×20-m quadrat across the FERP. Corner locations were surveyed using a hypsometer (Haglöf Vertex Laser VL400, Haglöf Inc., Langsele, Sweden) and sighting compass (Suunto KB14). We then measured the bearing (to 0.5°) and distance (to 0.1 m) from each individual to the hypsometer transponder placed on a tripod

immediately above a corner post no more than 25 m away. Adjusting the horizontal distance from the quadrat corner to include the radius of the tree stem, we then converted the radial measurements to global $x$, $y$ coordinates (in meters, with 0.1-m precision) from the southwest corner of the plot.

We gave each stem a metal numbered aluminum tag (Big City Manufacturing Inc., Houston, TX, USA), identified the plant to species, and measured its DBH. Diameters of stems smaller than 8 cm were measured with plastic calipers, whereas larger stems were measured with a diameter tape, recording diameter to 1-mm precision. For trees smaller than 30 cm, tags were tied to the base of the plant with 8-gauge grafting tape; for larger trees, the tags were nailed to the north side of the trunk at about 2-m height, with aluminum nails slightly angled so that rainwater would run down the nail away from the trunk. For multi-stemmed individuals, the DBH of the largest stem was recorded as the principle stem, along with the number and diameter of other stems $\geq$ 1-cm DBH. Variation in measuring DBH when stems were not cylindrical and recording auxiliary data about stems (e.g., multiple stems, stem leaning, etc.) followed the protocols and codes of the CTFS plots (Condit 1998). Initial mapping began on 8 December 2006, and main stem data were all completed by 13 September 2007. Counts and measurements of all stems DBH $\geq$ 1 cm on multi-stemmed individuals were completed in June–August 2008.

*Analyses*

**Species composition**

Species were identified morphologically and vouchers deposited in the UCSC Natural History Museum (UCSC). Taxonomic nomenclature follows that of the University of California Jepson Museum interchange (http://ucjeps.berkeley.edu/interchange. html, accessed 1 December 2008), which is the recognized standard reference for plant taxonomy in the state of California.

**Diversity**

We used individual-based rarefaction curves to evaluate the completeness of species sampling and the variation in woody species richness at different scales. We used EstimateS software (v. 8.0, Colwell, 2006) to calculate species accumulation curves (Mao Tau rarefaction) by dividing the entire 6-ha plot into non-overlapping quadrats of $5\times5$ ($25\,m^2$), $20\times20$ ($400\,m^2$), $50\times50$ ($2500\,m^2$), and $100\times100$ m (1 ha). We plotted species accumulation curves against the cumulative mean number of individuals (rather than quadrat size) because it is more robust for assessing

and comparing species richness, particularly when comparing across sites with different stem densities (Condit et al. 1996; Gotelli & Colwell 2001). Conducting the analysis at a range of different quadrat sizes allows us to evaluate homogeneity of habitat on the plot; if plant species are non-randomly distributed across the plot (i.e., high beta-diversity, with distinct habitat types within the plot), then the cumulative number of species should rise more quickly when smaller quadrats are sampled from across the plot, compared to a fewer larger quadrats, for the same number of individuals. Because more than half of the species were shrubs, vines, and treelets that are unlikely to ever reach larger size classes, we also calculated species accumulation curves that included only those 12 species able to achieve canopy tree stature.

Species richness data are most often available in the literature on a per hectare basis, and include individuals of different minimum diameters (e.g., DBH $\geq 1$, $\geq 10$, and $\geq 30$ cm) (Losos & Leigh Jr. 2004). As such, we present the average per hectare number of individuals, species, genera, and families, as well as mean Fisher's alpha as a measure of diversity, for different minimum DBH categories, by calculating each metric for six non-overlapping hectares on the plot, and then presenting the mean and standard deviation. We calculated Fisher's alpha as a common measure of species diversity that is more robust to variation in sample size (Condit et al. 1996) and more directly interpretable than other indices.

**Stem density and basal area**

We calculated the number of stems and basal area from counts and DBH of all stems larger than 1 cm, for minimum diameter classes of 1, 2, 5, 10, 20, 30, and 60 cm, following Losos & Leigh (2004). Stem densities count multi-stemmed individuals as just one; estimates of basal areas include the sum of all stems with DBH $\geq$ 1 cm.

In order to place these measures of stem density and basal area in the context of other forests, we co-plotted our results with comparable data for 14 tropical plots from the CTFS network and 12 mapped plots ($\geq 1$ ha) from temperate forests. We made every effort to include all plots outside of managed forests for which appropriate published data are available that can be compared directly to our plot. The temperate plots did not include data for the smaller stem diameters, so comparisons could not be made for size classes below 5 cm diameter. Several temperate plots did not provide the size-structured data required for some comparisons. Details of plot locations, extracted data used in the graphs, and references are presented in Appendices S2 and S3.

*Aggregation*

We evaluated spatial aggregation of species on the plot by calculating Condit et al.'s (2000) standardized index of relative neighborhood density ($\Omega$), which is a sample size-independent measure of aggregation based on the number of conspecifics in given annuli around focal individuals, allowing direct comparison among species. We chose this method because, in contrast to Ripley's $K$ (which is a cumulative distribution that confounds effects at long and short distances), $\Omega$ is a probability density function and, as such, allows the isolation of particular distances for analysis (described in Condit et al. 2000). It also permits direct comparison to published data from forest plots that used identical protocols. We calculated $\Omega$ for each successive 10-m annulus around each individual (e.g., 0-10, 10-20, to 80-90 m). If an annulus crossed a plot boundary, it was excluded from calculations. The 95% confidence intervals were calculated by determining $\Omega$ at each distance interval for random selections of half the stems. This was repeated 100 times, and the limits for the 95% CI calculated as $1.96 s^2/\sqrt{n}$. Following Condit et al. (2000), this value was then divided by $\sqrt{2}$ before applying to the full dataset. We excluded nine species found at densities $<1\,\mathrm{ha}^{-1}$. In addition, *Morella californica* and *Umbellularia californica* had no individual within the 0-10-m annulus, and were excluded from Fig. 4. Thus we were able to analyze spatial patterns for 20 of the 31 woody species.

To place these results into context, we co-plotted the data with the results from six CTFS tropical forest plots, taken from the analyses published in Table 2 of Condit et al. (2000). Directly comparable published data were not available for other tropical or temperate plots.

Statistical analyses were conducted using JMP (v 7.0, SAS Inc.), Excel 2004 (v11.4, Microsoft), and R (v2.6.2, The R Foundation for Statistical Computing). Data from figures in published papers used for comparative purposes were extracted using ImageJ (v1.41o, National Institutes for Health).

# Results

*Species composition*

The plot included 8180 individuals of woody trees, shrubs, and vines (Table 1). The woody vegetation comprised 31 species from 27 genera and 18 families. Rosaceae (five spp.), Ericaceae (four spp.), Fagaceae (three spp.), and Pinaceae (three spp.) were the most species-rich families, while Fagaceae and Pinaceae were by far the most common, with 41.1% and 26.7% of all stems, respectively. Canopy-stature trees (species that could potentially reach the canopy as free-standing trees) made up 79% of the stems, vines 11%, and shrubs/small trees 10%. The five most numerous species comprised 76.0% of the stems on the plot. The five leading species in terms of basal area comprised 95.4% of the total basal area on the plot, and 62.9% of the stems.

Oaks and conifers together comprise roughly three-quarters of the woody plants on the UCSC Forest Ecology Research Plot. Conifers (primarily Douglas-fir, *P. menziesii*) comprised 29% of the individuals and 54% of the basal area of woody individuals larger than 1-cm DBH. Three species of Fagaceae (two true *Quercus* oaks and tanoak *Lithocarpus*) contributed another 41% of the stems and 21% of the basal area. Ericaceae contributed four species, including the large canopy tree *A. menziesii*, the understory shrub *Vaccinium ovatum*, and the chaparral associates *Arctostaphylos tomentosa* subsp. *crustaceae* and *A. andersonii*. Just three species (*P. menziesii*, *L. densiflorus*, and *Q. parvula* subsp. *shrevei*) comprised more than half the stems (56.3%). Seven species were non-native invaders, representing 1% of the stems on the plot.

*Diversity*

The asymptotes of the species accumulation curves suggest that the woody plant diversity for this forest was well represented by the plot; at the full extent of the plot, one new species was added for each additional 400 stems. As expected when plant species are not randomly distributed, species accumulation tended to be more rapid when quadrat sizes were smaller, but 95% CIs were overlapping for even the smallest (5×5 m) and largest (100×100 m) quadrat sizes, indicating minimal beta diversity at the scale of the plot (Fig. 2a). The slope of the species accumulation curves declined significantly with number of stems sampled; about 80% of the 31 woody species would be encountered by sampling only half the plot area.

Much of the diversity was concentrated in smaller-diameter individuals, and in woody species of smaller potential stature (shrubs, understory treelets, and woody vines). Twenty-six per cent (eight of 31) of the woody species had no individuals larger than 5 cm. Only 18 of the 31 species (58%) included individuals larger than 10-cm diameter, and only eight species (25%) had individuals larger than 30 cm (Table 1). Just 12 species could be reasonably expected to reach canopy tree stature (Table 1). Accordingly, species

**Table 1.** Number of individuals by diameter class (DBH $\geq$ 1 cm) of all woody species on the 6-ha UCSC-FERP, and total basal area (m$^2$ ha$^{-1}$). Indicated are the six-letter codes (first four from genus, two from species name), family, origin (Native or Exotic to California), and potential plant stature (C = canopy tree; U = understory tree/shrub; V = vine). Basal areas include all stems larger than 1-cm DBH for multistem plants.

| Scientific name | Minimum stem diameter (cm) in class | | | | | | | | Basal area |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 5 | 10 | 20 | 30 | 60 | Total | |
| *Pseudotsuga menziesii* (Mirb.) Franco (PSEUME; Pin.; Nat.; C) | 265 | 569 | 435 | 341 | 159 | 268 | 125 | 2162 | 22.142 |
| *Lithocarpus densiflorus* (Hook. & Arn.) Rehder (LITHDE; Fag.; Nat.; C) | 492 | 472 | 173 | 69 | 16 | 34 | 2 | 1258 | 1.585 |
| *Quercus parvula* Greene var. *shrevei* (C.H. Mull.) Nixon (QUERPA; Fag.; Nat.; C) | 279 | 323 | 283 | 221 | 57 | 27 | | 1190 | 2.776 |
| *Quercus agrifolia* Née (QUERAG; Fag.; Nat.; C) | 127 | 161 | 165 | 196 | 142 | 120 | 8 | 919 | 5.607 |
| *Arbutus menziesii* Pursh (ARBUME; Eric.; Nat.; C) | 36 | 102 | 108 | 90 | 93 | 219 | 39 | 687 | 11.204 |
| *Toxicodendron diversilobum* (Torr.&A. Gray) Greene (TOXIDI; Anacardi.; Nat.; V) | 608 | 65 | 3 | | | | | 676 | 0.022 |
| *Rhamnus californica* Eschsch. (RHAMCA; Rhamn.; Nat.; U) | 152 | 120 | 17 | 4 | | | | 293 | 0.053 |
| *Vaccinium ovatum* Pursh (VACCOV; Eric.; Nat.; U) | 167 | 85 | | 1 | | | | 253 | 0.055 |
| *Lonicera hispidula* (Lindl.) Douglas ex Torr. & A. Gray (LONIHI; Caprifoli.; Nat.; V) | 178 | 39 | | | | | | 217 | 0.009 |
| *Sequoia sempervirens* (D. Don) Endl. (SEQUSE; Taxodi. = Cupress.; Nat.; C) | 30 | 36 | 36 | 32 | 21 | 17 | 14 | 186 | 3.431 |
| *Corylus cornuta* Marshall subsp. *californica* (A.DC.) E. Murray (CORYCO; Betul.; Nat.; U) | 60 | 84 | 2 | | | | | 146 | 0.050 |
| *Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *crustacee* (Eastw.) P.V. Wells (ARCTCR; Eric.; Nat.; U) | 4 | 9 | 23 | 2 | | | | 38 | 0.033 |
| *Cotoneaster pannosus* Franch. (COTOPA; Ros.; Ex.; U) | 6 | 15 | 16 | | | | | 37 | 0.017 |
| *Pinus ponderosa* Douglas ex Lawson & C. Lawson (PINUPO; Pin.; Nat.; C) | | 7 | 5 | 1 | | 2 | 2 | 17 | 0.217 |
| *Cotoneaster franchetii* Bois (COTOFR; Ros.; Ex.; U) | 7 | 9 | | | | | | 16 | 0.003 |
| *Arctostaphylos andersonii* A. Gray (ARCTAN; Eric.; Nat.; U) | 1 | 1 | 3 | 5 | 1 | | | 11 | 0.021 |
| *Heteromeles arbutifolia* (Lindl.) M.Roem. (HETEAR; Ros.; Nat.; U) | 4 | 1 | 4 | 2 | | | | 11 | 0.017 |
| *Ilex aquifolium* L. (ILEXAQ; Aquifoli.; Ex.; U,C) | 5 | 3 | 2 | 1 | | | | 11 | 0.007 |
| *Umbellularia californica* (Hook. & Arn.) Nutt. (UMBECA; Laur.; Nat.; C) | 4 | 5 | 2 | | | | | 11 | 0.003 |
| *Baccharis pilularis* DC. (BACCPI; Aster.; Nat.; U) | 6 | 4 | | | | | | 10 | 0.001 |
| *Morella californica* (Cham. & Schltdl.) Wilbur (MORECA; Myric.; Nat.; C) | 2 | 1 | 4 | 1 | | | | 8 | 0.007 |
| *Hedera helix* L. (HEDEHE; Arali.; Ex.; V) | 3 | 3 | 1 | | | | | 7 | 0.001 |
| *Eucalyptus globulus* Labill. (EUCAGL; Myrt.; Ex.; C) | 1 | 1 | 1 | 2 | | | | 5 | 0.004 |
| *Acer macrophyllum* Pursh (ACERMA; Sapind.; Nat.; C) | | | | | | 2 | | 2 | 0.063 |
| *Salix lasiandra* Benth. var *lasiandra* (SALILA; Salic.; Nat.; U) | | | 1 | 1 | | | | 2 | 0.003 |
| *Sambucus nigra* L. subsp. *caerulea* (Raf.) Bolli (SAMBNI; Caprifoli.; Nat.; U) | | 2 | | | | | | 2 | 0.0004 |
| *Ceanothus thyrsiflorus* Eschsch. (CEANTH; Rhamn.; Nat.; U) | | | | 1 | | | | 1 | 0.004 |
| *Crataegus monogyna* Jacq. (CRATMO; Ros.; Ex.; U) | | 1 | | | | | | 1 | 0.0003 |
| *Pinus attenuata* Lemmon (PINUAT; Pin.; Nat.; C) | | | | 1 | | | | 1 | 0.005 |
| *Pyracantha angustifolia* (Franch.) C.K. Schneid. (PYRAAN; Ros.; Ex.; U) | | 1 | | | | | | 1 | 0.0001 |
| *Ribes divaricatum* Douglas (RIBESA; Grossulari.; Nat.; U) | | 1 | | | | | | 1 | 0.0001 |
| TOTAL | 2437 | 2120 | 1284 | 971 | 489 | 689 | 190 | 8180 | 47.34 |

accumulation curves were much steeper when small-diameter classes were included than when only large individuals were included (Fig. 2b). When the analysis included only the 12 species that could be expected to reach canopy tree stature, the species accumulation curves were completely overlapping for all size classes (Fig. 2c), indicating that the greater diversity in smaller size classes is primarily a function of including shrubs, treelets, and vines. All the species with larger representatives (DBH $\geq$ 30 cm) except *Acer macrophyllum* ($N = 2$) also included small individuals (DBH < 5 cm). On the other hand, four species (*Eucalyptus globulus, Ilex aquifolium, Pinus attenuata*, and *U. californica*) could reasonably be expected to grow to large diameters, but were represented only by smaller individuals (Table 1).

Species diversity declined as the minimum diameter class increased from 1 to 60 cm (Table 2),

reflecting both the diversity of small-stature species and the absence of large individuals of several tree species capable of reaching canopy stature.

### Stem density and basal area

The density of woody individuals (DBH $\geq$ 1 cm) was 1363 stems ha$^{-1}$, and the density of large trees (DBH $\geq$ 30 cm) was 146 stems ha$^{-1}$ (Fig. 3a).

Multiple stems (DBH $\geq$ 1 cm) were found on 1214 individuals (14.8%), including 23 of the 31 species (74%). If all these stems were included in the density tally (instead of only the largest stem of each individual), this would increase the total number of stems across the 6-ha plot from 8180 to 11 671, increasing the overall stem density estimate by 42% to 1945 stems ha$^{-1}$.
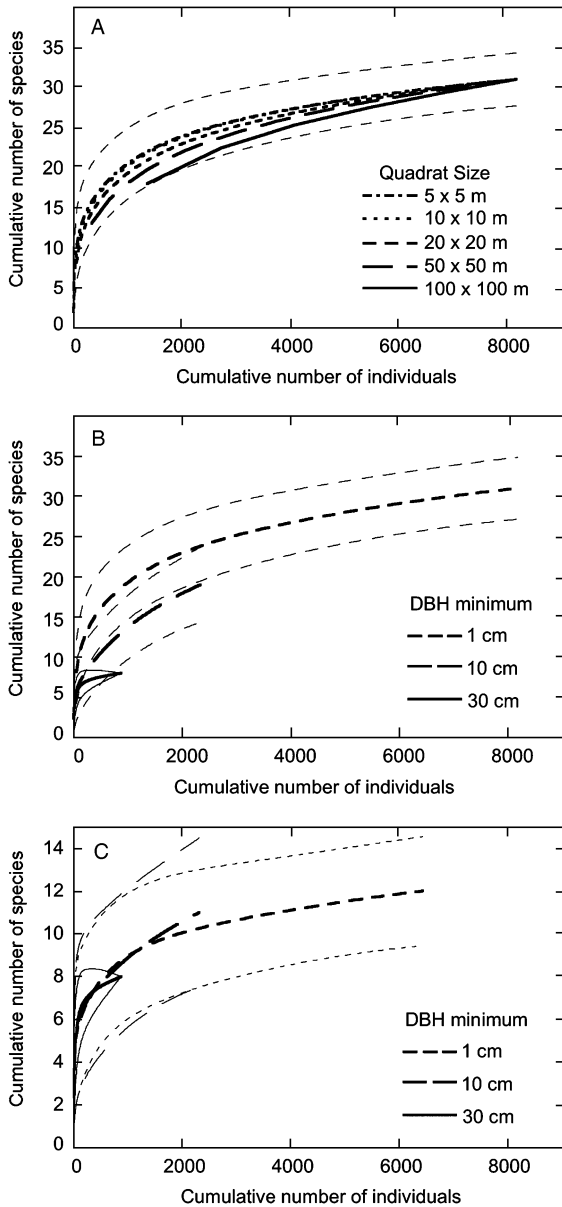
**Fig. 2.** Species accumulation (Mao-Tau) rarefaction curves on the 6-ha UCSC-FERP for (**a**) quadrats of different sizes, with all individuals DBH $\geq$ 1 cm, (**b**) individuals with different minimum diameters, all from 20×20-m grids, and (**c**) as in (**b**) but including only those 12 species able to grow to large tree stature. Fine dotted lines indicate 95% confidence intervals (for 5×5-m quadrats in **a**).

The basal area of woody plants was $47.3\,\mathrm{m}^2$ $\mathrm{ha}^{-1}$ ($42.4\,\mathrm{m}^2\,\mathrm{ha}^{-1}$ if only the largest stem of each individual were included in the calculation). Woody biomass was strongly concentrated in large individuals, with 97% of the basal area comprised of individuals with stems larger than 10-cm diameter, although those same individuals only represented 28.1% of the stems (Fig. 3b).

Stem density in the UCSC-FERP forest ($1363\,\mathrm{stems\,ha}^{-1}$ for DBH $\geq$ 1 cm) was lower than all but one of the methodologically comparable tropical CTFS plots. The one exception was the dry forest in Mudumalai ($353\,\mathrm{stems\,ha}^{-1}$), which suffers major disturbance from elephants; the range for remaining CTFS plots was 1450 to $12\,209\,\mathrm{stems\,ha}^{-1}$ (Fig. 3a). Interestingly, however, the density of larger individuals in the UCSC-FERP (i.e., $146\,\mathrm{stems\,ha}^{-1}$ for DBH $\geq$ 30 cm) was greater than in any of the tropical CTFS plots (range 46–143, mean $93.6 \pm 8.6$ $\mathrm{stems\,ha}^{-1}$; Appendix S3A). This bias towards larger stems compared to tropical forests is noteworthy in two ways. First, the total basal area of the FERP was greater than in any CTFS plot (Fig. 3b). The comparative data also support a generalization that temperate forests have a greater basal area than do tropical forests (Fig. 3b). Second, much more of the biomass of the FERP plot was contained in large trees: individuals larger than 30 cm comprised 81.4% of the UCSC-FERP basal area, whereas stems of that size represented 14.3% to 75.5% (mean 56.4%) of the stems DBH $\geq$ 1 cm in the 14 CTFS plots.

Stem density in the UCSC-FERP was comparable to that of most of the temperate plots when stems of DBH $\geq$ 5 cm or DBH $\geq$ 10 cm were included, but tended to be less than in other temperate plots for larger minimum size classes (Fig. 3a; Appendix S3B). Basal area appeared to be smaller than in comparable temperate forests for larger size classes (Fig. 3b; Appendix S3B), but comparisons for these diameter classes were only available for old-growth, mono-dominant conifer forests. For the range of temperate forest plots with minimum measured DBH $\leq$ 10 cm, basal area on the FERP was comparable to other temperate forests.

*Aggregation*

Of the 20 species that were more abundant than one per hectare, 15 were aggregated, and five were more regular than random. Rare species were more strongly aggregated, and the degree of aggregation decreased with increasing abundance on the plot (Fig. 4, Appendix S4). Species with densities greater than about $115\,\mathrm{ha}^{-1}$ were significantly more regular than random. Maps of each of the species are presented in Appendix S5.

We were surprised to find a substantial number of the species on the FERP (25%) were more regular than random. Of the six tropical CTFS plots so analyzed (Condit et al. 2000), none had more than 4% of its species that were not significantly *aggregated* at the same spatial scale. Aggregation decreased with stem

**Table 2.** Diversity and abundance measures for woody plants on the 6-ha UCSC-FERP, tallied for individuals larger than six minimum diameters. Shown are the number of stems (N), families (F), genera (G), and species (S), and Fisher's alpha ($\alpha$) (mean per ha $\pm$ sd),across the six non-overlapping hectares. Also shown are the values for the entire 6-ha plot.

| DBH (cm) | Mean per hectare | | | | | 6-ha plot | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | N | F | G | S | $\alpha$ | N | F | G | S | $\alpha$ |
| $\geq 1$ | 1364.5 $\pm$ 278.4 | 11.8 $\pm$ 2.0 | 16.2 $\pm$ 2.8 | 18.0 $\pm$ 2.7 | 3.0 $\pm$ 0.5 | 8180 | 18 | 27 | 31 | 4.08 |
| $\geq 5$ | 604.5 $\pm$ 41.3 | 7.8 $\pm$ 1.9 | 10.3 $\pm$ 1.9 | 11.5 $\pm$ 2.1 | 2.0 $\pm$ 0.4 | 3623 | 15 | 21 | 24 | 3.45 |
| $\geq 10$ | 390.3 $\pm$ 24.8 | 5.3 $\pm$ 1.8 | 7.2 $\pm$ 1.9 | 8.3 $\pm$ 2.1 | 1.5 $\pm$ 0.5 | 2339 | 11 | 16 | 19 | 2.83 |
| $\geq 20$ | 228.5 $\pm$ 27.9 | 3.7 $\pm$ 0.8 | 5.2 $\pm$ 0.4 | 6.2 $\pm$ 0.4 | 1.2 $\pm$ 0.3 | 1368 | 5 | 8 | 9 | 1.29 |
| $\geq 30$ | 147.0 $\pm$ 24.2 | 3.5 $\pm$ 0.8 | 4.8 $\pm$ 0.8 | 5.7 $\pm$ 1.0 | 1.2 $\pm$ 0.3 | 879 | 5 | 7 | 8 | 1.21 |
| $\geq 60$ | 31.7 $\pm$ 12.6 | 2.8 $\pm$ 0.4 | 3.5 $\pm$ 1.2 | 3.5 $\pm$ 1.2 | 0.7 $\pm$ 0.6 | 190 | 4 | 6 | 6 | 1.17 |

density (Fig. 4, Appendix S4), a pattern that was also found in analysis of the CTFS plots. For comparison with the tropical plots, we show the median aggregation indices against the minimum diameter size classes (Fig. 4), as presented in Condit et al. (2000). Of the six species with more than 100 stems ha$^{-1}$ on the FERP, five were significantly more regular than random (the woody vine poison oak, *Toxicodendron diversilobum,* was the exception). In contrast, the tropical trees were not significantly more regular than random at similar densities. Few tree species in the tropical forest plots, however, reach densities greater than 100 stems ha$^{-1}$ (2% of the 1768 species), whereas this is common on the FERP and in other temperate forests.
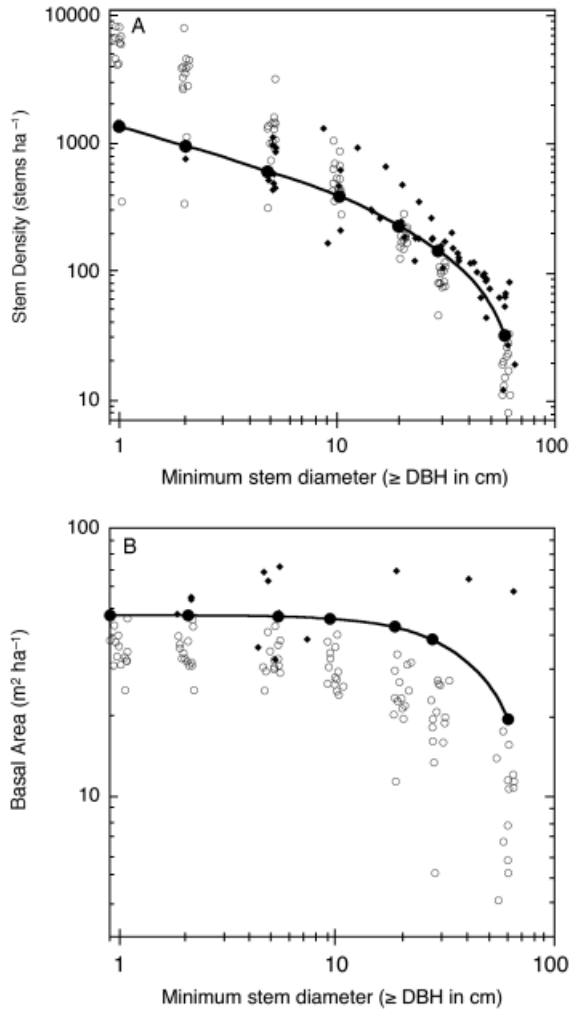
## Discussion

### Species composition

California includes two major types of broadleaf–sclerophyll vegetation: chaparral shrublands and forest dominated by sclerophyllous evergreens. Broadleaf–sclerophyll forest is distributed in discontinuous patches throughout much of the state, blending into chaparral in drier sites, and transitioning into an understory layer of *Sequoia* (coast redwood) or *Pseudotsuga* (Douglas-fir) forest where these tall conifers dominate (Cooper 1922). We see each of these three transitions within the 6-ha UCSC-FERP.

The forest is evergreen, with only three winterdeciduous species (*T. diversilobum*, *Corylus cornuta*, and *A. macrophyllum*). Of the deciduous species on the plot, only *A. macrophyllum* (N = 2 individuals) is an overstory species (although *Toxicodendron* can reach the canopy as a climber), so seasonal variation in canopy density should be subtle.

Rosaceae was the most species-rich family, with five species, but four of these were invasive nonnatives (*Pyracantha angustifolia*, *Crataegus monogyna*,
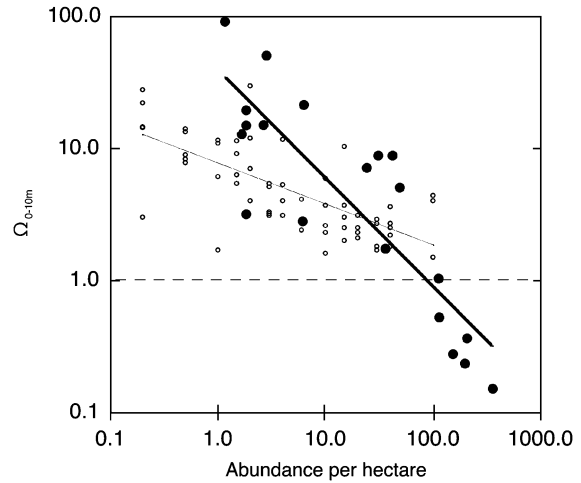
*Cotoneaster franchetii*, and *Cotoneaster pannosus*). Three additional non-native species, *I. aquifolium*, *E. globulus*, and the climber *Hedera helix*, were found on the plot. The *Eucalyptus* were progeny spreading from a row of large old trees planted in a line south of the FERP, separating campus lands from the Cave Gulch community, but the other species are found scattered throughout the plot and presumably arrived through animal dispersal. There is one reproductive *Ilex* (177 mm diameter, subcanopy height) on the plot that may be the source of the other small individuals. Although they are capable of achieving canopy stature, no individual of either species has yet reached such height, perhaps reflecting recent invasion. Together, the seven non-native species comprised 1% of the mapped individuals and 0.07% of the basal area. One valuable application of the mapped plot will be to document the spatial and numerical dynamics of these invaders.

The overall abundance of woody vines (poisonoak [*T. diversilobum*], honeysuckle, [*Lonicera hispidula*], and the invasive English Ivy [*H. helix*]) is strongly underestimated, because the majority of individuals of each of these three species are too small to be included in the census (DBH is often between 0.5 and 1.0 cm). Even so, the two natives (*Toxicodendron* and *Lonicera*) together represent 10.9% of the mapped stems on the plot (plus seven stems of *Hedera*). Woody vines (lianas) are important components of both diversity (to 25% of woody species) and stem density in tropical forests, with their diversity and abundance declining along a latitudinal gradient, down to about 10% of woody species in temperate forests (Schnitzer & Bongers 2002). The relative abundance of lianas has increased greatly in recent decades in non-fragmented tropical forests (Phillips et al. 2002) and at the edges of fragmented temperate zone forests (Londre & Schnitzer 2006). The reasons for such increases probably include increased light availability associated with disturbances, increased atmospheric $CO_2$, and increased temperature (Putz 1984; Londre & Schnitzer 2006;

**Fig. 4.** Aggregation of individuals of all size classes on the UCSC-FERP (DBH $\geq$ 1 cm) decreases with species density (filled circles and thick line, $\log(\Omega_{0-10}) = 1.5939 - 0.81767 \log(\text{abundance ha}^{-1})$, $R^2_{adj} = 0.72$, $F_{1,18} = 49.5$, $P \leq 0.0001$). Confidence intervals (95%) are smaller than the size of the symbol. Points above the dashed line are more aggregated than random, and those below are more regular than random. Data from six tropical plots (Table 2 in Condit et al. 2000) are shown as open circles for comparison; the regression for those combined data is shown as a fine line, where $(\log(\Omega_{0-10}) = 0.89 - 0.310 \log(\text{abundance ha}^{-1})$, $R^2_{adj} = 0.51$, $F_{1,80} = 84.5$, $P \leq 0.0001$).

**Fig. 3.** (**a**) Stem density and (**b**) basal area of the UCSC FERP (filled circles) compared to 14 CTFS tropical plots (open circles) and 12 temperate plots (closed diamonds), for different minimum stem diameters. Minimum diameters are 1, 2, 5, 10, 20, 30, and 60 cm for UCSC and CTFS plots, and are jiggered to aid viewing. The line through the UCSC plot data is a smooth curve. Minimum diameters vary for temperate plots, and size-structured data are not available for most temperate sites. Data and sources for each plot are given in Appendix S3. Two points are not shown because they strongly compress the scales, obscuring other data: in (**a**), stem density at DBH $\geq$ 60 cm for the tropical Nanjenshan plot = 1 stem ha$^{-1}$, and in (**b**), basal area DBH $\geq$ 10 cm for the temperate plot Sequoia = 329.5 m$^2$ ha$^{-1}$.

Mohan et al. 2006; Zotz et al. 2006; Isnard & Silk 2009). Given the negative impacts that woody vines can have on tree growth and regeneration after disturbances (Schnitzer et al. 2000; Schnitzer & Bongers 2002), and the possibility for their increased dominance over time, investigating the ecological determinants of their distribution, their impacts on other woody spe-

cies, and monitoring the population dynamics of lianas using standardized protocols (Gerwing et al. 2006) will be priorities for future research on the UCSC-FERP.

The UCSC-FERP forest showed stronger species dominance than most tropical forests, but fell within the range found in other temperate forests. The five leading species on the FERP comprised 95.4% of the total basal area (Table 1), far more than measured dominance in any of 16 CTFS tropical plots (range 15-78%, median 35.4% for % basal area) (Ashton & CTFS Working Group 2004). Those same five species represented 62.9% of all the stems, similar to that of the dry forest Mudumalai and monodominant and mixed forests at Ituri (60-65%), but far greater than the remaining tropical plots (range 3.3-24.5%, median 14.5%) (Ashton & CTFS Working Group 2004). The five most numerous species on the FERP comprised 76% of all stems, greater than all the CTFS tropical plots except the dry forest at Mudumalai, with 76.7% (range for all plots, 9.2-76.7, median 32.3).

Because temperate forest inventories generally have not included small-size classes, dominance on the UCSC-FERP could be compared to other temperate forests only for stems larger than 5-cm DBH. On the UCSC-FERP, stems larger than 5 cm represent

99.1% of the basal area (dbh $\geq$ 1 cm), but only 44.7% of all the stems. For stems in this size class, the five leading species (by basal area) represented 95.9% of the total basal area (dbh $\geq$ 5 cm) on the UCSC-FERP, within the range of dominance in the eight large temperate plots (64.0–97.9%; median 87.3%). The same five species comprised 88.6% of the stems (dbh $\geq$ 5 cm) on the UCSC-FERP. Dominance of the five leading species was much more variable in other temperate plots for which data were available, ranging from 33.2% to 98.6%, with a median of 76.0% (Tanouchi & Yamamoto 1995; Chen & Bradshaw 1999; Miura et al. 2001; Harcombe et al. 2002).

Half of the woody species and 10% of all stems on the plot mature as understory shrubs and treelets (Table 1). This more closely resembles the more even distribution of adult statures found in tropical forests (which have roughly equal numbers of canopy and subcanopy species) than the deciduous forests of the temperate east coast of North America, where only 11% of species mature in the subcanopy (King et al. 2006). In addition, the latitudinal gradient in woody species is primarily a product of the increasing diversity of subcanopy and understory woody species in tropical forests, rather than greater diversity of canopy-stature species (King et al. 2006). Whether the greater abundance of understory species in the UCSC-FERP forest compared to other deciduous temperate forests is a function of the Mediterranean climate deserves further inquiry; greater leaf longevity in the predominantly evergreen forest and greater understory light availability during the moist season may both favor the success of understory perennial plants in closed-canopy Mediterranean forests.

Understory shrubs have been shown to negatively affect recruitment of *P. radiata* seedlings, and canopy cover decreases understory shrub density in Mediterranean climate forests near to the UCSC-FERP (O'Brien et al. 2007). Temporal monitoring and experimental approaches are needed to evaluate the potential roles of competition, nurse plant effects, and shared enemies on the dynamic interactions between overstory- and understory-stature species in the mixed evergreen forest of the UCSC-FERP.

### Diversity

Species richness on the UCSC-FERP (Fisher's $\alpha$ = 1.6 for DBH $\geq$ 10 cm) was comparable to other temperate forest plots, and much lower than in tropical forests. Fisher's $\alpha$ ranged from 0.8 to 9.3 (median 4.4) for trees larger than 10-cm DBH in 29 temperate forest plots in Japan (0.12 to 6.5 ha, median 0.6 ha) (Takyu et al. 2005), and $\alpha$ = 0.9 for

the 12-ha Wind River plot in Pacific Northwest hemlock–Douglas-fir forest (North et al. 2004). For the 14 tropical CTFS plots, Fisher's $\alpha$ ranged from 5.3 to 153, with most above 20 (Appendix S2) (Losos & Leigh Jr. 2004). In 47 1-ha plots in tropical forests in Panama, Fisher's $\alpha$ ranged from 16 to 81 (Pyke et al. 2004). Comparable diversity data for stems DBH $\geq$ 1 cm are scarce from any forest, but species diversity for all stems with this minimum diameter on the UCSC-FERP (Fisher's $\alpha$ = 3.0) was much lower that that in the tropical CTFS plots (Appendix S2). Using Fisher's $\alpha$ (or other such diversity indices) for comparison of diversity with plots much smaller than 1 ha must be done with great caution, both because the index is sensitive to sample size for sample sizes < 500 stems (Condit et al. 1996) and because very small plots necessarily encompass much less potential habitat variation than do larger plots. It is clear, however, that the species richness from this Mediterranean forest plot is similar to that of a broad range of broadleaf, conifer, and mixed temperate forests from around the world, and much lower than that found in most tropical forests.

Mapped species on the UCSC-FERP included 31 of the 57 woody species (54%) ever recorded from the UCSC campus (Haff et al. 2008). Of the remaining 26 species, seven are generally restricted to riparian or wet habitat, four to grasslands or disturbed areas, and two to chaparral. Of the 13 remaining "missing" species that could be expected in mixed evergreen forest, nine are listed as uncommon, rare, or extirpated on the campus and one is a recent non-native invader. At least four of those 13 species are present on the plot, but did not reach minimum size requirements to be included in the mapping (G.S. Gilbert, unpubl. data). Taken together, the FERP includes 35 of the 38 woody species (92%) expected in the mixed evergreen forest; even if we consider rare and extirpated species previously recorded from campus, we still captured 80% of the possible 44 woody species. Mixed evergreen forest covers approximately 20% of the 8.1-km$^2$ campus ($\sim$162 ha), so we captured most of the local woody plant diversity in a sample of just 3.7% of the available habitat type.

By adopting a 1-cm minimum DBH rather than the 5-cm minimum often used in temperate plots, we included a full eight additional woody species that would otherwise have been excluded from our measure of species richness, an increase of 35%. As spatially explicit forest inventories attain smaller minimum sizes and larger plot scales, our ability to draw inferences increases for a number of important

issues, including the role of smaller stature species in overall community structure and dynamics, accurate estimates of community diversity, and the dynamics of species of conservation concern, such as rare and invasive species.

### Stem density and basal area

Temperate forests, including the UCSC-FERP, tend to have greater basal area than do tropical forests, at least in part because tropical forests have higher densities of small-diameter stems but lower densities of large-diameter stems (Fig. 3 and Hartshorn 1978; Enquist & Niklas 2001). These patterns might reflect a longer tenure of canopy trees in the dark understory of tropical forests compared to lighter understories of temperate forests (Clark & Clark 1992; Condit et al. 1993; Hunter & Barbour 2001; Metcalf et al. 2009).

Stem density on the UCSC-FERP was similar to other temperate forests for available diameter classes (Fig. 3a), and basal area was similar for studies with smaller minimum stem diameters (Fig. 3b). The estimates of basal area for larger minimum diameters appear to show that the basal area of the FERP forest is lower than that of other temperate forests. However, each of the estimates for larger diameter classes come from old-growth Douglas-fir (P. menziesii) or Coastal Redwood (S. sempervirens) stands, which would be expected to show extremely high values for basal area.

Many published estimates of stem density are available from transects, point-quadrat samples, and small-scale temperate forest plots, including some from Mediterranean forests. It is beyond the scope of this paper to summarize the entire literature on temperate forests. It is also important to note that density data from sample plots smaller than about 1 ha (depending on basal area) in most temperate forests are unlikely to capture enough stems in larger size classes to fill the stem size distribution (Rubin et al. 2006), which is critical in the evaluation of relationships between stem density and diameter (e.g., Fig. 3). Cross-site comparisons of stem density also depend critically on the minimum stem size included. For these reasons, we restrict our comparisons of stem density to plots larger than 1 ha (Fig. 3). As additional estimates of stand structure are generated from large-scale plots with small minimum diameters, it will be interesting to see if the patterns seen in Fig. 3 hold up, and whether UCSC-FERP is typical of temperate forests.

Two native species that are capable of reaching canopy height were present only in smaller size classes – P. attenuata and U. californica – and one

(A. macrophylla) only as large trees. Umbellularia and Acer are common in all size classes elsewhere on campus in moist ravines, and P. attenuata is common on drier ridges – it may be that environmental conditions on the FERP are not favorable to their growth in that area. Similarly, conditions may not be appropriate for survival and growth of Acer seedlings. Ecological limitations on growth and reproduction of the range of forest species are important areas of future inquiry.

### Aggregation

Trees on the UCSC-FERP tended to be less strongly aggregated than in tropical plots analyzed using the same metric; notably, the most common species were usually regularly distributed. If future comparisons of temperate and tropical forest spatial structure substantiate this pattern, it would suggest that the combination of efficient dispersal and density-dependent mortality patterns more strongly reduces aggregation in temperate forests than in tropical forests. If this were true, it would be a reversal of the assumption that Janzen–Connell mechanisms are of greater importance in tropical forests (Packer & Clay 2000; Gilbert 2002; Hille Ris Lambers et al. 2002).

We searched the temperate forest literature for evidence for or against the generality of this result. Single-species analyses of aggregation in temperate forests using a broad range of metrics, plot sizes, and size classes show that most woody species are significantly aggregated (Kenkel 1988; Busing 1998; Aldrich et al. 2003; Davis et al. 2005; Taylor et al. 2006). For example, Mediterranean Aleppo pines (P. halapensis) in monodominant forests in Spain (Moya et al. 2009) are significantly clustered in the absence of thinning practices. Two studies provided data more directly comparable to our result of variation in aggregation across density (Busing 1998; Aldrich et al. 2003). Busing (1998) examined patterns of aggregation for nine tree species in seven stands in the Great Smoky Mountains, USA (but with minimum size of 2 cm, rather than our 1 cm). Although juveniles were nearly always significantly aggregated, adults tended to be more regular. A total of 41 species/site analyses were presented; of the 21 more common species (densities $\geq$ 115 stems ha$^{-1}$), 71% were randomly ($n = 10$) or regularly ($n = 5$) distributed as adults. For the remaining 20 comparisons with less common species ($\leq$ 77 stems ha$^{-1}$), 35% were randomly ($n = 6$) or regularly ($n = 1$) distributed. In a broadleaf forest in Indiana, USA, Aldrich et al. (2003) found that, in

two adjacent plots, 39% and 53% of 18 tree species were randomly distributed and the rest were aggregated (dbh $\geq$ 10 cm; species with density 3 ha$^{-1}$ were not analyzed). In this case, however, the most common species were aggregated (Aldrich et al. 2003). Because of methodological and analytical differences, it is not possible to make direct quantitative comparisons of the degree of aggregation between these temperate plots and the UCSC-FERP or tropical plots, but available data suggest that tree species in temperate forests may be overall less aggregated than in tropical forests.

In both temperate and tropical forests, adults are often less aggregated than juveniles as a result of several different processes, often in combination, including gap-phase regeneration, dispersal limitation, microhabitat specificity, density-dependent impacts of natural enemies, and competitive and facilitative interactions (Gilbert et al. 1994; Harms et al. 2000; Harms et al. 2001; Pons & Pausas 2006; Taylor et al. 2006; Purves et al. 2007). A recent review suggests that spatial recruitment patterns in Mediterranean plant communities are much more strongly influenced by microhabitat specificity than by seed limitation (Gómez-Aparicio 2008). Ongoing studies on biotic and abiotic influences of species distribution, growth, and survival of woody species on the UCSC-FERP are designed to build on the pattern-based analyses presented here to understand more of the processes that shape the forest structure.

*Summary*

The University of California Santa Cruz – Forest Ecology Research Plot is the first large mapped forest plot in a mixed species Mediterranean climate forest, and will serve as the foundation for many studies on temporal dynamics and spatial process in forest ecology. It is part of a growing network of large mapped forest plots with high resolution that allow more specific quantitative comparisons of the structure and dynamics of forests from different climatic regions around the world. Our initial comparative analyses of spatial and structural snapshot data from more than 14 tropical and 12 temperate forests point to several patterns that merit additional research to verify the generality of the patterns and elucidate the underlying ecological processes. First, the UCSC-FERP shared with other temperate forests several consistent differences from tropical forests: temperate forests had greater basal area, lower overall stem density but more large-diameter stems, lower species richness, and greater species dominance than found in most tropical forests. Second, woody species tended to be aggregated in both temperate and tropical forests, with common species often less clumped than rare species. Trees in temperate forests may be more likely to be randomly or regularly distributed than in tropical forests. Finally, understory-stature woody species on the UCSC-FERP were much more abundant than in other temperate forests, and instead were more similar in importance to understory species in tropical forests. Whether this is a consistent difference between Mediterranean forests and other temperate forests remains to be tested.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Weather patterns for Santa Cruz, California (HCND station 047916). Shown are monthly averages (1948–2007) for minimum, average, and maximum daily temperatures, and total precipitation. Data are from the NOAA National Weather Service Cooperative Observer Network Program, available from the Western Regional Climate Center (http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca7916). Precipitation is highly seasonal, with 96% of the average yearly total of 776.3 mm falling between October and April.

**Appendix S2.** Location (country, latitude, meters above sea level), annual precipitation (mm),

number of months with $< 100\,\text{mm}$ rain, number of species per hectare (S), and Fisher's alpha ($\alpha$) by minimum stem diameter in 14 published tropical CTFS plots. Data are presented for comparative purposes in the text.

**Appendix S3.** Stem density (N) and basal area ($\text{m}^2$) per hectare from (A) 14 Center for Tropical Forest Science mapped forest plots and (B) published temperate forest plots. (C) Location, climate, and forest type for each of the temperate plots. These data are used in Figure 3.

**Appendix S4.** Indices of aggregation for all individuals on the UCSC Forest Ecology Research Plot, for an annulus from 0 to 10 m around each stem. *Umbellularia californica* and *Morella californica* had no individuals within this distance, and

so were excluded. These data are presented in Figure 4. $\Omega_{0-10\,\text{m}}$ and the 95% confidence interval were calculated as described in the text[1].

**Appendix S5.** Maps of the 31 woody species found on the UCSC Forest Ecology Research Plot. Shown are all individuals with $\text{DBH} \geq 10\,\text{mm}$. Symbol size is proportional to tree diameter. On the fourth page of graphs, the distribution of all species combined is shown for individuals with $\text{DBH} \geq 10$ mm, $\text{DBH} \geq 300\,\text{mm}$, and $\text{DBH} \geq 600\,\text{mm}$. The contour of the plot is shown with exaggerated scale for meters above sea level.