

# Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California

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**Abstract.** Community assembly processes are thought to shape the mean, spread, and spacing of functional trait values within communities. Two broad categories of assembly processes have been proposed: first, a habitat filter that restricts the range of viable strategies and second, a partitioning of microsites and/or resources that leads to a limit to the similarity of coexisting species. The strength of both processes may be dependent on conditions at a particular site and may change along an abiotic gradient.

We sampled environmental variables and plant communities in 44 plots across the varied topography of a coastal California landscape. We characterized 14 leaf, stem, and root traits for 54 woody plant species, including detailed intraspecific data for two traits with the goal of understanding the connection between traits and assembly processes in a variety of environmental conditions.

We examined the within-community mean, range, variance, kurtosis, and other measures of spacing of trait values. In this landscape, there was a topographically mediated gradient in water availability. Across this gradient we observed strong shifts in both the plot-level mean trait values and the variation in trait values within communities. Trends in trait means with the environment were due largely to species turnover, with intraspecific shifts playing a smaller role. Traits associated with a vertical partitioning of light showed a greater range and variance on the wet soils, while nitrogen per area, which is associated with water use efficiency, showed a greater spread on the dry soils.

We found strong nonrandom patterns in the trait distributions consistent with expectations based on trait-mediated community assembly. There was a significant reduction in the range of six out of 11 leaf and stem functional trait values relative to a null model. For specific leaf area (SLA) we found a significant even spacing of trait values relative to the null model. For seed size we found a more platykurtic distribution than expected. These results suggest that both a habitat filter and a limit to the similarity of coexisting species can simultaneously shape the distribution of traits and the assembly of local plant communities.

*Key words:* community assembly; environmental gradient; environment–species–trait relationship; habitat filtering; Jasper Ridge Biological Preserve, California, USA; limiting similarity; plant functional traits.

## INTRODUCTION

The fundamental connection between environmental conditions and plant characteristics was recognized very early in the development of plant ecology (Schimper 1898, Cowles 1899). Schimper's observation that different types of plants are successful under different environmental conditions is undoubtedly true, and yet more than a century later the ecological and physiological processes that drive these patterns are still areas of active research (Shipley et al. 2006, Westoby and Wright 2006), especially as a species' trait values have implications for both species interactions and ecosystem

processes (Hooper et al. 2005, Suding et al. 2005, McGill et al. 2006, Clark 2007).

Recent work synthesizing the role of traits in ecological interactions has identified a number of important strategy dimensions and their implications (Westoby et al. 2002). Leaf morphological and physiological traits show repeatable trends with environmental conditions on both global (Wright et al. 2004) and landscape (Cavender-Bares et al. 2004) scales. One outstanding problem identified in recent work is that a large portion of global trait diversity—for example, 36% and 38% of the interspecific variation in specific leaf area (SLA) and leaf nitrogen per mass ( $N_{\text{mass}}$ ), respectively—is found at the local scale within communities (Wright et al. 2004). This within-site trait diversity is relevant for understanding within-site species diversity (Mittelbach et al. 2001), and is also potentially important in its effect on ecosystem processes (Hooper et al. 2005). Patterns and processes underlying the dispersion of trait values

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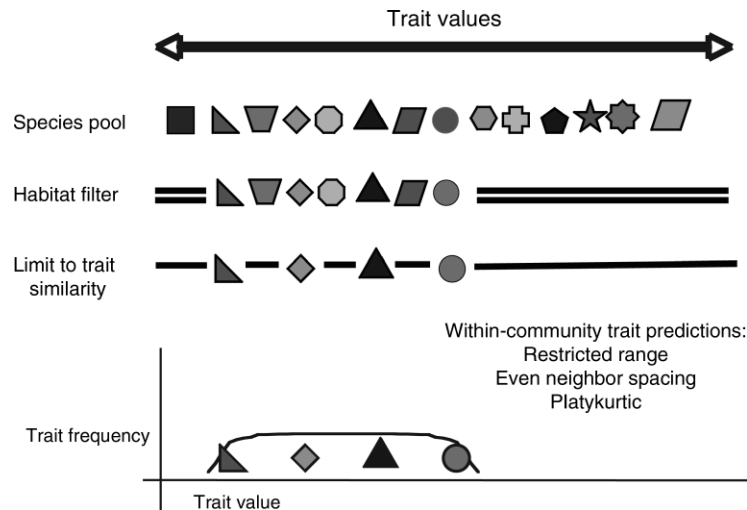


FIG. 1. A hypothesis for assembly effects on within-community trait distribution (following Diaz et al. [1998] and Weiher et al. [1998]). The strength of the habitat filter and limiting similarity is expected to depend on the identity of the trait in combination with the particular abiotic conditions at a site. Note that habitat filtering is hypothesized to affect the range of trait values; limiting similarity will affect the spacing and lead to a platykurtic (that is, flat-topped) distribution.

within communities are highly important but currently poorly understood (see Box 3 in McGill et al. [2006]).

Global trends in functional characteristics are congruent with another important concept in ecology—the limited nature of species distributions with respect to environmental gradients (Whittaker 1956). Community assembly theory has proposed a mechanism to explain these distributions (Diamond 1975): at a given site a series of nested processes allow some types of species and prohibit other types from successfully coexisting. These processes, a result of the multivariate relationships between each species' traits (including intraspecific variability), abiotic conditions, and species–species interactions, can be coarsely divided into two categories based on their effect on within-site trait distributions (see Fig. 1).

First, assembly processes can restrict the range of viable trait values at a given site; these processes have been described as a “filter” (van der Valk 1981, Keddy 1992, Weiher and Keddy 1995, 1999, Diaz et al. 1998, Weiher et al. 1998, Cornwell et al. 2006). For example, in a site that experiences a hard frost, species that cannot tolerate freezing will be excluded, resulting in a reduction in the range of a trait—freezing tolerance—at that site (Davis et al. 1999). There can also be a biotic component to a filter. For example, the reduction in soil water potentials due to transpiration by plants can create very negative soil water potentials that then lead to exclusion of other species that cannot both avoid catastrophic embolism and achieve a positive carbon balance in those conditions. This produces a reduction in the range of associated species traits (Pockman and Sperry 2000).

Second, another collection of processes can influence the spacing of trait values within that restricted range.

Classical models of competition predict a limit to the similarity of coexisting species (MacArthur and Levins 1967, Pacala and Tilman 1994). Evidence for this process has been presented from animal communities (Juliano and Lawton 1990, Wiens 1991). With respect to plant communities, species can coexist for extended periods of time if they have close-to-equal performance in the same environment (Hubbell 2001), if they regenerate in different microsites (Grubb 1977), and/or if they partition resources as adults (Chesson 2000). Examples of adult resource partitioning in plant systems include different rooting depths, uptake of different nitrogen compounds, light capture strategies, pollination traits or seasonal patterns of water use (Parrish and Bazzaz 1976, Davis and Mooney 1986, Stubbs and Wilson 2004, Grime 2006). To the extent that species' traits reflect regeneration microsite partitioning (Poorter 2007) and/or adult resource partitioning, we would then expect a non-random, even spacing of trait values within communities. Note that while a habitat filter restricts the range of trait values and a limit to similarity is thought to affect spacing (Fig. 1), both processes will affect the variance of trait values among species within the community. Matching these assembly processes to their effect on different measures of the within-community trait distribution is an important goal of this work.

Underlying the trait–environment relationship is the relative role of species turnover and intraspecific variation in determining the shift in trait values across sites along a gradient. Comparative efforts are usually focused on comparing species means (Wright et al. 2001, Cavender-Bares et al. 2004) or examining intraspecific variation due to plastic and/or heritable differentiation (Maherali et al. 2002). Here we seek to analyze the

effects of both intraspecific variation in functional traits and species turnover in the same framework.

The coastal California landscape is notable for its diversity of vegetation types with chaparral, oak woodland, and broadleaf evergreen forest all found in close proximity (Bakker 1984, Barbour and Billings 2000), allowing us to explore the multivariate relationship between species trait values, assembly processes, and abiotic gradients with a large degree of functional variation present across the landscape. Furthermore, unlike related efforts that focused on evolutionary patterns within a closely related group of species (e.g., Veech et al. 2000, Cavender-Bares et al. 2004), we examine the distribution of traits for all woody species in different communities.

Specifically, we ask the following questions: (1) Is there evidence in trait distributions for a restricted range (habitat filtering) and/or even spacing (a limit to similarity) of trait values as predicted by community assembly theory? (2) What environmental drivers are associated with trait variation in a coastal California landscape? (3) Does the relative importance of assembly processes with respect to different traits change across an ecological gradient? (4) To what extent do species turnover and intraspecific variability contribute to trends in the community mean trait values?

#### METHODS

##### *Study site*

Jasper Ridge Biological Preserve comprises a 481-ha area (roughly  $4 \times 2$  km) in the eastern foothills of the Santa Cruz Mountains, California, USA. The climate is mediterranean type with an average precipitation of 652 mm/yr (mean from 1975–2004); the vast majority of rain falls between November and April. The primary topographic feature in the preserve is a flat-topped ridge that runs northwest–southeast, with exposures to the northeast and southwest cut by seasonally dry, first-order streams. There is striking mosaic of vegetation in the physiognomy of the woody vegetation at Jasper Ridge (see Plate 1). Species characteristic of chaparral are abundant on higher ground and on southern exposures, while in lower areas and on north-facing slopes, broadleaf evergreen forest is common (see Bakker 1984).

Like the vast majority of California, Jasper Ridge has a long history of human land use by Native Americans (in this case the Muwekma-Ohlone) and later European missionaries and settlers. Most of the commercially useful lumber (especially that of *Sequoia sempervirens*) was cut by 1880. San Francisquito Creek, which bisects the preserve, was dammed in 1891, creating a delta where the creek entered the new Searsville Lake; willow woodlands rapidly developed on the expanding delta sediments. Since the late 1800s, the woody plant communities are thought to be relatively undisturbed, and the date of the last wildfire is unknown.

At Jasper Ridge the pattern of vegetation exists in a mosaic rather than a linear gradient. Possible drivers of the dramatic shift in physiognomy include the slow seep of water to lower topographic positions that ameliorates the long summer drought (Bakker 1984), north vs. south facing slopes mediating the amount of incoming radiation (Ackerly et al. 2002), and the effect of soil fertility especially where outcrops of ultramafic rock have influenced soil development (Kruckeberg 1984). One feature of the first two factors, topographic position and aspect, is that they could directly or indirectly influence the amount of water available to plants. Soils in the higher topographic positions dry out quickly after rain events, which can lead to very dry soils through the summer months (Bakker 1984), and south-facing slopes experience more incoming solar radiation through the year; increased solar irradiance could increase leaf and soil temperatures and therefore both evaporation and transpiration could dry the soil sooner (Ackerly et al. 2002). On the other hand, the greater leaf area development on north-facing slopes may lead to greater ecosystem transpiration, which could cause drier soils, as observed in southern California (e.g., Poole and Miller 1981). Cornwell et al. (2006) showed that for three traits (and their multivariate combination) local communities show evidence of habitat filtering at this site. Here, we expand on that work, consider a broader array of traits, and address the relationship between assembly processes and underlying abiotic gradients and the potential role of limiting similarity.

##### *Plot sampling and environmental characterization*

Forty-four  $20 \times 20$  m plots were located using a geographic information system (Arc-GIS; ESRI, Redlands, California, USA) within the woody plant communities at Jasper Ridge. Plots were located randomly within the woody plant dominated areas, with one caveat: to ensure adequate sampling of all of the common vegetation types, we required a minimum of five plots to be located in each of five woody vegetation types—chaparral, oak woodland, willow woodland, broadleaf evergreen forest, and open shrub land—as determined by a previous vegetation map drawn from aerial photographs. Locations that were disturbed by recent human activity (e.g., road building) were also excluded from sampling. During fieldwork from June–August of 2002 and 2003, within each plot all woody species were identified and recorded. The relative abundance of each species was estimated visually using 6% cover classes. Exotic species, which are a minor component of the woody flora at Jasper Ridge (<1% of sampled individuals), were recorded, but because most were represented by non-reproductive seedlings, the statistical power for examining trait-based assembly of invaders was too low, and they excluded from the subsequent analysis.

Arc-GIS was used to characterize the plots with respect to elevation and potential solar insolation

(Hendrick et al. 1993). In a subset of plots that could be sampled within a five-day period, we measured gravimetric soil water content of the 0–10 cm soil layer. We took three cores located haphazardly within each plot on 23–28 April 2004; the previous measurable rain was 5.3 mm on 20 April. This time point is at the end of the wet season, when warm temperatures and sufficient soil water allow for plant growth. Using the same methods, we also measured soil water 3–6 October of 2005 at the end of the four month dry season. No rain fell during either sampling period, and subsequent tests showed soil moisture was not related to the date of sampling within each sampling period.

Because woody vegetation is much more physiologically active at the end of the wet season relative to the end of the dry season, we also sampled for available soil N during the April sampling period. On the day of sampling, soil from each plot was extracted with 2.0 mol/L potassium chloride (KCl). Extracts were then analyzed for  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  on a AlpKem Auto-analyzer (OI Analytical, Wilsonville, Oregon, USA). The mean of the three separate within-plot measurements for gravimetric soil water content, available  $\text{NH}_4\text{-N}$ , and available  $\text{NO}_3\text{-N}$  for each time point were then used for subsequent statistical analysis.

#### Trait selection

Previous work on plant physiological and morphological traits has identified suites of functional variation that strongly influence plant growth and survival (Westoby et al. 2002). Specific leaf area (SLA, leaf area per mass), nitrogen per unit leaf mass ( $N_{\text{mass}}$ ), leaf life span, and photosynthetic rate per unit mass all covary strongly (Reich et al. 1997, Wright et al. 2004). This “economic” axis of variation represents a range from species that allocate resources to obtain a fast photosynthetic return on carbon investment vs. those that retain nutrients for longer periods and necessarily achieve a slower rate of carbon gain. Leaf economics traits have been shown to strongly affect plant growth rate in different conditions (Coley 1988, Poorter 1999, Walters and Reich 1999, Bloor and Grubb 2003, Poorter and Bongers 2006), and trade-offs in performance (Sack and Grubb 2001) suggest that different leaf traits are optimal in different regeneration opportunities (sensu Grubb 1977).

A second important suite of traits is related to the efficiency and safety of water transport including wood density and the characteristics of the conducting cells within the xylem; in chaparral species, this suite is orthogonal to the leaf economic traits above (Ackerly 2004), and has been shown to shift with macro-climate (Maherali et al. 2004, Cornwell et al. 2007) and affect the success or failure of species in particular sites (Pockman and Sperry 2000).

Other important axes of variation are represented by maximum plant height, which is related to successional status and shade tolerance (Falster and Westoby 2005,

Preston et al. 2006), and seed size, which is important for regeneration, the competition–colonization trade-off (Coomes and Grubb 2003), and tied to plant stature (Moles and Westoby 2006). Belowground attributes including mycorrhizal symbionts have been shown to be an important, though difficult to quantify, aspect of plant functional strategies (Read 1991).

#### Trait measurement

Traits were measured for this study at two scales. First, for two traits that can be easily measured—specific leaf area (SLA, leaf area per mass) and individual leaf area—we took two measurements from separate individuals for each species in each plot in which it was found. At the end of the survey in August 2002, drought deciduous species had lost their leaves and could not be sampled. When necessary for analyses relating to intraspecific variation across plots, those data points are excluded from the analysis.

For a second set of nine harder-to-quantify, and yet physiologically important traits, we obtained species means for the 54 species that occurred in our study (see Appendix E). In most cases, five (but up to 20) replicate measurements per species were sampled from separate individuals across each species’ distribution at Jasper Ridge.

While field protocols have been thoroughly developed for leaf and stem traits (Cornelissen et al. 2003), methods for quantifying belowground species characteristics are still being developed. To gain some information about the species strategies, we performed a literature survey for belowground symbiotic associations. These data are also reported on a presence/absence basis for species (see *Belowground symbioses*).

*Leaf traits.*—We sampled recently expanded sun leaves when possible. A small number of woody species at Jasper Ridge grow to maturity in the understory (e.g., *Rubus parviflorus*), and in these cases we sampled the most illuminated leaves on the plant. We quantified fresh leaf area using a leaf area meter (LI-COR 3100; LI-COR, Lincoln, Nebraska, USA). For calculation of SLA we dried leaves at 70°C for >3 days before weighing. Leaf nitrogen was measured by elemental analyzer (Turbo N, Costech, Italy). Both nitrogen per mass ( $N_{\text{mass}}$ ) and nitrogen per area ( $N_{\text{area}}$ ) were calculated on a species mean basis from these data.

*Stem traits.*—We measured wood density (dry mass/fresh volume), vessel cross-sectional area, vessel density (number per cross-sectional area), the proportion of the stem that is lumen, and the leaf area to sapwood area ratio (inverse of Huber value; LA:SA). Species-level data and methodological details related to the sampling of species for vessel traits are presented in detail by Preston et al. (2006).

*Seed traits.*—The seed mass data were assembled from several sources including new field collections for a majority of species, previous studies at Jasper Ridge (Ackerly et al. 2002, Ackerly 2004), and literature

sources (Baker 1972, Keeley 1991, Young and Young 1992). In cases where multiple measurements from different sources were available, we used the mean of all observations as the best estimate of a species mean value.

*Plant stature.*—At each plot, we assessed the height of the tallest individual of each species within each plot using, when necessary, a clinometer. We then used the maximum value of adult plants found in the survey as a measure of the tallest potential height given the range of environmental conditions found at Jasper Ridge (though some species are known to grow taller in other parts of their range, e.g., *Quercus kelloggii* farther north). As the forested areas of Jasper Ridge were likely logged in the 1860s and 1870s, very long-lived species including *Sequoia sempervirens* are likely still growing taller, and in these cases our measurements represent underestimates of the heights they could achieve at our site in the absence of disturbance.

*Belowground symbioses.*—Nitrogen fixing ability was assessed from a literature survey. Five native woody N-fixers were present in the sampled plots: *Ceanothus cuneatus*, *Ceanothus oliganthus*, *Cercocarpus betuloides*, and *Alnus rugosa* fix via actinorhizal symbionts, and *Lotus scoparius* has a *Rhizobium* symbiont. For the purposes of this analysis, potential ability to fix nitrogen was scored as presence/absence.

Using a literature survey, we also attempted to determine the type of mycorrhizal fungi associated with each species in this survey. We found no literature on the mycorrhizal status of many of the woody species at Jasper Ridge, but in many of these cases we did obtain records from congeners. Because the type of mycorrhizal associations tend to be conserved phylogenetically (Fitter and Moyersoen 1996, Cornwell et al. 2001), we chose to include these because of the general paucity of root trait information in comparative studies (e.g., Jackson et al. 1996, 2000); nonetheless, the following analysis should be seen as preliminary.

We found no species (or congeners) in which there was the documented absence of mycorrhizal fungi. On the other hand, both arbuscular mycorrhizas (i.e., association with *Glomalean fungi*) and ecto and arbutoid mycorrhizas (i.e., Ascomycete and Basidiomycete symbionts), are common. Including congeneric records, we found enough evidence for 51 out of 54 taxa in this study to include them in this analysis. A number of abundant species at Jasper Ridge form associations with both Glomalean and Ascomycetes/Basidiomycetes (e.g., *Salix* spp.), so we coded the presence or absence of arbuscular mycorrhizas (AM) and ecto- or arbutoid mycorrhizas as two binary traits.

#### Statistical analysis

The distributions of species means for SLA,  $N_{\text{mass}}$ , seed size, vessel area, vessel density, and maximum height were log-normal. To allow for parametric statistical analyses, we log-transformed these traits

values before analysis. Other traits were not transformed. Correlations among traits and multivariate analyses are discussed in Appendix A.

*Null model tests for habitat filtering and limiting similarity.*—We tested for nonrandom patterns of community assembly using a random (or lottery) assembly null model of species drawing with equal probability from the pool of 54 taxa found in the survey. In this analysis, we used the 20 × 20 m plots as our definition of a community (see discussion of community scale in Ackerly and Cornwell [2007]). It is important to note that both habitat filtering and limiting similarity processes can operate simultaneously in a community, both on separate traits and on the same trait (Fig. 1).

Community assembly theory suggests that a filter can limit the range of successful strategies at a site (Weiher and Keddy 1999). While range is useful in that it captures the “hard edge” effect of a habitat filter, it does have the statistical downside of being susceptible to extreme observations that could be due to mass effects (Shmida and Wilson 1985) or measurement error. For this reason we present results for both range and variance of functional traits in these communities. Note that variance may also be affected by limiting similarity (see Fig. 1).

We also examined the fourth moment of the trait distributions: kurtosis (Sokal and Rohlf 1995). We expect a process that spreads species trait values in communities to result in a more platykurtic (lower kurtosis value) than expected distribution within communities (see Fig. 1).

In many cases, the test statistics are highly correlated with sample size (=species richness) in both random draws and observed data. In order to incorporate this correlation into our null model, we conducted 9999 random draws at each species richness. We compared observed communities with a given number of species to the null draws at the same species richness. This approach to building a null model, known as the “RA3” algorithm, was first described by Lawlor (1980) and is discussed in detail by Gotelli and Graves (1996).

Tests for limiting similarity in natural communities have a long history, with many studies seeking to find evidence that species interactions produce nonrandom even spacing within communities (see references in Ricklefs 1990). However preliminary tests showed that many tests showed false positives for even spacing in the presence of a strong habitat filter, due to the presence of extreme trait values in the species pool.

To address this problem we present a two-step null model below, which produced a null distribution of trait values for each plot in the study (Fig. 2). In step 1 of the null model, we isolated the species whose niche breadth encompassed the abiotic conditions in each individual plot; these are defined as the “potential community members” for the null model specific to each plot. These species had distributions that spanned the conditions found in the plot of interest, that is, they were observed

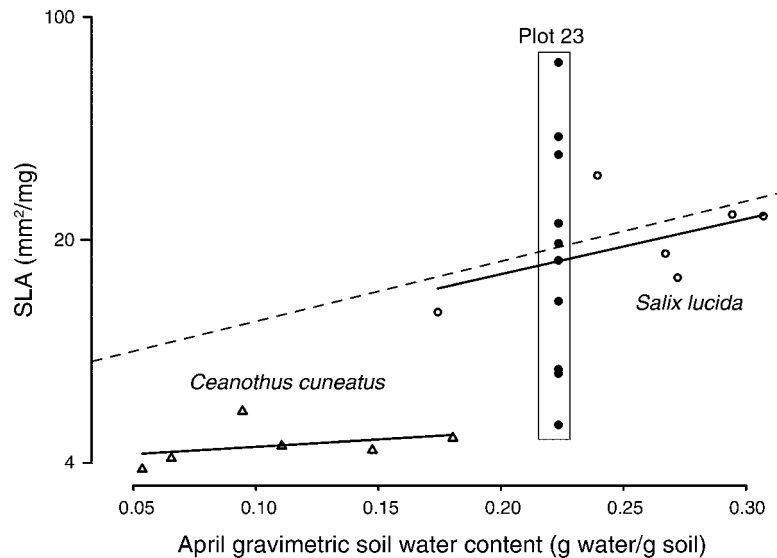


FIG. 2. An illustration of the plot-specific, more-restrictive, null model. All species in plot 23 are shown (solid circles) as well as two species, *Salix lucida* (open circles) and *Ceanothus cuneatus* (open triangles), that are not found in that plot. *S. lucida* is found across a range of soil water values that includes the value for plot 23; thus, we included it as a “potential community member” in our null model. The dashed line is the trend in community-mean SLA with April gravimetric soil water content (least-squares regression). *C. cuneatus* is not found in plots as wet as or wetter than plot 23 and was excluded from consideration in our null model. SLA is specific leaf area; note the  $y$ -axis log scale.

on both wetter and drier soils (see Fig. 2). Species whose niche breadths did not include the measured values were excluded from consideration. We also used community mean trait values to define a trait-based gradient and measure species niche breadth (see Ackerly and Cornwell 2007), and the results were very similar to using the abiotic measure.

In step 2, we quantified the even spacing of trait values within each plot relative to the null draws, using a modified version a statistical test put forward by Ricklefs and Travis (1980; see also Stubbs and Wilson 2004). We sort species with respect to their trait values and consider each gap between two community members to be a “neighbor distance.” (Note that this is analogous to the total length of the minimum spanning tree in multivariate space.) We then take the standard deviation of the distribution of these neighbor distances for the set of community members (sdND). If species are evenly spaced, then sdND will be lower than the expectation.

*Shifts in trait distributions with an environmental gradient.*—To test whether trait means shift across the environmental gradient at Jasper Ridge, we tested for a correlation between plot mean trait values and the abiotic conditions at each site. We also calculated the variance, range, and kurtosis for the 11 trait values and determined whether variation in those summary statistics is associated with the abiotic gradients at Jasper Ridge.

To reduce the number of statistical comparisons associated with all of the measured variables, for some calculations described below we chose one variable—April soil water—to represent the dominant abiotic gradient at Jasper Ridge. We chose this variable because

the end of the wet season is an active time for growth and photosynthesis for all species at Jasper Ridge, whether they are evergreen, drought deciduous, or winter deciduous. April soil water also had the highest predictive power with respect to plot mean trait values, and was highly correlated with September soil water (see *Results*).

*The role of intraspecific variation.*—To quantify the relative magnitude of the contribution of intraspecific variation and species turnover to observed trends in trait mean values, we calculated the slope of the log–log relationship between both SLA and leaf area with April soil water using all values measured for each species at each site. We then repeated this calculation using species means and calculated the percentage reduction in the slope when species means are used. We also calculated the slopes of the within-species relationship between April soil water and the leaf traits for species with observations in more than seven plots. We compared the slope of the plot mean relationship to that observed within each species.

Examining within species responses in more detail, Fig. 3A shows the pattern in plot mean SLA with April soil water. Decomposing the intraspecific response along this gradient there are five alternate hypotheses: (1) intraspecific variation could show no trend with the environmental gradient; (2) intraspecific variation could be shallower than the plot-mean trend but in the same direction; (3) the magnitude of intraspecific response could be equal to the trend in plot mean values; (4) intraspecific variation could be in the opposite direction as community trends; and (5) intraspecific variation

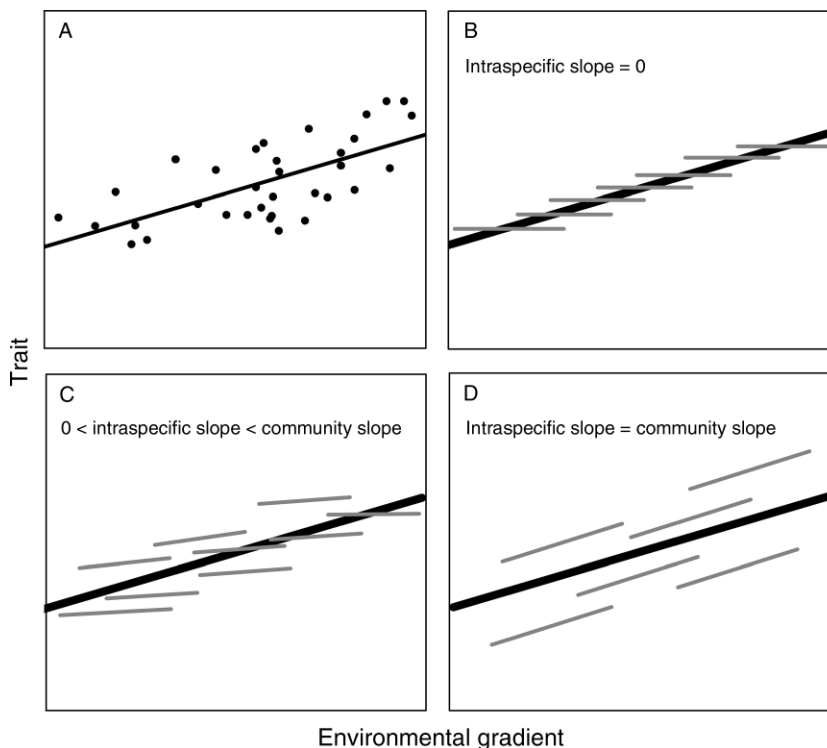


FIG. 3. Black lines show the mean plot trait value as it changes across the gradient of soil water availability. Each gray line represents a hypothetical species' response to the gradient in soil water. In panel A, the points are the plot values for an example trait, SLA, and environmental gradient, April soil water, at Jasper Ridge. Panel B shows a pattern with no intraspecific variation. Panel D shows a pattern with intraspecific variation of equal magnitude to the trend across plots. Panel C shows an intermediate pattern.

could be in the same direction and show a steeper slope compared to the community means.

Fig. 3B–D show the first three alternate hypotheses about how intraspecific variation could contribute to the plot mean trend. Hypotheses 4 and 5 are unlikely as we expected intraspecific variation to be in the same direction as the community trend because both community variation (due to assembly) and intraspecific variation (due to plasticity and heritable variation) are expected to be in the direction of increasing individual plant fitness.

## RESULTS

Fifty-four native species including two gymnosperms and three woody vines occurred in the 44 sampled plots (see Appendix E) across five habitat types that differ in environmental conditions (Table 4). Species mean trait data from this study is publicly available via the Jepson Herbarium's Ecological Flora of California (*available online*).<sup>4</sup> Species richness ranged from 3 to 18 species per plot with the median plot containing 12 species. There was no significant correlation between species richness of woody plants and any of the environmental variables at Jasper Ridge. For the 11 continuous and the three

discrete traits, species mean trait values ranged from orthogonal to highly correlated (see Appendix A).

### *Community assembly: evidence for habitat filtering and limiting similarity*

Relative to the null model, we found a significant reduction in the range of six traits: SLA, leaf area,  $N_{\text{mass}}$ , LA:SA, vessel area, and height (Table 1, Fig. 4). We found a significantly platykurtic distributions of trait values for seed mass (Table 2). We also found for SLA significant even spacing of trait values compared to the null model expectation ( $P < 0.05$ ; see Fig. 5 and example plot in Fig. 6); no other traits showed even spacing; this result is consistent both using April soil water and community mean trait values to constrain the null model to define potential community members.

### *Environmental gradient*

Gravimetric soil water sampled from 0–10 cm was 47% drier in September compared to April (paired analysis by plot); this was expected after the four-month summer dry season. Data from the two time points were highly correlated ( $r = 0.87$ ; Table 3; PCA axis 1 in Appendix C: Fig. C1) and showed a linear relationship. In bivariate analysis (Table 3), insolation and elevation were not tightly linked to soil water content, but in a multiple

<sup>4</sup> <http://ucjeps.berkeley.edu/efc/>



PLATE 1. Woody plant communities at Jasper Ridge, California (USA), showing riparian woodland in the foreground with chaparral and broadleaf evergreen forest in the background. Photo credit: Don Mason.

regression model both were significant predictors of April soil water ( $P=0.01$  and  $P=0.046$  for elevation and insolation, respectively; multiple regression  $r^2 = 0.25$ ), with wetter sites at lower elevations and experiencing less

TABLE 1. The range of trait values within a site: deviations from a null model and trends with soil moisture.

Trait	Cumulative significance testing across plots		Trend with April soil water	
	No. plots < expectation	Wilcoxon $P$	$r$	$P$
Leaf area	38 out of 44	****		NS
SLA	37 out of 44	****		NS
$N_{\text{mass}}$	33 out of 44	***		NS
$N_{\text{area}}$	27 out of 44	NS	-0.444	**
LA:SA	31 out of 44	**	0.441	**
Wood density	25 out of 44	NS	0.365	*
Vessel area	34 out of 44	***		NS
Vessel density	24 out of 44	NS		NS
Lumen fraction	26 out of 44	NS		NS
Height	28 out of 44	**	0.352	*
Seed mass	22 out of 44	NS		NS

Notes: Positive values of  $r$  indicate a larger range (relative to the null model) on wetter soils. Leaf area = the area of individual leaflets; SLA = specific leaf area (leaf fresh area/dry mass);  $N_{\text{mass}}$  = leaf nitrogen per mass;  $N_{\text{area}}$  = leaf nitrogen per area; LA:SA = leaf area per sapwood area (see Preston et al. [2006] for methods); wood density = wood dry mass per fresh volume; vessel area = mean cross-sectional area of individual vessel elements; vessel density = number of vessel elements per cross-sectional area of stem; lumen fraction = proportion of the stem cross-section that is devoted to water transport (the product of vessel area and vessel density); height = maximum height of the species at Jasper Ridge; seed mass = mean mass of seeds.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; \*\*\*\*  $P < 0.0001$ ; NS, not significant.

annual radiation. To a lesser extent, both April and September soil water also negatively correlated with available  $\text{NH}_4$  in April (Table 3 and Appendix C: Fig. C1). Chaparral and open woodland habitats were higher topographically with drier soils in both April and September when compared to broadleaf evergreen forest and riparian woodland (Table 4). Spatial autocorrelation of environmental variables was low; for example, a pairwise comparison of April soil water and spatial distances found an  $r=0.064$  with a Mantel test  $P=0.221$ .

#### *Shifts in trait distributions across an environmental gradient*

*Shifts in the plot-mean trait value.*—There were strong trends in the mean trait value for plots across the environmental gradient at Jasper Ridge (Table 5; abundance-weighted analysis found very similar patterns see Appendix B.) The strongest predictor of mean trait values was the gradient defined by April gravimetric soil water content: moving from dry to wet soils leaf area, SLA,  $N_{\text{mass}}$ , LA:SA, vessel area, and lumen fraction all increased. Values for  $N_{\text{area}}$  and wood density declined across the same gradient. Very similar results were found for the gradient in September soil water, April available  $\text{NH}_4$ , and elevation. In contrast, increasing insolation was associated with smaller leaves and smaller seeds.

There were also shifts in belowground traits. The proportion of species that form arbuscular mycorrhizas (AM) showed a triangular relationship with soil water, with AM species ubiquitous in plots on wetter soils. Plots on drier soils varied greatly in the proportion of species with AM (Appendix D: Fig. D2). N-fixing



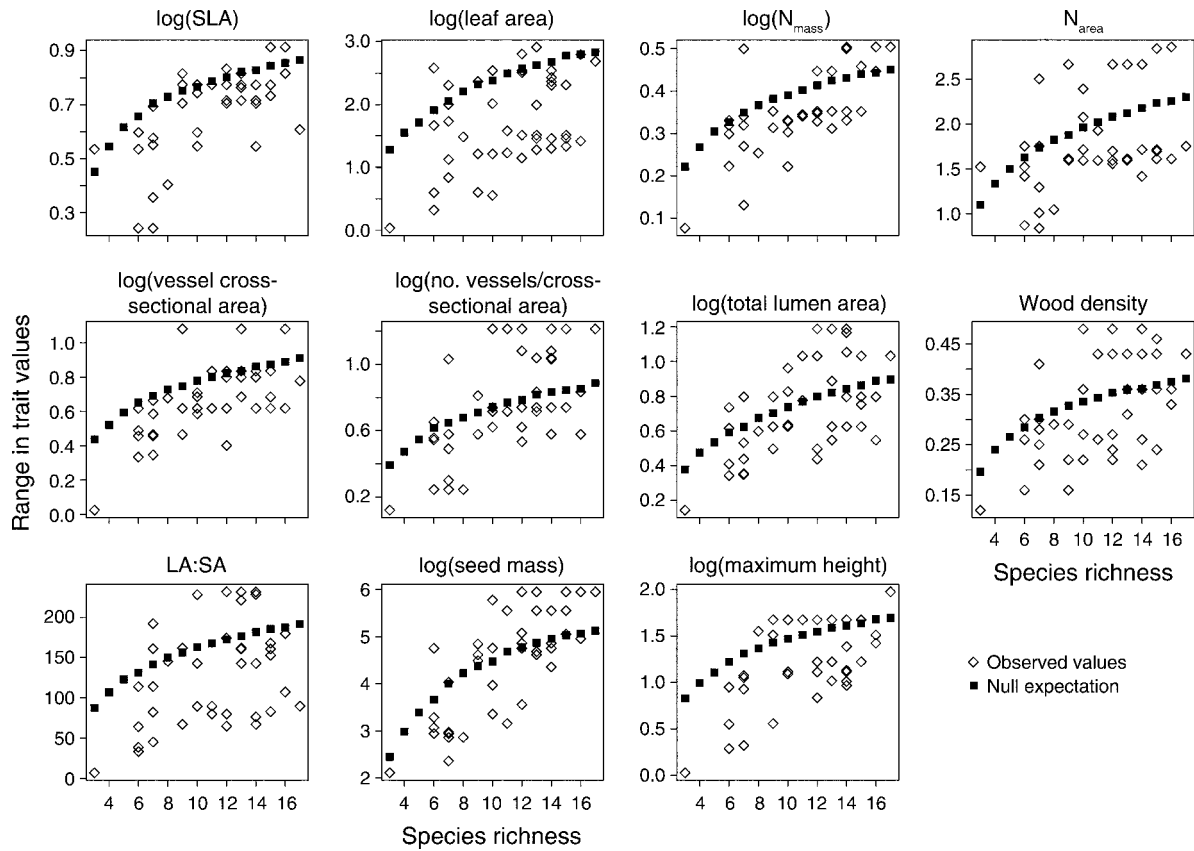


FIG. 4. The community-wide range of values for 11 leaf and stem traits at different levels of species richness. Open diamonds show the observed values for 44 plots; solid squares show the mean of 9999 null model trials at each of the corresponding levels of species richness. See Table 1 for a description of the traits; note that data have been log-transformed for all except  $N_{\text{area}}$ , wood density, and LA:SA.

symbionts were more common in high insolation environments (Appendix D: Fig. D2).

*Shifts in the spread of trait values.*—Many aspects of within-community trait distribution showed trends with April soil water. The range of LA:SA, wood density, and maximum height values present in a plot all increased with soil water, while the range in  $N_{\text{area}}$  values decreased (Table 1). For the kurtosis calculation, we found trends in the kurtosis of leaf area, vessel density, and height (Table 2). The distributions of max height values were more platykurtic on wetter soils, and more playkurtic distributions of leaf area and vessel density values were found on drier soils. We found no trend in the evenness of spacing of trait values for any of the measured traits.

We found significant shifts in the variance of eight out of 11 functional traits across environmental gradients (Table 6). We found greater variance in  $N_{\text{area}}$  at dry sites and greater variance in wood density in the wetter sites (see Fig. 7). In addition, with increasing September soil water the variance in log-transformed maximum height of species increased. This was consistent with the success of both short understory and tall canopy species in wetter sites. In the drier sites, all species tended to be of intermediate maximum height.

TABLE 2. The kurtosis of trait values within a site: deviations from a null model and trends with soil moisture.

Trait	Cumulative significance testing across plots		Trend with April soil water	
	No. plots < expectation	Wilcoxon $P$	$r$	$P$
Leaf area	22 out of 43	NS	0.36	*
SLA	29 out of 43	NS		NS
$N_{\text{mass}}$	17 out of 43	NS		NS
$N_{\text{area}}$	25 out of 43	NS		NS
LA:SA	22 out of 43	NS		NS
Wood density	23 out of 43	NS		NS
Vessel area	27 out of 43	NS		NS
Vessel density	23 out of 43	NS	0.52	**
Lumen fraction	24 out of 43	NS		NS
Height	26 out of 43	NS	-0.55	***
Seed mass	31 out of 43	*		NS

*Notes:* Lower than expected values indicate a more platykurtic distribution than expected. Negative values of  $r$  indicate a trend toward more platykurtic distribution (relative to the null model) on wetter soils.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

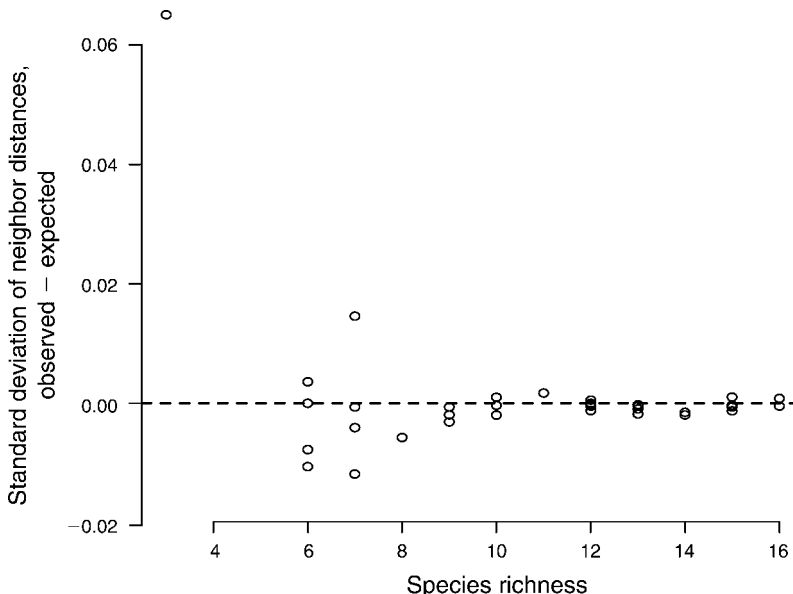


FIG. 5. Results of the more restrictive null model (see also Fig. 2). Each point represents the deviation from the null expectation for the spacing of SLA values within one plot. Values below the dashed line are indicative of even spacing relative to the null expectation. The distribution of plot values was significantly less than the expectation ( $P < 0.05$ ).

*The relative importance of intraspecific variation and species turnover*

The trends in trait values across ecological gradients are due to both intraspecific variation (due to plasticity and ecotypic differentiation) and species turnover. Using data for leaf area and SLA we can partition the strength of the pattern to these two drivers. For SLA, 14% of

slope of the plot mean response can be attributed to within species variation; the remaining 86% is due to species turnover. For leaf area, 21% of the slope of the plot mean slope is due to within species variation, while 79% is due to species turnover (see Fig. 8).

The within-species trait–environment scaling slopes were shallower than the community wide slope (Fig. 9).

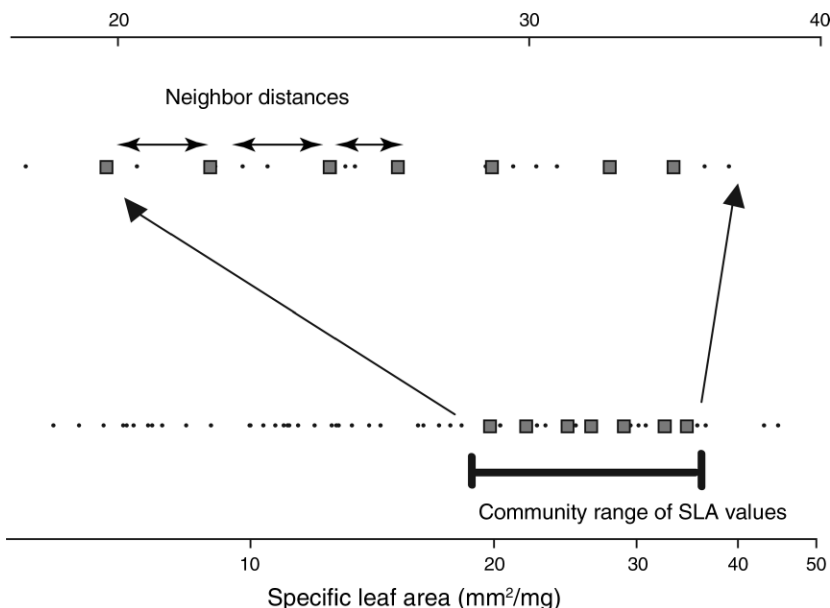


FIG. 6. Range in SLA values (log scale). Larger squares show SLA values from the species found in plot 31, a plot with relatively high soil water. Small circles show the species found at Jasper Ridge but absent from plot 31. The bottom panel shows the entire range for SLA values at Jasper Ridge; the upper panel narrows the extent of data presented to examine the spacing of trait values for coexisting species in more detail.

TABLE 3. Pearson correlation coefficients for environmental conditions among sampled plots at Jasper Ridge.

Condition	Sep soil water	Apr available NO <sub>3</sub>	Apr available NH <sub>4</sub>	Elevation	Insolation
Apr soil water	<b>0.87</b>	-0.11	<b>-0.44</b>	-0.37	-0.27
Sep soil water		<b>-0.44</b>	<b>-0.59</b>	-0.35	-0.21
Apr available NO <sub>3</sub>			0.12	0.09	0.13
Apr available NH <sub>4</sub>				<b>0.41</b>	-0.27
Elevation					-0.02

Note: Bold values indicate correlations with  $P < 0.05$ .

Species show some variation in slope of the response, though this is due at least in part to sampling theory: species that occurred in more plots showed slopes close to the median, and the very steep and very shallow slopes were species with fewer data points and large confidence intervals around our estimate of the slope (see also Ackerly and Cornwell 2007).

#### DISCUSSION

The goal of this study was to examine the trait–environment relationships in a coastal California landscape in the context of community assembly theory. Overall, we identified a topographically mediated gradient in water availability that strongly affects the within-community distribution of leaf, stem, and below-ground traits of successful species. The results of regression analysis suggest that on dry soils a coordinated leaf and stem strategy consists of low SLA, high  $N_{\text{area}}$ , low LA:SA, and high wood density (Table 5 and Appendix A).

These trends in plot mean trait values across a soil water gradient are consistent with the idea of habitat filtering (sensu Diaz et al. 1998): an exclusion of species outside of the viable range of trait values in each sampled habitat. A shift in the location of this allowed range across the soil water gradient then creates the observed trend in mean trait values. In the following section, we discuss community assembly processes and the within-plot trait distributions. We then compare the observed trends in plot mean values to previous studies of the functional ecology of these traits and discuss shifts in the spread or diversity of different functional traits with abiotic gradients. In the last section, we examine the relative contribution of intraspecific variation and species turnover to trends in plot mean trait values.

#### Community assembly and nonrandom aspects of trait distributions within communities (Question 1)

The distributions of trait values within Jasper Ridge woody plant communities were strongly nonrandom, suggesting an important role for species traits in determining the success or failure of species in particular sites. We found evidence of habitat filtering (sensu Diaz et al. 1998)—a smaller than expected range—for six traits: SLA, leaf area,  $N_{\text{mass}}$ , LA:SA, vessel area, and height (Table 1). In the case of SLA, we also observed more even spacing in trait space than expected using our null model, which included no species interactions. Our results support the idea that a restricted range and an even spacing of coexisting species can occur simultaneously, for the same trait. It is important to note that habitat filtering and limiting similarity, which are sometimes seen as competing models of assembly, both occur in this system, and can be seen as distinct steps in the assembly process that affects the distribution of functional strategies within communities.

The processes underlying even spacing of SLA values in this community are complex and relate to the more general debate regarding the processes allowing species coexistence. Two of the predominant niche-based hypotheses thought to underlie coexistence are spatial and temporal storage effects (Chesson 2000). Grubb's (1977) "regeneration niche," that is, the multidimensional, temporal windows for establishment of adult plants is thought to be especially important. Models have shown that coupling stochastic demography (i.e., mortality, establishment, and immigration from a meta-community) with species variation in niche parameters leads to the coexistence of a finite number of species evenly spaced in niche space (Pacala and Tilman 1994, Schilck and Ackerly 2005).

TABLE 4. Mean environmental parameters for the plots sampled within five a priori defined habitat types.

Habitat type	Elevation (m above sea level)	Insolation (MJ·m <sup>-2</sup> ·d <sup>-1</sup> )	Apr gravimetric soil water†	Sep gravimetric soil water†	Apr total available N (μg/g)†
Open scrubland	159	15.1	0.08	0.05	4.1
Chaparral	151	15.3	0.12	0.08	3.7
Open woodland	145	13.9	0.12	0.07	4.1
Broadleaf evergreen forest	124	13.1	0.14	0.09	3.2
Riparian woodland	105	14.3	0.28	0.25	1.8

† Variable is log-normally distributed, so geometric mean is reported.

TABLE 5. Correlations between mean plot value for plant functional traits and environmental variables at Jasper Ridge.

Trait	April soil water	September soil water	April NO <sub>3</sub>	April NH <sub>4</sub>	Elevation	Insolation
Leaf area	<b>0.60</b>	<b>0.54</b>	<b>-0.37</b>	<b>-0.44</b>	<b>-0.44</b>	<b>-0.49</b>
SLA	<b>0.71</b>	<b>0.77</b>	-0.31	<b>-0.58</b>	<b>-0.66</b>	-0.22
$N_{\text{mass}}$	<b>0.60</b>	<b>0.65</b>	-0.17	<b>-0.67</b>	<b>-0.64</b>	0
$N_{\text{area}}$	<b>-0.66</b>	<b>-0.71</b>	0.34	<b>0.42</b>	<b>0.55</b>	0.32
LA:SA	<b>0.70</b>	<b>0.74</b>	<b>-0.35</b>	<b>-0.65</b>	<b>-0.60</b>	-0.24
Wood density	<b>-0.70</b>	<b>-0.67</b>	0.22	<b>0.52</b>	<b>0.60</b>	0.29
Vessel area	<b>0.36</b>	0.28	-0.25	<b>-0.53</b>	<b>-0.45</b>	-0.19
Vessel density	0.13	0.14	0.16	0.13	0.2	0.11
Lumen fraction	<b>0.62</b>	<b>0.57</b>	-0.05	<b>-0.56</b>	-0.32	-0.05
Height	-0.04	-0.15	-0.15	-0.21	-0.12	-0.30
Seed mass	-0.13	-0.35	0.08	<b>0.39</b>	0.11	<b>-0.46</b>

Note: Bold values indicate correlations with  $P < 0.05$ .

Considering our results in the context of these models, in forests, there is a shifting mosaic of microsites created by disturbance at a range scales and intensities; each site has particular and fluctuating levels of light, water, and nutrients (Gray and Spies 1997). Because of the carbon capture trade-offs discussed above, each of these microsites likely favors a particular carbon capture strategy (Poorter and Bongers 2006). Thus, it is plausible that the trade-offs associated with SLA—one of a large number of complex trade-offs associated with coexistence (see Clark 2007)—and variation in regeneration opportunities could lead to the observed even spacing of species SLA values within communities.

Along the same lines, seed size had more platykurtic distribution within communities than expected (Table 2). This pattern can be interpreted as the result of a dispersion of successful regeneration strategies due to microsite variability within plots. This is consistent with the relationship between seed size and the competition–colonization trade-off (Jakobsson and Eriksson 2000, Moles and Westoby 2004), and provides further evidence for the idea that assembly processes generate communities with a wide array of regeneration strategies (Rees and Westoby 1997). A similar empirical result has

been found within Great Basin pine communities (Veech et al. 2000).

#### *Shifts in mean trait values across an environmental gradient (Question 2)*

*Leaf traits.*—We also found lower SLA and higher  $N_{\text{area}}$  in dry sites. SLA,  $N_{\text{area}}$ , and  $N_{\text{mass}}$  are mathematically related:  $N_{\text{area}} = N_{\text{mass}}/\text{SLA}$ . Increasing  $N_{\text{area}}$  in dry sites was due entirely to a very large reduction in SLA that more than balanced a trend toward lower  $N_{\text{mass}}$  in dry sites (Table 5). Low specific leaf area is strongly associated with long leaf life span and low  $N_{\text{mass}}$  (Reich et al. 1997) and with an allocation strategy that increases  $N_{\text{area}}$  and photosynthetic capacity per unit leaf area (Wright et al. 2002).  $N_{\text{area}}$  is also closely linked to the amount of rubisco per unit leaf area—the mechanism that draws down internal CO<sub>2</sub> concentrations (Field et al. 1983). As such, higher  $N_{\text{area}}$  will increase photosynthesis at a given stomatal conductance (“intrinsic water use efficiency”:  $A/g$ , where  $A$  is the photosynthetic rate per leaf area and  $g$  is stomatal conductance) (Wright et al. 2003). The advantage of higher  $A/g$  is thought to be larger at dry sites (Wright et al. 2003), leading to the success of the high  $N_{\text{area}}$  strategy when water is in short supply (Table 5); this is similar to the pattern observed

TABLE 6. Correlations between environmental variables and the variance of the traits within a community.

Trait	April soil water	September soil water	April available NO <sub>3</sub>	April available NH <sub>4</sub>	Elevation	Insolation
Leaf area	-0.20	-0.05	0.04	-0.19	0.27	<b>0.56</b>
SLA	-0.20	<b>-0.38</b>	0.13	<b>0.65</b>	0.15	-0.28
$N_{\text{mass}}$	-0.14	-0.22	0.31	-0.09	-0.09	0.29
$N_{\text{area}}$	<b>-0.48</b>	<b>-0.56</b>	0.25	<b>0.45</b>	0.34	0.23
LA:SA	<b>0.41</b>	<b>0.48</b>	-0.26	<b>-0.42</b>	-0.18	0.14
Wood density	<b>0.38</b>	0.25	0.15	0.02	-0.28	-0.33
Vessel area	-0.05	0.12	<b>-0.37</b>	0.28	-0.21	-0.14
Vessel density	-0.17	-0.25	0.17	<b>0.55</b>	0.05	-0.28
Lumen fraction	0.11	0.10	0.18	0.02	0.21	0.14
Height	0.33	<b>0.43</b>	-0.31	0.03	<b>-0.38</b>	<b>-0.47</b>
Seed mass	-0.32	-0.35	-0.07	0.35	0.03	-0.25

Notes: Bold values indicate correlations with  $P < 0.05$ . Traits are log-transformed when necessary to improve normality (see *Methods: Statistical analysis*).

across precipitation gradients in southeastern Australia (Wright et al. 2002) and in Hawaii (Cornwell et al. 2007).

We found smaller mean leaf area in drier sites, a result consistent with many previous studies at local and regional scales (Parsons 1976, Wilf et al. 1998, Fonseca et al. 2000). However the functional significance of leaf area is not entirely clear. Leaf area can influence the thermal conductance of the leaf boundary layer. The reduced boundary layer effect for smaller leaves may help keep leaf temperatures lower on exceptionally hot, windless days. In wet sites where stomata remain open throughout the day, evaporative cooling may serve to keep leaves from over heating. At dry sites, where limited soil water may lead to stomatal closure on a daily basis, closed stomata and large leaves could lead to high and potentially damaging leaf temperatures (Givnish and Vermeij 1976). Empirical evidence for a correlation between leaf area and leaf temperature is mixed (Givnish and Vermeij 1976, Smith 1978), possibly due to complex among-species variation in leaf angle and canopy architecture.

*Stem traits.*—In dry sites, a given sapwood area supports less leaf area, the plot mean LA:SA is lower. A similar pattern has also been found across precipitation gradients within species (Maherali and DeLucia 2001, Cornwell et al. 2007) and for closely related species (Preston and Ackerly 2003, Cavender-Bares et al. 2004). This increased allocation to sapwood could compensate for less conductive wood of dry-site species (see Preston et al. 2006). Also, when soil water potentials are close to a species' physiological limit and the differential between soil and leaf water potential is small, a lower LA:SA will facilitate keeping leaves hydrated and stomata open (Addington et al. 2006).

Species at dry sites had higher wood density, smaller vessels, and a smaller percentage of their stem cross-section area was lumen. Vessel and wood traits were correlated among species (see Preston et al. 2006 and Appendix A) suggesting that species with a specific suite of stem traits were successful on xeric soils. The ability to resist embolism while maintaining highly negative water potentials has been shown to be associated with dense wood (Hacke et al. 2001) as well as properties of the fibers (Jacobsen et al. 2005).

*Belowground traits.*—We found a higher proportion of species with arbuscular mycorrhizas with increasing soil water content (Appendix D: Fig. D2). Interestingly, we did not find a decrease in the proportion of ectomycorrhizal species with soil water. This is due to the abundance of species with both arbuscular and ecto-mycorrhizal associations at high soil water (e.g., *Salix* spp.).

Despite the presence of only five species with N-fixing capacity in this data set, the proportion of these N-fixers significantly increased with insolation at Jasper Ridge (Appendix D: Fig. D2). Species with the potential to fix N have higher  $N_{\text{area}}$  compared to obligate non-fixers (see Appendix A), which suggests a connection to operating

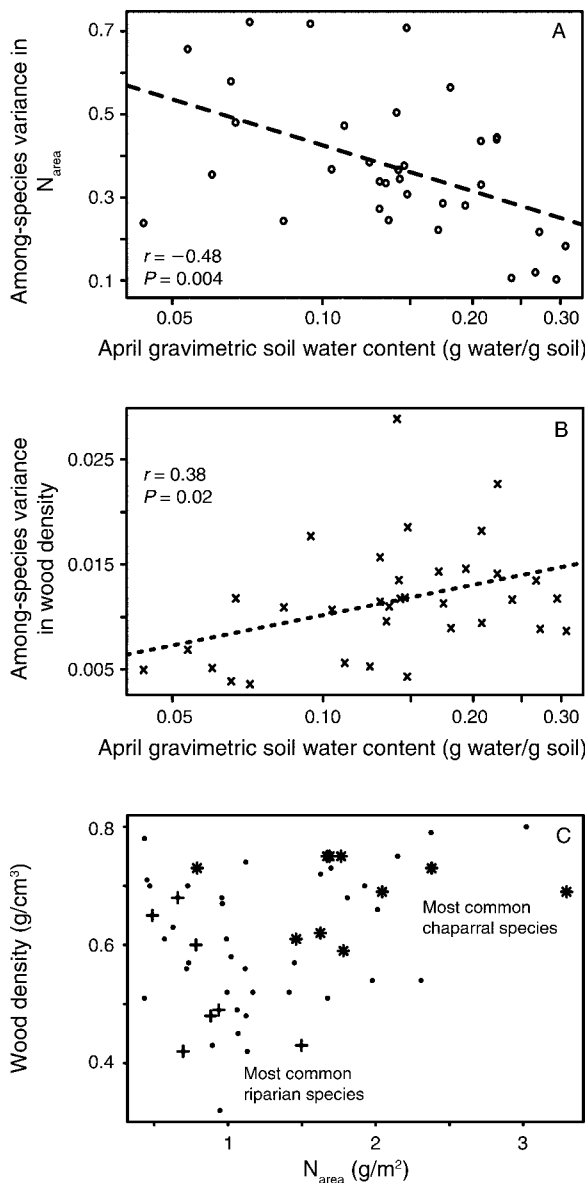


FIG. 7. Opposite shifts in the spread of different traits across the gradient in soil water content. In panels A and B, each point represents the within-plot variance in species trait values. In panel C, the same pattern is presented on a species basis, with each point a species mean. The species highlighted (crosses for the riparian woodland and stars for the chaparral) were selected as occurring in the largest number of plots within each habitat type. *Toxicodendron diversilobum*, which is common in both habitats, is not highlighted. Abbreviations are:  $N_{\text{mass}}$ , nitrogen per mass;  $N_{\text{area}}$ , nitrogen per area.

at a high  $A/g$  as discussed above and could be advantageous in high insolation habitats. Also, south-facing slopes that experience higher irradiance are known to be more likely to burn (Beatty and Taylor 2001), and could lose N in this process. It is possible that the ability to fix atmospheric N could be advantageous in higher fire frequency environments.

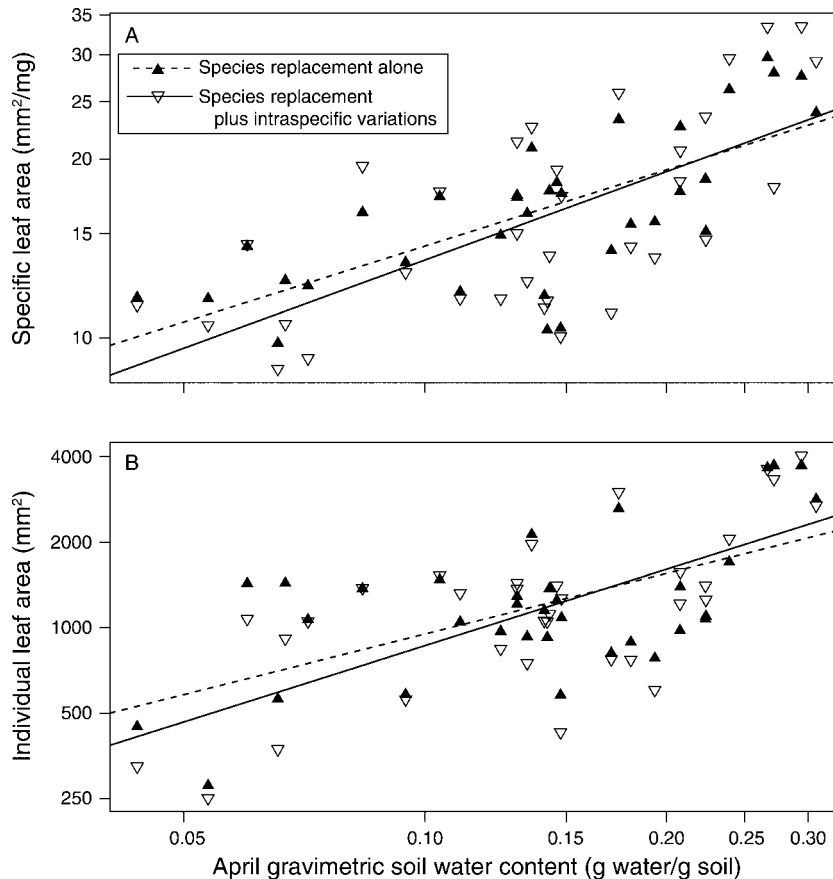


FIG. 8. The community mean trait–environment relationship with only species replacement considered and with species replacement plus intraspecific variation. Within-site measurements incorporating intraspecific variation are shown with the solid triangles and the dashed line; analysis using species means is indicated by open triangles and the solid line. Panel A shows SLA ( $r^2 = 0.51$  and  $0.44$  for the species mean and intraspecific analyses, respectively); panel B shows individual leaf area ( $r^2 = 0.47$  and  $0.38$  for the species mean and intraspecific analyses, respectively). Note the log–log scales.

### *Shifting trait distributions across an ecological gradient* (Question 3)

There was no trend in species richness across the environmental gradient at Jasper Ridge. This is unusual: a review of studies across environmental gradients found that the most common pattern is increasing species richness with gradients in water availability (Cornwell and Grubb 2003). The existence and the shape of the relationship between species richness and environmental gradients has been the subject of much debate (Mittelbach et al. 2001, Gillman and Wright 2006). Examining the distribution of traits within communities, and changes in that distribution, offers another line of evidence about the processes that control species richness and functional diversity within communities.

The range, variance, and kurtosis of trait distributions shift along the gradient in water availability at Jasper Ridge. The range of  $N_{\text{area}}$  values decreases with soil water while the range of max height, LA:SA, and wood density increases (Table 1). The variance of LA:SA and wood density also increases with April soil water; the

variance in  $N_{\text{area}}$  decreases (see Fig. 7). The degree of platykurtosis increases with soil water for height and decreases for leaf area and vessel density (Table 2).

In the wet sites, the increase in the range in the maximum height (log-transformed) is due to the presence of both canopy tree species and species that come to reproductive maturity in the understory. (This result is even more pronounced without log-transformation.) In contrast to the wetter sites, there are no woody understory species in the chaparral, leading to the observed trend in the range of maximum heights. The spread of species on the maximum height axis found in the forests on wetter soils has implications for other traits. For example, similar to what has been shown in tropical wet forests (Falster and Westoby 2005), understory species present on the wetter sites at Jasper Ridge (e.g., *Symphoricarpos* spp.) have high wood density and high leaf area per sapwood area compared to coexisting canopy species, leading to the wider range and variance in those traits on wet compared to dry soils.

In the chaparral, species are known to be differentiated on a rooting depth axis (Davis and Mooney 1986).

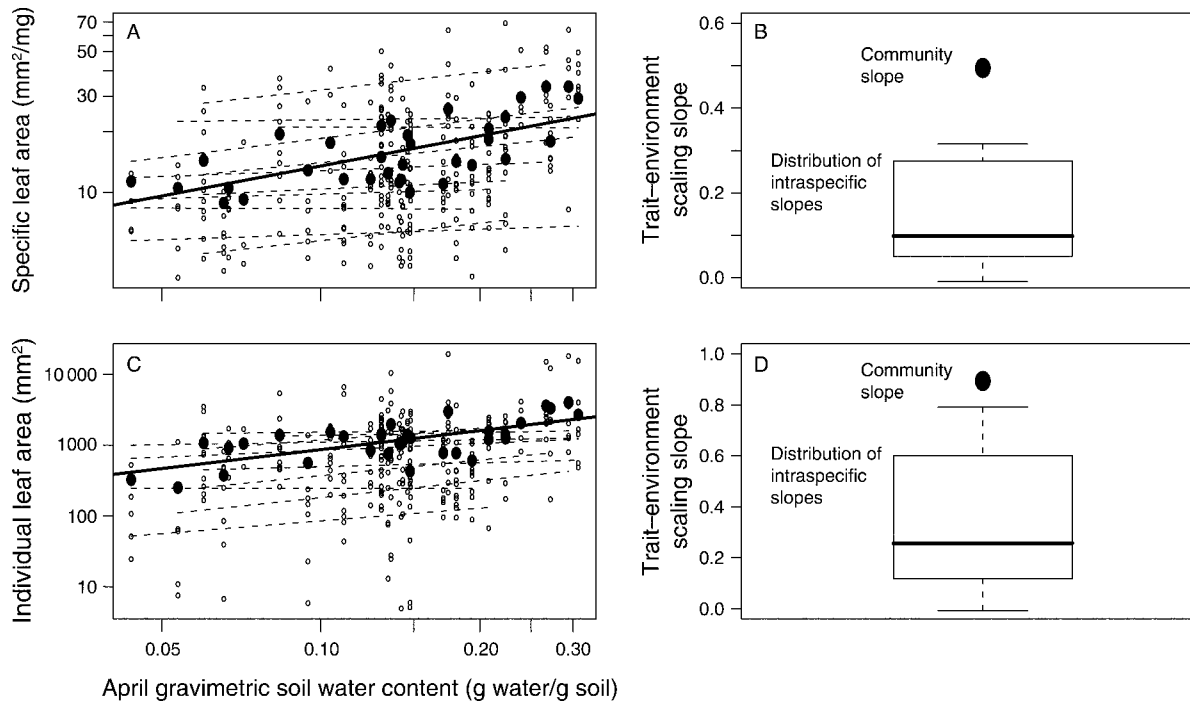


FIG. 9. Panels A and B show community mean trends and intraspecific variation for SLA. Panels C and D show data for individual leaf area. In panels A and C (note the log–log scales), dashed lines represent least-squares fits for intraspecific variation across the gradient in soil water (minimum of eight observations). Solid points and the solid line show the least-squares regression for the arithmetic mean plot value for each trait. The box extends from the first to the third quartile. The whiskers extend to the most extreme data point that is no more than 1.5 times the length of the box away from the box. Scaling slope is the log–log slope as depicted in panels A and C.

Ackerly (2004) showed that minimum seasonal water potentials, which are strongly associated with rooting depth, correlate with wood density and vessel traits. Here we show that moving toward the dry end of the gradient—the chaparral and the open scrubland (see Table 4)—the species show a more platykurtic distribution of vessel densities (Table 2) and an increasing range and variance of  $N_{\text{area}}$  (Table 1, Fig. 7), suggesting that species within the chaparral show a greater diversity of hydraulic strategies than is found in more mesic habitats.

Both wet sites and dry sites at Jasper Ridge support similar numbers of woody species. A multivariate analysis also found no trend in the multivariate volume of trait space occupied (Cornwell et al. 2006). This is in contrast to the trends observed in individual traits (Fig. 7). Collectively, evidence points toward a shift in the axes on which coexisting species are differentiated that allows for a similar number of coexisting species in wet and dry sites. In the wetter environments species spread out along a gradient in maximum stature which correlates strongly with light environment. In the drier sites, previous work at Jasper Ridge has shown that species are differentiated with respect to rooting depth and the soil water status into the summer drought (Davis and Mooney 1986, Ackerly 2004). In the dry

sites, we found greater spread in traits associated with this water transport and use.

#### *Species replacement and intraspecific variation* (Question 4)

For leaf area and SLA the strong trait–environment association is due to both species replacement and intraspecific variation, with species replacement playing a much larger role. This was due to the shallower slope of within–species trait variation (caused by plasticity and/or heritable variation) compared to the slope driven by species replacement (Fig. 9); in other words, our measurements support the hypothesis in Fig. 3C, that is that the intraspecific trait–environment relationship covaries in the same direction as the community slope but with a shallower slope. It is also worth noting that species turnover largely drove trait trends despite the near–ubiquitous presence of two species: *Toxicodendron diversilobum* and *Quercus agrifolia*.

The relative importance of species replacement and intraspecific variation is important in the context of a changing climate. The first functional response to a shift in environmental conditions is the plasticity of individual species. Secondly, species replacement and/or genetic shifts within the species will occur (Ackerly 2003). The result in this study argues strongly that within–species shifts in functional characteristics will be

small relative to the changes that could occur after species turnover.

### Conclusion

An understanding of the causes of functional diversity within communities will require three complementary approaches: observational studies, such as this one, process-based models, and experimental manipulations. In this study of the environment–species–trait relationship we find three main results. First, we find evidence for habitat filtering and limiting similarity—in one case for the same trait, SLA—in the same communities. Second, although we find no relationship between the environmental conditions and species richness, we find opposing shifts in the functional diversity of different traits, suggesting that the axes on which species are differentiated shift with the abiotic environment. Last we found that trends in trait means with the environment were due largely to species turnover, with intraspecific shifts playing a smaller role. This result has been predicted from theory but to the best of our knowledge has not been empirically demonstrated by previous work.

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#### APPENDIX A

Covariance structure of leaf, stem, and root traits for 54 woody species (*Ecological Archives* M079-004-A1).

#### APPENDIX B

Correlation between environmental variables and abundance-weighted mean plot value for plant functional traits (*Ecological Archives* M079-004-A2).

#### APPENDIX C

Principal components analysis of environmental variables (*Ecological Archives* M079-004-A3).

#### APPENDIX D

Additional plots of the relationships between environmental variables and traits (*Ecological Archives* M079-004-A4).

#### APPENDIX E

The 54 native woody plant species in this study (*Ecological Archives* M079-004-A5).