

A link between plant traits and abundance: evidence from coastal California woody plants

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Summary

1. A number of recent studies have demonstrated that plant traits play a crucial role in determining the success or failure of species in a given environment. However, whether traits play a role in determining species' abundance and rarity among the co-occurring species within a community remains an unresolved question.

2. To address this, we analysed the abundance of California coastal woody plant species at landscape and local scales in relation to 11 leaf, wood and seed traits.

3. At the landscape scale, we found no significant relationship between traits and abundance. In contrast, at the local scale we found significant relationships between abundance and four traits: specific leaf area (SLA), height, lumen fraction and wood density. For SLA and height, the relationship was linear; for lumen fraction, it was quadratic. For wood density, the direction of the trait–abundance relationship was dependant on the abiotic context, that is, it shifted across a gradient in soil water content.

4. *Synthesis.* Understanding the connections between traits and abundance is important for two reasons. First, there is an ongoing debate about the degree to which commonness and rarity are the result of drift among ecologically equivalent species or niche processes. These results suggest that there are non-random, trait-based processes affecting abundance and rarity. Secondly, species' traits have been shown to have a strong effect on photosynthesis and decomposition rates, mediated by the abundance of the species. The connections between traits and abundance presented here are crucial for scaling from measurements of species' traits to ecosystem-level processes.

Key-words: abundance, California, chaparral, community assembly, photosynthesis, plant traits, specific leaf area, wood density

Introduction

The question of why some species are common and others are rare has a long history in ecology. In 1948, Preston wrote:

It has often been a matter of comment by ecologists that one or two species are extraordinarily abundant at a particular time and place: all others seem rare in comparison.

Alongside this anecdotal observation, Preston (1948) showed that in several empirical data sets communities contain many rare taxa and few common ones. This pattern is widely found across both geography and taxa (Gaston & Blackburn 2000), and it represents one of the most consistently observed phenomena in ecology.

The mechanisms that influence relative abundance are a subject of ongoing debate, currently reflected in the dialogue on the importance of neutral versus niche-assembly processes

in structuring communities (Hubbell 2001; Murray *et al.* 2005; McGill *et al.* 2006, 2007; Shipley, Vile & Garnier 2006; Cingolani *et al.* 2007; Mouillot, Mason & Wilson 2007; McGill 2008; Levine & HilleRisLambers 2009). One theory holds that limited dispersal in space (e.g. meta-community dynamics), ecological equivalence and demographic stochasticity can, in certain conditions, create realistic abundance/rarity distributions measured as number of individuals (see theory and references within McGill *et al.* 2007; Morlon *et al.* 2009).

There has also been the suggestion that measurable traits of plant species play a crucial role for the success or failure – usually measured as presence/absence – of species in specific environmental conditions (Keddy 1992). There is now mounting evidence that plant communities in many different biomes show trait-based patterns of presence/absence (Diaz, Cabido & Casanoves 1998; Walker, Kinzig & Langridge 1999; Weiher & Keddy 1999; Stubbs & Wilson 2004; Engel Brecht *et al.* 2007; Kraft, Valencia & Ackerly 2008;

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Cornwell & Ackerly 2009). However, the observation that traits affect the presence/absence of species does not necessarily imply that *among the suite of co-occurring species*, traits determine which species are abundant and which are rare.

It is plausible that a species' presence in a community could be influenced by its traits, while its dominance or rarity could be the result of a series of solely stochastic events. For example, a species must be tolerant of highly negative water potentials to grow in the chaparral, but the identity of dominant species in the chaparral could be the result of apparently stochastic events. If this is the case, there will be no correlation between abundance and traits within communities. (There may still be a trait–abundance relationship if absent species are considered in the analysis (e.g. Shipley, Vile & Garnier 2006).) Alternately, the processes that affect abundance and rarity could be trait-based, similar to the assembly processes that affect presence/absence. If this is true, traits and abundance will be linked within communities, and the particular pattern will depend on the spatial and temporal frequency distribution of microenvironments (see Grime 2006) as well as the connection between traits and those microenvironments. It is important to note that any connection between traits and abundance does not preclude an effect of demographic stochasticity on abundance (see McGill *et al.* 2007). However, ecological equivalence and drift (*sensu* Hubbell 2001) do not predict any trait–abundance connection.

In woody vegetation of coastal California, we have previously demonstrated that plant functional traits, including specific leaf area (SLA), wood density and vessel traits, exhibit non-random distributions among communities arrayed along a gradient of soil moisture availability (Cornwell & Ackerly 2009). Here, we seek to use current understanding of plant functional variation to explain patterns in plant relative abundance. We consider abundance and rarity on two scales – local abundance and landscape abundance, asking the following questions: (i) Among co-occurring taxa, do species' traits correlate with abundance and rarity? (ii) Does the relationship between traits and abundance change at different spatial scales or in different abiotic contexts?

Materials and methods

MEASURING SPECIES ABUNDANCE

Using a stratified-random design, we sampled forty-four 20 × 20 m located across the woody plant communities at Jasper Ridge Biological Preserve, a 581-ha preserve located in the eastern foothills of the Santa Cruz Mountains, California, USA (Cornwell & Ackerly 2009). Sampling was stratified to sample a minimum number of plots within chaparral, oak woodland, riparian woodland and closed-canopy evergreen forest vegetation types. At Jasper Ridge, timber trees were removed prior to 1880, and fire was thought to be frequent prior to the arrival of Europeans. Since 1880, large-scale disturbance is thought to have been absent (for historical detail, see Cornwell & Ackerly 2009). Fifty-four native woody species (52 angiosperms and two gymnosperms), which ranged from sub-shrub to trees, occurred

in the sampled plots (Cornwell, Schwilk & Ackerly 2006; Cornwell & Ackerly 2009).

Abundance can be measured as number of individuals, biomass or resource use (Morlon *et al.* 2009). In this analysis, we focus on biomass (Species Biomass Distribution *sensu* Morlon *et al.* 2009), which is of special interest because it is the appropriate measure for scaling from plant traits to ecosystem processes (Lavorel & Garnier 2002; Cortez *et al.* 2007). Like many grasslands, shrublands and riparian forests world-wide, the woody plant communities at Jasper Ridge are dominated by plant species that include genetic individuals with multiple above-ground stems – clonal species. At Jasper Ridge, clonal species include both understorey woody species, e.g. *Symphoricarpos* spp., and canopy dominants, e.g. *Sequoia sempervirens*. In these communities, the prevalence of large clonal individuals makes measuring the size of genets intractable and precludes directly comparing our results to a genetic-individual-based measure of abundance.

In this data set, abundance was estimated visually using six abundance classes of percentage cover. We also measured the diameter at breast height (d.b.h.) for all individuals in each plot with a single stem at breast height and number of shoots per plot. In this analysis, we focus on percentage cover as the preferred measure of abundance for these systems, as it provides a common metric for abundance of shrubs and trees that correlates well with biomass (Murray *et al.* 2005). For quantitative analyses, we use the mid-point of each abundance class as our measure of the cover of a species in each plot. Biomass is likely to be less evenly distributed among species compared to individuals (see meta-analysis by Morlon *et al.* 2009).

FUNCTIONAL TRAIT DATA

Eleven traits (see Table 1) were selected to represent major axes of plant functional variation. We quantified the carbon and nitrogen economy of leaves by measuring SLA (leaf fresh area per dry mass) and nitrogen per leaf mass (N_{mass}), which can be thought of as part of the leaf economic spectrum, ranging from slow to fast return on carbon invested in leaves (Reich, Walters & Ellsworth 1997; Wright *et al.* 2004). Although nitrogen per leaf area (N_{area}) is mathematically related to N_{mass} and SLA, it behaves differently in a statistical sense (Wright *et al.* 2004) and has important implications for water use efficiency (Wright, Reich & Westoby 2003); we treat N_{area} as a separate trait.

We quantified light capture strategy via maximum plant height and leaf area. We measured traits that relate to the transport and use of water (leaf area : sapwood area, wood density, vessel density, vessel area and percentage of stem as lumen) and regeneration (seed mass). Note that in this system because of the prevalence of clonality and differential investment in below-ground biomass (Davis & Mooney 1986; Ackerly 2004), maximum height is not a proxy for the size of genetic individuals for this set of species.

Two traits, SLA and leaf size, were measured for each species in each plot allowing us to incorporate intraspecific variation into the analysis for those two traits. A few traits could not be measured for all species. For example, we did not include the maximum height of woody vines, which are not self-supporting, or vessel traits for gymnosperms, which lack vessels. In those cases, the species without trait values were excluded from the analysis for that trait.

For detailed discussion of the methods and functional significance of the traits, see Cornwell, Schwilk & Ackerly (2006), Preston, Cornwell & DeNoyer (2006) and Cornwell & Ackerly (2009).

Table 1. The relationship between 11 functional traits and abundance on two scales. The trait abbreviations are specific leaf area (SLA), nitrogen per leaf mass (N_{mass}), and nitrogen per leaf area (N_{area}). The significant relationships that were robust relative to the choice of null models are in bold. r is the Pearson product–moment correlation coefficient

	Landscape scale		Plot scale							
	r	Significance testing	Linear trait–abundance relationship				Quadratic trait–abundance relationship			
			Median r	Wilcoxon	‘Abund. shuffle’ null	‘Trait shuffle’ null	Median r	Wilcoxon	‘Abund. shuffle’ null	‘Trait shuffle’ null
SLA	–0.20	NS	–0.27	< 0.001	< 0.001	0.032	0.02	NS	NS	NS
Seed mass	0.17	NS	0.20	0.041	0.120	0.114	0.22	NS	NS	NS
Leaf area	0.03	NS	0.10	NS	NS	NS	0.01	NS	NS	NS
Wood density	0.13	NS	0.12	0.056	NS	NS	–0.05	0.021	NS	NS
N_{mass}	–0.10	NS	0.03	NS	NS	NS	–0.07	NS	NS	NS
Maximum height	0.25	NS	0.31	< 0.001	< 0.001	0.020	–0.03	NS	NS	NS
Vessel density	0.00	NS	–0.13	NS	0.046	0.166	–0.00	NS	NS	NS
Vessel area	–0.02	NS	0.15	0.070	0.022	NS	–0.16	0.007	0.060	NS
Leaf area : sapwood area	–0.08	NS	–0.16	0.003	0.018	0.134	–0.15	0.007	0.064	NS
Percentage of stem as lumen	–0.02	NS	0.06	0.090	NS	NS	–0.20	< 0.001	0.003	0.049
N_{area}	0.021	NS	0.19	< 0.001	< 0.001	0.116	0.08	NS	0.011	NS

Landscape-scale abundance and rarity

To estimate abundance at the landscape scale, we performed two analyses. First, we summed the cover values for each species in all plots to produce a measure of the abundance of each of 54 species at the scale of the entire 481-ha Jasper Ridge. We compared these values to the trait mean values for the 54 species. Secondly, we counted the number of plots in which a species was observed and compared the frequency of observation to the trait values for that species.

Plot-scale abundance and rarity

To test for non-random associations at the plot scale, we separately correlated percentage cover with trait values in each plot for each trait. This process was repeated for each plot in the study, generating 44 r -values, one for each plot, for each trait. We were then able to test whether the mean of the distribution of r -values was statistically different than zero. If the null hypothesis is correct, and there is no relationship between the trait value of a species and abundance, then the mean of this distribution is statistically indistinguishable from zero. A repeated and consistent within-plot relationship between the traits and abundance leads to, on average, a non-zero median value of within-plot r . We performed separate significance tests for each of the 11 traits.

In the cases where there was no significant relationship between relative trait value and abundance, we tested whether there was a non-random tendency for trait values to be located close to the unweighted trait mean value for species in the plot. To do this, we squared the standardized deviates:

$$a_i = ((t_i - t_{\text{mean}})/t_{\text{SD}})^2 \quad \text{eqn 1}$$

where t_i equals the trait value of the i th species. The term t_{mean} is the unweighted community mean, t_{SD} is the standard deviation of the trait values for the species in a plot, and a_i is the i th value of the test statistic vector. Note that this is similar to standard quadratic regression, and we will refer to this hereafter as ‘quadratic’.

However, there is an important difference compared to the typical quadratic regression case. In the typical case, there is also a linear term in the model, which allows the maximum of the function to vary (even outside the range of the data). In our analysis, we directly tested whether the abundant species are close to the unweighted mean. Because the maximum of the function is specified *a priori*, in all cases, the regression fit will be weaker, and the significance test will be conservative compared to the common implementations of quadratic regression.

We then calculated the correlation of this test statistic with abundance. If abundant species are located close to the unweighted mean, we would expect a negative relationship between the test statistic and abundance. We tested for a negative deviation from zero as above, using a one-sample Wilcoxon test.

Significance testing

Different null models for significance testing rely on different assumptions, and no single null approach can be seen as ‘correct’ (Gotelli & Graves 1996). Here, we present three methods that allow for significance testing. First, we used nonparametric statistics with each plot as a replicate, testing whether the mean of the 44 r -values collectively differs from zero. We tested the null hypothesis that the traits and abundance are uncorrelated.

We also used two null-model approaches: first, a null model in which for each plot we randomized abundances relative to species (‘abundance shuffle’ in Table 1). This approach maintained the observed distribution of abundance and trait values within each plot. This null model does not include any trait-based process affecting within-plot abundance.

Secondly, for an alternate null model, we randomized the species’ trait vector, while maintaining the species–plot and species–abundance relationships (‘trait shuffle’ in Table 1). In each randomization, each species’ abundance distribution is maintained, both within plots and on the landscape scale, but is assigned a random trait value. This approach does not maintain the presence/absence ‘filter’ and as such,

randomized plots have a larger range in trait values compared to the observed communities. It does account for the non-independence of trait values when species appear multiple times across plots.

Null models were run 9999 times. For both approaches, we calculated the median plot trait–abundance relationship for the 44 plots within a given randomization and compared the observed value to the distribution of null-model trials.

Trends across an ecological gradient

Related work on the ecological gradient at Jasper Ridge has shown that species and trait turnover is clearly associated with a topographically mediated gradient in water availability (Cornwell & Ackerly 2009). Of the suite of ways in which we characterized abiotic variation at Jasper Ridge, the strongest predictor of trait mean values was surface soil gravimetric water content (SGWC) sampled at the beginning of the dry season in April; it was also highly correlated with soil water content in September, available soil N and solar insolation (which integrates aspect and topography; see Cornwell & Ackerly 2009). These environmental factors are also strongly correlated with each other. Here, we use April SGWC and the r -values of traits and abundance (as described above) to test whether the relationship between trait values and abundance shifts across an ecological gradient at Jasper Ridge. A significant relationship between SGWC and the r -values would show that the strength and/or the sign of the correlation between traits and abundance is shifting across the ecological gradient.

Results

TRAIT CORRELATIONS WITH ABUNDANCE AND RARITY

We found no significant relationships on the landscape scale, neither examining the estimate of total cover at the landscape scale nor the frequency of observation across the 44 plots. The distribution of abundance was log-normal, with only a few very common species and many rare ones. Different trait strategies were abundant in different conditions, and there was no general trend towards higher landscape-level abundance among species with particular trait values.

We found significant relationships between traits and plot-level relative abundance. We focus here on the results that are robust with respect to null-model choices. Abundant species had lower SLA and taller maximum stature than the less abundant species, averaged over all sites. Incorporating intraspecific variation led to a very similar pattern for SLA (median $r = -0.25$ vs. $r = -0.27$). Some traits showed a quadratic relationship with abundance – species with intermediate values for percentage vessel lumen area were more abundant than expected by chance (Fig. 1b).

In general, the ‘trait shuffle’ null model produced relatively extreme trait–abundance correlations under the null model so observed results were less significant (Table 1). This was due to randomizations in which the species that were ‘most abundant’ on the landscape scale were assigned extreme trait values. The pattern observed in nature was considerably more nuanced.

For SLA, within each environment there was a restriction in the range of trait values (Cornwell, Schwilk & Ackerly 2006). Across plots, there was a shift in the mean trait values, with

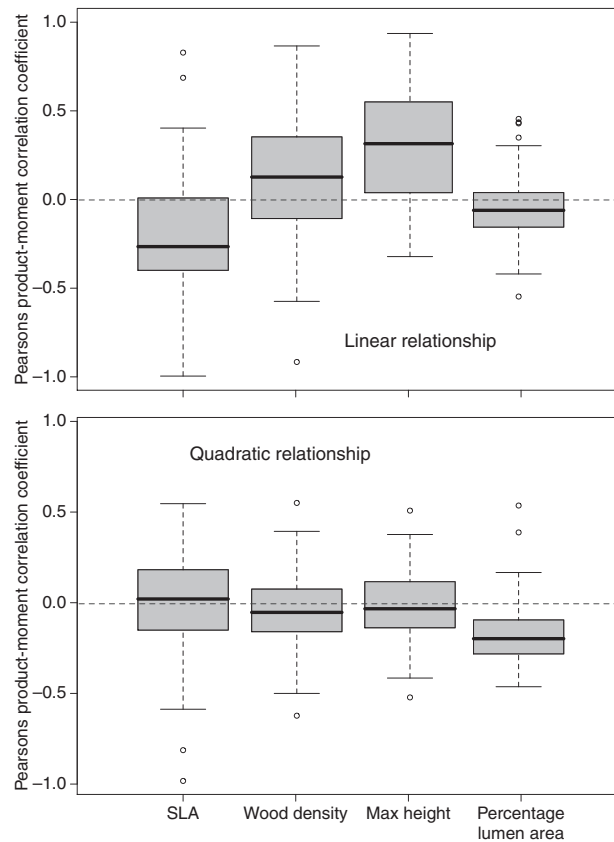


Fig. 1. Boxplots of the correlation between abundance and four traits, based on results across 44 plots. Top panel is for linear relationships. The bottom panel is for quadratic relationships with negative correlation coefficients, indicating a hump-shaped relationship between the trait and abundance with a peak near the plot mean. These panels show the traits for which there was a significant relationship; wood density is only significant when soil water content is taken into account (see Table 1 and Fig. 3).

higher mean SLA associated with higher April soil water content ($r = 0.71$, Fig. 2). Thus, species identity shifted across the abiotic gradient, and the abundant species in each location had different SLA values. Yet, abundant species had consistently lower SLA compared to the species they grew with. This can be visualized as trait–abundance relationships with a negative slope sequentially offset in the x -axis (see Fig. 2c).

TRENDS ACROSS AN ECOLOGICAL GRADIENT

There was a relationship between the correlation coefficient for wood density vs. local abundance and the April gravimetric soil water content in the plots. Across the soil water gradient, the direction of the abundance–wood density relationship reverses: the most abundant species on wet soils have low wood density and the most abundant species in dry sites have high wood density (see Fig. 3; $r^2 = 0.61$; $P < 0.0001$). At intermediate soil water content (that is, $0.15 < \text{SGWC} < 0.25$), wood density showed a quadratic relationship with abundance (Wilcoxon test: $P = 0.039$). No other trait–abundance relationships showed significant trends with April soil water content.

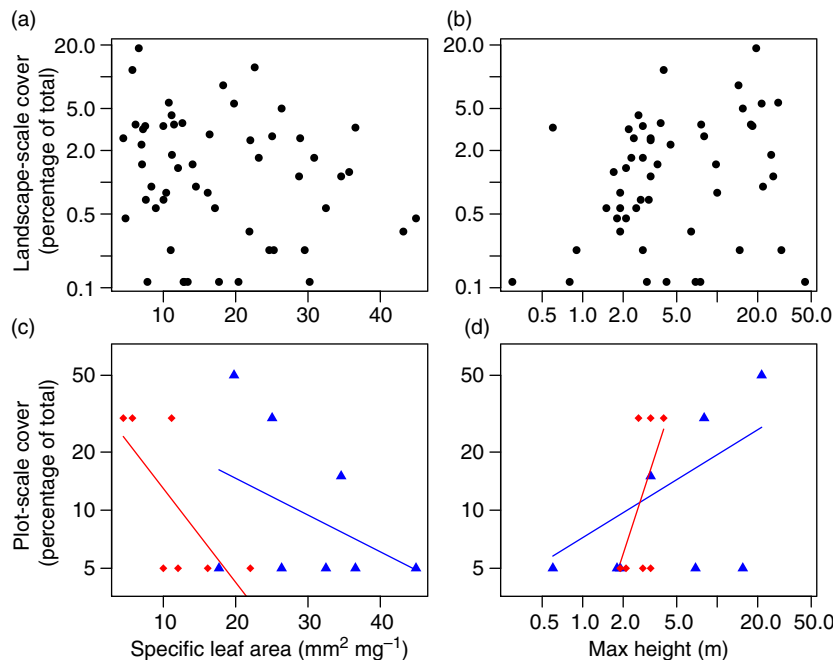


Fig. 2. Panels (a) and (b) show the lack of correlation between landscape-scale abundance and either specific leaf area (SLA; fresh leaf area per dry mass) or plant maximum height. Panels (c) and (d) show the within-plot trait–abundance relationship for two example plots: one from a hydric (blue triangles) and one from a xeric (red diamonds) position in the landscape. Note the shift in plot mean SLA between the two plots and also that roughly the same SLA values are abundant in the wet plot and yet rare in the dry plot. Within plot-correlation between SLA and the shift in plot means leads to the lack of correlation between SLA and landscape-scale abundance. Note also the shift in the range and variance in maximum-height values moving from wet to dry soils, which is discussed in detail in Cornwell & Ackerly (2009).

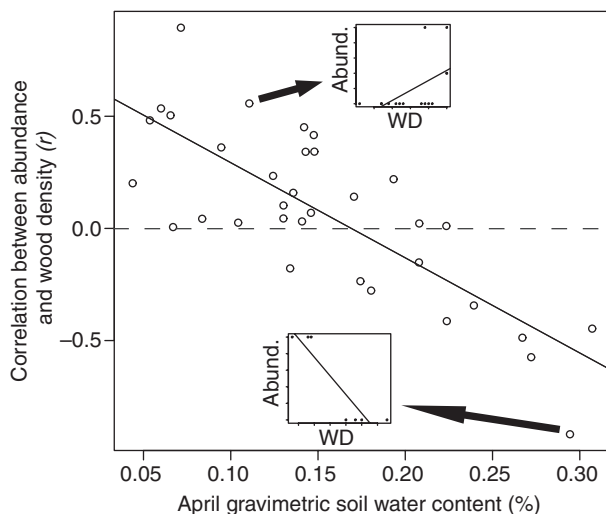


Fig. 3. Shifting correlation between wood density (WD) and plot-scale abundance (Abund.). At low soil water content, species with low wood density are abundant compare to the species they live with. At high soil water content, the relationship is reversed. Inset panels show two examples of the raw data that underlie the correlation coefficients. Arrows connect the correlation coefficients to the plots showing raw data for those plots.

Discussion

If exclusively stochastic processes affect abundance and rarity within suites of co-occurring species, then abundance should not be correlated with the traits of species. The existence of

within-community correlations between traits and abundance is strong evidence that there are non-neutral local-scale processes affecting the abundance and rarity of woody plant species in the coastal mountains of California.

This result supports other lines of evidence that non-neutral processes affect abundance and rarity at the local scale. A palaeontological study of mammal species abundance and rarity through time found that rare species stay rare and common species remain common much longer than expected based on a model of purely stochastic processes (McGill, Hadly & Maurer 2005). A study of Amazonian trees has also shown that patterns of abundance are consistent across vast spatial scales (Pitman *et al.* 2001). These observations suggest that the ecological processes that maintain abundance and rarity remain relatively constant through time and space. One possibility is that the three-way relationship between (i) the physiological and morphological traits of individual species (McGill *et al.* 2006), (ii) the relative abundances of different resources or microsites (Grime 2006), and (iii) abiotic conditions allow species with specific traits to become consistently common at a given site.

LINEAR TRAIT–ABUNDANCE RELATIONSHIPS

We found strong relationships within plots between abundance and two traits: maximum height and SLA. Species with low SLA and potentially tall ones were more abundant compared to co-occurring species (Table 1, Figs 1 & 2). Both SLA and maximum height are associated with the successional status of a species. Species with low SLA can retain resources for longer

periods of time (Reich, Walters & Ellsworth 1997). The combination of sequestering resources and the potential to reach a taller maximum height can be thought of as late-successional strategy (Bazzaz 1979) – a strategy that is successful in the absence of large-scale disturbance. Early successional species (e.g. *Lotus scoparius*) are found at Jasper Ridge and are dependent on local disturbance for regeneration microsites (Ackerly 2004). While Jasper Ridge has not had a documented large-scale disturbance in the last century, small-scale disturbances caused by animals, flooding near watercourses, small landslips, natural mortality and human activity (trails and roads) are common. However, in the absence of large-scale disturbance – especially, catastrophic fire – the gaps in the canopy are usually very small and at low frequency across the landscape.

Interestingly, although in other systems there is often a positive relationship between seed size and local abundance (Murphy *et al.* 2005), we found only very weak evidence for it at Jasper Ridge (Table 1). In fact, the most abundant species in the xeric sites (*Adenostoma fasciculatum*) has very low SLA (indicative of a slow carbon capture strategy) and yet very small seeds. In the more mesic sites, *Juglans californica* is relatively uncommon and has very high SLA and very large seeds. Overall, there was no correlation between SLA and seed mass for these 54 species ($r = -0.06$). For these taxa, regeneration ecology and carbon capture strategy appear to be decoupled (Ackerly 2004), and at least for the conditions currently found at Jasper Ridge after the long-term absence of large-scale disturbance, plot-scale abundance is more tightly linked to carbon capture strategy than to regeneration strategy.

QUADRATIC TRAIT–ABUNDANCE RELATIONSHIPS

We found a strong negative quadratic relationship for abundance relative to percentage lumen area, with peak abundance close to the plot mean. The size of the area in a stem that is lumen (i.e. the space inside vessels) represents a trade-off between high structural strength and resistance to embolism (at low percentage lumen area) versus the ability to transport a large amount of water per carbon invested in sapwood (Preston, Cornwell & DeNoyer 2006; Chave *et al.* 2009). The woody species with the highest percentage lumen area at Jasper Ridge are vines, which are not self-supporting and are often present at low abundance. Species with low percentage lumen area are relatively rare and differ among the habitats. In the chaparral, these species are highly drought-tolerant shrubs (e.g. *Ceanothus cuneatus*). In more mesic habitats, this functional strategy is associated with relatively uncommon understorey species (Preston, Cornwell & DeNoyer 2006). Note that this result is driven by a largely different set of species from the carbon capture pattern described above – while there are only a few abundant species, there are a larger number of rare species at any given site.

SHIFTING TRAIT–ABUNDANCE RELATIONSHIPS

At Jasper Ridge, the wood density of a given species is a strong predictor of its abundance, and this relationship is

dependent on the environmental context. There is a shift from a positive correlation coefficient at dry sites to a negative correlation coefficient at wet sites (see Fig. 3). In other words, species with high wood densities are abundant in dry sites while those with low wood densities are abundant at wet sites. This result is not surprising given the role of wood density in hydraulic strategies – higher wood density is associated with greater hydraulic safety but reduced conductive efficiency (Hacke *et al.* 2001; Pratt *et al.* 2007). This physiological trade-off apparently explains why species with higher wood densities – those capable of tolerating lower water potentials – are found in dry sites (Preston, Cornwell & DeNoyer 2006). The relationship between wood density and abundance is a variation on the result described above for percentage lumen area. Wood density and percentage lumen area are moderately correlated ($r = -0.56$). However, the moderate degree of decoupling between the traits appears to have important implication for abundance and rarity, suggesting an important role for the non-vessel parts (i.e. fibres and parenchyma) of stems. For example, the abundant species in dry sites have intermediate percentage lumen area but high wood density.

The shift in the relationship between abundance and wood density is coincident with a shift in plot mean wood density ($r = 0.70$, Cornwell & Ackerly 2009). This pattern is driven by community assembly processes leading to the absence of species with very light wood at dry sites and the absence of species with very dense wood at wet sites (Cornwell & Ackerly 2009). The abundance–wood density relationship could be thought of as the same process that creates the presence/absence pattern. For example, on dry soils species with wood density slightly lower than the mean are present at low abundance, and species with even less dense wood are excluded completely.

Conclusion

This work has three important implications: first, the leaf economic spectrum is a well-documented pattern of leaf physiological diversity that occurs within ecosystems across the globe (Reich *et al.* 1999; Wright *et al.* 2004). Here, we have shown that in the absence of large-scale disturbance, this variation correlates with abundance and rarity. Further investigating the relationship between disturbance, the leaf economics spectrum, and abundance and rarity within communities is an important next step connecting physiological trait measurements to community structure.

Secondly, these data will inform the effort to scale from plant traits to ecosystem processes (Cortez *et al.* 2007; Cornwell *et al.* 2008; Suding *et al.* 2008). Current vegetation models utilize trait data including SLA and plant maximum height in ecosystem models (Sitch *et al.* 2003). SLA and other traits can be estimated from the climate-adjusted mean of global species-based data sets (see Wright *et al.* 2005). This is a useful step forward. However, the data presented here demonstrate that for SLA in Californian woody vegetation, abundant species are not an unbiased sample of the species pool. Instead, species with low SLA are more abundant than co-occurring

species with high SLA in each vegetation type. If this pattern is widespread across biomes, it should be incorporated into the important effort to scale vegetation traits up to ecosystem and global models.

Lastly, the data presented here inform the ongoing debate about whether commonness and rarity are exclusively structured by stochastic processes (McGill *et al.* 2006, 2007; Shipley, Vile & Garnier 2006). Previous work has shown that rare and common species stay common through time (McGill, Hadly & Maurer 2005) and that common species are common in more places than expected by chance (Pitman *et al.* 2001). In this study, we have documented for the first time the connection between hydraulic traits and species' abundance at the plot scale, as well as shifts in the trait–abundance relationship across an ecological gradient. This supports the idea that non-neutral, trait-based processes play an important role in determining abundance within local communities. Continuing to consider the connections between the physiology of individual species and community-level organization offers a promising way forward.

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