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Trait-mediated effects of environmental filtering on tree community dynamics

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Summary

1. Individual performance is a function of an individual's traits and its environment. This function, known as an environmental filter, varies in space and affects community composition. However, filters are poorly characterized because dispersal patterns can obscure environmental effects, and few studies utilize longitudinal data linking individual performance to environment.

2. We model the effects of environmental filters on demographic rates of nearly all tree species (99) in a 25-ha subtropical rain forest plot. We develop a hierarchical Bayesian model of environmental filtering, drawing inspiration from classic studies of intraspecific natural selection. We characterize the specific environmental gradients and trait axes most important in filtering of demographic rates across species.

3. We found that stronger filtering along a given trait axis corresponded to less spatial variation in the value of favoured traits.

4. Environmental gradients associated with filtering were different for growth versus survivorship.

5. Species maximum height was under the strongest filtering for growth, with shorter species favoured on convex ridges. Shorter stature species may be favoured on ridges because trees on ridges experience higher wind damage and lower soil moisture.

6. Wood density filtering had the strongest effects on survival. Steep slopes and high available P in the soil favoured species with low-density wood. Such sites may be favourable for fast-growing species that exploit resource-rich environments.

7. *Synthesis*: We characterized trait-mediated environmental filters that may underlie spatial niche differentiation and life-history trade-offs, which can promote species coexistence. Filtering along trait axes with the strongest effects on local community composition, that is, traits with the strongest filtering, may necessarily have a weaker potential to promote species coexistence across the plot. The weak spatial variation in filters with strong effects on demography may result from long-term processes affecting the species pool that favour habitat generalist strategies.

Key-words: community assembly, functional traits, Fushan Taiwan, landscape, plant population and community dynamics, topography

Introduction

Quantifying mechanisms that determine spatial variation in community composition is a central goal in ecology. Although traditionally ecologists have used relationships between environmental gradients and species distributions to demonstrate environmental effects on communities (e.g. Whittaker 1960; Harms *et al.* 2001; Valencia *et al.* 2004), environmental conditions are indirectly linked to distributions. At a fundamental level, spatial distributions are determined by demographic rates such as birth, growth, death and dispersal (Clark *et al.* 2010). Variation in demographic rates is more directly linked to variation in environmental conditions and organismal physiology than presence/absence patterns are. However, environmental effects on community-wide demographic rates have rarely been quantified.

Researchers are increasingly studying community trait patterns to characterize niche processes of community assembly (e.g. Suding & Goldstein 2008; Swenson & Enquist 2009;

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Kraft & Ackerly 2010). Trait-based approaches may be more closely linked to ecophysiological mechanisms that shape community composition compared with species-specific approaches (McGill *et al.* 2006; Webb *et al.* 2010). Species are not completely idiosyncratic, and accounting for their functional similarities may reveal an important role for environmental filters (Cavender-Bares *et al.* 2004; Swenson & Enquist 2009; Kraft & Ackerly 2010). For example, co-occurrence of species with similar traits, such as sclerophyllous species co-occurring in xeric habitat, is considered to be evidence that communities are limited by environmental filters (Keddy 1992; Cavender-Bares *et al.* 2004).

Traditional studies of environmental filtering in tree communities have been limited by the use of temporally static distributional data (e.g. Harms *et al.* 2001; Swenson & Enquist 2009; Kraft & Ackerly 2010). Both dispersal and spatially autocorrelated environments can drive spatial community turnover, whilst their effects are often confounded because dispersal data are rarely available. For example, dispersal can mask environmental effects on the distribution of sink populations (Pulliam 1988). The role of environmental gradients in driving community variation at small spatial scales is particularly opaque, partly because dispersal regularly occurs across short distances (Clark, Clark & Read 1998). It is unclear whether commonly used null permutation models effectively reproduce seed dispersal patterns that are unobserved and often complex (Kembel 2009).

Rather than interpreting distributions along gradients as indicating optimal conditions for species, a more powerful approach is to analyse individual performance through time in different environments (Davies 2001; Baltzer *et al.* 2005; Uriarte *et al.* 2010). Studying longitudinal measurements of performance eliminates the confounding influence of dispersal and allows for a more direct assessment of environmental effects. Spatial variation in individual performance may reveal niche differentiation that is undetected when studying populations in aggregate (Clark *et al.* 2010).

Our primary goal is to characterize the environmental gradients and the species traits involved in community variation and species coexistence. Environmental filters that determine a large portion of performance variation amongst species may affect community composition (Webb *et al.* 2010). Spatial variation in filters can allow species coexistence across an area by spatially separating species niches (Pacala & Tilman 1994). Thus, we identified the trait–environmental axes with the strongest and most spatially variable effects on performance because such axes may drive community composition and species coexistence. However, the influence of environmental filters on community composition may be opposed by additional processes such as dispersal and competition (Mouquet & Loreau 2003; Swenson & Enquist 2009). Thus, we compared dynamic evidence for filters to static correlations between environmental conditions and community trait means.

We quantify the effects of environmental filtering on communities using a novel combination of techniques that synthesize recent advances (Clark *et al.* 2010; Kraft & Ackerly 2010; Uriarte *et al.* 2010) and classic approaches (Haldane 1954; Wade & Kalisz 1990). First, we study individual tree dynamics to infer environmental filtering, which eliminates dispersal as a confounding factor. Second, we model community demographic variation by allowing performance to vary as a function of trait values (McGill *et al.* 2006; Webb *et al.* 2010). Our approach is inspired by the classic work of Haldane (1954), who proposed estimating natural selection on a trait by quantifying the change in relative fitness across variation in the trait. Additionally, environmental gradients that covary strongly with selection may be associated with mechanisms of selection (Wade & Kalisz 1990). We extend these concepts to characterize the effect of environmental filters on communities. Finally, whilst previous trait-based studies of dynamics have been limited to a handful of abundant species (Davies 2001; Uriarte *et al.* 2010), we model nearly all species in our study plot using a hierarchical Bayes framework.

The objectives of this study were to address two questions. First, what are the quantitative effects of environmental filtering on spatial community variation? Second, which environmental and trait axes exhibit the strongest and most spatially variable filtering? We place axes of community demographic variation in a functional trait context, which we use to generate hypotheses about ecophysiological mechanisms of community variation.

Materials and methods

STUDY SITE

We studied the tree community at the 25-ha Fushan Forest Dynamics Plot (FDP) in northern Taiwan (24°45′40″N, 121°33′28″E, 600–733 m asl). Fushan FDP was established in 2004 following Centre for Tropical Forest Science protocols in which all trees with diameter at breast height (DBH, at 1.3 m height) ≥ 1 cm were mapped, tagged, identified and measured (Condit 1998). The forest at the site is a subtropical evergreen broad-leaved forest receiving 4271 mm year^{-1} rain. The soils are extremely acidic (pH 3.3–4.3) with low organic carbon content and fertility (for a detailed description of the plot, see Su *et al.* 2007).

TREE DEMOGRAPHIC DATA

We studied the growth and survival of 163 400 arborescent stems of 111 593 individuals belonging to 107 species recorded in 2004 (Table S1). 132 426 stems and 95 436 individuals survived to the second census completed in 2009. We divided the plot into 625 square quadrats with 20-m edges (quadrat area = 400 m^2). This scale offers a reasonable trade-off between sample sizes at two levels: (i) number of trees within quadrats, required to model local relationships between traits and performance and (ii) number of quadrats within the plot, required to model spatial heterogeneity of filtering (Swenson & Enquist 2009).

ENVIRONMENTAL CONDITIONS

Topographical, soil moisture and soil nutrient gradients may have strong effects on tree demography (Engelbrecht *et al.* 2007; Russo *et al.* 2008). Topographical gradients are typically correlated with variation in soil moisture in tropical forests (Daws *et al.* 2002).

Previous analyses of the Fushan forest have suggested that tree survivorship is significantly greater on convex ridges compared with concave basins (I-F. Sun, *unpublished data*). With respect to soil nutrients, subtropical rain forests in Taiwan are thought to be highly P-limited (Wu *et al.* 2007). Additionally, tropical forests are often N-limited, especially in young soils such as those in Taiwan (Lebauer & Treseder 2008). We measured 2 topographical and 2 soil attributes of 20 × 20 m quadrats: convexity, slope, available N and available P (Table 2; Supporting Information).

TRAIT DATA

Following established protocols, we measured traits on 6–12 individuals of each tree species found in the plot (Supporting Information; Cornelissen *et al.* 2003). We studied five traits that correspond to life-history trade-offs and niche variation: (i) leaf area, which is subject to a trade-off between light capture and increased temperature (Dolph & Dilcher 1980), (ii) specific leaf area (SLA; leaf area/dry mass), which represents a trade-off between the cost of leaf growth versus photosynthetic rate (Wright *et al.* 2004), (iii) leaf succulence [(fresh mass – dry mass)/leaf area], which is subject to a trade-off between high productivity versus long leaf life span (Garnier & Laurent 1994), (iv) wood density, which represents a trade-off between growth and survival (Muller-Landau 2004), and (v) maximum height, which represents the light niche of adults (King, Wright & Connell 2006). We obtained leaf trait data for a total of 99 species, maximum height data for 96 species and wood density for 75 species. Because traits do not vary independently, we extracted the first two principal components axes of the combined leaf and maximum height variation for the 96 species having these data (Table S2).

MODELS OF TRAIT-BASED ENVIRONMENTAL FILTERING

We used a hierarchical Bayes approach to statistical inference, primarily because such models are flexible enough to allow integration over many sources of uncertainty. Simultaneously, modelling spatial variation in the performance of many species is a challenging high-dimensional problem: species vary in their ontogeny, and environmental filtering varies in space. A hierarchical approach simplifies high-dimensional uncertainty and facilitates model convergence by constraining parameters to hyperdistributions (Clark & Gelfand 2006).

Table 1. Summary statistics of the trait and environmental variables studied. Environmental variables were analysed at the quadrat level, whilst traits were analysed at the species level.

		Mean	SD	Min.	Max.
Environment	Convexity (m)	0.0	1.9	−6.2	5.7
	Slope (°)	21.4	10.6	2.1	46.8
	Ava. N (mg kg^{-1})	126.7	28.1	61.3	208.9
	Ava. P (mg kg^{-1})	3.6	1.2	1.5	8.8
Traits	Leaf area (cm^2)	52.3	169.3	4.4	1658.8
	Specific leaf area (cm^2 g^{-1})	171.8	61.7	89.3	400.2
	Leaf succulence (mg cm^{-2})	12.0	3.0	6.5	20.1
	Height (m)	13.0	6.7	2.3	28.6
	Wood density (g cm^{-3})	0.53	0.11	0.22	0.79

The structure added by modelling hyperdistributions over parameters lends stability to even rare species, which might, if modelled independently, lack sufficient data to give an interpretable result. We assume that each species-specific parameter is drawn from a common hyperdistribution for all species, although this approach may be limited by the accuracy of our assumption.

In Bayesian inference, we seek the probability of parameter values given the observed data, known as the posterior distribution. The posterior is proportional to the likelihood of the data given the parameters, multiplied by the prior probability of the parameter values. We assumed essentially no prior information about parameters, that is, all parameter values have approximately equal prior probability. Below, we present equations used to calculate the expected growth or survival given the parameters.

Our ability to accurately model environmental filtering can be aided by accounting for the variation in mean vital rates amongst species and across ontogeny (Davies 2001; Uriarte *et al.* 2004). Our model builds on the ontogenetic growth and survival functions of Uriarte *et al.* (2004) by adding in environmental filtering and hierarchical organization of community dynamics. The expected growth of an individual stem i of species s in quadrat q is

$$E(g_i) = \exp(g_s + \delta_i + F_{sq}) \qquad \text{eqn 1}$$

where g_s determines maximal growth of species s, δ_i is the reduction in growth of stem i due to its size, and F_{sq} is the reduction in growth due to environmental filtering against the species in quadrat q. When the last two terms in the exponent equal zero, they have no effect, and the expected growth is the species maximum g_s. Survival models are a logistic version of eqn 1:

$$E(p_t) = \frac{\exp(S_t)}{1 + \exp(S_t)} \qquad \text{eqn 2}$$

$$S_t = S_s + \delta_t + F_{sq} \qquad \text{eqn 3}$$

where p_t is the probability of survival of individual tree t, which can be comprised of multiple stems. S_s determines the maximal survival probability of species s, δ_t determines the size-dependent reduction in survival probability of individual tree t, and F_{sq} determines the reduction in survival probability due to environmental filtering.

Following Uriarte *et al.* (2004), species-specific ontogenetic growth patterns (δ_i) are modelled using a lognormal function:

$$\delta_i = -\frac{1}{2}\left[\frac{\ln(DBH_i/(X_{0s}))}{X_{bs}}\right]^2 \qquad \text{eqn 4}$$

where DBH_i is the DBH of stem i, X_{0s} is the DBH at which maximum growth or survival occurs for species s, and X_{bs} determines the dispersion of the function. When $DBH_i = X_{0s}$, $\delta_i = 0$ and performance is at its ontogenetic peak. The equation is the same for ontogenetic survival, except that it is a function of the largest stem of an individual tree, which can be multiple-stemmed. This lognormal function is flexible and allows us to model U-shaped ontogenetic mortality, that is, greatest mortality for seedlings and large adults. The lognormal is flexible enough to model monotonic functions as well (*e.g.* when $X_{0s} \rightarrow 0$). We constrain species-specific ontogenetic parameters to hyperdistributions:

$$X_{0s} \sim \gamma(k_0, \theta_0) \qquad \text{eqn 5}$$
$$X_{bs} \sim \gamma(k_b, \theta_b) \qquad \text{eqn 6}$$

Gamma distributions are appropriate because they constrain parameters to be positive and can model the strong right skew in distributions of these species-specific parameters (Uriarte *et al.* 2004). Maximum growth for each species g_s is also modelled as a random variable

$$g_s \sim N(\mu_g, \sigma_g^2) \qquad \text{eqn 7}$$

Hyperdistributions are the same for species-specific survival parameters.

We represent local environmental filtering within a quadrat by considering performance a Gaussian function of the difference between the optimal trait (Gaussian mean) and each species' trait value. We allow this function to vary in space; so that each quadrat has a function describing the decay in performance as a species trait is farther from the local optimum (Fig. 1). The Gaussian form follows the hypothesis that environmental filtering reduces trait variance (*e.g.* Kraft & Ackerly 2010). Additionally, our model is similar to theoretical models (*e.g.* MacArthur & Levins 1967) that assume a Gaussian function to describe performance along a niche axis. The filtering effect in quadrat q on species s with trait value T_s is the following:

$$F_{sq} = -\frac{(T_s - \mu_q)^2}{2\sigma_q^2} \qquad \text{eqn 8}$$

where μ_q is the optimal quadrat trait value, that is, the trait value for which performance is maximal, and σ_q determines the strength of filtering (as σ_q decreases, filtering becomes stronger). The optimal trait value need not occur within the observed trait range, allowing us to model gradients where all species perform best in favourable conditions, but under poor conditions, species with certain functional traits have less reduction in performance (*e.g.* Sterck *et al.* 2011). Note that our approach does not preclude the possibility that environmental filtering is mediated by competition (Mayfield & Levine 2010), but merely allows different traits to confer greater relative performance in different locations.

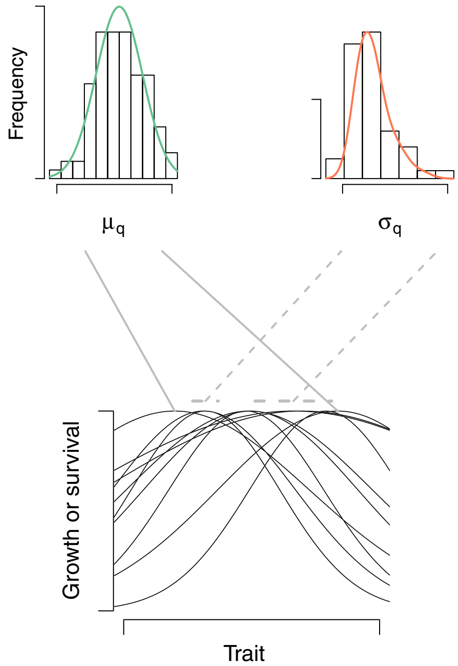

Fig. 1. Illustration of environmental filtering functions for tree performance in different quadrats q. In each quadrat, a different Gaussian filtering function is estimated (curves in the lower panel) with a local optimal trait value (μ_q, the mean of the local Gaussian filtering function) and a local strength of filtering (determined by σ_q, the standard deviation of the Gaussian). Each quadrat q has separately estimated μ_q and σ_q, constrained by hyperdistributions shown in the top panels. Histograms represent the distribution of quadrat filtering function parameters, with the curves showing fitted hyperdistributions of filtering parameters.

We assume that filtering is determined by environmental conditions (Weiher & Keddy 1995). We model the optimal trait value as a function of four variables, although additional variables likely affect filtering. The optimal trait value in a quadrat is linearly related to a vector of observed local conditions $\boldsymbol{X_q}$:

$$\mu_q = \mu + \boldsymbol{X}_q\boldsymbol{\beta} + \varepsilon_q \qquad \text{eqn 9}$$

where μ is the mean plot-wide trait optimum, $\boldsymbol{\beta}$ is a vector of environmental effects on trait optima, and ε_q is the random error in optima. The filtering function varies amongst quadrats q and affects all species in a quadrat. Random errors in quadrat-specific filtering parameters are constrained to hyperdistributions:

$$\varepsilon_q \sim N(0, \sigma_\mu^2) \qquad \text{eqn 10}$$

where σ_μ is the standard deviation of random error in optimal quadrat trait values. Variation amongst quadrats in the strength of filtering is also modelled:

$$\sigma_q \sim Inv - \gamma(k_F, \theta_F) \qquad \text{eqn 11}$$

We include error terms at the level of the individual (sometimes comprised of multiple stems) and the quadrat. The observed growth of stem i of species s (y_i) is the expected growth plus random error:

$$y_i = \exp(g_s + \delta_i + F_{sq} + v_q + \tau_t) + \varepsilon_i \qquad \text{eqn 12}$$

where ε_i is stem error, τ_t is individual tree-level error, and υ_q is error at the quadrat level. Error distributions are Gaussian with mean 0. The full joint posterior probability, BUGS code, methods for posterior sampling and sampled posterior densities are included in the Supporting Information. For simplicity, in the text, we focus on reporting credibility intervals (CIs) and point estimates of parameters (the posterior mean), although this necessarily gives an incomplete description.

COMPARING FILTERING ALONG DIFFERENT TRAIT AND ENVIRONMENTAL AXES

We fit a model of growth and a model of survival for each of the five traits and the first two principal components of traits (Table S2). We modelled the performance of all species with data along a given trait axis. Each trait model included four potentially important environmental variables (eqn 9) that were relatively uncorrelated: topographical convexity, topographical slope, available N and available P in the soil (Table S3). We limited the number of environmental variables in the model to avoid problems with collinear covariates.

We compared spatial variation in filtering and the strength of filtering across different trait axes. We estimated spatial variation in filtering as the standard deviation of quadrat optimal trait values μ_q. This metric describes how the best trait value for local performance varies in space. The strength of filtering along a trait axis (irrespective of spatial variation in filtering) was estimated as the average quadrat strength of filtering, given by $1/\sigma_q$.

We compared models of growth versus survival for the same trait to study life-history trade-offs. Environmental conditions that cause spatial variation in performance may affect species growth and mortality in correlated ways if favourable conditions promote both growth and survival. Under this hypothesis, optimal traits for growth should be positively correlated with optimal traits for survival. Alternatively, environmental conditions may affect different aspects of demography so that conditions favouring certain species for growth may also increase their mortality. We calculated Pearson's correlations between optimal traits (μ_q) for growth versus survival across quadrats.

COMPLEMENTARY ANALYSES

We compared results from our model of dynamics to static correlations between quadrat environmental conditions and quadrat mean traits. Quadrat mean trait was calculated as the mean trait value for all species present in a quadrat in the 2009 census, weighted by the number of stems for each species. Quadrat mean traits and environmental conditions were approximately normally distributed. Thus, we tested the association between quadrat mean trait and environmental conditions using general linear models. Each of the four environmental variables was tested separately as predictors of quadrat mean trait.

Finally, we conducted three additional complementary analyses that may provide evidence for environmental filtering. These analyses tested whether environmental filtering inferred above was concordant with (i) the change across size classes in static correlations between environment and community mean traits, (ii) the difference in neighbourhood trait diversity between trees that survived versus those that died (Uriarte *et al.* 2010) or (iii) changes in trait diversity of trees surviving in quadrats from one census to the next (see Supporting Information).

Results

GROWTH

Estimated filtering functions differed widely amongst traits, with some showing low spatial variation and very strong trait filtering and others showing high spatial variation with weaker filtering. Across traits, the strength of filtering (average $1/\sigma_q$) was significantly negatively correlated with the standard deviation of quadrat trait optima, μ_q (rank correlation, $\rho = -0.86$, $P = 0.02$; Fig. 2). The strongest environmental filtering on growth occurred along an axis of species maximum height variation (Fig. 3, Table S4). Species with smaller maximum height were favoured for growth as soil available N and quadrat convexity increased; indicating shorter stature species were favoured on ridges (Fig. 4). PC2, which was highly correlated with maximum height ($r = -0.6$), had the next strongest filtering.

The most spatially variable filtering occurred along an axis of wood density. However, the strength of filtering $1/\sigma_q$ for wood density was lowest, fitting the overall pattern amongst traits (Fig. 2). Species with greater wood density had increased growth in quadrats with greater convexity and greater available N (Fig. 4). Convexity and available N were also the environmental variables most often associated with filtering for growth along trait axes, indicated by a high frequency of models where 95% CIs for β excluded zero (Fig. 3). Local optima μ_q for SLA, leaf succulence, maximum height, wood density and PC1 were all correlated with convexity and available N. Traits with weaker filtering such as wood density were still implicated in filtering, as fitted quadrat trait optima were far from the trait values of most species.

SURVIVAL

As with growth, the expected strength of filtering $1/\sigma_q$ on a given trait was negatively correlated with the standard deviation in quadrat optima μ_q of that trait (rank correlation, $\rho = -0.83$, $P = 0.02$; Fig. 2). The strongest environmental filtering on survival occurred along PC1. Species with greater PC1 scores were favoured for survival as the quadrat slope became steeper and soil available P increased. Amongst raw trait axes, wood density (negatively correlated with PC1, $r = -0.32$) had the strongest filtering (Table S4, Fig. 4).

The most spatially variable filtering occurred along an axis of leaf area, although filtering was weakest along this axis. Quadrats with steeper slope and greater available N favoured species with larger leaves (Fig. 4). Available P and slope were the environmental variables most often associated with filtering for survival along trait axes, indicated by a high frequency of models where 95% CIs for β excluded zero (Fig. 3). Local optima μ_q for SLA, leaf succulence, maximum height, wood density and PC1 were all correlated with available P, whilst leaf area, leaf succulence, height, wood density and PC1 correlated with slope (Fig. 5).

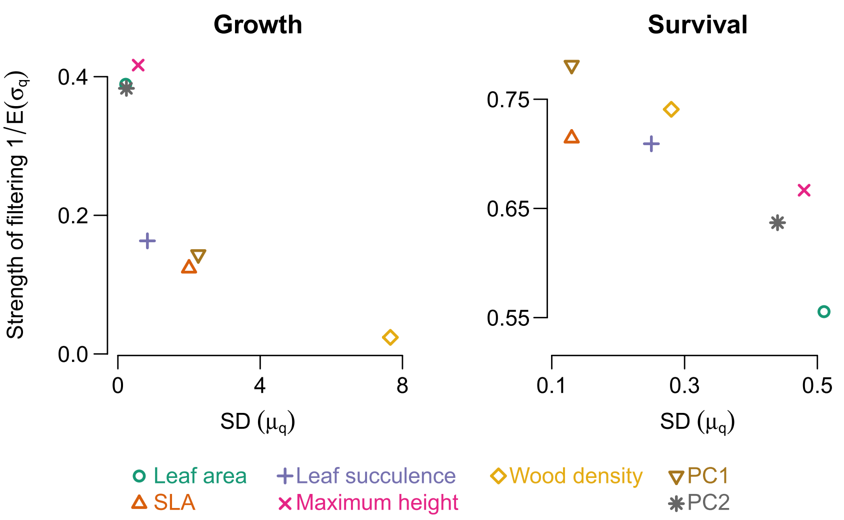

Fig. 2. The average strength of filtering on a given trait axis ($1/\sigma_q$) declines as the spatial variation (SD) in optimal trait values (μ_q) increases. For comparison and consistency amongst traits, traits are scaled to have unit standard deviation. Symbols (and colours) indicate different trait models.

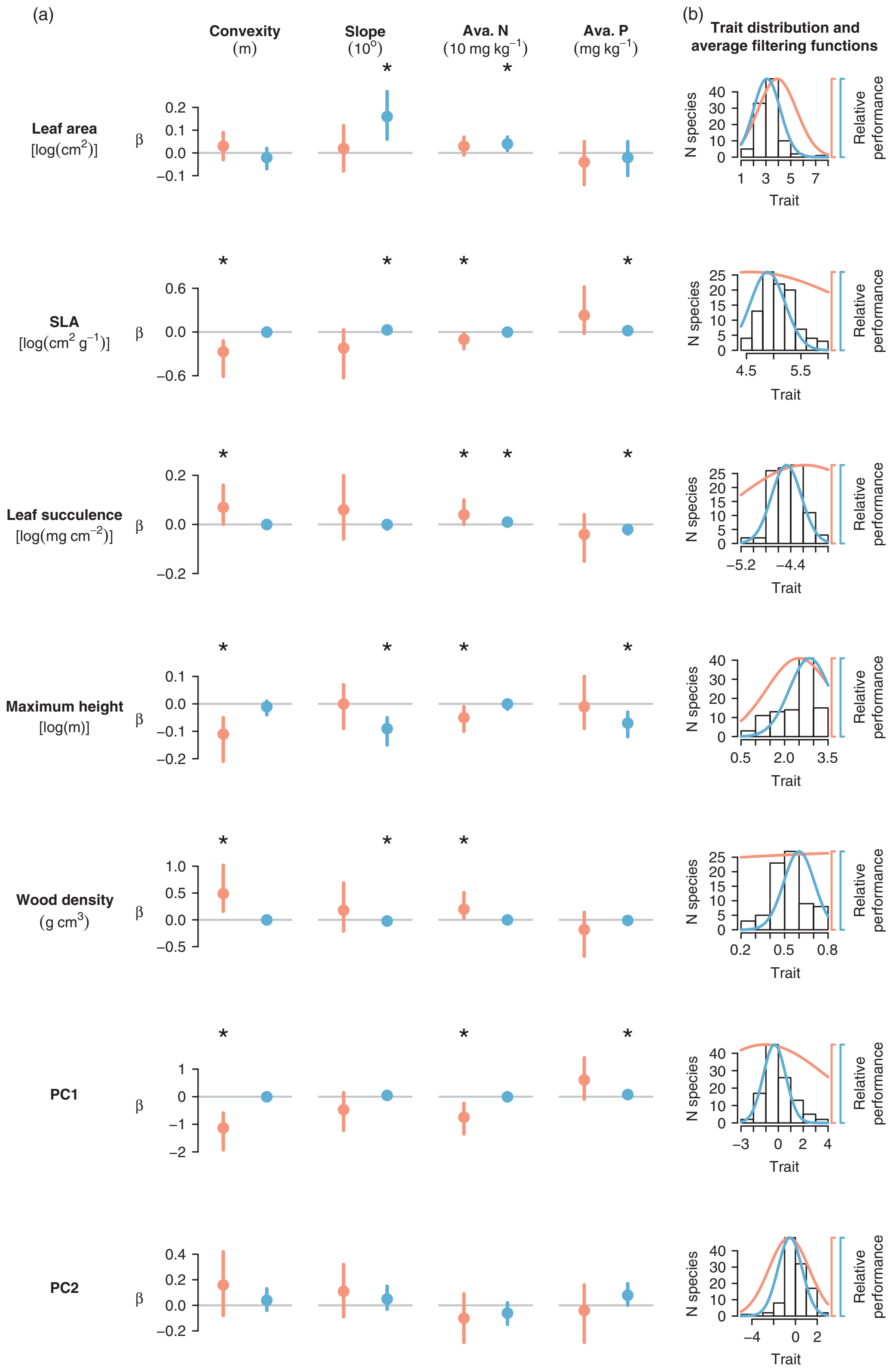

Fig. 3. Growth model (red) and survival model (blue) posteriors for environmental filtering. (a) Slopes of environmental effects β on the optimal trait value in each quadrat (dots show posterior means, and lines show 95% credibility intervals). Asterisks indicate environmental effects with a 95% CI excluding zero. The slopes of environmental effects are shown as trait units divided by environmental units. For example, for a 10° increase in quadrat slope, the optimal leaf area for survival is estimated to increase by 0.16 log(cm^2). (b) Histograms show distributions of species mean trait values. Red (growth) and blue (survival) curves show filtering functions ($\exp(F_{sq})$ from eqn 8) in the average quadrat (using posterior means of filtering functions). Note that because growth and survival link functions are different, the magnitudes of displayed filtering functions are not directly comparable.

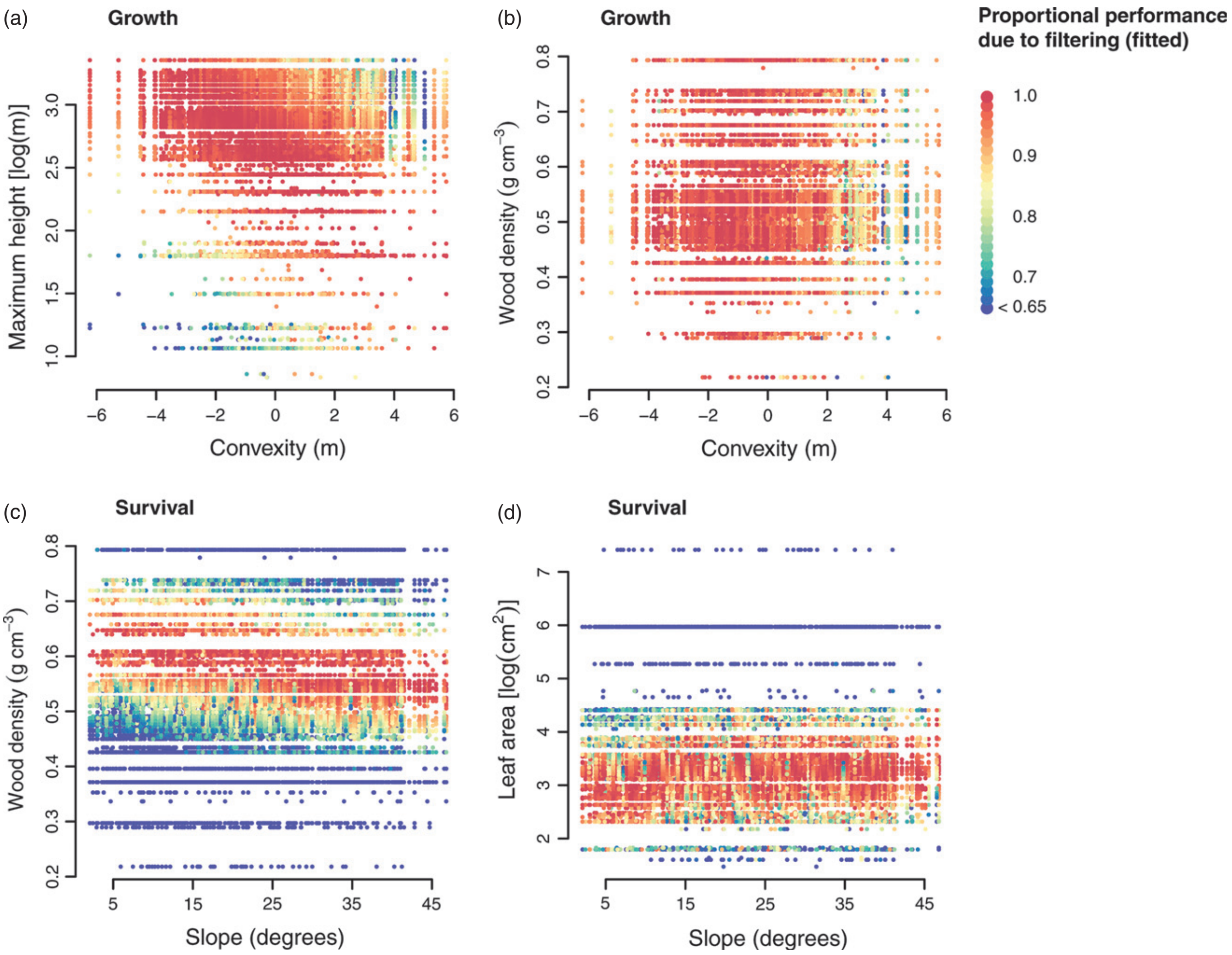

Fig. 4. Proportional growth (a & b) and survival (c & d) of individual trees due to filtering on trait axes. The trait axes with the strongest estimated filtering function (a & c) and the axes with the greatest spatial variability in trait optima (b & d). Species with the optimal value of each trait for their quadrat, μ_q, have proportional growth or survival equal to unity (red dots). Species experiencing the strongest negative effects of filtering because of their trait value are shown in blue. (a) As quadrat convexity increases, there is a decrease in the optimal value of maximum height for growth. (b) As quadrat convexity increases, there is an increase in the optimal value of wood density for growth. (c) As quadrat slope increases, there is a decrease in the optimal value of wood density for survival. (d) As quadrat slope increases, there is an increase in the optimal value of leaf area for survival.

LIFE-HISTORY TRADE-OFFS

Optima for growth versus survival were significantly positively correlated for four traits (leaf area, leaf succulence, maximum height and PC2), and leaf area showed the strongest correlation (Pearson's correlation, $\alpha = 0.05$, $P < 10^{-8}$, $R^2 = 0.05$, Fig. S1). Whereas growth and mortality optima were correlated along some trait axes, correlations were very noisy and the slope of the relationship was not unity for any trait. Differences in quadrat and plot-wide trait optima between growth and survival for the same traits indicate life-history trade-offs along trait axes (Fig. 3). However, life-history trade-offs were not apparent along individual environmental gradients. When trait optima were correlated with environmental variables (*i.e.* 95% CI of β excluded zero) for one demographic variable such as growth, trait optima for the other demographic variable were correlated with the environment in the same direction or were uncorrelated (Fig. 3).

COMPLEMENTARY ANALYSES

Complementary analyses using static data were partially concordant with our results. For growth, four of the 11 β with 95% CIs that excluded zero in our models (Fig. 3) were matched by significant correlations in the same direction between stem-weighted mean trait values in a quadrat and environmental conditions (general linear model, $\alpha = 0.05$, Table 2). For survival, five of the 14 β with 95% CIs excluding zero in our models were matched by significant static trait–environment correlations in the same direction. Static correlations were only slightly more concordant with our estimated β when we stratified comparisons by tree size class (Table S5).

Change in abundance-weighted trait variance of surviving trees revealed the strongest evidence for filtering amongst trait diversity metrics (Supporting Information). Five of seven traits showed significantly lower trait variance amongst surviving stems in quadrats when compared with null simula-

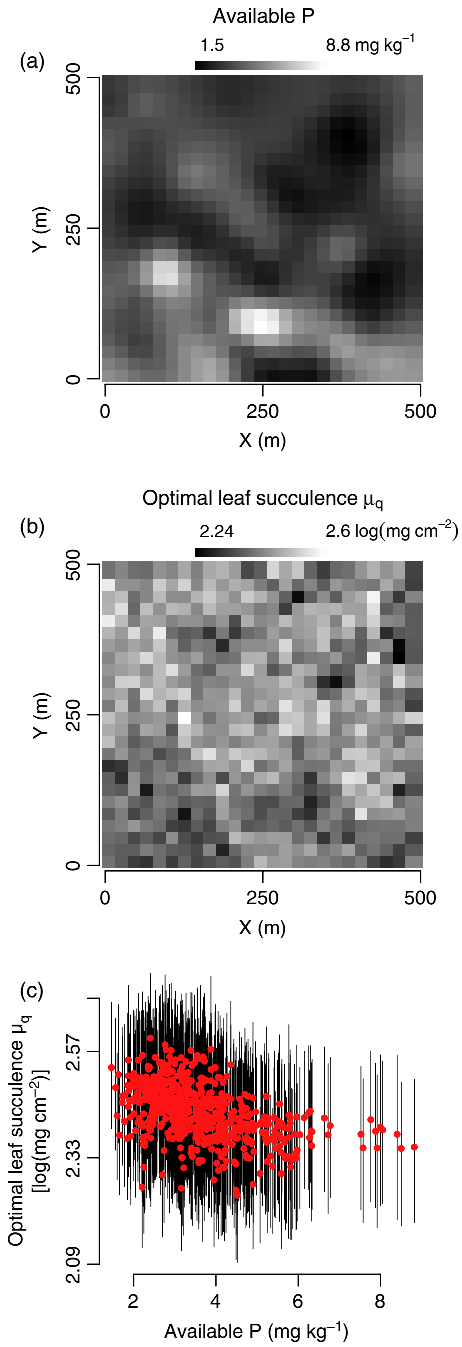

Fig. 5. As quadrat available P (a) increases, the optimal value of leaf succulence for survival (b) decreases (c). (a) A map of available P at the quadrat level. (b) A map of posterior means of optimal leaf succulence μ_q for survival across quadrats. (c) Dots show posterior means of optimal quadrat values of leaf succulence μ_q, and black lines indicate 95% CIs.

tions of mortality (Fig. S2, permutation test, $\alpha = 0.05$). Maximum height and PC2 diversity in the neighbourhood of surviving trees were significantly lower than those of dying trees (linear mixed effects model, $P < 10^{-5}$ for both traits), which were also the two traits with the strongest filtering for growth in our hierarchical models. For the other five traits, the neighbourhood trait diversity of living trees was significantly greater than that of trees that died (linear mixed effects model, $P < 0.01$ for all).

Discussion

Traditional studies of the environmental drivers of community composition largely rely on static community–environment correlations (Whittaker 1960; Harms *et al.* 2001; Valencia *et al.* 2004). Borrowing approaches from studies of natural selection (Haldane 1954; Wade & Kalisz 1990; Nagy & Rice 1997), we advanced beyond existing research by characterizing the relationship between environmental conditions and the performance of over 100 000 individual trees belonging to over 90 species. We placed axes of community-wide demographic variation in a functional trait context, which we use below to generate hypotheses about ecophysiological mechanisms of community variation. Additionally, we found broad evidence for filtering constraints across trait axes that may indicate a link between small-scale dynamics and long-term processes governing the species pool.

Our results suggest that the strength and spatial variability of environmental filters were constrained to a negative relationship. Thus, filtering on trait axes with the greatest potential effects on local community composition, i.e. traits with the strongest correlation with performance, were less likely to be involved in spatial niche differentiation that would promote species coexistence. We know of no theoretical prediction of this relationship. Part of the relationship stems from the lack of trait axes with both very strong *and* spatially variable filtering, which is likely due to the interaction between the plot environment and its species pool. For example, the elevation range on the plot was 113 m, which may be too limited to have dramatic effects on performance of most species present. Forces that shape the species pool, such as evolution, speciation and extinction, may have limited the presence of species that are highly specialized on a subset of conditions at Fushan FDP (Ricklefs 1987; Cornell & Lawton 1992). Low-magnitude environmental differences, fine-grained environmental heterogeneity and a limited ability for directed dispersal (*e.g.* as in most plants) can inhibit the evolution of specialization (Levins 1962, 1968; Futuyma & Moreno 1988). The environmental gradients in Fushan are probably fine-grained across the highly rugose surrounding mountainous region. Additionally, the spatial scale of analysis can affect whether environmental filtering is observed (Swenson & Enquist 2009; Pinto & MacDougall 2010), and future studies should examine smaller-scale filtering effects.

Environmental gradients associated with trait filtering were often different when considering growth versus survival, which could be a consequence of (i) distinct ecophysiological pathways affecting growth and survival and (ii) life-history trade-offs where increased growth in one environment is associated with increased mortality in another environment (Davies 2001; Russo *et al.* 2008). Principally, convexity and available N were associated with trait-based filtering of growth, whilst slope and available P were associated with

Table 2. Estimated slopes of general linear models, which relate interspecific mean trait values in quadrats (weighted by stem frequency) to quadrat environment

	Convexity (m)	*P*	Slope (10°)	*P*	Ava. N (10 mg kg^{-1})	*P*	Ava. P (mg kg^{-1})	*P*
Leaf area [log (cm^2)]	−0.040	< 0.0001	0.000	0.1999	−0.020	< 0.0001	0.016	0.0382
Specific leaf area [log (cm^2 g^{-1})]	−0.010	< 0.0001	−0.017	< 0.0001	−0.001	0.3482	0.007	0.0336
Leaf succulence [log (mg cm^{-2})]	0.000	0.6887	0.007	0.0024	−0.002	0.0169	0.005	0.0141
Max. height [log (m)]	0.010	0.0025	0.012	0.0354	0.001	0.5961	−0.024	< 0.0001
Wood density (g cm^{-3})	0.005	< 0.0001	0.003	0.0019	0.001	0.0003	−0.002	0.0501
PC1	−0.034	< 0.0001	−0.061	< 0.0001	−0.004	0.4567	0.028	0.0357
PC2	0.026	< 0.0001	0.009	0.1953	0.016	< 0.0001	0.009	0.1207

Slopes are given in units of trait/environment. *P*-values show results for testing the null hypothesis that slope = 0.

trait-based filtering of survival. Such alternate axes of resource specialization combined with life-history trade-offs may increase the number of coexisting species (Tilman 1994). Additionally, the weak correlations between environmental filtering for growth versus survival may serve as a demographic equalizing mechanism that promotes unstable species coexistence (Chesson 2000). Finally, four of the trait axes had significant positive relationships between optimal trait values for growth versus survival, indicating that a modest portion of spatial demographic variation was consistent across different vital rates.

Filtering along an axis of maximum height variation was the strongest for growth, and optimal height was negatively correlated with convexity and available N. Greater quadrat convexity, such as on ridges, may be associated with increased exposure to wind and with reduced soil moisture (Daws *et al.* 2002), especially at Fushan where summer typhoons and winter monsoon occur regularly. Shorter stature species may be favoured in higher-wind environments because they avoid damage, which if not fatal could impact negatively on growth (Lawton 1982; Sun, Hsieh & Hubbell 1998). Reduced soil moisture could also favour species with short growth forms that are less vulnerable to hydraulic limitation (Ryan, Phillips & Bond 2006). Note that maximum size is a strong predictor of absolute growth rates (Hérault *et al.* 2011), which may also be subject to filtering by convexity and available N. Previous studies in the region suggest that topographical disturbance patterns underlie tree community variation (Su *et al.* 2010). On Borneo, convex ridges and steep slopes had an increased rate of gap formation, higher light availability and a greater risk of mortality for large trees (Ohkubo *et al.* 2007). In Hainan, frequently disturbed stands were subject to less trait filtering than old-growth stands (Ding *et al.* 2012).

For wood density, survival filtering was strongest amongst the raw trait axes, and growth filtering was the most spatially variable. Slope was the strongest correlate of wood density survival filtering, favouring lighter wood on steeper quadrats and heavier wood on flat quadrats. Steep slopes are often associated with more frequent disturbances, shorter canopy height and greater light availability (Sun, Hsieh & Hubbell 1998; Ohkubo *et al.* 2007; Su *et al.* 2010). Increased disturbances on slopes may, thus, favour more rapid generation times and associated physiological traits such as low wood density. High light availability may increase the survival of fast-growing species with light wood that often have poor survival in shade (Augspurger 1984). Greater available P also favoured survival of species with light wood, consistent with findings that tropical trees with greater wood density tend to occupy poorer soils at the landscape scale (Gourlet-Fleury *et al.* 2011). However, high wood density species also had greater growth under high available N.

Environmental filtering has been proposed as an important driver of community variation on forest plots (Harms *et al.* 2001; Swenson & Enquist 2009; Kraft & Ackerly 2010; Shipley, Paine & Baraloto 2012), but environmental effects have rarely been documented where dispersal effects were definitively separated. By studying individual trees through time, we have avoided this problem. Similarly, Clark *et al.* (2010) tracked spatial variation in tree dynamics in the southeast of the USA. They found that heterospecific neighbours tended to have asynchronous dynamics, even though aggregate dynamics across plots were synchronous amongst species. Small-scale variation in environmental filtering was a likely explanation for locally asynchronous dynamics. Metcalf *et al.* (2009) showed that the growth and survival of nine species of Costa Rican rain forest trees responded differently to variation in light availability. We build upon such previous research by explicitly linking dynamics to species traits and environments.

We found that our estimated filtering functions were only partly concordant with static distributions (Table 2). However, we only modelled filtering of growth and survival, whereas spatial distributions were also likely affected by spatial variation dispersal, fecundity and recruitment (Uriarte *et al.* 2005). Although studies of static community patterns are limited in their ability to tease apart community drivers, such studies have the advantage of including effects at additional life stages that are difficult to observe, such as fecundity (*e.g.*

Kraft & Ackerly 2010). Our finding that static distributional patterns were incongruent with some environmental filters is unsurprising given that dispersal can obscure environmental effects. Dispersal may have had particularly strong effects on community composition in our 20 × 20 m quadrats because tree dispersal is highly variable at this scale (Clark, Clark & Read 1998) and species in diverse tropical forests are likely dispersal limited (Hubbell *et al.* 1999; Muller-Landau *et al.* 2008). Similarly, Pinto & MacDougall (2010) found that species distributions showed weaker correlation with environmental gradients than performance measures, possibly due to dispersal patterns. Finally, our study was conducted over a 5-year period, whereas distribution patterns are integrated over many tree generations. It is likely that our study overlooked the long-term effects of environmental filters and their temporal fluctuations.

There are multiple applications for the demographic models of trait-based environmental filters that we generated. A quantitative understanding of community mechanisms may be required to predict community dynamics under novel environmental conditions where phenomenological models fail (Webb *et al.* 2010) and to predict high-dimensional community dynamics with applications for biodiversity conservation (Keddy 1992). Our modelled environmental filters could form some of the building blocks of more process-oriented models of community assembly, which would permit detailed investigation into how underlying processes affect community composition and diversity (*e.g.* Levine & HilleRisLambers 2009). However, note that the traits we studied are sometimes indirectly linked to tree ecophysiology, and future studies would benefit from more detailed physiological measurements of an entire community (cf. Sterck *et al.* 2011). Finally, models of community-wide demography can be used to study trait and niche evolution of competing species (Hubbell 2006). Environmental filters at Fushan likely generate non-random phylogenetic patterns in community dynamics (Swenson & Enquist 2009), although we did not address phylogenetic patterns here.

Integration of filtering effects on seedling recruitment and fecundity would complete the modelled life cycle (Clark *et al.* 2010) and allow us to study population persistence and species diversity. We modelled the trait–performance relationship along a single trait axis at a time. However, performance may be affected by a many traits, and future studies should model multidimensional filtering. Future research could incorporate biophysical models of resource acquisition (Sterck *et al.* 2011), links between environmental conditions and the strength of filtering (Russo *et al.* 2008) and neighbourhood interactions (Cavender-Bares *et al.* 2004; Uriarte *et al.* 2010). Additionally, future studies of trait-mediated environmental filtering should incorporate intraspecific trait variation, which can be substantial and increase power to reveal filtering effects (Paine *et al.* 2011).

Conclusions

Our approach to elucidating environmental filtering was largely inspired by classic studies of natural selection, a field with a long tradition of linking trait variation to performance (Wright 1932; Haldane 1954). Environmental filters can drive spatial community turnover, just as environmental variation in the fitness–trait relationship can cause niche differentiation amongst genotypes, local adaptation and spatial diversity within species (Nagy & Rice 1997). We believe that additional insights may be gained by transferring ideas between environmental filtering and natural selection research because of the common focus on the interaction between environment, traits and fitness (Keddy 1992; Weiher & Keddy 1995; Webb *et al.* 2010).

We characterized environmental filters whose effects are mediated by interspecific trait variation, using a novel approach to study a large number of trees. The trait–environment axes we identified may underlie spatial niche differentiation and life-history trade-offs, promoting species coexistence. Filtering on trait axes with the strongest effects on local community composition may be constrained to weaker impacts on species coexistence across the plot. The weak spatial variation in filters with strong demographic effects may result from a preponderance of habitat generalists in the species pool.

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Supporting Information

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

Figure S1. Quadrat trait optima in each quadrat for growth compared to survival.

Figure S2. Four metrics designed to test evidence for environmental filtering based on trait diversity metrics.

Figure S3. Model of growth selection along an axis of leaf area.

Figure S4. SLA - growth.

Figure S5. Leaf Succulence - growth.

Figure S6. Height - growth.

Figure S7. Wood density - growth.

Figure S8. PC1 - growth.

Figure S9. PC2 - growth.

Figure S10. Leaf area - survival.

Figure S11. SLA - survival.

Figure S12. Leaf succulence - survival.

Figure S13. Maximum height - survival.

Figure S14. Wood density - survival.

Figure S15. PC1 - Survival.

Figure S16. PC2 - Survival.

Table S1. List of 110 tree species on the study plot in 2004 and 2009.

Table S2. Cross-trait correlations (Pearson product-moment correlation coefficient).

Table S3. Correlation (Pearson product-moment correlation coefficient) between environmental variables and the first five principal components of environment.

Table S4. Posterior estimates for selected parameters.

Table S5. Mean stem standardized trait value correlations to standardized quadrat environments (general linear model), stratified by tree size class.