In the lack of extreme pioneers: trait relationships and ecological strategies of 66 subtropical tree species

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Abstract

\textbf{Aims}

Despite the growing interest in the topic of functional ecology, there are still forest regions that have not been examined, as most work has been done in the tropics. Unresolved issues include the strength of a growth-mortality trade-off in trees (originally identified for seedlings) and the nature of the association between plant traits and vital rates, if any. Our objectives were to examine whether (i) ecological strategies in South American mixed forests are organized along the fast competitor \times slow stress-tolerator and height gradients as the main strategy axes depicted in the overall trait and vital rate correlation structure, and (ii) a tentative path model we proposed can explain the patterns of covariation among traits and vital rates.

\textbf{Methods}

We studied a different habitat (subtropical mixed conifer-hardwood forests) and region (Brazilian Atlantic Forest) from the majority of related studies in forests, carried out in the Neotropical region. Data on total height, stem slenderness, crown depth, wood density, specific leaf area, leaf and seed length, seed dispersal mode, annual mortality, diameter relative growth rate and relative growth rate under favorable conditions were measured in southern Brazil for 66 tree species. Data were subjected to principal components analysis and path analysis. Restricted data on saplings and treelets were analyzed through correlation.

\textbf{Important Findings}

Studied traits were reduced to four principal components. Principal components analysis produced axes that fit the resource acquisition versus resource-conservation and the height-mortality trade-offs, although the former was split into two distinct axes. Seed size and seed dispersal mode appeared independently of these axes. A path model showed that leaf length and specific leaf area caused direct changes in trunk slenderness and, indirectly through growth, affected mortality. Expected trade-offs between growth and survivorship and between wood density and stem slenderness trade-offs were not found. This may result from the lack of extreme pioneers and over-representation of slow-growing hardwood species found in Atlantic subtropical forests of South America. This suggests that the fastest growing species in the region do not grow so fast as to compromise wood density and survivorship, but grow fast enough to benefit from increased size. Relationships between traits and vital rates seem to be mediated by the assembly process of regional floras, and the relative importance of traits like SLA and wood density may vary between floristic regions.

\textbf{Keywords:} Araucaria angustifolia, Atlantic forest, ecological strategies, life-history trade-offs, mixed forests

Received: 29 April 2014, Revisited: 5 October 2014, Accepted: 12 October 2014
INTRODUCTION

Tropical and subtropical forests are rich ecological systems not only because of their high species diversity but also because of the high diversity of traits and ecological strategies shown by their constituent species. Strategy diversity evolved in the form of multiple correlated traits and vital rates in life-history trade-offs (Adler et al. 2014), as a response to competing demands on organisms (Grime and Pierce 2012). Ecological strategies are more than simple sets of correlated variables. They also include cause and effect relationships between traits, which are only beginning to be understood (Adler et al. 2014; Falster and Westoby 2005; McGill et al. 2006; Westoby et al. 2002). Additionally, ecological strategies form the basis for the identification of groups of species capable of simplification of complex systems while retaining key information for modeling (Gourlet-Fleury et al. 2005; Souza et al. 2014), management and restoration purposes (Turner 2001). For these reasons, the ecological and functional diversity of tree species requires understanding and simplification, particularly so in the tropics and subtropics.

Despite the growing interest in the topic of functional ecology (Vielle et al. 2007; Wright et al. 2010), there are still forest regions that have not been examined, as most work has been done in the tropics (Adler et al. 2014; Kraft et al. 2010; Wright et al. 2007). Evolutionary, climatic and historical constraints in the assembly of regional floras can affect relationships between traits and demographic performance. The austral origin of many taxa in subtropical Atlantic forests of South America (Gonçalves and Souza 2014) makes this an interesting case, with high density of groups such as Myrtaceae, known to lack a wood density-survivorship trade-off (Kraft et al. 2010). Here, we ask whether South American subtropical forests reveal the same ecological strategy trends and trait relationships found in regions with other phylogeographies.

Theoretical models and empirical observations suggest the existence of a few main axes of trait and vital rate variation in plants (Loehle 2000; Reich 2014; Westoby and Wright 2006). One of these axes represents a resource acquisition × stress tolerance or fast–slow trade-off (Grime 1977; Grime and Pierce 2012; Reich 2014). It has been proposed (Grime and Pierce 2012) that competitor or pioneer species are characterized by a fast use of readily available resources as light, nutrients and water through the production of large and inexpensive leaves with high specific leaf areas (SLAs), shallow crowns, low wood density, fast growth, slender trunks and high mortality (Condit et al. 1996; Diaz et al. 2004; Fan et al. 2012; Gourlet-Fleury et al. 2005; Kraft et al. 2010; Loehle 2000; Picard et al. 2012; Poorter et al. 2006, 2008; Reich 2014; Van Gelder et al. 2006; Wright et al. 2003, 2004, 2010). Stress-tolerant or shade-tolerant/late successional species would be adapted to withstand the stress represented by deep shade, being characterized by the opposite traits and vital rates except crown depth (Grime and Pierce 2012). Another important axis would be based on potential size. It has been assumed to represent the vertical partition of the light resource and should correlate with potential height (positive correlation), crown depth (positive correlation), mortality (negative correlation) and longevity (positive correlation; Deng et al. 2008; Loehle 2000; Picard et al. 2012; Poorter et al. 2006; Turner 2001; Westoby 1998). Reproductive traits are expected to form independent strategy axes (Loehle 2000; Sutherland et al. 2000; Westoby 1998; Westoby and Wright 2006; Westoby et al. 2002; but see Deng et al. 2008). Unresolved issues include the strength of a growth-mortality trade-off in trees (originally identified for seedlings, Condit et al. 1996; Poorter et al. 2008; Wright et al. 2003, 2010) and the nature of the association between plant traits and vital rates (if any, e.g. Kraft et al. 2010).

These major trade-offs involved in the evolution of ecological strategies (Onoda et al. 2013; Wright et al. 2004) may not exhaust all possible relationships between traits and vital rates. The usual dimensionality reduction approach employed in the analysis of trait and vital rate relationships (Easdale et al. 2007; Falster and Westoby 2005; Loehle 2000; Onoda et al. 2013; Westoby and Wright 2006; Wright et al. 2004) has left this complexity unexplored (but see Wright et al. 2007). We advanced a tentative model for some of the main direct and indirect relationships between size, leaf and vital rates that comprise tree life histories (Fig. 1). It was based on the premise that in closed-canopy forests, relationships between traits and vital rates include among-axes as well as within-axis relationships, and also that plant morpho-structural traits determine tree architecture both directly and indirectly through growth and mortality rates. In this model, leaf size and SLA are strongly related to light capture and use efficiency (Cerabolini et al. 2010; Reich 2014; Wright et al. 2004; but see Poorter et al. 2008). High wood density is thought to limit growth but increase stress tolerance through endurance of resource deprivation, and resistance against natural enemies (Chave et al. 2006; Fan et al. 2012; Kraft et al. 2010; Poorter et al. 2008). We thus expected that leaf length and SLA increase the relative growth rate (RGR) while wood density decreases it. Growth is expected to trade-off survivorship (i.e. to be positively related to mortality, Condit et al. 1996; Poorter et al. 2008; Wright et al. 2003, 2010). High growth rates and the accompanying resource-acquiring traits mentioned previously were expected to produce slender trunks that favor height over stability (Poorter et al. 2003; Falster and Westoby 2005; but see Méndez-Alonzo et al. 2012). Larger tree sizes are expected to be correlated with reduced mortality and higher growth rates necessary to produce them (Easdale et al. 2007; Poorter et al. 2008; Turner 2001; but see Wright et al. 2010). Deep crowns should be associated with increased tree size as a solution to both increased exposure to light and respiration loads (Poorter et al. 2006).

Our objectives were to examine whether (i) ecological strategies in South American mixed forests are organized along the fast competitor × slow stress-tolerator and height gradients as the main strategy axes depicted in the overall
trait and vital rate correlation structure, and (ii) the tentative path model presented in Fig. 1 can explain the patterns of covariation among traits and vital rates. We studied a different habitat (subtropical mixed conifer-hardwood forests) and region (Brazilian Atlantic Forest) from the majority of related studies. The biodiversity-rich (Souza et al. 2012) subtropical mixed forests in southern Brazil are dominated by the conifer Araucaria angustifolia, represent a transitional zone between the floras of southern and eastern South America (Gonçalves and Souza 2014), and are threatened by a recent history of heavy logging and fragmentation (Souza et al. 2012).

MATERIALS AND METHODS

Ten 1-ha plots were used to sample tree species at the São Francisco de Paula National Forest (29°25'S, 50°23'W), southern Brazil (Fig. 2). The National Forest is covered by biodiversity-rich subtropical mixed rainforest dominated by the emergent conifer A. angustifolia. Mixed Brazilian forests represent southern extensions of tropical and semideciduous Atlantic forests into subtropical latitudes (Gonçalves and Souza 2014). The National Forest stands as a well-conserved 1600-ha reserve in a landscape dominated by logged and grazed forest fragments (Souza et al. 2012). Five of the studied plots have never been logged, and the others suffered selective logging until 1955 or 1987 (find a detailed analysis of the plots and their history in Souza et al. 2012). Apart from selective logging history, the plots are similar in physiognomic, topographic and edaphic features. The diameter at breast height (dbh) and total height of all trees (dbh ≥ 9.5 cm) in each plot were recorded. Treelets (4.8 ≤ dbh < 9.5 cm) were sampled within each sample plot in randomly chosen 10 × 10 m subplots covering 10% of each sampled area (0.1 ha). Within each of the subplots used to sample treelets, saplings (0.95 ≤ dbh < 4.8 cm) were sampled in a 3.16 × 3.16 m (10.0 m²) subplot. Plots were investigated annually from 2000 to 2008. In 2000, bole (trunk segment from ground up to the first branch) height was measured for all trees.

We chose functional traits and vital rates (sensu Violle et al. 2007) known to reflect species adaptations to the horizontal and vertical light gradients, to reflect the fast–slow continuum (acquisitive versus conservative trait values) in the vegetative stage and the seed size colonization trade-off in the regenerative stage. Vital rates represent synthetic measures of a plethora of morphological, physiological and phonological traits besides biotic and abiotic factors that are hardly accessible in most part, and for this reason have been used alongside with functional traits in a number of studies (e.g. Poorter et al. 2008; Reich et al. 2003; Wright et al. 2003, 2010). RGRs equaled

$$RGR = \frac{\ln(DBH_f) - \ln(DBH_i)}{(t_f - t_i) \ln(DBH_f)},$$

where dbh is diameter at breast height, \(t\) is year and the subscripts \(f\) and \(i\) are final and initial values, respectively (Wright et al. 2003). Growth rates under favorable conditions equaled 95th percentile RGRs (growth_{95}, Wright et al. 2010). Although it is generally assumed that RGRs are an appropriate correction for size (e.g. Condit et al. 1996; Wright et al. 2003, 2010), Paine et al. (2012) have recently shown that, almost universally, RGR decreases with increasing plant size. This was not an issue for our analyses, however, as growth-mortality trade-offs were tested for saplings and treelets separately from trees, and our ordination and path model only include trees, for which RGRs are not expected to respond intensely to size (see Data analyses). Annual mortality rates equaled

$$M = 1 - \left[1 - \left(\frac{N_f - N_i}{N_i}\right)^{1/97.46}\right],$$

Figure 1: theoretical path model to test all hypothesized causal relations.
for $N_i$ initial individuals and $N_f$ survivors (Sheil et al. 1995). We excluded palms because most palm species lack dbh growth, and species with fewer than five individuals to calculate RGR and mortality. We used larger seed length (excluding wings or other structures that aid wind dispersal) as a proxy for seed size and measured it with a digital caliper from herbarium Anchieta samples (PACA). When reproductive material was not available in the herbarium, seed length was obtained from the literature (See Supplementary Material for references). Seed dispersal mode (zoocoric or anemocoric) was obtained from the same literature as seed length. Wood density for each species was obtained from the literature (see Supplementary Material for references). Wood density values for *Cestrum intermedium* and *Ilex dumosa* correspond to genus means, a procedure supported by the finding that genus-level means give reliable approximations of values of species (Chave et al. 2006). The value for *Symplocos uniflora* could not be found in the literature and is the mean of the values for all species originally in our database ($N = 78$, Hair et al. 1998).

Maximum height (height hereafter) was used as a proxy for species size and was calculated as the 95th percentile of the height values in each species’ population (Poorter et al. 2003). Crown depth was the difference between a tree total height and bole height in 2000. Species-level crown depth was the average crown depth of all co-specifics for each species. Stem slenderness was the species-specific expected tree height for a standard dbh of 15 cm (Poorter et al. 2003) and was calculated from species-specific regression equations between height and dbh. SLA was obtained following Cornelissen et al. (2003). Blade length (leaf length hereafter) was used as a proxy for leaf size. Leaf length measurements were made on five fresh or herbarium leaves collected from different individuals per species. Traits and vital rates for each studied species can be found in Supplementary Tables S1 and S2.

**Data analysis**

Many multivariate analyses we applied are based on the premise that ecological traits and vital rates are independent from the phylogeny of the studied species (Webb 2000). To test this premise, a phylogenetic distance matrix was built according to the APG III (2009) using Phylocom 4.1 (Webb et al. 2008) and the supertree R20100701 (available at http://svn.phylodiversity.net/tot/megatrees/R20100701.new). Branch length at the species level was obtained using the ‘branch length adjustment’ procedure, following Wikström et al.’s (2001) minimum age estimates for families and genera. The independence between the trait and vital rate matrix and the phylogenetic matrix was tested through a Mantel test (Borcard et al. 2011) and a phylogenetic signal analysis, using the ‘philosig’ function of the PHYTOOLS 0.1–9 R package. We also performed a phylogenetic signal analysis using the evolutionary model-based metric of phylogenetic signal K (Blomberg et al. 2003). K has an expected value of 1.0 and otherwise provides a measure of the excess (when >1.0) or shortage (when <1.0) of statistical dependence among the tips compared with that expected when the data have evolved by Brownian motion.
Analyses involving saplings and treelets were restricted to the 26 species for which the above-mentioned sample size requirements could be achieved. For this data set, multivariate analyses like principal components analysis (PCA) could not be performed due to small sample size (Hair et al. 1998). We performed correlation analyses to evaluate the growth-survivability trade-off and pairwise relationships between traits and vital rates for saplings and treelets. We applied the Benjamini–Hochberg adjustment (Waite and Campbell 2006) to the 0.05 significance level, as the Bonferroni adjustment would risk greatly inflating the Type II error rate relative to the possible increase in the Type I error rate without adjustment.

To analyze large-tree trait and vital rate covariation patterns, we conducted a PCA on a correlation matrix using function ‘principal’ of the package Psych 1.3.2 in the RStudio 0.97.320 software. Saplings and treelets could not be included in this analysis due to sample size restrictions. When needed, traits and vital rates were log-transformed to achieve normality and all variables were standardized prior to analysis. Dispersal mode was included in the analysis as a dummy or indicator variable in which all wind-dispersed species were represented (indicated) by ‘1’ and all other species (animal-dispersed) were represented by ‘0.’ Principal components with eigenvalues ≥1.0 were retained for analysis. A varimax rotation method was employed to minimize the number of variables that have high loadings on each factor (Hair et al. 1998). Significance of component loadings was obtained from Hair et al. (1998) based on sample size needed to attain significance based on a 0.05 significance level, a power level of 80% and standard errors assumed to be twice those of conventional correlation coefficients. Following Hair et al. (1998), we regarded loadings ≥0.68 as of statistical significance and ≥0.50 as of practical significance. To more comprehensively test the causal model presented in Fig. 1, a complete path model was computed in AMOS 18.0 by using maximum likelihood (ML) estimation procedures (Grace 2006). Standard error estimates were obtained through standard ML bootstrapping techniques by using 5000 bootstrap iterations. Pathways were regarded whenever $P < 0.05$ or critical ratios $> 1.5$. Due to its high redundancy with average growth, the variable growth$^{95}$ was not included in the model.

### RESULTS

Size (maximum height), and leaf traits and vital rates were independent of the studied species’ phylogeny. The phylogenetic and the trait-vital rate matrices were not correlated (Mantel test, $r = 0.059; P = 0.17$, Supplementary Figure S1). Furthermore, mean phylogenetic signal ($K = 0.50, P = 0.06$) was not significantly different from $K = 1.0$ and 9 out of 10 variables had non-significant K values (data not shown, $K_{\text{min}} = 0.36, K_{\text{max}} = 1.00$).

Bivariate relationships involving saplings and treelets could be calculated for 26 species and are thus restricted to bivariate analyses. Treelet average growth (but not growth under favorable conditions, $P = 0.02$) was significantly correlated with tree growth ($r^2 = 0.73, P < 0.001$). Sapling average growth and growth under favorable conditions were highly correlated ($r^2 = 0.85, P < 0.00001$), but were neither related to sapling mortality nor to tree and treelet growth ($P > 0.15$). There was a marginally significant trade-off between sapling growth under favorable conditions and wood density ($r^2 = -0.52, P = 0.0059$, Benjamini–Hochberg corrected significance threshold = 0.0024).

The 11 tree trait and vital rate variables measured for 66 tree species (44.9% of the 147 species found in the 10-ha study area) were reduced to four principal components, which explained 75.0% of the variation in the data (Table 1, see species scores in Supplementary Table S2). The first ordination axis had large positive component loadings for stem slenderness and SLA (Fig. 3). The second axis had positive loadings for maximum height and crown depth. Wood density was

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**Table 1**: results of the PCA on traits of 66 tree species

<table>
<thead>
<tr>
<th>Traits</th>
<th>PCA axes</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(24%; 1.9)</td>
<td>(19%; 1.5)</td>
<td>(17%; 1.3)</td>
<td>(15%; 1.3)</td>
</tr>
<tr>
<td>Slenderness</td>
<td>0.83</td>
<td>0.15</td>
<td>−0.01</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Leaf length</td>
<td>0.44</td>
<td>0.16</td>
<td>−0.61</td>
<td>0.15</td>
<td></td>
</tr>
<tr>
<td>SLA$^*$</td>
<td>0.85</td>
<td>−0.01</td>
<td>−0.12</td>
<td>−0.06</td>
<td></td>
</tr>
<tr>
<td>Crown depth</td>
<td>0.18</td>
<td>0.86</td>
<td>0.12</td>
<td>−0.16</td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>−0.02</td>
<td>0.84</td>
<td>−0.13</td>
<td>0.24</td>
<td>0.72</td>
</tr>
<tr>
<td>Wind dispersal of seeds</td>
<td>0.34</td>
<td>0.07</td>
<td>0.28</td>
<td></td>
<td>0.76</td>
</tr>
<tr>
<td>Seed length</td>
<td>−0.36</td>
<td>0.01</td>
<td>−0.24</td>
<td></td>
<td>0.08</td>
</tr>
<tr>
<td>Wood density</td>
<td>0.03</td>
<td>0.07</td>
<td></td>
<td>0.88</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Loading components (eigenvectors) for each variable associated to each axis are shown. Percentage of the variance explained by each axis and eigenvalues are shown in parenthesis. Bold and underlined figures are of statistical ($P \geq 0.68$) and practical ($P \geq 0.50$) significance, respectively. $^*$SLA (m² kg⁻¹).


positively loaded on the third axis, whereas leaf length was negatively loaded on the same axis. Seed size and seed dispersal mode appeared positively on the fourth axis (Table 1).

The causal model fit the correlation structure between the trait and vital rate variables \(\chi^2 = 11.51; df = 7; P = 0.12\); normed fit index = 0.91; root mean square error of approximation = 0.10 (90% confidence interval: 0.00–0.20). However, 9 of the 18 path coefficients and the covariance between SLA and wood density were not significant. Leaf resource-capture traits caused direct changes in trunk slenderness and, indirectly through growth, affected mortality. Leaf length had a positive effect on growth, whereas wood density acted negatively on it. The causal model explained from 0.1% to 42.9% of the interspecific variation in growth, mortality, maximum height, slenderness and crown depth. Mortality was negatively affected by direct effects of height and crown depth, and also indirectly by resource-capture variables (leaf length and SLA) and wood density mediated by growth (Table 2). Maximum height had a strong negative effect on mortality due to reinforcing direct and indirect (through crown depth) effects. We ran the path model without the conifer A. angustifolia, but results were similar (not shown).

**DISCUSSION**

**Ecological strategies**

The tree species in our subtropical forest were distributed along four main strategy axes, which in turn indicate the existence of

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**Figure 3:** PCA ordination diagram of 66 subtropical forest tree species in southern Brazil. Lines represent correlations between PCA ordination axes and traits and vital rates. Traits that did not have significant loadings in the displayed PCA axes are not shown here. Sapling and treelet data were not available for the majority of species and were not included in this analysis.

**Figure 4:** Fit path model with significant paths. Standardized and unstandardized (within parentheses) path coefficients (along paths), correlations (along double-headed arrows) and squared multiple correlations \(R^2\), beside the boxes in bold are shown. The width of each line is proportional to the strength of the relationship. The U’s account for unexplained variance. Sapling and treelet data were not available for the majority of species and were not included in this analysis.
ecological strategies (Easdale et al. 2007; Falster and Westoby 2005; Loehle 2000; Westoby and Wright 2006). The first and third axes kept represented different aspects of the fast resource acquisition × slow stress tolerance trade-off, which has been predicted to occur in plants along light nutrient, and water gradients (Grime 1977; Grime and Pierce 2012; Reich 2014), and also underlies successional gradients (Condit et al. 1996; Easdale et al. 2007; Wright et al. 2005). Increased light acquisition capacity in the form of leaves that spread their mass over large areas (high SLA) was associated to slender stems, able to place leaves at comparatively large heights. Large leaves, on their turn, were related to lower wood densities (axis 3). The opposite of these traits are frequently linked with slow growth rates and stress-tolerating strategies and vital rates (Grime and Pierce 2012; Souza et al. 2014). This result lends support to the recognition of a universal trade-off in plant ecology (Cerabolini et al. 2010; Grime and Pierce 2012; Reich 2014) and its application to trees as well as herbaceous plants (Kilinç et al. 2010). Its separation in two distinct axes, however, indicates that the traits involved with this trade-off present more complex relationships than initially thought (see below). The universality of this trade-off is also in line with the global leaf economic spectrum (Diaz et al. 2004; Onoda et al. 2013; Reich 2014; Wright et al. 2004). As has been increasingly recognized (Deng et al. 2008; Falster and Westoby 2005; Loehle 2000; Picard et al. 2012; Poorter et al. 2006; Turner 2001; Westoby 1998), potential size formed a second strategy axis, with tree height associated with deeper crowns and denser woods. The segregation of reproductive traits, in our case seed size and dispersal mode, in separate strategy axes, has been detected as an ecological avenue for diversifying regeneration strategies (Loehle 2000; Sutherland et al. 2000; Westoby 1998; Wright et al. 2007) much broader than the traditional association with successional status (Loehle 2000; Westoby et al. 2002). This means that a diversity of strategies related to reproduction probably exist overlaid to the more traditionally recognized strategies related to resource acquisition (see Sutherland et al. 2000 for a purely reproductive classification of ecological groups).

### Traits and vital rates causal relationships

Our path model (Fig. 1) helped to uncover the causal relationships between the variables involved in the ecological strategies detected in the PCA and also revealed more complex relationships crossing such strategies. Broadly, the fit model reinforced the two main ecological axes uncovered by the PCA. This occurred because relationships between observed variables were segregated into two main sets of paths, that kept some correspondence to the resource acquisition × stress tolerance (leaf size, SLA and stem slenderness) and tree architecture (height and crown depth) strategy axes. Contrary to our expectations and in partial agreement with findings by Wright et al. (2007) for Neotropical forests, most relationships between strategy axes were not supported by the data (but see Deng et al. 2008 for a counterexample). Relationships between axes were mediated by the vital rates such as growth and mortality and, to a lesser extent, by wood density, through both direct and indirect effects. SLA (and leaf size by correlation) is a key trait underlying the leaf economic spectrum, which summarizes variation in several traits concerning carbon fixation and nutrient use (Onoda et al. 2013; Wright et al. 2004). Despite this, and as found by Wright et al. (2007) and Poorter et al. (2008) for Neotropical forests, SLA was only modestly informative of architecture variation and not associated to vital rates.

Although wood density had a weak negative relation with growth, it was positively related to mortality and stem slenderness. Fan et al. (2012) showed that diameter growth is limited by xylem anatomy and the lack of a strong correlation between wood density and growth rates is likely from the fact that wood density emerges from complex xylem properties. Stem slenderness increases with the light requirements of the species (Poorter et al. 2003), and species with slender stems grow more efficiently in height and have better access to light, than species with stouter stems (Gourlet-Fleury et al. 2005; Poorter et al. 2005). However, tropical species’ slenderness is negatively related to wood density and stiffness (Van Gelder et al. 2006), whereas at São Francisco de Paula, the reverse was found. A possible explanation for this unexpected result is the lack of extreme pioneers in this study forests (more on this point below). This complexity warns against the restriction of the discussion about ecological strategies to PCA-based results (Condit et al. 1996; Deng et al. 2008; Easdale et al. 2007; Grime and Pierce 2012; Sutherland et al. 2000), as they alone may be too limited to provide a deeper understanding of the ecological relationships on which strategies are based upon. Indeed, Adler et al. (2014) found that raw morphological traits underlie fast versus slow life histories despite weak correlation with vital rates.

Contrary to what has been found in tropical forests (Condit et al. 1996; Poorter et al. 2008; Wright et al. 2003, 2010), a

### Table 2: standardized total, direct (on the left within parentheses) and indirect (on the right within parentheses), effects from the path analysis; the direct effects represent path coefficients

<table>
<thead>
<tr>
<th></th>
<th>Growth</th>
<th>Mortality</th>
<th>Slenderness</th>
<th>Maximum height</th>
<th>Crown depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf length</td>
<td>0.29 (0.29; 0.00)</td>
<td>−0.13 (0.00; −0.13)</td>
<td>0.30 (0.26; 0.04)</td>
<td>0.01 (0.00; 0.01)</td>
<td>0.07 (0.02; 0.05)</td>
</tr>
<tr>
<td>SLA</td>
<td>0.10 (0.10; 0.00)</td>
<td>−0.14 (0.00; −0.14)</td>
<td>0.49 (0.48; 0.01)</td>
<td>0.04 (0.00; 0.04)</td>
<td>0.17 (0.10; 0.07)</td>
</tr>
<tr>
<td>Wood density</td>
<td>−0.18 (−0.18; 0.00)</td>
<td>−0.002 (0.00; −0.002)</td>
<td>0.25 (0.28; −0.03)</td>
<td>0.003 (0.01; −0.01)</td>
<td>0.04 (0.00; 0.04)</td>
</tr>
<tr>
<td>Growth</td>
<td>−0.27 (−0.23; −0.04)</td>
<td>0.14 (0.14; 0.00)</td>
<td>0.04 (0.04; 0.00)</td>
<td>0.04 (0.00; 0.04)</td>
<td></td>
</tr>
<tr>
<td>Maximum height</td>
<td>−0.44 (−0.28; −0.16)</td>
<td>0.11 (0.11; 0.00)</td>
<td>0.43 (0.41; 0.02)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crown depth</td>
<td>−0.34 (−0.34; 0.00)</td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
growth-survivorship trade-off (growth positively related to mortality) was not found in either saplings or seedlings (or which this trade-off is expected to be stronger, Wright et al. 2010) or trees. In fact, mortality was negatively correlated with growth and was associated with the stress (shade)-tolerance strategy (review in Pierce et al. 2005). This suggests that shade-tolerant species are more prone to and do not survive stem breakage due to falling debris better than fast-growing species (Van Gelder et al. 2006). Rather, they may persist due to high rates of recruitment (Easdale et al. 2007).

Another potential explanation for the lack of overall importance of SLA as well as growth-mortality and wood density-stem slenderness and wood density-mortality trade-offs is that our studied forests, due to its austral-Antarctic and chilling-sieved tropical flora (Gonçalves and Souza 2014), lack extreme pioneers and have an over-representation of slow-growing hardwood species and families. Some of these, like Myrtaceae, are known to lack a wood density-survivorship trade-off due to uniformly high wood density and generally low mortality rates attributable in part to elevated investment in defenses (Kraft et al. 2010). Fast-growing pioneers are responsible for corresponding extremes of growth and death rates and low-density wood and stem slenderness (Méndez-Alonzo et al. 2012; Turner 2001; Van Gelder et al. 2006; Wright et al. 2003, 2010). They also present high SLA, with corresponding low leaf structural resistance, and high rates of herbivory (Méndez-Alonzo et al. 2012; Onoda et al. 2013). The tree species in our study site presented low mortalities and had higher wood densities and slower growth rates than species in tropical Panama (Wright et al. 2003; their Fig. 2 compare with Fig. 1) and even in subtropical Argentina (Easdale et al. 2007). This suggests that the fastest growing species in Atlantic subtropical forests of South America do not grow so fast as to compromise wood density and survivorship (Chave et al. 2006; Kraft et al. 2010; Méndez-Alonzo et al. 2012; Van Gelder et al. 2006), but grow enough to benefit from increased size (Easdale et al. 2007). The recent history of selective logging in half of our study plots excludes the possibility of lack of pioneers due to homogeneous mature successional stage.

Overall, our results confirm the emerging suggestion that factors responsible for the relationship between traits vary at large spatial scales, at least between biomes and climate zones (Adler et al. 2014; Kraft et al. 2010), and thus, although the ecological interpretation of vital rates is largely unambiguous, this is not yet the case with plant traits (Fan et al. 2012; Violle et al. 2007; Wright et al. 2007). Relationships between traits and vital rates seem to be mediated by the assembly process of regional florras, constrained as it is by evolutionary, climatic and historical factors (e.g. Gonçalves and Souza 2014). Hence, the ecological significance of traits like SLA (Poorter et al. 2008; Wright et al. 2007) and wood density (Fan et al. 2012; Kraft et al. 2010) may vary between floristic regions. The strategy axes and relationships between traits and vital rates we studied may provide a useful approach for more realistically representing large and diverse sets of tree species in forest ecosystem models (Mcgill et al. 2006).

SUPPLEMENTARY MATERIAL
Supplementary material is available at Journal of Plant Ecology online.

FUNDING
Funding was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) through the grant ‘PELD - Bioma Araucária e suas Transições’ and by Energética Barra Grande (BAESA).

ACKNOWLEDGMENTS
We thank Arselino P. Morais (o Cabo), José R. Souza (o Bepe) and Tania Mara V. F. Souza for logistical support. Thanks to the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) and Artur J. Soligo for facilitation of access to the São Francisco de Paula National Forest, Renato Záchia for providing Annona seed length data, Vanderlei Debastiani and Leandro Duarte for helping with the phylogenetic analyses and Márcio Cunha for writing a C+ program for data handling. Elgin S. Perry suggested a practical way of classifying external species into the k-means groups. Comments by Courtney G. Collins, Edu Eliom, Robert C. Morrissy and two anonymous referees greatly helped to improve an earlier version of this manuscript. Conflict of interest statement. None declared.

REFERENCES


