Tree life histories in a montane subtropical forest: species differ independently by shade-tolerance, turnover rate and substrate preference

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Summary

1. To investigate life-history differentiation and an objective functional classification of tree species we analysed the demography of 29 species in subtropical montane forests in north-western Argentina.

2. We computed 13 growth, demographic, abundance and distribution variables based on: (i) two 5-year re-measurements of stems ≥ 10 cm diameter at breast height (d.b.h.) in 8 ha of old growth forest and 4 ha of secondary forest; (ii) assessments of tree crown illumination; and (iii) sapling counts under shade and on landslides.

3. We assessed the potential confounding effects of stem size and crown illumination on absolute stem diameter growth rate for the 24 most abundant species. As diameter increased, one species showed significant increases in growth rate and five showed significant reductions. Seventeen species grew significantly faster with increased exposure to light and we controlled for this confounding effect in the computation of diameter growth rates for subsequent analyses.

4. A principal component analysis resulted in three meaningful and interpretable axes of demographic variation across species. The first axis (interpreted as shade tolerance) indicates that trees of species with inherently high growth rates tend to have well-exposed crowns at 10–30 cm d.b.h., have high density of trees in secondary forest and are less tolerant of shade.

5. The second axis (turnover) shows that in old-growth forest short-lived species, with high mortality rates, size-class distributions with a steep negative slope and low dominance, persist due to high rates of recruitment (to ≥ 10 cm d.b.h.).

6. The third axis indicates that species that colonize landslides have lower tree recruitment rates and greater growth variability in secondary forest, reflecting spatio/temporal differences in species' recruitment linked to differences in their substrate requirements for regeneration.

7. Maximum height and diameter are correlated with the first and second axes, indicating that higher rates of both growth and survival permit some species to attain large size.

8. All three demographic axes depict separate trade-offs that confer competitive advantage to each 'demographic type' under contrasting ecological conditions (of light availability, disturbance frequency and disturbance intensity), thus underpinning species' coexistence in dynamic forest landscapes.

Key-words: demography, forest dynamics, functional classification, longevity, maximum height, species coexistence, trade-off

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Introduction

The wide variation in the life histories of tree species implies that studies at the whole-stand level are poor descriptors of the diversity of dynamic processes occurring within a forest. Research on inherent demographic differences amongst species (e.g. Alvarez-Buylla & Martínez-Ramos 1992; Clark & Clark 1992; Hubbell & Foster 1992; Swaine 1994; Turner 2001) allows us to discriminate both the fundamental demographic types that comprise forest communities and the main features that distinguish them. This then provides insight into ecological processes and mechanisms such as species coexistence and abundance structure (Condit *et al.* 2006).

A functional classification of species based on demography has good potential for simplification. Demographic performance not only reflects the intrinsic life-history features of a species but also integrates its ecophysiological response to a diverse set of biotic and abiotic factors in a 'top-down' approach (cf. Zeide 2003). For example, growth rate is the outcome of numerous traits that underlie trade-offs amongst resource acquisition, defence against natural enemies, and allocation to reproduction and storage (Bazzaz & Pickett 1980; Clark & Clark 1999; Baker *et al.* 2003). As a result, a separation of species based on growth rates summarizes their response to a series of ecological factors, some of which are difficult to measure or may be ignored. Similar reasoning can be applied to other demographic descriptors. At the same time, this indicates that demography-based classifications carry a risk of oversimplification because similar demographic outcomes (e.g. growth rates) can result from different processes.

Three main sets of relationships between life history traits have been reported in quantitative comparisons amongst coexisting tree species in lowland tropical rain forest (Fig. 1). One set of associations involves population turnover rates: species' longevity correlates inversely both with recruitment rate (Lieberman *et al.* 1985; Laurance *et al.* 2004) and mortality rate in mature forest (Korning & Balslev 1994; Laurance *et al.* 2004), and recruitment and mortality rates are positively correlated (Lieberman & Lieberman 1987). In general this means short-lived species with fast rates of population turnover can be differentiated from long-lived species with slow population turnover.

A second set of associations is linked to a species' shade tolerance. The common observation that light-demanding species grow faster in the seedling/sapling stage seems to hold for larger trees. Growth rates of pioneer trees were found to be double those of more shade-tolerant species (Swaine 1994); and species' 'colonizing index', defined as the proportion of recruits found in canopy gaps, was positively correlated with tree (10–20 cm diameter) growth rates across a wide range of shade conditions (Condit *et al.* 1996). Manokaran & Kochummen (1987) also found that light-demanding
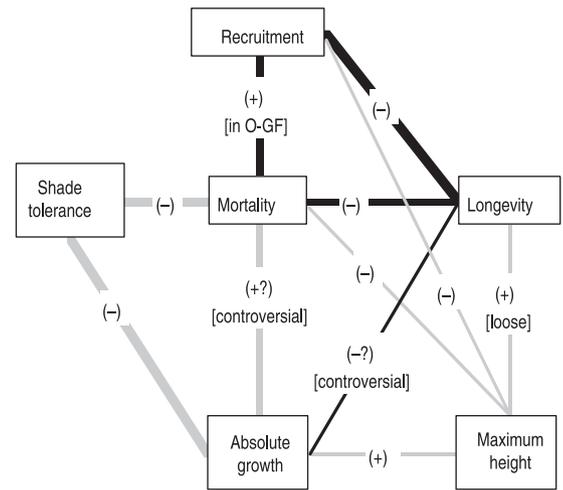
Fig. 1. Interspecific relationships between demographic variables in old-growth lowland tropical rain forest reported by comparative studies with permanent sample plots throughout the world. Associations connected with turnover rates are indicated by thick black lines, with shade tolerance by thick grey lines, the relationship between growth and longevity by a thin black line, and maximum height by thin grey lines.

species have high inherent mortality rates. The compromise between high growth rate in well-lit conditions and high mortality rate under shade for light-demanding species, and the opposite trend for shade-tolerant species, is frequently observed in saplings (e.g. Kobe *et al.* 1995). However, this pattern is more contentious for large trees (Clark & Clark 1992). For example, Condit *et al.* (1996) found it to apply to canopy species but not to subcanopy species.

A third consistent set of associations has been reported between a species' maximum height and several demographic variables (Fig. 1). Tall-growing species tend to have higher average and maximum growth rates in comparison with understorey species (Lieberman *et al.* 1985; Manokaran & Kochummen 1987; Korning & Balslev 1994; Swaine 1994; Thomas 1996; Clark & Clark 1999; Turner 2001). These associations could be attributed to a differentiation in species responses to vertical gradients of light, analogous to the differentiation between pioneer and shade-tolerant species in response to horizontal gradients of light (Thomas & Bazzaz 1999). Some studies also report that short species exhibit higher mortality rates than tall species due to the effects of shade, falling debris and earlier senescence (Manokaran & Kochummen 1987; Clark & Clark 1992; Korning & Balslev 1994; Condit *et al.* 1995; Nascimento *et al.* 2005). In addition, species that reach tall stature have lower relative recruitment rates (Kohyama *et al.* 2003; Nascimento *et al.* 2005) and a weak tendency to achieve greater longevity (Lieberman *et al.* 1985; Korning & Balslev 1994).

The degree of collinearity among the sets of relationships summarized in Fig. 1 is uncertain. For example, the relationship between growth and longevity is

controversial. The r–K and related fast–slow continuum axes of life-history differentiation suggest that fast-growing species tend to be short-lived while slow-growing species tend to be long-lived (Silvertown & Charlesworth 2001). However, while this trend seems to apply in some empirical studies (Loehle 1988; Laurance *et al*. 2004), Lieberman *et al*. (1985) and Lusk (1999) found maximum growth rates to be largely independent of longevity.

CONFOUNDING FACTORS: SIZE AND RESOURCES

A number of authors have recognized that average demographic variables are imperfect descriptors of species' life histories (Sheil 1995; Clark & Clark 1999; Wright *et al*. 2003). The intrinsic variability of demography within each species and the influence of confounding factors (i.e. tree size and growth conditions) partially explain the lack of clear and consistent relationships between demographic variables amongst coexisting species. Tree size and age may affect growth, survival and fecundity (Harper 1977) due to ontogenetic changes in morphology and ecophysiology, and due to size-related variation in resource conditions. Examples are the shifts in light response of non-pioneer light-demanding trees (Oldeman & van Dijk 1991; Whitmore 1998) and of trees that establish in well-lit conditions but can later tolerate substantial shade (Oldeman & van Dijk 1991; Clark & Clark 1992; Whitmore 1998; Dalling *et al*. 2001).

In addition to their inherent differences among species, recruitment, growth and mortality rates are also moderated by resource levels (Swaine 1994; Baker *et al*. 2003). Therefore, when comparing species' life histories, demographic rates should be measured under comparable resource conditions. Otherwise similar average demographic rates may disguise significant life-history differences among species, e.g. between those that are unresponsive to the environment and those whose performance in optimal conditions is counteracted by poor performance in unfavourable conditions.

OBJECTIVES

The general purpose of this study was to assess the associations between demographic and population-structure variables amongst co-occurring tree species in the under-studied subtropical montane forest. The objectives were to (i) find out if these correspond to the associations previously found for lowland tropical rain forest (Fig. 1) and (ii) determine if they can be reduced to an objective framework for ecological classification of tree species. In particular, the following questions were addressed. (i) How does absolute diameter growth vary with stem size and light environment? (ii) With the confounding effects of tree size and light level controlled, are the associations among demographic variables identified in previous studies (Fig. 1) identifiable and

separable from each other as independent multivariate axes? For instance, does a single pioneer/shade-tolerance axis account for most variation in recruitment, growth, mortality and longevity? Or are there other important axes of life-history variation? (iii) How are abundance and population structure variables, such as stem density and size-class distribution, related to demographic variables/axes? (iv) Are the structural characteristics, (a) maximum tree size and (b) mean number of stems per individual, correlated with demographic variables and axes?

Methods

STUDY SITE

The study was undertaken within the Argentinean *Yungas* forests (Cabrera & Willink 1980), a subtropical extension of tropical Andean montane forests, in Parque Biológico Sierra de San Javier (27°S), Tucumán, Argentina. The sample plots are situated between 700 and 1010 m a.s.l., within the elevation belt known as Selva Montana or lower montane forest (Grau & Brown 1995). The park is a nature reserve of semi-deciduous forests with an uneven canopy reflecting frequent natural disturbance. Mean annual rainfall fluctuates between 1300 and 1600 mm and is distributed in a seasonal monsoonal regime with a dry winter season (Bianchi & Yáñez 1992). Mean annual temperature is 18 °C, with the absolute minimum of –5 °C expected to occur once every 10 years (Torres Bruchman 1977).

PERMANENT SAMPLE PLOTS

The study was carried out in 1-ha permanent sample plots established in old-growth forest (O-GF, $n = 8$) across different topographic positions and in closed-canopy post-agricultural secondary forest (SF, $n = 4$) of different relative abundance of species (Grau & Brown 1998). The four SF and two of the O-GF plots were established in 1991; the six other O-GF plots were established in 1992 (Appendix S1 in Supplementary Material). Three SF plots are on sites with slope < 15% in forests that were, respectively, 11–12, 20–25 and 45–50 years old in 1991; the fourth plot is on a steeper slope (40–55%) in 45–50-year-old forest (Grau *et al*. 1997). A map and more detailed descriptions of the plots are provided in Appendix S1.

All stems ≥ 10 cm diameter at breast height (d.b.h.) were identified to species, marked with aluminium tags at breast height (1.3 m), mapped, and had their girth at breast height measured with a tape. Trees were considered alive when they had living tissue above the tag. Two re-measurements were carried out at 5-year intervals to record growth (change in diameter) and survival of pre-existing tagged trees, and new recruits ≥ 10 cm d.b.h.

We recorded the Dawkins's (1958) Crown Form Index and Clark & Clark's (1992) Crown Illumination

(or Crown Position) Index (CII) for every tagged tree during the late and early growing seasons in 2003. The CII classifies trees into seven categories based on the proportion of their crown that is exposed to direct vertical and lateral light (Table 1). We modified it to split the largest category, 3 (≥ 10 to $\leq 90\%$ of the vertical projection of the crown exposed to vertical light) to distinguish trees with less than half of their crowns exposed to vertical light (category 3 for ≥ 10 to $< 50\%$ vertical light) from those with at least half of their crowns exposed (category 3.5 for ≥ 50 to $\leq 90\%$ vertical light). All CII assessments were carried out by a team of six persons who followed a standard protocol (adapted from Clark & Clark (1992)) and used clinometers for assessment of vertical projections. The fairly open and relatively short forest canopy (9.7–16.8 m in height, Appendix S1) facilitated the discrimination of adjacent tree crowns and increased the reliability of our CII measurements.

Of 45 species recorded in the plots, we analysed only the 29 species with ≥ 13 living individuals ≥ 10 cm d.b.h. at the last census. This cut-off corresponds to a break in the species rank-abundance curve and represents a compromise between acceptable sample sizes and comparing as many species as possible. Sixteen of these species had at least seven individuals ≥ 10 cm d.b.h. recorded in both O-GF and SF at the last census, eight other species were mainly confined to O-GF, and the remaining five species were confined to SF (Appendix S2).

SPECIFICATIONS FOR DEMOGRAPHIC AND STRUCTURAL VARIABLES

We computed 16 variables for the 29 tree species (Table 1). (a) Response to illumination variables: (i) demographic shade-tolerance index, (ii) average crown illumination index and (iii) extreme pioneer index. (b) Growth variables: (iv) maximum growth rate, (v) average growth rate under more shaded conditions ($< 50\%$ of crown exposed to direct vertical light), (vi) average growth rate in more open conditions ($\geq 50\%$ of crown exposed to direct vertical light), (vii) growth rate variability. (c) Strictly demographic variables: (viii) relative recruitment rate, (ix) relative mortality rate and (x) minimum longevity (to reach the maximum measured d.b.h.). (d) Abundance and population structure variables (that can be interpreted as outcomes of demographic processes): (xi) stem density, (xii) basal area and (xiii) slope of population size-class distribution. (e) Structural variables: (xiv) maximum unified stem diameter at breast height (d.b.h.), (xv) maximum height and (xvi) average number of stems per individual.

These variables were selected to best meet the study's purpose because previous studies indicate that they are ecologically meaningful or have controversial inter-relationships. Four different growth variables were used to describe the large intraspecific variation in growth rate detected within natural populations of trees. Maximum growth rate isolates species' inherent growth potential from other demographic and environmental factors (Clark & Clark 1999); mean growth rates in open and in shaded conditions summarize growth in contrasting light environments; and the coefficient of variation of growth rate reveals the species' potential to react to changes in resources or environmental conditions (Korning & Balslev 1994).

The relationship between population size-class distribution and other demographic variables remains unclear; the shape of the size-class distribution appears to be a poor indicator of rates of population change but can be related to individual growth and survival rates (Condit *et al.* 1998). Size is a critical factor in the life history of tree species because forests exhibit strong vertical gradients of light (in addition to horizontal gap–shade gradients). Multiple stems can have important implications for transport of nutrients and reserves within a tree, and can increase longevity, but the demographic implications of this trait have not yet been examined in depth.

All demographic variables are based on 'individuals' with separate trunks at ground level. Each individual with multiple stems was transformed into a single virtual stem (by back-computing the d.b.h. from the summed basal area of joined stems) for computations that involve measures of stem diameter (i.e. growth rate, longevity, size-class distribution and maximum d.b.h.). Only stems that were alive in each census interval were included for computations of growth. All demographic variables were computed as 5-year rates. This avoided potential underestimation of recruitment and mortality rates (Sheil & May 1996) and errors in the estimates of growth rates that result from transforming 5-year rates to annual rates (Clark & Clark 1999).

To control for the impact of crown health on growth rate, all trees with 'very poor' crowns (Crown Form Index = 1) were omitted from computations of growth rates. Average CII was used as an indicator of each species' degree of affinity with exposed positions in the canopy, and the computations were limited to trees ≥ 10 and ≤ 30 cm d.b.h., to control for differences in maximum tree size and population size structure (i.e. crown exposure) amongst species. Clark & Clark (1992) and Davies *et al.* (1998) report that CII measured on saplings/juveniles is strongly correlated with canopy openness measured with hemispherical lens photographs.

Growth was represented as absolute rather than relative rate because there was no general correlation between the absolute diameter growth rate and size of individuals ≥ 10 cm d.b.h. when light conditions were controlled for. However, all four growth variables were restricted to trees 10–40 cm d.b.h. to control for interspecific differences in maximum size and the effect of size in the seven species that showed significant size–growth relationships. For computations of growth in open or shaded conditions, all records of trees that were judged to have experienced a clear change in crown light conditions since the last census (i.e. trees bordering or within recent tree-fall gaps) were omitted.

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Table 1. Variables computed for the 29 most common tree species in permanent sample plots at Sierra de San Javier, Argentina. * Treated as separate variables for old-growth and secondary forests

Variable	Abbreviation	Possible link with shade-tolerance axis	d.b.h./size	Temporal specifications	Measurement specifications	Measurement unit	Variable transformation
Response to illumination							
Shade-tolerance index	Shade tolerance	Recruitment under closed-canopy conditions	0.3–1.5 m tall	2004	Average density of saplings (> 0.3 and < 1.5 m) growing in the shade (i.e. below closed-canopy cover, indicated by a sapling crown illumination index of 2.5 or lower) divided by average density of large trees (≥ 10 cm d.b.h) in the three subplots (20 × 20 m) with the highest density of trees (≥ 10 cm d.b.h) for each species	Adimensional	Log
Crown illumination Index	CII	Close link with shade tolerance; large differences in species' rank compared with sapling shade tolerance may indicate ontogenetic changes in light response	10–30 cm d.b.h., to control for the effect of maximum height	2003–2004	Average CII (8 categories: 1 (no direct light); 1.5 (low lateral light); 2 (medium lateral light); 2.5 (high lateral light); 3 (crown lit with lateral light and ≥ 10% to < 50% vertical light); 3.5 (crown lit with lateral light and ≥ 50% to ≤ 90% vertical light); 4 (> 90% vertical light with lateral light blocked within some of a 90° inverted cone encompassing the crown); 5 (crown completely exposed to vertical and to lateral light))	CII units	None
Extreme pioneer index	Pioneer index	Indicates requirement for large gaps and/or denuded soil for recruitment	0.3–2 m tall	2004	(3: recruits on landslides only, 2: recruits on landslides and under forest canopy shade, or not found on landslides nor under forest canopy shade, 1: recruits under forest canopy shade only)	Adimensional	None
Growth variables							
Maximum growth rate	Maximum growth	Decreases with shade tolerance	10–40 cm initial d.b.h.	For individuals with two 5-year growth records measured within this size range, the larger record was used	Growth is change in d.b.h. over five years. The 90th percentile of 5-year growth records was computed for the population of each species	cm 5-year^{-1}	Log
Average growth rate in shaded conditions*	Growth shaded	Controversial: recent literature indicates that light demanders grow faster in shade (at least under some shade levels)	10–40 cm initial d.b.h.	1997–2002 only (immediately before the CII measurements)	Average growth rate (5-year^{-1}) of trees with < 50% of their crown exposed to direct vertical light	cm 5-year^{-1}	Log

Table 1. *Continued*

Variable	Abbreviation	Possible link with shade-tolerance axis	d.b.h./size	Temporal specifications	Measurement specifications	Measurement unit	Variable transformation
Average growth rate in well-lit conditions	Growth well-lit	Light demanders grow faster in open conditions	10–40 cm initial d.b.h.	1997–2002 only (immediately before the CII measurements)	Average growth rate (5-year^{-1}) of trees with ≥ 50% of their crown exposed to direct vertical light	cm 5-year^{-1}	Log
Growth rate variability*	CV growth	Controversial: are shade-tolerant species more variable in growth rate?	10–40 cm initial d.b.h.	The successive two 5-year growth periods were split as independent data points for each tree	CV of growth	Adimensional	None
Strictly demographic variables							
Relative recruitment rate*	Recruitment	Association with shade tolerance will depend on light conditions	≥ 10 cm d.b.h.	Averaged out over the two periods	Five-year recruitment rate of individuals in old-growth and secondary forests was divided by the number of individuals ≥ 10 cm d.b.h. alive at the start of each period (potential seed parents). This relative recruitment rate was then averaged between the two periods. Minimum tree size of seed set is not precisely known, but was < 10 cm d.b.h. for some species and 10 cm was taken as the minimum threshold	Trees recruited tree^{-1} 5-year^{-1}	Log
Relative mortality rate	Mortality	No simple relationship with overall mortality rate known	≥ 10 cm d.b.h.	Averaged out over the two periods	Proportion of individuals which died in each 5-year period relative to the number of individuals ≥ 10 cm d.b.h. alive at the start of the period; averaged over the two periods	Dead trees tree^{-1} 5-year^{-1}	Log
Minimum longevity	Min. longevity	A weak trend of increase with shade tolerance	Since reached 10 cm d.b.h.	Both 5-year census intervals were included	The boot-strapping method of Lieberman & Lieberman (1985), with modifications and Matlab code by Bullock *et al.* (2004), was used to estimate maximum growth curves (taken as the 90th percentile of growth). From these growth curves, minimum expected longevities to reach the maximum measured d.b.h. were calculated for each species. A window was defined for each species for the selection of growth increments that was proportional to its sample size. Zero growth autocorrelation was assigned when running the program	Year	Square root

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Table 1. *Continued*

Abundance and population structure variables (resulting from demography)

Variable	Abbreviation	Possible link with shade-tolerance axis	d.b.h./size	Temporal specifications	Measurement specifications	Measurement unit	Variable transformation
Stem density*	Density O-GF and SF	Density in O-GF increases with shade tolerance and density in SF decreases with shade tolerance	≥ 10 cm d.b.h.	2002 census	Computed with individuals, not stems	Individuals ha^{-1}	Log
Basal area*	Basal area O-GF and SF	Basal area weakly increases in O-GF with shade tolerance and decreases in SF with shade tolerance	≥ 10 cm d.b.h.	2002 census	For trees that were overlooked in the 2002 census (with no positive indication that they were dead) their BA records in the previous census were used	m^2 ha^{-1}	Log
Slope of size-class distribution*	Slope O-GF and SF	The slope is more negative for shade-tolerants in both forest types (after the initial establishment phase of SF)	10 cm d.b.h. to the 95th percentile of size	2002 census	The size range of each species (from 10 cm d.b.h. to the 95th percentile of size) was divided into eight equal size-classes (to control for the effect of maximum size on the slope of the regression line) and the slope of a linear regression computed between ln(N + 1) and the midpoint of each size class (N being the number of individuals per size class)	Adimensional	3-power O-GF/ 2-power SF
Structural variables							
Maximum unified d.b.h.	Maximum d.b.h.	No association known	n.a.	All three censuses were screened	Data from PSPs, cored trees and trees measured for maximum height outside the plots; d.b.h. was unified for multiple stems	cm	Log
Maximum height	Maximum height	No association known	Trees which had either large d.b.h. or seemed tall from visual estimations were selected for measurement	2003–2004	The average of the three tallest from the measured heights of six or more trees within the 12 ha of plots plus some large trees measured outside the plots	m	
Number of stems per individual	Stems per individual	No association known	≥ 10 cm d.b.h.	2002 census	Average number of stems alive at 1.3 m height per individual (individuals were those identified as separate trees at their trunk base). No distinction was made between individuals branched near ground level (real multistemmed trees) or between the base of the trunk and breast height (branched trees).	Stems per individual	Log

Analysis of correlations between growth and other variables was subjectively restricted to the 24 species with at least 15 individual growth records for trees 10–40 cm d.b.h.

Due to limitations in sample size, mortality rate was assumed to be constant with size. The boot-strapping technique of Lieberman & Lieberman (1985) was used to estimate growth curves for fast-growing trees, and thus the minimum life span ($\geq$ 10 cm d.b.h.) required to reach their largest unified d.b.h. Maximum, average and minimum estimated longevities were initially estimated, and were found to be well correlated with each other. Minimum longevity was used, however, because it showed a closer correspondence both with dendrochronological estimations of longevity available for some of the species and with the occurrence of pioneer species in SF of known age (Grau *et al*. 2003). As multistemmed trees have the potential for longer life-spans due to stem replacement, we may have underestimated their longevity.

DATA ANALYSIS

Partial correlations were used to test (i) the effect of (unified) stem diameter on absolute growth rate whilst controlling for the increase in crown exposure with size, and (ii) the effect of crown exposure on stem growth rate whilst controlling for stem diameter.

Principal components analysis (PCA) was used to summarize (i) the association amongst demographic variables, and (ii) the main trends of demographic differentiation amongst species. Seven variables were computed with the combined OG-F and SF data sets, but the two data sets were kept separate for the computation of (i) the three abundance and population structure variables (density, basal area and size-class distribution), for which difference between the two forest types was a powerful indicator of ecological differences amongst the species, and (ii) three other variables (average growth under shade, CV of growth and relative recruitment rate), which did not correlate between O-GF and SF amongst the species (see Results). Therefore, the PCA was based on 29 species and 19 variables (three light response, six growth, four strictly demographic, and six abundance and population structure). Following McCune & Grace (2002), variables with skewness > 1 were transformed (by $\log_{10}$ or square root as appropriate) to reduce the effect of asymmetry and (natural) outliers, and to improve the performance of the PCA. Logarithmic transformations were computed with a generalized procedure that tends to preserve the original order of magnitudes in the data (McCune & Grace 2002). The slope of size-class distribution regressions in O-GF and SF had negative skew and, after rescaling to positive values, we, respectively, cubed and squared them. Those variables that were computed separately for OG-F and SF (size-class structure, growth variability, and growth under shade) could only be computed for a subset of

species occurring in each forest type. The values for the missing species were replaced by the all-species mean, a conservative approach that has little effect on the outcome of the analysis when few means are introduced (McCune & Grace 2002).

We used the broken-stick method to identify interpretable ordination axes (Jackson 1993). This method discards ordination axes with eigenvalues that are lower than expected from a random partitioning of variance, which is predicted by the broken-stick distribution. A similar procedure, the bootstrapped broken-stick method, was used to evaluate the confidence of component loadings (Peres-Neto *et al*. 2003). This method re-samples entire rows from the original data with replacements and computes ordinations for each bootstrapped sample. The confidence of loadings was calculated by comparing the loadings generated by the bootstrapped samples with those predicted by the broken-stick distribution (Peres-Neto *et al*. 2003). For this purpose we used a Borland Pascal computer routine supplied by Pedro Peres-Neto, and based the analysis on 10 000 samples.

Results

CHARACTERISTICS AND TRENDS IN THE TREE COMMUNITY

A total of 3111 individual living trees (multiple stems unified) $\geq$ 10 cm d.b.h. were recorded in the last census of O-GF plots (388 ha^{-1}) and 1692 individuals in the SF plots (423 ha^{-1}). These correspond to 44 tree species in 41 genera and 25 families (Appendix S2). The density of trees $\geq$ 10 cm d.b.h. in SF remained stable through the 10 years of monitoring, with 435 trees ha^{-1} in 1991 and 423 trees ha^{-1} in 2001, but there was a clear change in species relative abundance. Of the 21 species with 10 or more individuals recorded in any one SF census, nine increased by more than 30% of their initial abundance over 10 years and two decreased by more than 30%. In contrast, there was a notable increase in density of all species in the O-GF, from 258 trees ha^{-1} in 1992 to 389 trees ha^{-1} of all species in 2002, accompanied by a change in species relative abundance (Appendix S2). Of the 24 species with 10 or more individuals none decreased by more than 20% of its initial abundance but 13 increased by more than 30%.

GROWTH VS. STEM SIZE AND CROWN ILLUMINATION

Of the 24 species tested, six showed significant associations between stem growth and size when the effect of crown illumination was controlled for; five of these (*Solanum riparium*, *Juglans australis*, *Allophylus edulis*, *Heliocarpus popayanensis*, *Pisonia zapallo*) were negative correlations and just one (*Morus alba*) was positive (Appendix S3). The partial correlations between stem diameter growth rate and crown illumination were

positive for 23 of the 24 species with ≥ 15 individual growth records and were strongly significant for 17 of these species (Appendix S3). We found no visual evidence for any clear nonlinear relationship between growth rates in open or shaded conditions and trunk diameter.

DEMOGRAPHY IN OLD-GROWTH VS. SECONDARY FOREST

CII for trees between 10 and 30 cm d.b.h. was the only variable with a significantly higher interspecific mean in SF than in O-GF (paired-sample *t*-test, $t = 4.9$, $P < 0.001$) in a comparison of 14 species with seven or more individual growth records in each forest type. The four growth variables and recruitment and mortality rates showed no significant differences between SF and O-GF. Correlation analyses of the mean values for these 14 species indicated that three variables, species' growth rate under shade ($r = 0.10$, $P = 0.73$), variability in growth rate ($r = 0.36$, $P = 0.20$) and recruitment rate ($r = 0.38$, $P = 0.18$), were not correlated between SF and O-GF and so they were kept separate for subsequent analyses. CII ($r = 0.84$, $P < 0.001$), maximum growth rate ($r = 0.71$, $P = 0.004$), growth rate in open conditions ($r = 0.74$, $P = 0.004$) and mortality rates ($r = 0.52$, $P = 0.05$) were correlated between SF and O-GF and so were recomputed with the combined data sets for subsequent analyses. Appendix S4 provides species' values for all demographic and population structural variables.

DEMOGRAPHIC TRENDS ACROSS SPECIES

The PCA ordination of tree species based on demographic variables resulted in four meaningful components when compared with the broken-stick distribution. These explain 74% of the total variance in the data (Table 2). The first PCA axis (variance explained = 30.9%) integrates all growth variables except growth variability and growth under shade in SF (Table 2). This axis also integrates species' dominance in SF, density in both forest types, and distribution of saplings and trees in relation to light conditions (Table 2). Shade tolerance and density in O-GF have a negative association with the other variables grouped by this axis. The importance of the associations amongst the variables linked to this axis is confirmed by the strength and sign of the bivariate correlations between them (Table 3). Some pairs showed highly significant correlations; the strongest was between maximum growth and growth in well-lit conditions (Fig. 2). Although variability of growth rates in O-GF did not have a significant association with the first axis according to the bootstrapped broken-stick method, this variable is significantly associated with several others that define the axis (Table 3), indicating that species with lower average growth rates and more shaded crowns tend to have greater growth variability.

The second PCA axis (explained variance = 18.4%) integrates the strictly demographic variables: estimated

Table 2. Cumulative percentage of variance explained by the components of a principal components analysis of 29 tree species and loadings of the 19 variables on the first four components extracted by the PCA. Bold numbers indicate significant loadings according to the bootstrapped broken-stick method (10 000 permutations)

	Axis 1	Axis 2	Axis 3	Axis 4
Percentage variance explained	30.9	18.4	13.7	11.3
log Maximum growth Co	**0.86**	0.00	0.33	−0.17
log Basal area SF	**0.81**	0.09	0.04	0.34
log Growth well-lit Co	**0.81**	−0.14	0.45	−0.12
log Growth shaded O-GF	**0.73**	−0.11	0.18	0.28
Crown illumination index Co	**0.70**	−0.12	0.03	0.38
log Density SF	**0.68**	0.03	−0.05	0.45
log Density O-GF	**−0.66**	0.22	0.30	0.35
log Shade tolerance	**−0.63**	−0.01	0.37	0.30
log Recruitment O-GF	−0.32	**−0.85**	0.16	0.07
Min. longevity ½	−0.39	**0.81**	0.06	0.13
Slope O-GF³	0.49	**0.76**	0.14	0.09
log Basal area O-GF	−0.36	**0.66**	0.34	0.38
log Mortality Co	−0.04	**−0.57**	−0.51	0.25
Slope SF²	0.42	**0.45**	0.22	−0.42
Pioneer index	0.58	−0.04	**−0.70**	−0.22
CV Growth SF	0.05	0.38	**−0.64**	0.26
log Recruitment SF	−0.31	−0.48	**0.61**	−0.03
log Growth shaded SF	0.24	0.06	0.38	**−0.74**
CV Growth O-GF	−0.47	0.31	−0.39	**−0.54**

Co = both forest types combined (SF = secondary forest; O-GF = old-growth forest); ½, ² and ³ are power transformations.
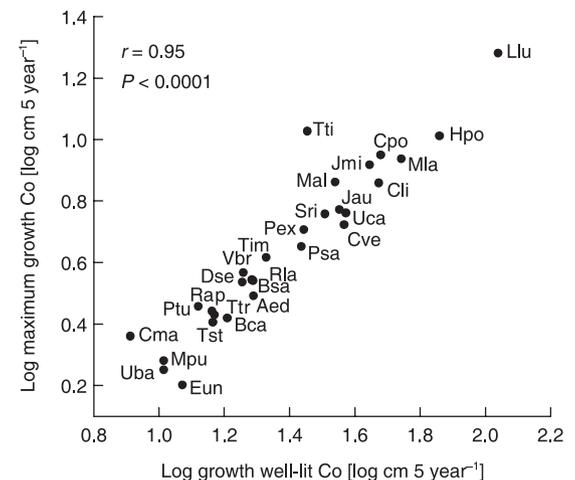
Fig. 2. Relationship between maximum growth rate and growth rate in well-lit conditions amongst tree species. Both variables are computed with the combined old-growth forest and secondary forest data sets. Growth in open conditions exceeds maximum growth values due to the artefact of using different order of magnitude constants for the log transformations (see McCune & Grace 2002). Species abbreviations are defined in Appendix S2.

longevity, recruitment rate in O-GF and mortality rate (Table 2). It also includes three population abundance/ structure variables: the regression slope of the size-class distribution in each forest type, and dominance in O-GF.

Table 3. Correlation matrix for demographic and structural variables for 29 montane forest tree species. Frames that expand from the upper–left corner discriminate traits grouped by each of the four Principal Components. Cases with a grey background and coefficients in bold show significant correlations at $P < 0.05$, underlined coefficients are significant at $P < 0.01$. Significance may differ for a given correlation coefficient due to varying degrees of freedom for variables that were estimated for only some species in old-growth forest (O-GF) or secondary forest (SF); Co is both forest types combined; $\frac{1}{2}$, ^{2} and ^{3} are power transformations. [Correction added after publication 31 August 2007: in Table 3 the entry −0.56 in for log Mortality Co/Slope O-GF^3 corrects the previously published value of 0.56]

Pearson correlation coefficient	log Maximum growth Co	log Basal area SF	log Growth well-lit Co	log Growth shaded O-GF	Crown illumination index Co	log Density SF	log Density O-GF	log Shade tolerance	log Recruitment O-GF	Min. longevity ½	Slope O-GF ³	log Basal area O-GF	log Mortality Co	Slope SF ²	Pioneer index	CV Growth SF	log Recruitment SF	log Growth shaded SF	CV Growth O-GF	Maximum height	log Maximum DBH	PCA Axis 1	PCA Axis 2	PCA Axis 3	PCA Axis 4
log Basal area SF	0.62																								
log Growth well-lit Co	0.95	0.61																							
log Growth shaded O-GF	0.73	0.72	0.68																						
Crown illumination index Co	0.61	0.50	0.59	0.59																					
log Density SF	0.44	0.94	0.46	0.59	0.39																				
log Density O-GF	−0.50	−0.30	−0.44	−0.49	−0.39	−0.21																			
log Shade tolerance	−0.48	−0.35	−0.37	−0.36	−0.31	−0.28	0.46																		
log Recruitment O-GF	−0.29	−0.30	−0.09	−0.12	−0.05	−0.25	0.22	0.25																	
Min. longevity ½	−0.31	−0.25	−0.39	−0.37	−0.25	−0.26	0.36	0.33	−0.63																
Slope O-GF ³	0.51	0.56	0.37	0.37	0.30	0.44	−0.23	−0.30	−0.85	0.55															
log Basal area O-GF	−0.23	−0.07	−0.27	−0.23	−0.17	−0.08	0.80	0.31	−0.39	0.67	0.54														
log Mortality Co	−0.25	0.04	−0.22	−0.01	0.13	0.10	−0.12	−0.04	0.53	−0.38	−0.56	−0.36													
Slope SF ²	0.61	0.45	0.56	0.33	0.23	0.09	−0.25	−0.24	−0.58	0.22	0.66	0.09	−0.31												
Pioneer index	0.30	0.36	0.19	0.32	0.29	0.32	−0.60	−0.73	−0.33	−0.35	0.17	−0.50	0.27	0.14											
CV Growth SF	−0.20	0.32	−0.41	−0.11	0.00	0.48	0.08	−0.24	−0.55	0.24	0.22	0.14	0.09	−0.05	0.44										
log Recruitment SF	−0.08	−0.29	0.10	−0.23	−0.34	−0.12	0.36	0.42	0.66	−0.29	−0.52	−0.03	−0.02	−0.35	−0.55	−0.51									
log Growth shaded SF	0.52	0.14	0.49	0.16	−0.28	−0.04	−0.16	−0.30	−0.13	−0.26	0.23	−0.12	−0.36	0.51	0.08	−0.24	0.25								
CV Growth O-GF	−0.59	−0.47	−0.66	−0.67	−0.70	−0.45	0.19	0.03	−0.22	0.36	−0.12	0.11	−0.04	−0.01	0.11	0.28	−0.25	0.25							
Maximum height	0.57	0.52	0.54	0.37	0.34	0.36	−0.12	−0.10	−0.50	0.32	0.75	0.31	−0.48	0.67	−0.14	−0.12	−0.18	0.15	−0.37			0.50	0.51	0.46	0.12
log Maximum DBH	0.51	0.47	0.42	0.28	0.24	0.31	0.03	−0.05	−0.65	0.55	0.78	0.49	−0.53	0.72	−0.16	0.08	−0.24	0.19	−0.13	0.86		0.39	0.72	0.41	0.09
log Stems per individual	−0.15	−0.01	−0.16	0.19	−0.34	0.05	0.25	−0.04	0.07	−0.07	−0.13	0.10	0.12	−0.09	−0.11	0.01	0.38	0.37	0.18	−0.30	−0.08	−0.13	−0.07	0.10	−0.09

The relationship amongst these variables is confirmed by the correlation matrix and, in particular, by the negative association of both recruitment in O-GF and combined mortality with the other four variables (Table 3). These relationships are underlain by the ecologically important negative associations between longevity and both recruitment rate in O-GF and mortality rate (Fig. 3).

The third PCA axis (explained variance = 13.7%) indicates that species that colonize landslides have greater variability of growth rate in SF, but lower recruitment rate to 10 cm d.b.h. in SF. This separation is more notable for species with intermediate to high light demand (i.e. those with high values along the first PCA axis; Fig. 4). Recruitment into ≥ 10 cm d.b.h. at the current stage of SF stand development is dominated by species (upper part of Fig. 4b) with high recruitment rates and size-class distributions with steep negative slopes in O-GF (Table 3). The associations between the variables are again reflected in the correlation matrix (Table 3).

Finally, growth rate of shaded trees in SF and variability of growth rate in O-GF are associated with the fourth PCA axis according to the bootstrapped broken-stick method (Table 2). However, these two variables are not significantly correlated (Table 3), which together with the low percentage of variance explained (11.3%) lessens the importance of this axis.

Although the PCA identifies orthogonal axes, the correlation matrix (Table 3) shows that some variables are associated with variables linked to another axis. This is notable for the slopes of the regressions of size-

class distributions in both forest types, which, in addition to the dominant association with Axis 2, are significantly correlated with variables linked to Axis 1, such as maximum growth rate and basal area in SF.

STRUCTURAL VS. DEMOGRAPHIC VARIABLES

Species' maximum d.b.h. and maximum height were significantly correlated with the species' scores along all the first three principal demographic components (Table 3). However, when single demographic variables are taken into account, maximum d.b.h. and height only correlate with variables linked to the first and second demographic axes. No association was detected for number of stems per individual tree.

Discussion

Consistent associations were found between demographic and population structure variables amongst the species examined. Tree species can be differentiated into demographic types or syndromes within the multidimensional space defined by three axes that are independent of each other; as such, this provides an objective framework for classification.

SHADE-TOLERANCE VS. POPULATION TURNOVER

Two of the life-history dimensions represented by the PCA axes, shade tolerance and population turnover

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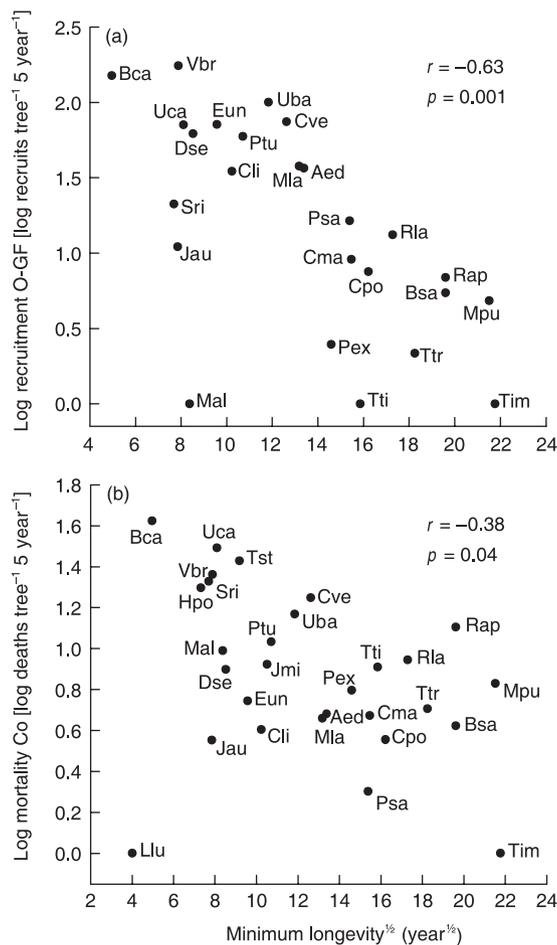
Fig. 3. Relationships between longevity of montane tree species and (a) recruitment rate in old-growth forest and (b) mortality rate in old-growth and secondary forests combined. Correlation coefficients and significance levels are shown for linear regressions. Recruitment rate in old-growth forest and mortality rate are positively correlated (Table 3). Species abbreviations are defined in Appendix S2.

rate, match well with the findings of previous studies in lowland tropical rain forest (Fig. 1). Our central finding is that these axes are orthogonal of each other. This is consistent with the observations of Lieberman *et al.* (1985) that species with slow maximum growth rate can be either understorey trees of short life span or subcanopy trees with longer life spans, whereas fast-growing species can be either short-lived shade intolerants or long-lived canopy species that tolerate shade but respond opportunistically to increased light levels. This indicates that the assumption that growth potential and longevity are negatively correlated (e.g. Condit *et al.* 2006) is not as strong or as universal as commonly thought.

As revealed by PCA axis 1, species with inherently fast growth (across a range of shade conditions) tend to recruit less commonly under shade, have more exposed crowns, and have larger populations in SF than O-GF. The positions of species along this axis follow a trend from species associated with shade towards the negative end of the axis, typical tree-fall gap colonizers in the middle, and species that commonly recruit after large-scale

disturbance (i.e. in SF) towards the positive end (Fig. 4). This interpretation is based on (i) the associations of this axis with species' relative abundances in SF and O-GF, and shade tolerance and crown illumination indices, and (ii) the observation that three of the four species (*Urera caracasana*, *Solanum riparium* and *Boehmeria caudata* but not *Urera baccifera*) classified as 'gap-dependent tolerant' by Grau & Brown (1998) were ordered in the middle of this axis (Fig. 4). This trend agrees with observations from several controlled studies that many (but not all) tree species perform differently in terms of establishment, growth and survival along light–resource gradients characteristic of the gap–understorey continuum (Brokaw & Busing 2000).

Previous work has indicated that early-successional species have more flexible physiological responses to light than late-successional plants (Bazzaz 1996). However, we observed a trend that species with high mean growth rates and more exposed crowns have less variable growth rates across a range of light conditions in old-growth forest, which does coincide with recent observations by Nascimento *et al.* (2005). One possible explanation for our result is the superior survival of shade-tolerant species at slow growth rates compared with light demanders (Kobe *et al.* 1995; Kobe & Coates 1997). Lieberman *et al.* (1985) observed that populations of long-lived species have more variable growth rates than those of short-lived species, but we found no association between longevity and variability in growth rate.

The second demographic axis shows that shorter-lived species, with high mortality rates, maintained their populations in O-GF through higher recruitment rates (to ≥ 10 cm d.b.h) during the 10-year study period. The axis also indicates that longer-lived species are more dominant in O-GF, where they have flatter size class distributions (i.e. a higher ratio of large to small trees). These results support the observation of Swaine *et al.* (1987) that the pattern of mortality in time and space is closely tied to species' maximum longevity and their distribution amongst size classes. They also accord with findings of a significant negative correlation between species' longevity and recruitment rate (Fig. 1, Lieberman *et al.* 1985; Laurance *et al.* 2004), and between longevity and mean annual mortality rate (Fig. 1, Korning & Balslev 1994; Laurance *et al.* 2004). On the whole, PCA axis 2 suggests that recruitment and mortality rates compensate each other for most species in O-GF and this will maintain the species abundance structure within the community (Lieberman & Lieberman 1987; Swaine *et al.* 1987; Burslem *et al.* 2000; Nascimento *et al.* 2005). This contrasts with the compensatory hypothesis of Connell *et al.* (1984), which proposes that the richness and abundance of species in old-growth forest is maintained due to compensatory mechanisms that favour rare species (in terms of density and basal area) over common species by means of higher growth, recruitment and survival rates. We did find a compensatory negative correlation between growth rate and density in
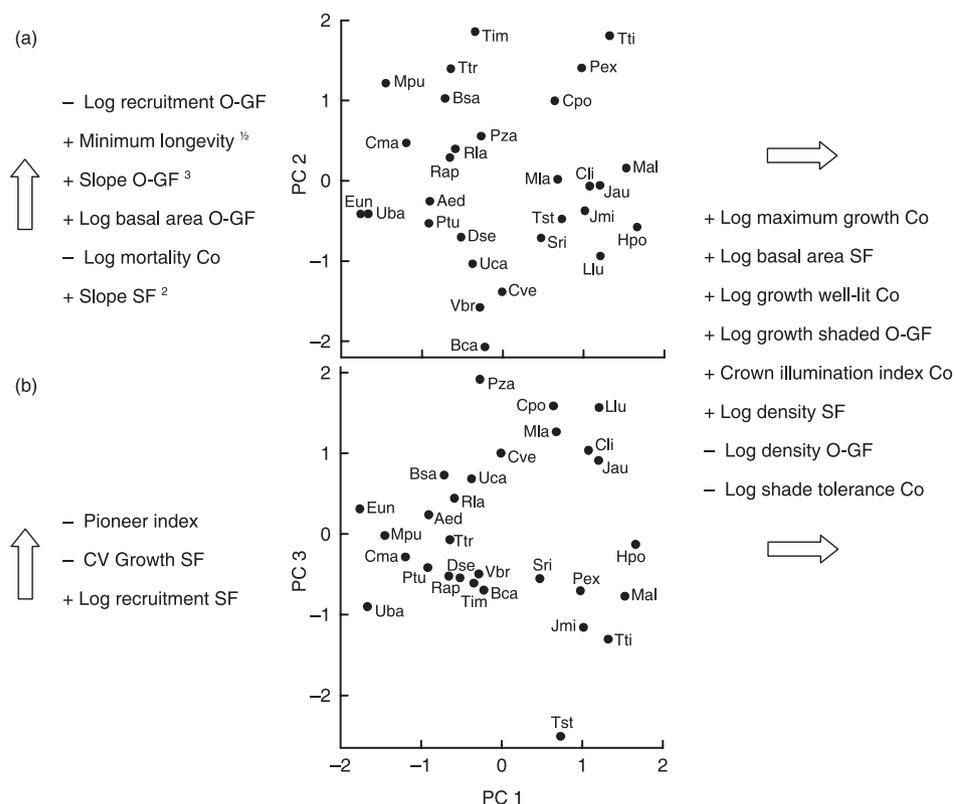
Fig. 4. Principal components (PC) ordinations of 29 montane tree species based on 19 demographic variables: (a) principal components 1 and 2, and (b) principal components 1 and 3. Components 1, 2 and 3 explain 31%, 18% and 14%, respectively, of the demographic variation amongst species. Variables with significant loadings on each axis are listed from strongest to weakest strength of association; signs indicate the direction of association. Species abbreviations are defined in Appendix S2.

O-GF but no such compensation in terms of recruitment and mortality rates; although species with low basal area in O-GF displayed a (non-significant) tendency to high recruitment in O-GF, the effect was cancelled by their high mortality rates.

SIZE-CLASS DISTRIBUTION

The size-class distribution of a species is typically interpreted as an indication of future population growth. This interpretation has been challenged by the finding that size-class distribution was only a poor predictor of the projected population growth rates of 216 tree species in tropical lowland moist forest (Condit *et al.* 1998). In theory, higher growth and survival rates have the potential to flatten size-class distributions. Indeed, Condit *et al.* (1998) did find that population size-class distributions were well correlated with growth rates of trees in small (but not in large) size-classes, but they failed to find any correlation with mortality rates. In contrast, in the subtropical montane forest of the present study, static information on species' size-class distributions was correlated with longevity and turnover rates but less strongly with tree growth potential. Interestingly, the slope of size-class distribution in O-GF had a loading of 0.76 on PCA axis 2 (Table 2), suggesting that it can be used as an easily measurable static surrogate of population turnover rates.

SUBSTRATE REQUIREMENTS FOR RECRUITMENT

Species that recruit well as saplings onto landslides (as indicated by the 'pioneer index') are distinguished in PCA axis 3 from species that recruit well to ≥ 10 cm d.b.h. in SF stands that are going through a stem-exclusion phase (*sensu* Oliver & Larson 1996). The latter are dominated by light-demanding species that have high recruitment rates in O-GF. In contrast, it is notable that species' potential to colonize landslides does not have a close association with some measures of light demand, such as CII and growth rate in well-lit conditions. This is in accordance with previous studies showing a lack of linkage between substrate requirements for recruitment and juvenile light requirements (Lusk 1995; Lusk & Kelly 2003), whereas some earlier studies had found evidence for such a linkage (Putz 1983; Nakashizuka 1989). Most of the species that recruit well on landslides (*Tecoma stans, Tipuana tipu, Jacaranda mimosifolia* and *Parapiptadenia excelsa*) are also common colonizers of bare river terraces, but are rare colonizers of sites with herbaceous and/or thick litter cover (T. A. Easdale personal observations).

The third demographic axis therefore appears to discriminate species according to their capacity for dispersal and establishment on large open areas, with bare mineral soil and dry microenvironments, rather

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than just well-illuminated sites. This reflects confusion in the ecological literature over the use of the term 'pioneer' in the context both of stand succession and of regeneration within established forest ecosystems (e.g. Swaine & Whitmore 1988).

The independence between species' recruitment rate in SF and density and basal area in SF during the study period gives a clear indication of the temporal transition in species' relative recruitment rates during the process of secondary succession. Those fast-growing pioneer species that recruit in abundance early in the succession, and then dominate the stand, have much less recruitment after canopy closure when non-pioneer light-demanding and shade-tolerant species take over.

LINKS BETWEEN LIGHT EXPOSURE, ACTUAL SIZE, MAXIMUM SIZE AND DEMOGRAPHIC PERFORMANCE

Interspecific differences in mean growth rates can result from (i) inherent differences in growth potential at equal irradiance or (ii) a size effect, due to differences in diameter distribution combined either with allometric correlations between trunk diameter and absolute diameter growth or higher crown illumination of tall (large-diameter) trees (Thomas 1996; Clark & Clark 1999; Baker *et al.* 2003). Distinguishing between these alternative explanations requires comparisons that control for diameter and light environment. We found that trunk diameter affected the absolute growth rate of only one-quarter (6/24) of the species (after controlling for light environment) and the association was negative in a majority (5/6) of these. However, CII had a significant positive influence on the stem growth rates of approximately two-thirds (17/24) of the species (after controlling for tree diameter). The results for the majority of the species are similar to the finding of Clark & Clark (1999) that the growth rates of six out of nine species were unrelated to trunk diameter once the positive effect of crown illumination was factored out (but these results differ from ours in that the three species with significant growth-size relationships had positive associations). However, our results for the five species are in accordance with the finding of Vanclay (1991) that the intrinsic diameter growth rates of mature trees often decrease with increasing stem diameter at fixed competitive effects. This suggests that observations of increases in radial stem growth capacity with trunk size (e.g. Pacala *et al.* 1994; King *et al.* 2006) result from the overcompensating positive effect of increasing irradiance with tree size (i.e. crown height) and not from the effect of diameter *per se* (King *et al.* 2006). For instance, in a growth analysis of nine temperate species, the addition of a basal area regression term added little to the variance in basal area growth already explained by a term representing the crown area exposed to direct sunlight (Wyckoff & Clark 2005).

Although individual growth rate decreased with stem size within a few species, species' average growth rate increased with their maximum d.b.h. and height. This second relationship is in agreement with previous comparative studies (Fig. 1), but we know of only two studies that controlled for the effect of individual size. Thomas (1996) found significant but low-magnitude correlations between species' asymptotic height and growth rate of saplings 1–2 cm d.b.h. amongst 38 shade-tolerant species, and King *et al.* (2006) found positive correlations between maximum trunk diameter and growth rate within different diameter classes across species of varied shade-tolerance. This phenomenon was attributed to (i) the higher leaf photosynthetic capacity (A_{max}) of congeneric species that achieve greater heights (Thomas & Bazzaz 1999), (ii) stature-dependent shifts in allometry, and (iii) differential size at onset of reproduction between short- and tall-statured species (King *et al.* 2006).

Species that reach large size also have slower rates of population turnover, are more dominant in O-GF, and have flatter population size-class distributions (PCA axis 2). Although longevity was estimated on the basis of maximum size, maximum diameter is also significantly correlated with all other variables represented by the axis that are not liable to circularity. This result is consistent with the observations of Condit *et al.* (1998) that species with very few juveniles and the flattest population size-class distributions were long-lived and reached the largest statures. The relationship between maximum size and both the shade-tolerance and turnover axes supports previous findings (Fig. 1) and suggests that maximum size is 'oblique' to these orthogonal axes; species reach a large tree size not only by high survival rates and longevity but also by faster growth (Swaine & Hall 1983).

IMPLICATIONS FOR SPECIES COEXISTENCE

Previous studies have focused on species' niche differentiation in light requirement but have generally found it wanting as an explanation for species coexistence (e.g. Hubbell *et al.* 1999; Brokaw & Busing 2000; Lusk *et al.* 2006). However, we found three orthogonal demographic axes each indicating trade-offs: (i) species with high inherent growth (both at high and low light levels) have low sapling density under shade and low tree density in O-GF, (ii) within O-GF, less dominant, short-lived species have high recruitment rates and population turnover compared with long-lived species, and (iii) species that are good colonizers of landslides have poor recruitment after canopy closure in SF. This increases the potential for niche differentiation created by trade-offs to explain species coexistence at local scales, provided that the environment exhibits a variety of resource levels and/or disturbance regimes (Tilman 1990).

The first two axes correlate with species' maximum size and match well with results from previous studies (Fig. 1). Axis 1 reflects the compromise commonly reported for saplings between fast growth in high light

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and survival in shade; a trade-off that is generally proposed as the primary (but not sole) mechanism allowing the coexistence of light-demanding and shade-tolerant species (Leigh *et al.* 2004). However, this interpretation is challenged by studies that fail to detect a clear partitioning in species' distribution or performance across the gap-to-forest light gradient and, instead, give a greater weight to stochastic processes, such as occupation of canopy gaps by advanced regeneration and dispersal and recruitment limitation, for the explanation of species coexistence (reviews by Brokaw & Busing 2000; Leigh *et al.* 2004). Although we have not analysed here the implications of differential light response for species coexistence, a previous analysis of 6 ha of O-GF PSPs used in the present study (Grau 2002) demonstrated that gaps of similar age are spatially clustered at scales smaller than 5000 m^2. Grau (2002) also found that although isolated tree-falls (100–400 m^2) have little effect on species composition and richness, the tree-fall regime at scales > 1000 m^2 is a good predictor of species richness and discrimination among regeneration groups. Aggregations of tree falls and expansion of gaps appear to increase the probability of neighbouring tree falls being colonized by light-demanding species, thus improving the environmental partitioning among regeneration groups and favouring coexistence. Although the secondary forests studied here were initiated by anthropogenic disturbance, the first axis also shows a clear separation in species distribution between SF and O-GF and much potential for niche differentiation with large-scale natural disturbance.

Axis 2 represents two alternatives for species persistence: either high recruitment (with a limited probability of survival) or long life spans. This trade-off provides an opportunity for species coexistence; Shmida & Ellner (1984) showed with a modelling exercise that two species occupying the same niche could coexist in a single patch of identical microsites and unchanging environment if one species has greater fecundity and the other, greater adult survivorship.

The third axis reflects spatio/temporal differences in species' recruitment that seem to result from different regeneration requirements (e.g. bare soil or herbaceous/thick litter cover) amongst species with intermediate to high light demand. As indicated across a range of forest environments by Putz (1983), Nakashizuka (1989) and Lusk & Kelly (2003), this indicates the importance of variation in disturbance intensity (usually associated with disturbance size) for the maintenance of landscape-level species richness (i.e. some species maintain their populations with tree-fall disturbance, while others require more intense disturbances and bare mineral soil).

This study identifies a set of key questions for future research that ought to be addressed with a balanced sample size amongst the species compared. Does the performance of saplings match that observed here for large trees? Is reproductive investment independent of

the axes identified? Are these axes still identifiable after controlling for soil fertility and soil moisture? The present study shows the power of comparative analyses of a wide range of stages in the regeneration cycle of coexisting species for identifying independent axes of tree life history differentiation.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Location and description of permanent sample plots in Sierra de San Javier, Tucumán, Argentina.

Appendix S2. Abundance of all tree species > 10 cm d.b.h. recorded in the permanent sample plots in O-GF and SF throughout three censuses.

Appendix S3. Partial correlations among diameter growth, diameter, and crown illumination.

Appendix S4. Demographic and structural description of 29 common tree species in the 12 ha of permanent sample plots within Sierra de San Javier.

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