

Changing drivers of species dominance during tropical forest succession

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Summary

1. Deterministic theories predict that local communities assemble from a regional species pool based on niche differences, thus by plant functional adaptations. We tested whether functional traits can also explain patterns in species dominance among the suite of co-occurring species.

2. We predicted that along a gradient of secondary succession, the main driver of species dominance changes from environmental filtering in the relatively harsh (dry and hot) early successional conditions, towards increased competitive interactions and limiting similarity in later successional conditions (when light is limited).

3. We used the Kurtosis (K) (a measure of peakedness) of the functional trait distribution of secondary forest communities in high-diversity tropical rain forest in Chiapas, Mexico. The forests ranged 1–25 years in age, and we used eight functional leaf traits related to a plants' carbon, water and heat balance. We calculated the functional trait distribution based on species dominance, where trait values were weighted by species' relative basal area, as well as based on species presence, all species counting once. 'K-ratio' was subsequently computed by dividing kurtosis based on species dominance by kurtosis based on species presence. If the K-ratio is high, the dominant species are functionally similar and we interpreted this as environmentally driven functional convergence allowing species to become dominant. If the K-ratio is small, dominant species are a functionally dissimilar subset of the species present and we interpreted this as competitively driven functional divergence allowing species to become dominant.

4. We found that in early succession, dominant species represent a functionally narrow subset of species with similar traits, and in late succession, dominant species increasingly represent a wide subset of the species present. This trend was found for traits that reflect photosynthetic performance and light capture, and indicates increased competition for light with succession. No trend was found for traits that indicate defence against herbivory, suggesting no successional changes in herbivore pressure.

5. *Synthesis*. This is one of the first studies showing that drivers of species dominance change along a gradient of secondary succession. During the early successional time window we evaluated, the importance of environmental filtering as a driving force fades away rapidly, and the importance of niche partitioning for species dominance starts to emerge.

Key-words: Chiapas, environmental filtering, functional convergence/divergence, functional traits, kurtosis, light gradient partitioning, Mexico, secondary succession

Introduction

Community assembly processes are crucial for explaining species coexistence and maintenance of biodiversity

(Hubbell 2001; Wright 2002). The mechanisms by which local communities assemble remain debated however, although many advances have been made in the last decade (e.g. Davis, Thompson & Grime 2005; Ackerly & Cornwell 2007; Chase 2010; Uriarte *et al.* 2010). Deterministic theories predict that niche differences create

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differential responses of species to environmental conditions and to different interspecific interactions. The environmental filtering hypothesis (Weiher & Keddy 1995; Díaz *et al.* 1999), for example, predicts that species are functionally adapted to survive and grow under specific environments, and species with similar traits are therefore found in similar habitats, a phenomenon also known as *trait convergence* (e.g. Pavoine *et al.* 2011). The limiting similarity hypothesis (MacArthur & Levins 1967) postulates that under resource-limiting conditions, competition leads to niche differentiation of co-occurring species (Hardin 1960; Grime 1973). Competing species can therefore only coexist if they differ in their traits (limiting similarity), a phenomenon which is also known as *trait divergence*. Alternatively, biodiversity is the result of neutral drift, in which all species of the same trophic level have equal chances of becoming abundant and are functionally equivalent, despite having different functional traits (Hubbell 2001). Different assembly processes may simultaneously affect local community structure (Helmus *et al.* 2007; Cornwell & Ackerly 2009), and their relative importance may change along environmental gradients (Mason *et al.* 2007, 2013).

Secondary succession is community assembly in action (Lebrija-Trejos *et al.* 2010) and therefore provides an ideal setting to test whether functional traits are indeed important for community assembly. In this study, we analyse functional trait distributions as indicators of changing drivers of species dominance during secondary succession. Although we consider species dominance one aspect of community assembly, this contrasts with the commonly used concept of community assembly processes where the focus is on assembly of local communities from a regional species pool. To avoid confusion and to underline the difference, we use the term *drivers of species dominance*, not community assembly processes. Previous studies have explored the relative importance of the process of environmental filtering and competition by comparing trait characteristics of species in the local community with that of the regional species pool, demonstrating a link between species presence (and sometimes also abundance) and their traits (e.g. de Bello *et al.* 2009; Marteinsdóttir & Eriksson *in press*). This does not necessarily imply that functional traits can also explain patterns in species dominance among the suite of co-occurring species (Cingolani *et al.* 2007). Cornwell and Ackerly (2010) have shown that species' abundances are correlated with functional traits, and recent advances have modelled species abundances based on functional traits (using methods like maximum entropy and hierarchical Bayesian models) (Merow, Latimer & Silander 2011; Shipley *et al.* 2011; Laughlin & Laughlin 2013).

Recognizing two alternative drivers of species dominance, the environmentally driven process selecting individuals with similar traits versus the competitively driven process selecting individuals with dissimilar traits, we ask what drives species dominance, and whether the relative

importance of these drivers changes along a successional gradient. We do so by using kurtosis to describe the 'peakedness' of the trait distribution of the community (in line with Kraft, Valencia & Ackerly 2008) for the species present in a site and based on species dominance (weighted by relative basal area) in a site. Subsequently, the logarithm of the ratio (kurtosis based on species dominance)/ (kurtosis based on species presence), hereafter referred as *K-ratio*, is tested for changes along the successional gradient. We thereby evaluate successional shifts in the relative contribution of environmentally driven and competitively driven processes that underlie species dominance: when *K-ratio* is positive, the main force driving species dominance is environmental filtering as filtering selects species with similar traits; in contrast, when *K-ratio* is negative, the main force is the competitively driven process leading to limiting similarity as competition selects species with dissimilar traits (cf. Webb *et al.* 2002; Grime 2006; Kraft, Valencia & Ackerly 2008; Mouchet *et al.* 2010). Conceptually, Fig. 1 shows how the predicted decrease in *K-ratio* during succession is translated into a shift in relative importance from environmentally driven to competitively driven processes.

Previous studies have shown that different trait values become important for species success at different points along habitat gradients (e.g. Lebrija-Trejos *et al.* 2010; Violle *et al.* 2010; Lohbeck *et al.* 2013). Early in succession resources (e.g. light) are abundant and dominant species are likely the ones that successfully exploit these resources for growth and reproduction (few functional strategies dominate). It is expected that the importance of competition increases with succession because resources become limited as stand biomass increases (Grubb 1977). Such

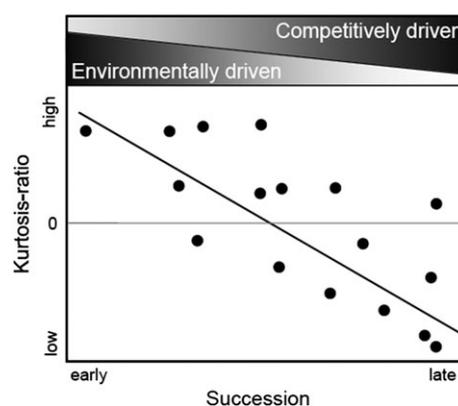


Fig. 1. Conceptualized changes in *K-ratio* (kurtosis change, or trait distribution change, from species presence to species dominance) during secondary succession. The *K-ratio* is expected to shift from high values early in succession ($K_{\text{dominance}}$ exceeds K_{presence}) to lower values late in succession (K_{presence} exceeds $K_{\text{dominance}}$), indicated by a negative relationship. This reflects a shift in the relative importance of environmental filtering in early stages of succession towards competitively driven processes leading to limiting similarity in later stages, recognizing that both drivers are influencing species dominance at all times.

increased competitive pressure will lead to differentiated strategies to obtain the increasingly scarce resources, with concomitant different functional traits, a process leading to increasingly limited trait similarity.

In this study, we evaluate whether and how the relative contribution of environmentally and competitively driven processes to species dominance changes with succession and whether functional traits can be used as indicators of this change. We evaluated functional traits for 81 woody species occurring along a chronosequence of secondary forests in high-diversity tropical rain forest in southern Mexico. We selected eight functional traits that are important for the carbon, water and heat balance of plants and hence for species success. These eight traits can be divided into two groups: traits reflecting photosynthetic performance and light capture and traits related to herbivore defence. We hypothesized that early successional forests are mostly shaped by environmentally driven processes (higher kurtosis when weighted by species dominance), and as forests get older and structurally more complex, they are increasingly shaped by competitively driven processes leading to limiting similarity (lowered kurtosis when weighted by species dominance). As light is the major factor limiting growth in wet tropical forest, we expect this to be true for leaf traits reflecting photosynthetic performance and light capture. We expect no pattern for defence traits as we predict no successional change in herbivore pressure. To assess these hypotheses, we compared the empirical (observed) successional trajectory of K -ratio with randomly generated trajectories.

Materials and methods

RESEARCH SITE AND SPECIES SELECTION

Research plots are located in the wet tropical forest surrounding the village of Loma Bonita in the Marqués de Comillas region in Chiapas, southeast Mexico (16°01'N, 90°55'W). Mean annual temperature is 24 °C, and mean annual precipitation is 3000 mm, with a dry period (<100 mm per month) from February through April (van Breugel, Martínez-Ramos & Bongers 2006). The research area is characterized by small hills and valleys with sandy, limestone or clay soils of low pH (<5.5). Seventeen secondary forest plots (0.1 ha) with different fallow ages (<1–25 years) were established on abandoned maize fields. Each plot was divided into two 10 × 50 m subplots. In one subplot, all individuals with d.b.h. ≥ 1 cm were identified and measured; in the second, all individuals d.b.h. ≥ 5 cm. Species-level variables were scaled up according to sampling effort per size-class (i.e. sampling effort for 1 ≤ d.b.h. ≤ 5 is half the sampling effort for d.b.h. ≥ 5). For functional trait measurement, those species were selected that made up at least 80% of the stand basal area (average 92%) in each plot, being 81 species in total.

FUNCTIONAL TRAITS

For each species, eight leaf functional traits were considered: leaf area, specific leaf area (SLA), leaf dry matter content (LDMC),

leaf density, leaf thickness, petiole length, chlorophyll content and specific force to punch. These were measured on two sun-lit leaves per individual, on 10 replicate small adult trees of *c.* 5 m high per species. The leaf mechanical resistance (specific force to punch) and chlorophyll content were measured for five individuals per species. Traits were measured following standardized protocols (Cornelissen *et al.* 2003). For analyses, we used species' mean functional trait values, although we acknowledge that intraspecific functional trait variation could have improved the accuracy (Baraloto *et al.* 2010). However, given the extensive species-level trait data set (81 species) and the high species turnover during succession, for the purpose of this research, we consider the use of species mean trait values meaningful.

Chlorophyll content per unit area (Chl, in SPAD-units) was measured directly on the tree with a SPAD meter (Minolta SPAD-502; Spectrum Technologies, Plainfield, IL, USA). SPAD values correspond closely with independent measurements of chlorophyll contents (Coste *et al.* 2010). After collection, the leaves were rehydrated after which fresh weight was determined. Petiole length (cm) and leaf thickness (mm) were measured with a tape measure or a digital calliper. Leaves were photographed on a light box after which leaf area was calculated using pixel counting software IMAGEJ (Rasband 2008). Leaves were dried until constant weight (at 70 °C) and weighed. Specific leaf area (SLA, m² kg⁻¹) was calculated as fresh leaf area divided by oven-dried mass and leaf dry matter content (g g⁻¹) as leaf oven-dry weight divided by fresh weight; leaf density (g cm⁻³) was calculated as leaf dry mass divided by leaf volume (in which volume is calculated as leaf area multiplied by thickness).

Fresh leaf laminae were punched with a penetrometer built with a flat-end nail attached to the inner part of a syringe and a water-basin on top. The total weight added to penetrate the leaf was converted to Mega Newton. The specific force to Punch (sFtP, MN m⁻²) was calculated as the force divided over the breaking surface of the hole (circumference of the nail × thickness of the leaf). This alternative punching method is comparable to cutting and tearing tests and is a good indicator of leaf mechanical resistance (Onoda *et al.* 2011).

STATISTICAL ANALYSES

We use stand basal area, instead of fallow age, as the successional variable. Stand basal area logarithmically increases with fallow age ($R^2 = 0.70$, $P < 0.001$), it is a good descriptor of above-ground biomass, and it correlates closely with light interception and changes in environmental conditions (Lebrija-Trejos *et al.* 2011) and may reflect competitive interactions (Paquette & Messier 2011). To quantify the distribution of trait values in the community, the Pearson's measure of Kurtosis (K) was calculated for each of the eight traits in each community using the package 'moments' in R (Komsta & Novomestky 2012). Pearson's Kurtosis implies that a mesokurtic distribution has a value of 0 and platykurtic distributions are indicated by negative values (lower bound -2), suggesting limiting similarity and leptokurtic distributions by positive values suggesting environmental filtering. Kurtosis was calculated in two ways: for the species present in a site (all species counted once; K_{presence}) and for species dominance (species weighted by relative basal area, $K_{\text{dominance}}$) (see also Fig. S2, Supporting Information for rank-dominance curves). We chose to weight by the relative basal area, rather than abundance, because it better reflects the species' biomass, an indicator of plant performance and adaptation to local conditions. To determine $K_{\text{dominance}}$, species present were multiplied by their percentage of the stand basal area (species contributing <1% were excluded). Subsequently, the relative change in kurtosis from species presence to dominance was calculated as:

$$K\text{-ratio} = \ln \frac{K_{\text{dominance}}}{K_{\text{presence}}}$$

When K -ratio is higher than zero, $K_{\text{dominance}}$ exceeds K_{presence} ($K_{\text{dominance}}$ is more peaked than K_{presence}) and indicates that dominant species are convergent in functional characteristics, which we interpret as environmental filtering being the main driver of species dominance. When K -ratio is lower than zero, K_{presence} exceeds $K_{\text{dominance}}$ ($K_{\text{dominance}}$ is more evenly spread than K_{presence}) and the competitively driven process resulting in limiting similarity is the main driver of species dominance. Changes in K -ratio with stand basal area were tested using linear regression.

To test whether the observed changes of K -ratio are ecologically meaningful, we also generated random values for K -ratio. Doing so, a random $K_{\text{dominance}}$ is computed by randomly attributing trait values from within the community to the communities' dominance structure (see Fig. S2, for the rank-dominance curve of some plots). This is carried out 999 times for each of the communities and for all traits, after which a random K -ratio was calculated by dividing the random $K_{\text{dominance}}$ over K_{presence} . The randomly generated K -ratio values were then regressed against stand basal area, resulting in an average randomized regression coefficient and corresponding confidence intervals (95%). These were compared with the regression coefficient of the observed K -ratio with stand basal area. All statistical analyses were carried out using R v. 3.0.0 (R Development Core Team 2011).

Results

For four of the eight traits (SLA, leaf area, leaf thickness and chlorophyll content), the K -ratio decreased significantly as stand basal area increased (Fig. 2). These patterns indicate that, during stand development, the functional distribution of dominant species is more leptokurtic (peaked) in early succession and becomes increasingly platykurtic (more evenly spread) compared with the functional distribution of the species present in the community. Randomly generated functional trait distributions (random K -ratio) for each of the existing communities showed no pattern with stand basal area (grey line in Fig. 2). Indeed, the slope of the observed trends differed significantly from the randomly generated functional trait distributions (Table 1, Supporting Information).

Discussion

We used kurtosis to describe the distribution of functional traits in the community and showed that in early succession, dominant species are a functionally narrow subset of the species present and that this subset widens with succession. We interpret this as a gradually shifting importance of different drivers of species dominance, environmentally driven filtering decreases and competitively driven limiting similarity increases with succession.

GRADUAL CHANGE IN DRIVERS OF SPECIES DOMINANCE DURING SUCCESSION

For four functional traits, the trait distribution of the dominant species became relatively more evenly spread

during succession compared with the trait distribution of the species present in the community. This is in line with our hypothesis that the dominant species become functionally less similar and more divergent during secondary forest succession. This suggests that during succession, the competitively driven process leading to limiting similarity becomes gradually more important and the process of environmental filtering less important in shaping species dominance. Although at later successional stages, the observed trend approaches the randomized trend, the observed K -ratio never drops below the random K -ratio, with the exception of SLA (Fig. 2). Never do we find that observed communities are more platykurtic, dominants representing a wider subset of species present, than the randomly generated communities. Possibly, our successional gradient is too short (up to 25 years after abandonment) or our plots are too large, as biotic interactions that result in limiting similarity predominantly take place at smaller spatial scales (Swenson *et al.* 2007).

The trends in drivers of species dominance are largely consistent with findings in the literature on community assembly processes. Letcher *et al.* (2012) found increasing phylogenetic evenness during succession in a study on secondary forests across the Neotropics (including our study region). Similarly, Holdaway & Sparrow (2006) found increasing evenness in functional group abundances with successional age on riverbeds and explain this by increased importance of competition at later stages of succession. Also Cardinale *et al.* (2007) concluded in their review article that, as a result of niche partitioning, species become increasingly complementary in their resource uptake with time (in experiments). This suggests that the increasing functional trait complementarity among dominants during tropical forest succession may reflect general patterns of natural population dynamics that can be found across vegetation types.

SPECIES PRESENCE AND SPECIES DOMINANCE MAY BE DRIVEN BY DIFFERENT FACTORS

The focus of this study is *drivers of species dominance*, emphasizing the functional traits of species that are dominant, compared with the traits of the species that are present in the community. As explained, this is distinct from those studies emphasizing community assembly processes selecting species present in a plot from the regional species pool. These distinct methods may reflect different processes, one shaping species presence and the other shaping species dominance, which may be driven by different mechanisms (Keddy 1992; Cingolani *et al.* 2007). Choice of the method thereby depends on the research interests. For example, species presence is determined by species' establishment success and mechanisms thereby include natural regeneration, dispersal limitation, and connectivity to the species pool within the landscape matrix. This line of research is crucial for assessing the impact of habitat fragmentation on natural regeneration and maintenance of

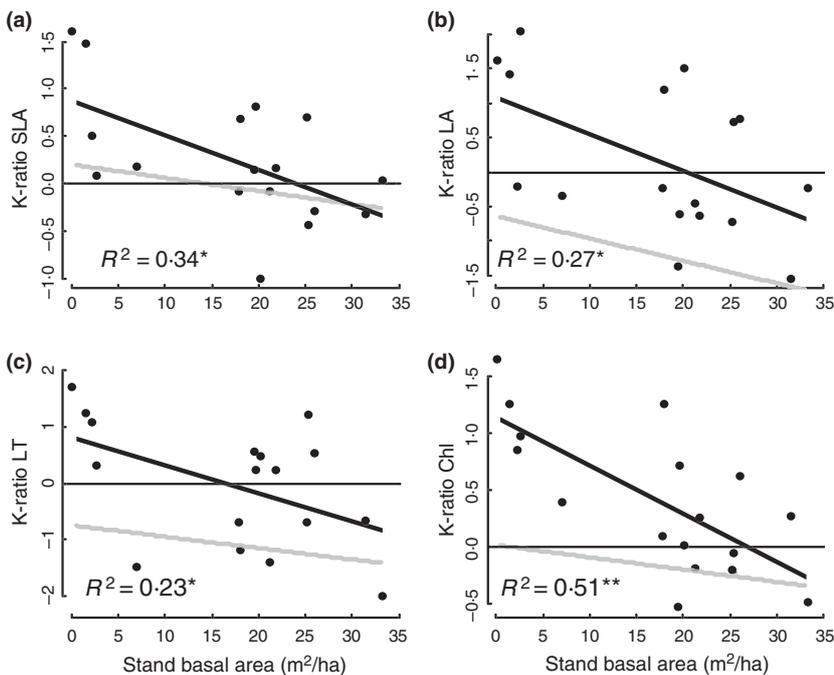


Fig. 2. The relative change in kurtosis from species presence to species dominance ($K\text{-ratio} = \ln(K_{\text{dominance}}/K_{\text{presence}})$) decreases with succession expressed as stand basal area ($\text{m}^2 \text{ha}^{-1}$), indicating a decreased effect of environmentally driven filtering and an increased effect of competitively driven processes shaping species dominance. (a) Specific Leaf Area (SLA), (b) Leaf Area (LA), (c) Leaf Thickness (LT), (d) Chlorophyll content (Chl). Given are the linear model R^2 , * $P < 0.05$, ** $P < 0.01$ of the observed trend (solid line), in grey, the median regression through the randomized data is given (not significant), slopes of the observed trends are significantly different from the randomized trends (999 randomizations, see Table S1).

biodiversity in fragmented landscapes. Instead, species dominance (the focus of the current study) is mainly influenced by species' adaptations to local conditions and biotic interactions affecting plant growth and population dynamics. This line of research matters more for assessing land-use impacts on ecosystem properties and functions, which are largely driven by the characteristics of dominant species (Grime 1998; Smith & Knapp 2003).

The rationale behind this paper is that species dominance is influenced by local adaptation to environmental conditions and competitive interactions. Of course, the species present at the site have passed a dispersal filter already (Myers & Harms 2009), which may indirectly influence the patterns found in this study. For example, pioneers species with productive, high SLA leaves that reach high abundances in early successional stages may also have arrived in large numbers because of the correlated suite of regenerative traits (i.e. many small seeds), which allows them to become dominant. We recognize the important role of seed dispersal and dispersal limitation in community assembly during secondary forest succession (Guariguata & Ostertag 2001). However, we feel that this affects our results only to a limited extent, as we focus on the species that have already successfully dispersed to our sites, and we evaluate then what factors shape their subsequent dominance.

LIGHT CAPTURE TRAITS, NOT DEFENCE TRAITS, SHAPE SPECIES DOMINANCE DURING EARLY SUCCESSION

Declining K -ratio during succession is an indicator that competitive interactions become more important over time. Traits central to the leaf economics spectrum are

important indicators of changing drivers of species dominance, because above-ground competition for light is more important than below-ground competition for water and nutrients at early stages of secondary tropical forest succession (van Breugel *et al.* 2012). In our study sites, SLA, leaf area, leaf thickness and chlorophyll content of the dominant species became more divergent with increasing stand development (Fig. 2). These traits are central to species' photosynthetic performance and growth potential and vary along light gradients. SLA is a strong driver of interspecific variation in growth responses to the light gradient (e.g. Poorter 1999). A large leaf lamina indicates an efficient light foraging strategy (Bazzaz & Pickett 1980; Takenaka 1994). Leaf thickness has been related to high photosynthetic capacities per unit leaf area (Niinemets 2001), and thick leaves are expensive to construct and are associated with a longer leaf life span (Reich *et al.* 1991; but see Kitajima & Poorter 2010). Chlorophyll content reflects light capture efficiency per unit leaf area (Rozendaal, Hurtado & Poorter 2006), which is important for individuals growing in the shade (Poorter & Bongers 2006). During succession, understorey light availability decreases rapidly, inducing the creation of different light niches. Our results thereby suggest that increased light gradient partitioning drives species dominance as the forest becomes structurally more complex during succession.

K -ratio of the traits LDMC, leaf density, specific force to punch and petiole length do not change with succession (see Fig. S1, Supporting Information). LDMC, leaf density and specific force to punch represent defence traits. Even though pioneers suffer more from herbivory than late successional species (Coley, Bryant & Chapin 1985; Poorter *et al.* 2004), and community-weighted mean of defence traits increased with succession (Lohbeck *et al.* 2013), we

hypothesized that herbivore *pressure* shows no clear successional pattern. Lack of changes in *K*-ratio with succession confirms that herbivore pressure may indeed remain constant. In fact, surprisingly little research has been carried out on presence and abundance of herbivores with succession. One may also expect increasing numbers of herbivores during succession due to improved habitat complexity and resource availability (Brown 1985). This would cause defence traits to be increasingly filtered for along the successional gradient and would increase *K*-ratio with succession (showing the reverse pattern from what is expected for light capture traits). Further research needs to clarify how changes in herbivore pressure affect species performance and community structure, which may be related to defence traits.

In sum, we show that leaf trait values are more constrained among species dominating early successional forests than among species dominating late successional forests. This suggests an increased effect of light gradient partitioning to more optimally use the increasingly scarce irradiation during succession. The use of kurtosis for describing trait distributions is intuitive, straightforward and applicable to many data sets. We show that it can be applied successfully to environmental gradients and is able to detect shifts in the relative importance of different processes driving species dominance.

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Data accessibility

Data are deposited in the Dryad repository: doi:10.5061/dryad.v2v83.

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Supporting Information

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

Fig. S1. The relative change in kurtosis from species presence to species dominance ($K\text{-ratio} = \ln(K_{\text{dominance}}/K_{\text{presence}})$) with succession for the following traits shows no significant trend: (a) Leaf Dry Matter Content (LDMC), (b) Leaf Density (LD), (c) specific Force to Punch (sFtP), (d) Petiole Length.

Fig. S2. Rank-dominance curves for three sites with low basal area ($<2.5 \text{ m}^2 \text{ ha}^{-1}$): Fig. a, b, c, for three sites with intermediate basal area ($18\text{--}20 \text{ m}^2 \text{ ha}^{-1}$): Fig. d, e, f, and for three sites with high basal area ($> 26 \text{ m}^2 \text{ ha}^{-1}$): Fig. g, h, i.

Table S1. Regression coefficients of $K\text{-ratio}$ against stand basal area (Fig. 2).