



**ARETHA FRANKLIN GUIMARÃES GOMES**

**TREE FUNCTIONAL TRAIT PATTERNS  
ACROSS A CHRONOSEQUENCE**

**LAVRAS – MG**

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CHRONOSEQUENCE**

**TRAÇOS FUNCIONAIS DE ÁRVORES EM UMA  
CRONOSSEQUÊNCIA**

Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Engenharia Florestal, área de concentração em Ecologia Florestal, para a obtenção do título de Mestre.

Orientador

Prof. Dr. Eduardo van den Berg

**LAVRAS-MG**

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*“You were wild once.  
Don't let them tame you!”*  
Isadora Duncan

## RESUMO

Entender como as características funcionais variam para espécies com nichos mais amplos (generalistas) e espécies com nichos mais estreitos (especialistas) em relação às variações ambientais inerentes ao processo de sucessão ecológica é fundamental para compreender como ocorre a substituição e manutenção de espécies durante este processo. Até o presente momento, poucos estudos exploram as diferenças nos traços funcionais de espécies de plantas generalistas e especialistas dentro de uma trajetória sucessional nos Neotrópicos. Nosso estudo visa preencher esta lacuna. Nós investigamos os traços funcionais de espécies generalistas e especialistas de plantas em três estágios de uma cronossequência (inicial, intermediário e avançado) em florestas neotropicais do Reservatório do Funil (Eletrobrás Furnas), Rio Paraíba do Sul, estado do Rio de Janeiro, Brasil. Encontramos evidências de que, para espécies generalistas, os valores de área foliar específica, conteúdo de clorofila, resistência à perfuração e espessura foliar permanecem constantes em todos os estágios da sucessão ecológica. A área foliar específica não mostrou diferença em todos os estágios sucessionais tanto para espécies generalistas quanto para especialistas. Encontramos diferença nos valores do conteúdo de clorofila (menor para especialistas do estágio inicial e maior para generalistas), resistência à perfuração (menor em especialistas do estágio inicial e maior nos demais estágios), densidade da madeira (não apresentou um padrão claro) e espessura da folha (maiores em especialistas do estágio inicial e menores nas demais especialistas) para especialistas dos estágios inicial e avançado. Os valores de densidade da madeira são similares para especialistas dos estágios iniciais e intermediários da sucessão. Nossos resultados contribuirão para seleção de espécies em programas de reflorestamento e manejo florestal.

**Palavras-chave:** Generalistas. Especialistas. Sucessão Ecológica.



## ABSTRACT

Understanding the characteristics that allow some species to survive in broader ranges of the ecological succession and how do they vary from those of the other species that are restricted to certain successional stages is an important aspect of ecosystem functioning. To date, few studies proceeded on exploring the differences in the functional traits of generalist and specialist plant species along successional trajectories in neotropical forests. We aim to fill this gap in our study. We investigated generalist and specialist plant species functional traits of three successional stages (early, intermediate and late) in neotropical forests in Reservatório do Funil (Eletróbrás Furnas), Rio de Janeiro state, Brazil. We used five functional traits (specific leaf area, chlorophyll content, resistance to drill, wood density and leaf thickness) to compare generalist and specialist plant species in early, intermediate and late successional stages of a chronosequence. We found evidence that, for generalists species, specific leaf area, chlorophyll content, resistance to drill and leaf thickness values remain constant in all the successional stages. Also, we found that specific leaf area values have no difference in all the successional stages for both generalists and specialists species. There is difference in the chlorophyll content (smaller for early specialists e higher for generalists), resistance to drill (smaller for early specialists and higher on the other stages), wood density (no clear pattern) and leaf thickness (higher on early specialists and lower for intermediate and late specialists). We found that wood density values are similar for early and intermediate specialists. Our results will help guiding the selection for species to be used on forest management and restoration programs.

**Keywords:** Generalists. Specialists. Ecological Succession.

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## PRIMEIRA PARTE

### 1 INTRODUÇÃO

Compreender como as plantas respondem a variações temporais e espaciais tem sido um dos assuntos mais abordados dentro da ecologia. Entender como determinadas espécies se comportam durante a sucessão ecológica pode nos ajudar a traçar estratégias mais efetivas para a recuperação de ambientes degradados, contribuindo assim para uma otimização de recursos aplicados e aumento do sucesso de programas de reflorestamento. Uma abordagem pouco estudada para o reflorestamento de determinadas áreas é a abordagem funcional, que retira o peso de saber quem e quais são as espécies presentes em um determinado local, colocando o foco no papel que aquela espécie desempenha e nos seus atributos chave que lhe permitem prosperar naquele ambiente.

Os atributos chaves das plantas são conhecidos como traços funcionais, e podem ser entendidos como características que atuam no *fitness* de um organismo, atuando em sua reprodução e desempenho. Apesar de amplamente estudados, pouco se sabe sobre o papel destes traços funcionais durante a sucessão ecológica e como eles se diferenciam entre espécies de planta especialistas e generalistas. Este estudo aborda esta lacuna, contribuindo para o entendimento de como os traços funcionais de plantas generalistas e especialistas se comportam durante o processo de sucessão ecológica.

O objetivo deste trabalho foi, portanto, entender quais são as variações nos traços funcionais entre espécies generalistas e especialistas dentro de três diferentes estágios de uma cronossequência definida para representar o processo de sucessão (inicial, intermediário e avançado). Nosso objetivo geral foi identificar como os traços funcionais de algumas espécies se variam e permitem com que estas sejam bem adaptadas e distribuídas durante a sucessão ecológica, com fins de corroborar em projetos de reflorestamento, manejo e recuperação da área da UHE Funil (Eletrobrás Furnas), situada no Estado do Rio de Janeiro.

### 2 REFERENCIAL TEÓRICO

Classificar a natureza de acordo com grupos é uma ciência que remonta ao período Helenístico, onde se classificavam os organismos de acordo com seu elemento (ar, terra, fogo e água) mais proeminente. Na ciência das plantas, Theophrastus (372-287 AC) já utilizava este tipo de classificação para separar ervas, arbustos, árvores e subarbustos baseado em alguns atributos, tais como densidade da madeira e altura (WEIHER et al., 1999). Com o passar dos anos, vários outros cientistas buscaram selecionar uma lista de características chave dentro de grupos de organismos que pudessem auxiliar no entendimento do funcionamento dos ecossistemas. No século 19 essa abordagem ganhou força com os estudos de Alexander von Humboldt, que foi o primeiro a reconhecer a relação entre forma da planta e função, desenvolvendo um sistema de classificação baseado em tipos de crescimento da planta (GARNIER et al.,

2016). Em 1903, Schimper identificou convergências adaptativas entre plantas taxonômica e geograficamente distantes, porém inseridas em locais com climas parecidos. Modernamente, Grime desenvolveu um sistema de classificação de plantas baseado em seu tipo funcional e estratégias evolutivas - competitivas, tolerantes ao stress e ruderais (GRIME, 1977). Após estas, várias tentativas vem sendo lançadas no sentido de tentar criar um protocolo universal para o tratamento de dados destas características, que receberam então a alcunha de traços funcionais (CORNELISSEN et al., 2003; PÉREZ-HARGUINDEGUY et al., 2013).

Mudanças globais no clima e meio ambiente (e.g. aquecimento global, expansão da fronteira agrícola) têm desencadeado uma série de processos ecossistêmicos, que podem ser amplamente verificadas através das respostas dos organismos vegetais em mudanças nos traços funcionais (PÉREZ-HARGUINDEGUY et al., 2013). Tais mudanças podem ser verificadas através de alterações nos padrões de crescimento em altura e diâmetro, quantidade de clorofila da folha, quantidade e densidade de raízes secundárias, densidade da madeira, conteúdo de carbono da folha, capacidade de tolerância à herbivoria, área foliar e outros (GRIME, 1977; LAVOREL & GARNIER, 2002; DIAZ *et al.*, 2004). As mudanças globais podem se refletir em traços funcionais ligados à resistência a dessecação, como, por exemplo, na eficiência do uso da água e resistência a cavitação, mostrando um padrão diverso em plantas de estágios iniciais da sucessão ecológica (maior resistência a seca) e plantas de estágios mais avançados (menor resistência a seca) (APGAUA *et al.*, 2015).

Em consequência direta de diversos impactos antrópicos (corte seletivo de madeira, exploração agropecuária, construção de estradas e outros), as florestas secundárias têm crescido amplamente (CHAZDON et al., 2009), se tornado os tipos predominantes de floresta (ITTO, 2002). Apesar de existirem vários estudos sobre florestas secundárias, ainda existe uma grande demanda no sentido de entender os processos de sucessão ecológica nesses locais para manejar corretamente seus recursos (GUARIGUATA & OSTERTAG, 2001). Desta forma, a investigação de estágios sucessionais baseados em cronosequências são elementos fundamentais no estudo de florestas secundárias (CHAZDON et al., 2007).

Em muitos países tropicais, as florestas secundárias têm se tornado os tipos predominantes de floresta (ITTO, 2002). Como consequência direta de diversos impactos antrópicos (corte seletivo de madeira, exploração agropecuária, construção de estradas e outros), as florestas secundárias têm crescido amplamente no cenário mundial (CHAZDON et al., 2009). Dado o panorama atual de fragmentação das Florestas Atlânticas, que constam com apenas 8% da sua distribuição original (MITTERMEIER et al., 2005), é possível

que pequenos fragmentos de florestas secundárias remanescentes sejam representativos de refúgios de vegetações naturais da paisagem tropical, sendo extremamente importantes para a conservação (SANTOS et al., 2007). Este tipo de floresta pode ser estudada investigando-se os estágios sucessionais baseados em cronosssequências (CHAZDON et al., 2007), aumentando desta forma o conhecimento de como se dão as mudanças nos remanescentes de Floresta Atlântica ao longo do tempo.

As florestas tropicais apresentam alta diversidade de espécies, com uma estimativa de mais de 40.000 espécies de árvores (SLIK et al., 2015). Diante desta megadiversidade, o Brasil figura entre um dos países com maior número de espécies na lista vermelha da IUCN, com aproximadamente 1209 espécies vegetais ameaçadas, extintas, criticamente ameaçadas de extinção, extintas na natureza ou vulneráveis (IUCN, 2015). A Mata Atlântica foi o primeiro Domínio brasileiro a ser explorado pelos europeus, sofrendo com a retirada de recursos naturais que culminou na redução da vegetação a pequenos remanescentes esparsos (OLIVEIRA-FILHO & FLUMINHAN-FILHO, 1999). A extensão dessas florestas cobria de forma contínua a costa brasileira, abrangendo um amplo rol de zonas climáticas e formações vegetacionais com flora altamente heterogênea e diversa (TABARELLI et al., 2005). Figurando no segundo lugar entre as florestas úmidas mais importantes da América do sul (OLIVEIRA FILHO; FONTES, 2000), o domínio consta como um dos *hotspots* da biodiversidade mundial desde 1998 (FUNDAÇÃO SOS MATA ATLÂNTICA; INPE, 2014).

Estudar traços funcionais de plantas é importante, pois estas respondem por 99% do material vivo presente em ecossistemas terrestres, ou seja, seu funcionamento afeta diretamente a qualidade de habitat para os outros organismos terrestres, bem como os ciclos naturais da terra (carbono, nitrogênio e chuva) (GARNIER et al., 2016). A abordagem funcional possibilita o entendimento das respostas da vegetação em relação às mudanças nos padrões de alterações globais de clima e meio ambiente, enfatizando os serviços ecossistêmicos, transcendendo análises descritivas (PLA et al., 2015). Assim, através do estudo de traços funcionais de plantas, podemos entender como as espécies são afetadas pelas condições ambientais, sendo ou não favorecidas.

Os traços funcionais podem ser definidos como características que afetem direta ou indiretamente o *fitness* de um organismo, contribuindo para alterações em sua taxa de sobrevivência, tolerância à herbivoria e ataques de patógenos, fertilidade e outros (GEBER & GRIFFEN, 2003). Um traço funcional é aquele que influencia fortemente a performance de um organismo dentro de uma comunidade (VIOLLE et al., 2007). Um conhecimento mais aprofundado sobre os traços funcionais pode ajudar a mitigar as perdas na

biodiversidade as quais as florestas vêm sofrendo ao longo dos anos (CHAI et al., 2016).

Folhas verdes são fundamentais nos ciclos biogeoquímicos da terra, sendo amplamente utilizadas por animais, fungos e outras plantas, além de funcionarem como combustível de construção para outras partes do vegetal (WRIGHT et al., 2004). Traços funcionais de folhas são bons preditores da performance da planta e estão intimamente associados com taxa de crescimento, sobrevivência e requerimento de luz das espécies (POORTER & BONGERS, 2006).

A habilidade de um organismo de captar recursos do meio em que está inserido é uma resposta direta do desenvolvimento de determinados traços funcionais fisiológicos e morfológicos moldados ao longo do processo evolutivo (FERRY-GRAHAM et al., 2002). Essas habilidades se baseiam na captação de recursos e sobrevivência, sendo impossível investir em ser bom competidor em todas as frentes, ou seja, existe um *trade-off* entre as habilidades de um organismo (FUTUYMA & MORENO, 1988). Como padrão geral, há duas estratégias distintas na captação de recursos do ambiente: estratégias aquisitivas (maior investimento em crescimento rápido e estruturas com menor custo de construção) e conservativas (investimento mais robusto em construção de estruturas e crescimento lento) (POORTER & BONGERS, 2006). Desta forma, uma gama de características sofre a ação da seleção natural dentro de um pool de espécies, persistindo apenas aquelas que forem mais aptas.

O ambiente pode atuar como um filtro seletivo, removendo de uma comunidade espécies que não possuam determinadas características para persistir sob determinadas condições (KEDDY, PAUL A., 1992). Estes filtros podem ser devido a distúrbios climáticos, interações bióticas e regime de perturbação. As associações de atributos específicos em um rol de espécies distintas de plantas mostram um efeito direto da ação desses filtros (KEDDY, PAUL A., 1992). Mudanças na estrutura da floresta e na composição de espécies ao longo da sucessão ecológica também afetam significativamente a diversidade funcional de uma área, entretanto, como se dão essas mudanças em florestas secundárias permanece pobremente estudado (LOHBECK et al., 2012).

Mudanças nos traços funcionais de plantas refletem padrões de alterações climáticas, distúrbios ambientais e diferenças no estágio sucessional de uma comunidade, sendo importantes para o desenvolvimento e aprofundamento do estudo da ecologia de comunidades (DÍAZ et al., 1998). Ao longo de uma cronossequência, espécies que ocupam diferentes posições ao longo de um gradiente de luz e altura (generalistas altamente requerentes de luz e com crescimento rápido e especialistas de crescimento lento e baixo requerimento de luz) devem possuir diferentes traços funcionais de folhas

(POORTER et al., 2006). As diferenças nos traços funcionais das espécies frente a estes gradientes podem se refletir em estratégias de vida distintas, como as estratégias aquisitivas (maior investimento em crescimento rápido e folhas com menor custo de construção) e conservativas (investimento mais robusto em construção de folhas e crescimento lento, capazes de tolerar herbivoria) (POORTER & BONGERS, 2006). Utilizando a abordagem funcional, espécies generalistas e especialistas de ambiente contribuem de forma significativa para um aumento na diversidade funcional de uma área, ou seja, a cada nova espécie adicionada ao pool local, aumentam as chances de haver um novo traço que contribua para uma maior diversidade funcional no local (LOHBECK et al., 2012).

Devido ao alto grau de distúrbio ao qual remanescentes florestais no Domínio Atlântico estão sujeitos, existe uma grande demanda no sentido de entender os processos de sucessão ecológica e como se dão as mudanças nestes ambientes (GUARIGUATA & OSTERTAG, 2001). Padrões de mudanças ao longo de cronossequências em florestas tem sido estudados (WALKER et al., 2010), entretanto, nenhum estudo, que seja de nosso conhecimento, foi realizado aplicando diferenças nos traços funcionais em espécies generalistas e especialistas de ambiente em uma cronossequência.

Este trabalho busca entender como os traços funcionais se comportam e influenciam as espécies vegetais. Buscamos compreender de que forma os traços funcionais contribuem para que algumas espécies (generalistas) se sobreponham na captação e aquisição de recursos, permitindo que estas ocupem posição dominante em comunidades em diferentes estágios sucessionais. Averiguamos também como os traços funcionais de determinadas espécies (especialistas) contribuem para que estas ocupem florestas em estágios sucessionais específicos, desaparecendo em outros estágios.

### **3 CONCLUSÃO**

Traços funcionais têm sido amplamente utilizados para compreender os padrões ecológicos da vegetação ao longo de trajetórias sucessionais, entretanto, poucos são os estudos que avaliam suas respostas dentro de grupos funcionais distintos (espécies especialistas e generalistas de habitat). Nosso estudo se propôs a investigar esta questão.

Demonstramos ao longo deste trabalho que traços funcionais podem ser utilizados como bons preditores de mudanças nas trajetórias sucessionais dentro de grupos de espécies generalistas e especialistas. Ao final do trabalho, sugerimos quais grupos podem ser utilizados preferencialmente para auxiliar o sucesso de programas de reflorestamento ambiental.

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**SEGUNDA PARTE – ARTIGO 1**

**ARTIGO 1 TREE FUNCTIONAL TRAIT PATTERNS ACROSS A  
CHRONOSEQUENCE**

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**ABSTRACT**

Generalist species are those with widespread distribution, and can be found in three different types: polymorphic species, phenotypically plastic and “jack-of-all-trades” Specialist species are those with narrow ranges of distribution, restricted to certain environmental conditions. A possible approach to study the differences between the leaf economics of specialist and generalist plant species is utilizing functional traits. In our study, we utilized functional traits of fourteen tree species to address the main question: are generalist species going to exhibit a constant trait value along the ecological succession? We studied three stages of a chronosequence: Early, Intermediate and Late. We measured specific leaf area, leaf thickness, persistence to drill, wood density and chlorophyll content for all the species selected. We constructed GLM's for each of the functional traits and performed a posthoc contrast analyze with Tuckey test to see if there was difference between the functional traits ant the chronosequence stages. We found that there is no difference in specific leaf area, chlorophyll content, persistence to drill and leaf thickness for the generalist species. There was no clear pattern for wood density in all the stages of the chronosequence. Specific leaf area were not different for specialist species. Chlorophyll content was different for early and late specialists. Persistence to drill was different from intermediate and late specialists. Leaf thickness was different for intermediate and late specialists. We hope that our findings can be used in selecting best models for forest and managements projects to restore the successional trajectories with success.

**Keywords:** Chronosequence. Specialists. Generalists. Ecological succession.

## 1 INTRODUCTION

Vascular plants continually invest and re-invest resources (mineral nutrients and photosynthate) in the construction of leaves, a process also known as leaf economics (WRIGHT et al., 2004). Tropical Forests accounts for more than one third of terrestrial primary productivity (FIELD et al., 1998), where the leaf economics processes contribute to CO<sub>2</sub> reductions and stabilization (HOUGHTON et al., 2015), and carbon storage (MAGNAGO et al., 2016), which highlights its importance to Earth's biogeochemical cycles. Despite Tropical Forests global importance, human activities (e.g. logging, agriculture and fragmentation) have been increasing the amount of secondary forests where the original vegetation was suppressed (CHAZDON et al., 2009). Therefore, secondary forests are becoming the predominant type of forest in the majority of the tropical countries (ITTO, 2002). A possible way to study those forests and understand their importance in ecosystems functioning is approaching them as chronosequences (CHAZDON et al., 2007), investigating successional trajectories in places where the land uses, environmental conditions and the anthropic activities historic are similar (CHAZDON, 2012).

Brazilian Atlantic Forest is considered a hotspot for the global biodiversity because of its high number of species and the extensive reduction of its original area (less than 10% of original cover) (FUNDAÇÃO SOS MATA ATLÂNTICA; INPE, 2014). This forest is now mostly composed by small fragments of secondary forests (OLIVEIRA-FILHO; FLUMINHAN-FILHO, 1999). Understanding the relationships between the functional groups such as

specialists, generalists, and its functional traits might help to assist forest management and restoration programs (RUIZ et al., 2005).

Highly specialized species are commonly described as those restricted to certain environmental conditions, while generalists can widespread to broader environmental ranges (MARINSEK et al., 2015). It's been described in the literature that there are three prevalent types of generalists: polymorphic species (genotypes are maintained for various ecological conditions), phenotypically plastic (genotypes express the correct phenotypic response for the ecological conditions needed) and “jack-of-all-trades” (the specie has a phenotypic optimum value for all the ecological conditions experienced) (MCPEEK, 1996). Phenotic plasticity is considered here as differential genotypic response on traits to different environments (RICHARDS et al., 2006). The most accepted definition for specialization is when a species is restricted to a narrow range of resources (FERRY-GRAHAM et al., 2002), where the specie trades the capacity to widespread for the ability to use resources (DEVICTOR et al., 2010). A specie can be defined as specialist or generalists based on many aspects of habitat utilization (FERRY-GRAHAM et al., 2002), and in this article we focus on niche breadths to describe patterns of resource utilization.

In nature, the trade-offs between the ability to widespread for the ability to use resources represent the ecological cost to be paid on fitness by a certain organism when there is a beneficial change in a functional trait that is

detrimental to another (STEARNS, 1989). Using functional trait approach is a robust tool to investigate those trade-offs (PÉREZ-HARGUINDEGUY et al., 2013), allowing us to quantify parameters of species niche (VIOLLE & JIANG, 2009). In this sense, functional traits can thus be defined as the characteristics that affect directly or indirectly the fitness of an organism, changing its survival rates, fertility, tolerance to herbivore and pathogen attacks (GEBER & GRIFFEN, 2003). A functional trait approach will help us to predict and identify which are the key traits that allow some groups of species to succeed during the ecological succession and see if those traits vary from those of the other species that are limited to certain stages of the succession.

Therefore, our aim in this study is to understand how the variations in functional trait values allow some species to occupy a broader range of the ecological succession (generalists) and how those species compare, in terms of functional trait values, to species that are more restricted to certain successional stages (specialists). We hypothesize that A) generalists are going to exhibit similar trait values along the ecological succession, with the alternative hypothesis of plasticity, which states that generalists are plastic and exhibit different trait values as the successional pathway goes on and B) specialists of different successional stages will differ in terms of functional traits values. We also expect that C) functional traits such as specific leaf area and chlorophyll content will have higher values for early specialists and lower values for late



specialists, as plants in the beginning of the ecological succession needs invest in larger leaf areas and more chlorophyll to grow faster, rising above their neighbors (POORTER & BONGERS, 2006). On the other hand, we expect lower wood densities, leaf thickness and resistance to drill for early specialist and higher values for late specialists, as plants at the beginning of the ecological succession favor fast-growing structures in detriment of expensive structures related to persistence in poor resources conditions (POORTER & BONGERS, 2006; PÉREZ-HARGUINDEGUY et al., 2013).

## **2 MATERIALS AND METHODS**

### **2.1 Study area**

Field work was carried out in Semideciduous Forest fragments, in Atlantic Domain, localized on the marginal area of reservoir of Eletrobrás Furnas, between Resende and Itatiaia municipalities, Vale do Rio Paraíba do Sul region, Rio de Janeiro state, Brazil. The dam is located on the coordinates 22°31'43.80"S e 44°34'7.95"W. Climate on the region is characterized as Cwa on Köppen scale (BERNARDES, 1952), with dry winters and hot summers (KOTTEK et al., 2006).

The forest fragments analyzed were selected from a previous study performed by MEIRELLES (2015), who had investigated the structure and floristics in the area. Fragments were distributed in a chronosequence with three different successional stages: early (10 to 20 years), intermediate (30 to 40

years) and late successional stage (more than 60 years). MEIRELLES (2015) accessed information about the successional stages of the chronossequence by interviewing the owners of the areas. The ages of the chronossequence were defined, then, as the age of cessation of human activities plots (coffee plantations and cattle activities) and posterior regrowth of the vegetation. Our samples were collected inside MEIRELLES (2015) plots, utilizing 5 plots for each stage of the chronossequence (total 15 plots) with 400 m<sup>2</sup> (20 x 20 m) extension.

## **2.2 Tree species selection**

Employing the data abundance collected by MEIRELLES (2015), we performed previous an analysis using the method proposed by CHAZDON et al. (2011) to investigate the existence of generalist and specialists in each of the stages of the chronossequence using software CLAM – Classification Method (CHAO & LIN, 2011). The CLAM (CHAO & LIN, 2011) uses a multinomial approach based on the relative abundance of the species to compare pairs of habitats, generating information about the generalists and specialists in each area. We used this approach to compare the abundance of species in pairs of different chronossequence stages (early × intermediate, early × late, intermediate × late) defining generalists and specialist species according to the chronossequence stages. The generalists did not show any preference for any of the stages of the chronossequence and specialists occurred preferentially in one

of three chronosequence stages (Figure 1). As a result, we selected six generalist species, two specialist species for the early successional stage, three specialist species for intermediate stage and three for the late successional stage (table 1). Generalist species were: *Ferdinandusa elliptica* (Pohl) Pohl, *Cupania oblongifolia* Mart., *Brosimum guianense* (Aubl.) Huber ex Ducke, *Siparuna guianensis* Aubl., *Cupania vernalis* Cambess. and *Platypodium elegans* Vogel. Generalist species were sampled in all the successional stages (early, intermediate and late) to test for differences between them in each of the successional stages. Early successional stage specialist species were *Zeyheria tuberculosa* (Vell.) Bureau ex. Verl. and *Croton floribundus* Spreng. Early successional stage only had two specialist species because those were the only ones selected by Program CLAM (CHAO & LIN, 2011). Intermediate successional stage specialist species were *Luehea grandiflora* Mart., *Myrcia splendens* (Sw.) DC. and *Xylopia brasiliensis* Spreng. Late successional specialist species were *Amaioua intermedia* Mart. ex Schult. & Schult. f., *Guapira opposita* (Vell.) Reitze and *Sorocea bonplandii* (Baill.) W. C. Burger, Lanj. & de Boer).

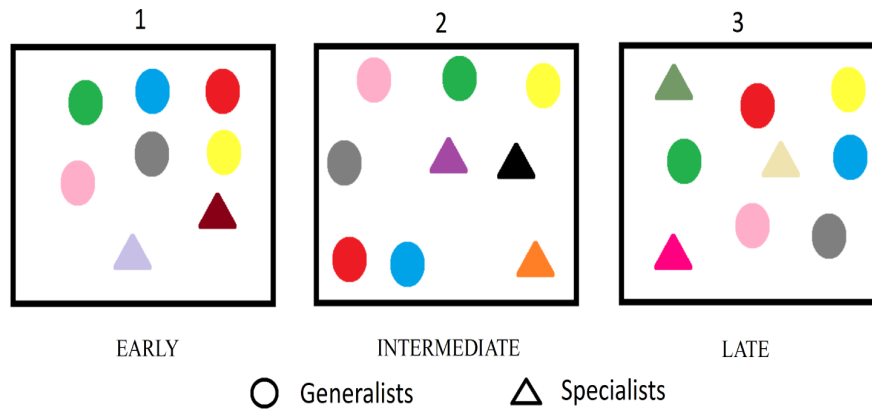


Figure 1: Three different stages of a chronossequence in Reservatório da Eletrobrás Furnas, Rio de Janeiro state. Numbers mean the age of the chronossequence: early (1), intermediate (2) and late (3). Circles are the generalist tree species and triangles are specialist tree species. Circles with the same color mean the same species in all the stages of the chronossequence. All the triangles have different colors meaning seven different species along the chronossequence.

### 2.3 Functional traits

For each species matching the criteria described above, we collected samples from five adult trees, totaling thirteen sampled species. From each of those thirteen species, we collected six leaves, totaling 390 samples. We analyzed the following functional traits: leaf area –  $\text{cm}^2$  (LA), leaf dry mass content –  $\text{g/g}$  (LDMC), leaf thickness –  $\text{mm}$  (LT), wood density –  $\text{g/cm}^3$  (WD), chlorophyll content (CLO), persistence do drill –  $\text{g}$  (PEN) and leaf macronutrients content N, P, K, Ca, Mg and S. We used LA and LDMC ratio to construct specific leaf area (SLA) values. We processed these traits using the methods proposed by PÉREZ-HARGUINDEGUY et al. (2013).

Table 1: Selected species, three families and functional group and for each successional stage of a chronosequence in Furnas dam in Rio de Janeiro state.

Successional stage	Functional group	Specie	Family
Early	Specialist	<i>Zyheria tuberculosa</i> (Vell.)	Bignoniaceae
	Specialist	<i>Croton floribundus</i> Spreng.	
	Specialist	<i>Luehea grandiflora</i> Mart.	Malvaceae
Intermediate	Specialist	<i>Myrcia splendens</i> (Sw.)	Myrtaceae
	Specialist	<i>Xylopia brasiliensis</i> Spreng	Annonaceae
	Specialist	<i>Amaioua intermedia</i> Mart. Ex Schult. & Schult. F.	Rubiaceae
Late	Specialist	<i>Guapira opposita</i> (Vell.) Reitze	
	Specialist	<i>Sorocea bonplandii</i> (Baill.) W. C. Burger	Moraceae
	Generalist	<i>Brosimum guianense</i> (Aubl.) Huber ex Ducke	Moraceae
	Generalist	<i>Cupania oblongifolia</i> Mart.	Sapindaceae
Early, Intermediate and Late	Generalist	<i>Cupania vernalis</i> Cambess.	Sapindaceae
Late	Generalist	<i>Ferdinandusa elliptica</i> (Pohl) Pohl	Rubiaceae
	Generalist	<i>Platypodium elegans</i> Vogel	Fabaceae

## 2.4 Samples treatment

Fresh samples were processed in 24h. We used black bags to avoid desiccation and transported the samples to laboratory facilities next to the study area, where they were processed and analyzed. We chose fully expanded green leaves, without herbivore attacks and next to the canopy. We excluded the first 4 pairs of leaves next to the apical buds to standardize the ontogenetic stage of the leaves. Fresh leaves were weighted on a precision scale and after that digitalized using a digital scanner. We calculated leaf area based on images, using ImageJ software. Latter, fresh leaves were dried at 70°C temperature in a greenhouse to determine leaf dry mass content. Chlorophyll content was measured using a field

SAPD to avoid its degradation during the transport. Leaf thickness was measured using a field micrometer. To analyze leaf nutrient contents, we grinded the dried leaves in a Willey mill and sent the samples to the Leaf Analysis Laboratory, at Chemistry Department at Universidade Federal de Lavras, for macronutrients (N, P, K, Ca, Mg and S) assessment..

We measured the amount of water required to drill a leaf (persistence to drill) using a penetrometer mounted on a stationary platform with a hole following the method described by KITAJIMA & POORTER (2010) and POORTER (2009). The equipment needs to be filled with water in a container as a needle is pushed through the leaf. We putted the leaves in the platform avoiding primary and secondary veins and weighted the amount of water in the container needed to tear them in a precision scale (g).

We collected wood samples by cutting 4<sup>th</sup> order branches for each of the selected species in each of the successional stages. Samples were processed in laboratory, where we removed the bark and medulla. We submerged the samples on water within a graduated cylinder to estimate the wood density ( $\text{g}/\text{cm}^3$ ) using Archimedes principle (water displacement method) following the method described by FALSTER & WESTOBY (2005).

## **2.5 Data analysis**

We separated the species according to their successional stage and functional group (generalist or specialist) to access four categories: early specialists, intermediate specialist, late specialists and generalists. We built Generalized Linear Models (GLM) for each of the following functional traits (SLA, CLO, PEN, LT e WD), using macronutrients as explanatory variables to see which of the macronutrients was influencing the functional traits analyzed. We tested the correlation among the leaves macronutrients using “Performance Analytics” package and Spearman correlation in R software. We built the models in a way that correlated variables would be presented in separate models. Distribution families were tested separately using “gofstat” function from “fitdistrplus” package. To determine the best distribution family, we used Akaike Information Criterion of Selection Order (AIC), where the AICc selected is the one with lower value (BURNHAM & ANDERSON, 2002). Gamma family was selected and residuals were checked to see the model adjustment. We used the “dregde” function from “MuMin” package to test all possible combinations. Again, the best models were selected based on AICc approach. We performed a *posthoc contrast* analyze with Tukey test to see if there was difference between the functional traits and the chronossequence stages within all the functional groups. Those analyzes were performed on R (TEAM, R. C., 2015), using R studio platform (R Development Core Team, 2009).

### **3 RESULTS**

We analyzed 390 samples across all the stages of the chronosequence belonging to 14 species and 11 families. Spearman correlations showed that the levels of P and N in the leaves were correlated ( $p = 0.72$ ), followed by Ca and Mg ( $p = 0.68$ ). Those correlated macronutrients didn't appear together on the same model when we build the GLM's. Based on AICc values, the best model selected for SLA had K, N and S influencing positively this trait, while Ca had a negative influence. For the chlorophyll content, the best model had K, Mg and N influencing positively the variable. The best model for persistence to drill had Ca, K, P and S influencing positively the variable. Leaf thickness was most affected (positively) by N and S contents. For the wood density, the best model was the one with Ca, N and S influencing positively the variable.

*Posthoc contrast* analysis with Tukey test (table 3) showed that there is no difference in specific leaf area, chlorophyll content, persistence to drill and leaf thickness for the generalists in all the stages of the ecological succession (Figure 2). The same analysis showed that wood density was different when comparing generalist species in all the stages of the ecological succession. Wood density was higher on early generalists and lower for intermediate generalists.

For the specialist species group, we found that there is no difference in SLA in all the stages of the ecological succession. Chlorophyll content was different (with lower values) only for early and late specialist species (higher values). Also for the chlorophyll content, generalist species had similar values



only to the late specialist species and differ from early and intermediate specialist species. Early specialists persistence to drill is lower and different from intermediate and late specialist. Early specialist species persistence to drill is different from all the generalists. Leaf thickness is higher and different when comparing early specialists to intermediate and late specialists. There is no difference for intermediate and late specialist species persistence to drill. Generalists persistence to drill is different from early, intermediate and late specialist species. Wood density was different for early and late specialist species and intermediate and late specialist species

Table 3: P values from posthoc contrast analysis with Tuckey test for functional groups and functional traits SLA (specific leaf area), CLO (chlorophyll content), PEN (persistence to drill), WD (wood density) and LT(leaf thickness) in a chronosequence on Furnas dam in Rio de Janeiro state.

Functional Group	SLA	CLO	PEN	WD	LT
Early Specialist x Early Generalist	0.9999	0.0001	0.0001	0.0056	0.0031
Early Specialist x Intermediate Specialist	0.4953	0.8960	0.0163	0.9016	0.0001
Early Specialist x Intermediate Generalist	0.9868	0.0001	0.0001	0.9690	0.0001
Early Specialist x Late Specialist	0.9308	0.0050	0.0001	0.0001	0.0001
Early Specialist x Late Generalist	0.9177	0.0001	0.0002	<.0001	0.0001
Early Generalist x Intermediate Specialist	0.0913	0.0079	0.9780	0.0008	0.0001
Early Generalist x Intermediate Generalist	0.8455	1.0000	0.7002	0.0001	0.2891
Early Generalist x Late Specialist	0.5491	0.9092	0.2553	0.0584	0.0001
Early Generalist x Late Generalist	0.6023	0.6378	1.0000	0.0365	0.5395
Intermediate Specialist x Intermediate Generalist	0.2857	0.0041	0.4817	0.9931	0.0011
Intermediate Specialist Late Specialist	0.3866	0.0643	0.0625	0.0001	0.9095
Intermediate Specialist x Late Generalist	0.9555	0.0001	0.9619	0.0001	0.0004
Intermediate Generalist x Late Specialist	0.9839	0.8785	0.7656	0.0001	0.0070
Intermediate Generalist x Late Generalist	0.9644	0.5493	0.7983	0.0001	0.9993
Late Specialist x Late Generalist	0.9999	0.1600	0.1558	1.0000	0.0021

Table 2: Summaries of the generalized linear models (GLM) used to verify if there are differences for specialists and generalist species in different stages of a chronosequence. Values were adjusted for the effects of variables on each functional trait parameters: SLA - Specific Leaf Area (A), SPAD - Chlorophyll Content (B), PEN\_WM - Persistence to Drill (C), D - Wood Density (E) and LT - Leaf Thickness (F). Coef: coefficient, SE: standard error. All the macronutrients that were not selected on the best models have “-” sign.

Variables	A) SLA		B) SPAD		C) PEN_WM		E) D		F) LT	
	Coef. (contrast)	SD	Coef. (contrast)	SD	Coef. (contrast)	SD	Coef. (contrast)	SD	Coef. (contrast)	SD
Early Specialist	212.59	0.002	34.92	0.003	250.92	0.001	0.36	0.27	-13.65	0.39
Early Generalist	204.83	0.001	46.15	0.001	600.60	0.001	0.45	0.16	1.33	0.22
Intermediate Specialist	344.29	0.0010	37.56	0.002	512.16	0.001	0.33	0.25	0.39	0.36
Intermediate Generalist	240.14	0.0008	46.11	0.001	746.55	0.001	0.35	0.17	0.85	0.23
Late Specialist	263.53	0.0009	43.84	0.002	982.51	0.001	0.53	0.17	0.46	0.29
Late Generalist	276.74	0.0011	49.13	0.001	606.50	0.001	0.53	0.17	0.90	0.22
Nitrogen (N)	315.97	0.0003	36.23	0.0004	-	-	0.39	0.06	1.57	0.12
Phosphorus (P)	-	-	-	-	58.18	0.003	-	-	-	-
Potassium (K)	130.82	0.001	31.12	0.001	411.95	0.0004	-	-	-	-
Calcium (Ca)	-289.47	0.002	-	-	141.40	0.001	0.66	0.36	-	-
Sulfur (S)	78.79	0.002	-	-	199.94	0.001	0.49	0.21	0.36	0.58
Magnesium (Mg)	-	-	58.83	0.002	-	-	-	-	-	-

#### 4 DISCUSSION

Our results partially supported our hypothesis. The studied generalist species had similar functional trait values in all the stages of the chronosequence, except for wood density agreeing, mostly, with the idea of “jack-of-all-trades” strategy to the detriment of high plasticity one. On the other hand, hypothesis B proved to be wrong and much more complex than expected, as we could not find any clear pattern for the specialist species analyzed in our study. The latest hypothesis – C – proved also to be wrong too, as the SLA values were the same for both generalist and specialist species. Chlorophyll content values were higher in the final stages of the ecological succession, while there is no clear pattern for wood density. The only trait that behaved as predicted was persistence to drill, with lower values for early specialist species and higher for the other groups. Leaf thickness exhibited a contrary behavior than expected, with higher values at the early stage of the chronosequence.

We expected that SLA values would be higher in the early stages of the succession for specialists as a reflection of efficiency for light capture, which means more productive leaves (PÉREZ-HARGUINDEGUY et al., 2013). Though our results showed no difference in SLA for the functional groups analyzed in our study, it is widely described that higher values for SLA and chlorophyll content are typically found for fast growing species on the early stages of the succession (BONAL et al., 2007). For the chlorophyll content

values, there are no differences for the generalist species as we expected, and Mg was selected in the best model as the nutrient that affects the most in this trait, which highlights its importance on the formation of the chlorophyll (EPSTEIN, 1975). It is possible that there's a trade off between leaf area and leaf dry mass content values that allows all species in all the stages along the succession to access and utilize the sunlight with the same efficiency, leading to no differences in SLA ratios. On the other hand these results also indicate that SLA can be a tricky trait for characterizing light use changes along succession.

We found higher values for leaf thickness for early specialists and lower in the late stages, and the contrary pattern for the persistence to drill. Ca and P appears on GLM as some of the macronutrients influencing positively the persistence to drill, and their high concentrations are widely described in the literature as related to higher pH and palatability for herbivores (PÉREZ-HARGUINDEGUY et al., 2013). It is possible that early specialists species are in a quick-return end of the functional spectrum (WRIGHT et al., 2004), reflecting a leaf that is easier to construct, but less resistant and possibly more susceptible to herbivore attacks (POORTER, 2006). Higher leaf thickness values for early specialists could indicate that, though it is easier to drill those leaves, they have thicker leaves to deal with sunnier environments such as those of the early stages of the ecological succession. Leaves full exposed to sunlight can extra layers of parenchyma as a filter against excessive radiation and, therefore,

be thicker (PÉREZ-HARGUINDEGUY et al., 2013). Early, intermediate and late generalist species leaf thickness values are similar in all the stage of the chronosequence, which shows that there is a general pattern for this functional trait that allows them to deal with light capture and water loss the same way during the ecological succession. There is no clear pattern for wood density values. We found no clear pattern for wood density values. There was no difference between early and intermediate specialist species, but these two groups are different from late specialist species wood density. Wood density was similar for the generalist across the chronosequence.

Except for the persistence to drill, nitrogen appears on the best model for all the other functional traits, highlighting it's importance on plants life. It is documented on literature that high nitrogen and phosphorus contents are strongly correlated with maximum photosynthetic rates and SLA, indicating high nutritional availability for the food web consumers (PÉREZ-HARGUINDEGUY et al., 2013).

Early and late specialist species had values of chlorophyll content, persistence do drill, wood density and leaf thickness different, which shows that traits behave unequal on early and late stages of the ecological succession. Also for specialist species, traits do not seem to experience major variations from intermediate to the late stages of the ecological succession, as all the traits values were similar in these two stages, except for wood density.

Although our results only partially supported our hypothesis, the variations we found on the functional traits for generalist and specialist species are expected in the context of the ecological succession, representing plant economy and resource allocation strategies as light, nutrient, water and competition with neighbors changes (WESTOBY et al., 2002). However, there is an unmistakable difference in the perception of the selected groups as the succession goes on: while specialist species captures the changes in the environment and perish easily, generalists tend to persist in all habitats seeming not to be affected by the same changes (MCPEEK, 1996). Making an odd comparison, generals in the army are so called because they can see the big picture and process it in a way that will allow them to persist, while soldiers (specialized in certain functions) are more probably to perish because their abilities are restricted to deal with some conditions. For plants in a world of constant environmental changes, the ones with generalized abilities are more likely to persist because of their wider niches and would be the best choices for management and reforestation programs, because of their higher chances of success in unpredictable conditions.

Trait variation is an important to understand how species deal with variations across successional stages. Our findings suggest the idea that some generalist species experience a medium value (“jack-of-all-trades” generalists) (MCPEEK, 1996) in their functional traits that allows them to do well along the

environment changes that happen across succession. If phenotype plasticity were the key driver in for species persistence in all the stages of the chronosequence in our case, we would expect that functional traits would be different for generalist species. Since we used traits mostly recommended to ecological studies approaching plant functions, we suggest caution on attributing to trait plasticity a main role on the species adjustment along succession gradients.

We found the largest differences between early specialist species and the other specialists and generalist species, suggesting that the bottleneck for specialization is in the beginning of the succession. Early specialists had trait values that varied from high to low, contrary to generalist species that had medium values for their functional traits. Those variations found on early specialist species trait values could have made them unable to maintain their population as the complexity of the environment increases. Early specialist species appears to invest on building structures very quickly to acquire most of the resources as possible, favoring fast-growing structures in place of persistence in time (POORTER; BONGERS, 2006). This behavior is important if you think about the beginning of the successional trajectories, when you have open and sunny environments. In these conditions, fast-growing colonizers are able to grow and reproduce fast (MCCOOK, 1994), however, as the forest canopy closes, traits that favor stability and persistence over time are favored (LOHBECK et al., 2012; LASKY et al., 2014).

Because generalist species can easily adapt to different stages of the succession, forest restoration programs should focus on trying to identify them, we mean, plant species that exhibit constant functional trait values that allow them to persist in different environments across the forest development. Those species have higher chances to persist as the ecological succession goes on. Specialists could then be used combined with generalists to create the conditions which will allow the maintenance of the successional pathway, improving forest management projects success.



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