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Research Article

Effects of environmental heterogeneity and temporal variation on ecological relationships of vegetation in a seasonally dry tropical forest in Brazil

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Abstract: Species distribution patterns, community structure, and dynamics are determined on a small scale by soil and habitat heterogeneity. The aim of this work is to evaluate the temporal changes in composition and structure of a tree community, revealing the ecological drivers of the observed vegetation patterns. For 16 years (2000, 2005, 2010, and 2016) we monitored the temporal variations in structure and floristic composition of a semideciduous seasonal forest through 20×20 m² (400 m²) plots, totaling 2.08 ha of sampled area encompassing Cambisol (0.4 ha), Oxysol (1.12 ha), and Nitosol (0.56 ha) soil classes. These tree communities were different in floristic and structural composition and showed oscillations over the years. The individual density and temporal beta diversity did not show differences among the soil classes in any of the monitoring intervals. In the other parameters, the Cambisols differed from the other soil classes, presenting the lowest species richness, greater floristic dissimilarity, and a structural pattern characterized by the dominance of Galipea jasminiflora (A.St.-Hil.) Engl. in all measurement years. From these results, we conclude that the temporal oscillations did not alter the original characteristics of the vegetation due to the species' adaptations to the environment, entailing the maintenance of the habitat characteristics and the directional development of the communities.

Key words: Environmental filtering, assembly rules, structural modifications, floristic modifications, forest dynamics, diversity patterns

1. Introduction

The search for the understanding of ecological processes that determine species distribution patterns, tree community structure, and dynamics is one of the main challenges in plant ecology (Tilman et al., 1997; Begon et al., 2007; Leps, 2013). The occurrence of a species in a given area is determined by its colonization capacity and environmental conditions that act as a filter to colonization. mediated by evolutionary factors (Leps, 2013). When environmental conditions are spatially heterogeneous, competitors may coexist for long periods of time through species differentiation in their ability to acquire and use resources (Chesson, 2000).

On the small scale, heterogeneity in soil and habitat conditions is an important driver of plant community structure (Baldeck et al., 2012). On these scales, soil variation in fertility and texture may be so pronounced as to act as filters, influencing tree species distribution, composition, and substitution (Figueiredo et al., 2018; Medvigy et al., 2019), community structure (Peña-Claros



et al., 2012; Martins et al., 2015), and temporal variations in demography and biomass (Russo et al., 2008; Quesada et al., 2012).

For instance, soils play an important role in post disturbance dynamics, being a potentially decisive factor in determining the successional trajectories of tropical forest regeneration (Chazdon et al., 2007; Martins et al., 2015). Under these conditions, the environmental heterogeneity produced by variation in soil type, coupled with forest age, explains changes in basal area, species, and tree density that occur along the successional gradient (Martins et al., 2015).

Environmental heterogeneity plays a major role in the evolutionary differentiation across communities dwelling in different habitats (Leps, 2013), especially in seasonally dry tropical forests (Pennington et al., 2000; Neves et al., 2015). Pennington et al. (2009) found high niche conservatism among seasonally dry tropical forests and demonstrated the importance of the evolutionary dimension for determining the patterns of

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these communities. Thus, seasonally dry tropical forests provide a good study case for understanding community assembly rules, given their disjunct distribution and past connections resulting in high environmental heterogeneity (Pennington et al., 2000).

Studies have shown this floristic differentiation and environmentally driven distribution patterns in the Brazilian semideciduous seasonal forests and related this physiognomy to other physiognomies of the Atlantic domain (Oliveira-Filho and Fontes, 2000; Oliveira-Filho et al., 2005). Ecological patterns in semideciduous forest fragments have been investigated through tree community structure and ecological guilds (Nunes et al., 2003), as well as through the role of environmental heterogeneity for species distribution (Espirito-Santo et al., 2002). However, studies that investigate the effects of temporal variation and its interactions with environmental variables in this vegetation type are scarce (Higuchi et al., 2008). Higuchi et al. (2008) demonstrated that soil variability might not reflect the dynamic community rates (or the community temporal change in demography and biomass). However, it is not yet known whether the variability in soils can affect beta diversity and community structural processes over time.

Tree communities are dynamic elements and changes occur over time at population levels of species and individuals (Felfili, 1995a). Changes include edaphic, climatic, and biogeochemical factors that influence the colonization of the environment and vegetation dynamics by affecting the success of different life strategies (Phillips et al., 2004). Thus, in spite of the great diversification of habitats among fragments of seasonally dry forests and temporal changes, communities tend to maintain a composition pattern depending on the evolutionary adaptations of the species to that habitat.

By examining the temporal changes in the composition and the structure of a community, it is possible to reveal the ecological processes that affect vegetation patterns (Chazdon et al., 2007). Understanding the temporal changes in heterogeneous communities on forest fragments is of paramount importance for the understanding of ecological processes, allowing conservation, management, and restoration actions for these environments (Higuchi et al., 2008). Accordingly, the aim of this study was to evaluate the floristic and structural changes of the tree community in a fragment of semideciduous seasonal forest present in three soil classes over a period of 16 years (2000-2016). We hypothesized that: (1) communities on different soil classes exhibit directional changes in dynamic behavior and (2) such temporal changes do not alter floristic and structural differences between communities. Specifically, the tree communities showed similar changes in the floristic and structural parameters, maintaining the pattern of three

distinct communities in terms of floristics and structure, determined by edaphic heterogeneity.

2. Materials and methods

2.1. Characterization of the study area

The study was undertaken in a fragment of semideciduous seasonal forest (Oliveira-Filho and Fontes, 2000) located on the campus of the Federal University of Lavras, Lavras, Minas Gerais, Brazil (Figure 1). The fragment is situated at coordinates of 21°13′17.29″S and 44°57′47″W, covering an area of 8.75 ha, with elevations ranging from 890 m to 948 m. The climate of the region according to the Köppen classification is Cwb, with mild summers and dry winters. The average rainfall and temperature between the years 1965 and 2016 was 1428.92 mm and 20.05 °C, respectively (INMET, 2017).

The studied fragment occurs within an agricultural matrix, surrounded by farmland and pasture. According to reports from Espírito-Santo et al. (2002) and Higuchi et al. (2008), the area underwent clear-cutting in the 1950s, with rapid natural regeneration mainly through resprouting. After the clear-cutting and the beginning of the regeneration process, the area did not suffer considerable anthropogenic disturbances, except in plots that were withdrawn from sampling.

2.2. Vegetation sampling

The first measurement occurred in 2000, when 52 contiguous plots of 20×20 m (400 m²) were allocated, constituting a total area of 2.08 ha, encompassing 0.4 ha in Cambisol, 1.12 ha in Oxysol, and 0.56 ha in Nitosol. Tree individuals within the inclusion criterion of diameter at breast height of ≥ 5 cm were measured, numbered, and identified. The trees within the plots were measured again in 2005, 2010, and 2016, and because in the year 2005 a road was opened near the forest fragment, five plots were removed from the sample (Higuchi et al., 2008; present study). In the measurement years, all surviving individual trees were remeasured. New individuals that reached the inclusion criterion (recruits) were identified in the field with the aid of specialists, marked with aluminum tags, numbered, and measured in terms of circumference and height. Dead individuals were recorded.

2.3. Soil types of the sampling units

The forest fragment presents three types of soil: Red-Yellow Oxysols, Haplic Cambisols, and Red Nitosols (Espírito-Santo et al., 2002; Higuchi et al., 2008), which differ in terms of fertility, texture, and drainage, classified according to EMBRAPA (2013). Nitosols are at the base of the slope, showing a medium texture and moderate drainage. This class has the highest K, Ca, and Mg and lower Al levels, which favors a higher effective cation exchange capacity and higher values for sum of bases (S) and base saturation



Figure 1. Location of the city of Lavras in the State of Minas Gerais, Brazil and in South America.

(V), besides showing the highest pH and highest organic matter and silt. Cambisols are also found at the base of the slope, with a medium texture, well drained and showing the highest values of P and sand and the lowest clay content, characterized by sandy soils. Oxysols, the most acidic soil type among the three, are found on top of the slope of the fragment, display a clayey texture, are well drained or significantly drained, and present the highest values of K, clay, H+AL, and aluminum saturation.

2.4. Data analysis

Vegetation structural patterns on each of the three soil classes was evaluated by using the value of phytosociological importance (VI) and the value of cumulative phytosociological importance (VIA), obtained for the species through their relative participation in density (RD), dominance (RDo), and frequency (RF). These parameters were calculated based on the following formulae:

$$ADi = \frac{ni}{A} ; \quad RD = \left(\frac{ADi}{\sum ADi}\right) \times 100$$
$$ADoi = \frac{bai}{A} ; \quad RDo = \left(\frac{bai}{\sum ADo}\right) \times 100$$
$$AFi = \frac{ui}{ut} ; \quad RD = \left(\frac{AFi}{\sum FAi}\right) \times 100$$

The expressions use the absolute density of the species (ADi), number of individuals of the species in the sample (ni), total area sampled in hectare (D), relative density (RD), absolute dominance of the species (ADoi), basal area of the species (bai), relative dominance (RDo), relative frequency of the species (AFi), number of sampling units

in which the species was sampled (ui), and total number of sample units (ut). VIA is the cumulative sum of species VIs.

Richness within soil classes was analyzed through rarefaction curves of estimated species richness as a function of individual abundance (Gotelli and Colwell, 2001). The rarefaction curve is created by repeated resampling of the pool of individuals (N) randomly and thus generates the expected number of species in a sampled number of individuals, and it can be viewed as the statistical expectation of the accumulation curve, although without the bias promoted by the second (Gotelli and Colwell, 2001). The phytosociological structure and richness were compared spatially (among soil classes) and temporally (within each soil class).

Differences concerning the floristic composition among soil classes were verified through analysis of similarities (ANOSIM) (Anderson 2013) at 5% significance level using the Bray–Curtis index (Magurran, 2003) as a measure of similarity among sample units. Temporal changes in within-class floristic composition were evaluated through temporal beta diversity (https:// CRAN.R-project.org/package=betapart) for each soil class among measurement intervals. All statistical analyses performed for soil attributes, structure, and temporal variation were performed with R Studio software 3.3.1 using the packages "vegan" (https://CRAN.R-project.org/ package=vegan) and "betapart" (https://CRAN.R-project. org/package=betapart).

3. Results

The three soil classes showed particular structural characteristics, with differences concerning the most

important species (VIs), the structural pattern, richness, and floristic composition. Despite substrate differences, the density of individuals was similar among soil classes, characterized by a reduction in the number of individuals over time. Species richness was similar between the Oxysol and Nitosol communities, but superior to the Cambisol soil class in all measurement years (Figure 2). Richness displayed an increasing trend throughout the monitoring period that was consistent in the Oxysol class (131 species in 2000, 132 in 2005, 143 in 2010, and 145 in 2016), while in the Cambisol (89 species in 2000, 92 in 2005, 98 in 2010, and 95 in 2010) and Nitosol (121 species in 2000, 125 in 2005, 126 in 2010, and 114 in 2016), richness decreased in the last interval, between 2010 and 2016 (Figure 2).

Besides presenting the lowest richness, the floristic composition of Cambisols was similar with the richest classes. The number of species exclusive to Cambisol ranged from four in 2000 and 2005 to 11 in 2016. In Nitosol, the largest number of exclusive species was observed in 2000, 24 species, and the smallest in 2016, 15 species. Oxysol showed the highest number of exclusive species, ranging from 26 in 2005 to 38 species in 2016 (Figure 3). The number of species shared among the three communities increased over the first two measurement intervals, from 69 species in 2000 to 72 in 2005 and 73 in 2010, but declined in 2016 to a total of 62 species.

The soil classes differed significantly in relation to the floristic composition in all measurement years, Oxysol and Nitosol showing less dissimilarity than Cambisol (Figure 4). Temporal beta diversity did not significantly differ among the classes in any of the intervals, indicating that species substitution occurs similarly in each of them (Figure 5).

The vegetation structure on Cambisols was characterized by the dominance of Galipea jasminiflora (A.St.-Hil.) Engl., while Oxysol and Nitosol communities were not dominated by any species (Figure 6). Some changes in the species hierarchy of the community occurred across the 16 years of monitoring. From the five species of major importance in the Nitosol and Cambisol classes, three remained in this group over time. In the Oxysol, only Eugenia acutata Miq. remained among the five most important species during the 16 years. The species E. acutata also increased in importance over



Figure 2. Rarefaction curves for the three soil classes in the four years of measurement in a semideciduous seasonal forest in southeastern Brazil. The y axis represents the estimated richness (created by resamplings of individuals' pools, randomly) and the x axis represents the number of individuals sampled (n).



Figure 3. Venn diagram of floristic composition (species richness) by soil class in a semideciduous seasonal forest in southeastern Brazil.

the monitoring period in all soil classes, resulting in the presence of this species among the five most important in all soil classes in the last measurement year (Table).

4. Discussion

The tree communities on the three soil types investigated here were found to be distinct in terms of floristic composition and structure, and they varied in species composition and structural patterns over the years. However, these temporal modifications did not alter the original characteristics of the vegetation, corroborating our hypothesis. The floristic-structural distinction among soil types may be related to the diversification of these habitats (distinct niches), while the maintenance of existing patterns among communities over time may be associated with temporal differentiation of niches (Begon et al., 2007). This environmental heterogeneity is an important controlling factor of species distribution (Réjou-Méchain et al., 2008), and the maintenance of the environmental characteristics over time contributed to the maintenance of community temporal patterns. Thus, through specific environmental filters, habitats select ecologically equivalent species that maintain the already existing relationships in the community, producing a directional establishment.

Soil spatial heterogeneity may offer a wider range of niches so that species with different resource needs coexist locally, thus promoting high species substitution within small distances (Tilman and Pacala, 1993). The role of niche in structuring plant communities and maintaining diversity in tropical forests is widely recognized (Baldeck et al., 2012; Maia et al., 2020), together with the evolutionary



Figure 4. Average dissimilarity of the soil classes found in the semideciduous seasonal forest sampled in southeastern Brazil, analyzed for the years of measurement using Bray-Curtis dissimilarity. Error bars represent the sample's standard error.

coexistence ability of plant species (Leps, 2013). In the present study, the highest species richnesses found in the Nitosol and Oxysol, as well as the lowest richness of the Cambisol community, were maintained over time. This greater richness may have been conditioned by the higher fertility in the Nitosol and the higher water availability in the Oxysol, characteristics that contribute to maintaining high species diversity (Tuomisto et al., 2014). John et al. (2007), analyzing soil maps of three plots in neotropical forests, found a distribution from 30% to 40% of the tree species associated with soil nutritional variation. Fertile soils tend to be more species-rich because they allow the coexistence of more species (Dantas and Batalha, 2011; Figueiredo et al., 2018), mainly due to a decrease in resource competition (MacArthur, 1972).

The strong influence of soils on the floristic composition of tropical forests has been discussed before (Espirito-Santo et al., 2002; Figueiredo et al., 2018; Medvigy et al., 2019). Texture and fertility variations can be limiting factors (environmental filters) for the establishment of species, thus reflected directly on their abundance and distribution (Botrel et al., 2002; Rodrigues et al., 2007; Fagundes et al., 2019) and, consequently, on the species richness of a site (Lemos et al., 2013). Species distributions are typically associated with habitat conditions, which act as environmental filters for plant colonization, survival, and growth (Cadotte and Tucker, 2017; Maia et al., 2020). The higher quality and quantity of resources will enable more species-rich areas (such as the Nitosol and Oxysol areas of our study) to be occupied by species with different life strategies. Cambisols are sandier in texture, with reduced water availability and lower fertility, all factors that can act as environmental filters in this community. The restrictiveness imposed by the Cambisol may exceed the physiological tolerance threshold of many species (Reich et al., 2003), reducing the number of species that



Figure 5. Temporal beta diversity of the three soil classes in the intervals between measurements in a semideciduous seasonal forest in southeastern Brazil. Beta temp = beta temporal diversity.

are able to colonize this area, as we show with our results. The higher dominance found in the Cambisol community is a typical pattern on forest formations under unfavorable environmental conditions (Souza et al., 2007; Fagundes et al., 2019).

On small scales, soil is the main driver of vegetation patterns in space (Arruda et al., 2013; Chase 2014; Fagundes et al., 2019). Pedogenesis is a slow process, and because the fragment has not undergone any disturbance capable of altering soil properties (e.g., the occurrence of fire) (Rheinheimer et al., 2003; Lorenzon et al., 2014), the communities are structured according to the attributes of each soil type. Differences in habitat resources and the ability of species to colonize these areas are an expression of different anatomical, physiological, and functional traits in different ecological strategies (Wright et al., 2004; Chave et al., 2009; Mayfield et al., 2010; Adler et al., 2014). Highly fertile soils tend to favor the existence of good competitor species, with fast growth and recruitment, high resource acquisition, and low internal conservation of resources, while poorer soils tend to favor slow-growth species that invest in survival more than growth (Wright et al., 2004; Chave et al., 2009; Adler et al., 2014). Thus, species fitness and representativity in the habitats are niche-determined, with plant-soil associations acting as an important mechanism shaping the plant community structure (Terra et al., 2018; Maia et al., 2020). On a small scale, the soil selected the most adapted individuals to explore the available resources, whereas other variables (e.g., precipitation and temperature) shaped the evolution of species on major scales (e.g., biomes) (Oliveira-Filho and Fontes, 2000). Evolutionary factors may have conditioned the coexistence of a pool of species that are able to persist in this area with similar life histories. Therefore, within the same fragment and the same physiognomy, habitat diversification contributes to supporting floristically and structurally different communities, but maintaining their patterns through temporal directional processes.

Studies that bring about the temporal dimension of forest community floristics and structure derive important insights on the direction of modifications verified among communities occurring in different environments (Botrel et al., 2002), such as the different soil types investigated here. Condit et al. (2002) highlighted that the substitution of species among communities may reflect the adaptation processes to different substrates, resulting from limited



Figure 6. Structural pattern of the three soil classes for each of the years of measurement in a semideciduous seasonal forest in southeastern Brazil. The y axis represents the value of phytosociological importance (importance value – IV) and the x axis presents the value of cumulative phytosociological importance (accumulated importance value – AIV).

dispersal associated with speciation or other historical factors. In the present study, similar temporal beta diversity among soil classes may also be associated with the fact that the tree community has not experienced significant anthropogenic interference since the 1950s (Espírito-Santo et al., 2002), being already established in the area. Swanson et al. (2011) emphasized that disturbances are the main factors driving changes in forests due to the opening of clearings, which are the basis for the renewal of floristic composition of communities in tropical forests (Jardim et al., 2007). However, small clearings have little influence on recruitment rates, as they result in the appearance of few new individuals (Paula et al., 2004), and therefore in low species substitution over time. This substitution occurs by species with ecological equivalence (due to environmental filtering) and is constant over time, showing evolutionary adaptation of the communities to the soil types.

The results corroborate one of the main hypotheses about the origin and maintenance of beta diversity, which relates species distribution with environmental conditions, whereby a mosaic of areas with different species compositions would be controlled by the site's environmental characteristics (Whittaker, 1956; Legendre et al., 2005). The presence of environmental filters in a community (as in the Cambisol class) results in the species of this community being a subset of a species group from a richer community, such as the entire studied fragment (Keddy, 1992). Thus, the presence of environmental filters makes the environment more selective, causing the recruited species to be eliminated before reaching the intermediate and upper strata of the forest (Carvalho et al., 2009). Consequently, only species that are functionally adapted to survive and grow under the specific conditions of that environment are able to establish themselves in the community (Lohbeck et al., 2013). This selectivity of the environmental conditions leads to a lower species richness and greater dominance (Keddy, 1992; Botrel et al., 2002; Fagundes et al., 2019). In the Cambisol, the structural

SANTOS et al. / Turk J Bot

2000			
Class	Species	VI	Rank
Cambisol	Galipea jasminiflora (A.StHil.) Engl.	9.44	1°
	Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	6.26	2°
	Platycyamus regnellii Benth.	3.93	3°
	Machaerium stipitatum (DC.) Vogel	4.20	4°
	Albizia polycephala (Benth.) Killip ex Record	4.08	5°
Nitosol	Casearia sylvestris Sw.	4.64	1°
	Albizia polycephala (Benth.) Killip ex Record	4.61	2°
	Cupania vernalis Cambess.	3.98	3°
	Machaerium stipitatum (DC.) Vogel	3.71	4°
	Platycyamus regnellii Benth.	3.20	5°
	Croton floribundus Spreng.	4.73	1°
	Colubrina glandulosa Perkins	3.44	2°
Oxysol	Albizia polycephala (Benth.) Killip ex Record	3.30	3°
	Eugenia acutata Miq.	3.28	4°
	Piptadenia gonoacantha (Mart.) J.F.Macbr.	3.23	5°
2005			
	Galipea jasminiflora (A.StHil.) Engl.	10.29	1°
Cambisol	Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	5.84	2°
	Piptadenia gonoacantha (Mart.) J.F.Macbr.	5.40	3°
	Platycyamus regnellii Benth.	4.15	4°
	Machaerium stipitatum (DC.) Vogel	3.87	5°
	Casearia sylvestris Sw.	4.61	1°
	Albizia polycephala (Benth.) Killip ex Record	4.52	2°
Nitosol	Cupania vernalis Cambess.	4.20	3°
	Machaerium stipitatum (DC.) Vogel	3.92	4°
	Eugenia acutata Miq.	3.07	5°
Oxysol	Croton floribundus Spreng.	4.01	1°
	Eugenia acutata Miq.	3.66	2°
	Colubrina glandulosa Perkins	3.31	3°
	Ixora brevifolia Benth.	3.22	4°
	Ocotea corymbosa (Meisn.) Mez	3.21	5°
2010			·
Cambisol	Galipea jasminiflora (A.StHil.) Engl.	10.65	1°
	Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	5.90	2°
	Piptadenia gonoacantha (Mart.) J.F.Macbr.	4.63	3°
	Platycyamus regnellii Benth.	4.52	4°
	Machaerium stipitatum (DC.) Vogel	3.76	5°
Nitosol	Albizia polycephala (Benth.) Killip ex Record	4.54	1°
	Casearia sylvestris Sw.	4.54	2°
	Cupania vernalis Cambess.	4.10	3°
	Machaerium stipitatum (DC.) Vogel	3.71	4°
	<i>Eugenia acutata</i> Mig.	3.57	5°

Table. Importance values (VI%) of the five most important species in the years 2000, 2005, 2010, and 2016 by soil class in a semideciduous seasonal forest in southeastern Brazil.

	<i>Eugenia acutata</i> Miq.	4.05	1°
	Croton floribundus Spreng.	3.37	2°
Oxysol	Ixora brevifolia Benth.	3.33	3°
	Ocotea corymbosa (Meisn.) Mez	3.23	4°
	Piptadenia gonoacantha (Mart.) J.F.Macbr.	3.18	5°
2016		·	
	Galipea jasminiflora (A.StHil.) Engl.	10.95	1°
	Piptadenia gonoacantha (Mart.) J.F.Macbr.	6.33	2°
Cambisol	Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	6.23	3°
	Platycyamus regnellii Benth.	4.53	4°
	Eugenia acutata Miq.	3.53	5°
	Machaerium stipitatum (DC.) Vogel	5.42	1°
	Galipea jasminiflora (A.StHil.) Engl.	4.76	2°
Nitosol	Casearia sylvestris Sw.	4.51	3°
	Cupania vernalis Cambess.	4.27	4°
	Eugenia acutata Miq.	4.15	5°
	Eugenia acutata Miq.	4.57	1°
	Ixora brevifolia Benth.	3.55	2°
Oxysol	Mollinedia widgrenii A.DC.	3.45	3°
	Colubrina glandulosa Perkins	3.35	4°
	Albizia polycephala (Benth.) Killip ex Record	3.05	5°

Table. (Continued).

pattern of the tree community was characterized by the dominance of the species *Galipea jasminiflora*, which did not change over time. This shows that this species is more efficient in exploring the available resources in this area (Felfili, 1995b), due to its adaptations to the environmental conditions that allow its dominance (Lohbeck et al., 2013). Therefore, in the absence of major disturbances, it is unlikely that this species will alter its participation in the community structure (Pinto and Hay, 2005).

Niche conservatism was discussed by Pennington et al. (2009) for seasonally dry forests and it allows us the inference about the importance of evolutionary factors in choosing a pool of species able to coexist in the climatic and soil conditions of these areas. This long-term stable coexistence is possible because species differ in their ability to acquire and use resources as the environment varies (Chesson, 2000). In this study, we observed that changes in

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Adler PB, Salguero-Gomez R, Compagnoni A, Hsu JS, Ray-Mukherjee J et al. (2014). Functional traits explain variation in plant life history strategies. Proceedings of the National Academy of Sciences of the USA 111: 740-745. soil conditions promote changes in semideciduous seasonal forest community structure and composition. Despite the soil types acting as an environmental filter, selecting the functionally more skilled in each soil condition (and promoting a high beta diversity), community dynamics were maintained over time, displaying a directional establishment and evolutionary adaptation to soil type in the community.

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