ABSTRACT

VARIATIONS IN ANGIOSPERM LEAF VEIN DENSITY HAVE IMPLICATIONS FOR INTERPRETING LIFE FORM IN THE FOSSIL RECORD

by Camilla Crifò

This work analyzes leaf vein density variation in flowering plants and proposes it as a new tool to trace the first occurrence of angiosperms as canopy members in the fossil record. Comparisons of vein density between canopy and understorey plants show that vein density variation mainly reflects the position of the leaf in the canopy. Vein density values of a standing forest are reflected in its leaf litter, suggesting that a fossil floral assemblage is also representative of a past forest ecosystem. Vein density measurement on leaf cuticles from a Miocene fossil flora suggest that vein density can be successfully measured on fossils. Comparison of vein density distributions of a leaf litter assemblage and those of several Cretaceous-Paleocene paleofloras (132.35 to 58 Ma) suggests that angiosperms emerged in forest canopies at least 58 Ma.

VARIATIONS IN ANGIOSPERM LEAF VEIN DENSITY HAVE IMPLICATIONS FOR
INTERPRETING LIFE FORM IN THE FOSSIL RECORD

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TABLE OF CONTENTS

	Page
List of Tables	iv
List of Figures	v
ACKNOWLEDGMENTS	vi
Section 1: Modern data, leaf litter, and fossil floras	
INTRODUCTION	1
SITES OF THE STUDY	3
Panama Forests	3
<i>Parque Natural Metropolitano</i>	3
<i>Parque Nacional San Lorenzo</i>	3
Maryland Forest	4
METHODS	4
Leaf sampling	4
<i>Panama samples</i>	4
<i>Maryland samples</i>	5
<i>Leaf litter samples</i>	5
Laboratory protocol for leaf clearing, staining, and photographing	5
Leaf vein density measurements	6
Statistical Analysis	7
RESULTS	7
DICSCUSSION	8
Canopy versus understorey trees	8
Differences between sites	9
Sun-established versus shade-tolerant species	9
Early-diverging versus late-diverging angiosperms	10
Leaf litter	10
Vein density and the fossil record	10
CONCLUSION	11

Section 2: The Mush Valley paleoflora: a preliminary case study of vein density as a proxy for canopy closure

INTRODUCTION	12
METHODS	12
RESULTS	13
DISCUSSION	13
CONCLUSION	13
REFERENCES CITED	15
FIGURE 1	19
FIGURE 2	20
FIGURE 3	21
FIGURE 4	22
FIGURE 5	23
TABLE 1	24
TABLE 2	25
SUPPLEMENTARY MATERIAL	
SUPPLEMENTARY MATERIAL I – Figures	26
SUPPLEMENTARY MATERIAL II – R codes	29
SUPPLEMENTARY MATERIAL III – Row data	38

List of Tables

Table 1. Average D_v values of sun-demanding and shade tolerant species in both canopy and understorey strata in PNM, FTS, SERC forests, and all forests together (TOTAL).

Table 2. Table of specimen names, corresponding morphotypes, area measured and vein densities.

List of Figures

Figure 1: Photo of a leaf of *Miconia borealis* (Melastomataceae) for vein density estimation.

Figure 2. Comparison of canopy and understorey at FTS, SERC, and PNM, and PNM litter.

Figure 3. Comparisons of the PNM litter and Cretaceous-Paleocene fossil floras.

Figure 4. Phylogenetic distribution of leaf vein density.

Figure 5. Comparisons of the PNM litter and the Mush Valley fossil assemblage.

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Section 1: Modern data, leaf litter, and Cretaceous-Paleocene fossil floras

INTRODUCTION

Plant remains are usually found as isolated organs. Their morphology, anatomy, and taxonomy can provide information on species composition of ancient ecosystems, plant evolution, paleogeography, paleoecology, and paleoclimate, yet they have been scarcely used to infer the structure of past ecosystems. Hence, key questions for the history of terrestrial ecosystems, such as when angiosperms emerged and dominated forest canopies, remain unsolved. In this study I present vein density (D_v), a trait visible on fossil leaf imprints, as a tool to shed light on the origin of forest types. Vein density (the vein length per unit leaf area) correlates with transpiration capabilities (Brodribb *et al.*, 2007) and maximum conductance to water vapor (Boyce *et al.*, 2009). Increased D_v allows a leaf to deliver water as close to the epidermis as possible, overcoming the low hydraulic conductivity that characterizes the leaf mesophyll, and optimizing water transportation (Brodribb *et al.*, 2007). Leaf D_v is also a tradeoff between the investments for more efficient transpiration and the costs of building vascular tissues (Noblin *et al.*, 2008; Beerling and Franks, 2010; McKown *et al.*, 2010). A four-fold increase in D_v during flowering plant evolution led to higher transpiration rates and contributed to the domination of this group in most terrestrial ecosystems (Boyce *et al.*, 2009; Boyce and Leslie, 2012). de Boer *et al.*, 2012 have interpreted angiosperms D_v increase as a response to the lower atmospheric humidity of the upper strata of the canopy and the falling CO_2 concentration during the Cretaceous: in fact, under these conditions, high D_v may have allowed plants to face the higher transpirational demand associated with higher stomatal conductance typical of upper canopy environments (de Boer *et al.*, 2012). Similarly, Feild *et al.*, pointed out that the long-term decrease in CO_2 and increase in O_2 atmospheric concentrations during the Cretaceous represented an environmental pressure supporting higher vein density.

In some temperate and almost all tropical modern forests, angiosperms inhabit a wide range of microhabitats (strata), where they fulfill their different resource needs by a variety of ecological strategies (Denslow, 1987; Rijkers *et al.*, 2000; Rueger *et al.*, 2009). Some of these strategies are reflected in their life forms, morphology and physiology. Leaf trait variations between trees living in different forest strata have been documented and traditionally attributed to the local light regime (Sack & Frole, 2006) or to differential hydraulic limitations at the top and bottom of the canopy (Zwienieck *et al.*, 2004; Meinzer *et al.*, 2008; Boyce, 2009; Cavaleri *et*

al., 2010). In fact, the main limiting factor in angiosperm-dominated forests is light irradiance (Campanello *et al.*, 2008), which decreases descending from the upper to the lower levels of the forest. Mulkey *et al.* (1996) documented a high light extinction (>90%) below the uppermost canopy leaves of a tropical forest in Panama; similarly, light transmittance in the understorey of temperate deciduous forests drops below 5% (Brown and Parker, 1994). In general, upper canopy leaves that have access to a higher light irradiance have higher stomatal density (Panditharathna *et al.*, 2008; Yáñez-Espinosa *et al.*, 2003), allowing higher transpiration rates and more efficient carbon gains (Rijkers *et al.*, 2000). Similarly, shade-tolerant and sun-established tropical forest species show differences in leaf hydraulic architecture, leaf conductance (K_{leaf}) and leaf mass per area (LMA) (Sack *et al.*, 2005; Sack and Frole, 2006; Campanello *et al.*, 2008) associated to respectively lower (shade-tolerant) and higher (sun-established) whole plant relative growth, carbon assimilation, and transpiration rates.

Here I test 3 hypotheses. (1) My first hypothesis is that differences between understory and canopy leaves are reflected in higher D_v values in the canopy than in the understorey, according to differential transpiration and metabolic needs at different forest strata. To test this, I have measured D_v variation among canopy and understorey plants in two forests in Panama and one in Maryland. (2) My second hypothesis is that the variation in D_v within a forest is reflected in its leaf litter. In order to know if both canopy and understorey values are present in the leaf litter, D_v values measured in a tropical leaf litter assemblage were compared to those of the corresponding standing forest. (3) My last hypothesis is that the first forests characterized by an angiosperm-dominated canopy present similar D_v values to modern forests. Present data from a tropical forest litter assemblage were compared with fossil data from Feild *et al.*'s (2011), which encompass a time period from the Hautaverian to the Paleocene (132.35 to 58 Ma). This comparison assumes that fossil flora assemblages reflect the forest as closely as litter assemblages do. Fossil and molecular data indicate that the rise of angiosperm-dominated forests took place either in the Late Cretaceous (Crane *et al.*, 1995; Davis *et al.*, 2005; Wang *et al.*, 2009) or in the Paleocene (Bunnham and Johnson, 2004; Wing *et al.*, 2009; Wing *et al.*, 2012). I propose vein density as a new tool to better define when the emergence of angiosperms as canopy members took place.

SITES OF THE STUDY

Panama Forests

The two forest sites in Panama, Parque Natural Metropolitano (PNM) and Fort Sherman Crane (FTS) at the Parque Nacional San Lorenzo are located respectively on the Pacific and Caribbean coasts of Panama, near the cities of Panama and Colón.

Parque Natural Metropolitano

Parque Natural Metropolitano is located at 30 m above seal level on the Pacific coast, fifteen-minute drive from downtown Panama City (8°59'N, 79°33'W). This site represents one of the few remaining tropical dry coastal forests in Central and South America and it has been protected since the construction on the Panama Canal (1903). Parque Natural Metropolitano is a tropical dry semi-deciduous rainforest with a mean annual rainfall of 1865 mm and mean annual temperature of 26.3°C. The canopy is 30-40 m high and it is dominated by the species *Anacardium excelsum* (Anacardiaceae). Other abundant tree species are *Luehea seemanii* (Tiliaceae), *Cordia alliodora* (Boraginaceae), *Ficus insipida* (Moraceae) and *Castilla elastica* (Moraceae). 0.85 hectares of the forest are accessible by canopy crane, which is 42 m high with a 52 m long arm. 316 trees with a minimum diameter at breast height (dbh) of 10 cm have been censused and mapped in a 1-hectar-plot area surrounding the crane. Of the 284 species of trees present in the park, 36 species, belonging to 20 families, are reachable by the crane (STRI, 2013).

Parque Nacional San Lorenzo

Parque Nacional San Lorenzo (Fort Sherman Crane, FTS) is located 130 m above sea level on the Caribbean coast, near the city of Colón (9°17'N, 79°58'W). This forest is 300 years old and is part of the Mesoamerican Biological Corridor and the forested area of the Panama Canal Basin. After having been used as a jungle warfare-training site by the U.S. army in the second half on the 1900's, the site was declared a protected area. Parque Nacional San Lorenzo is a tropical evergreen humid rainforest with annual rainfall of 3152 mm and a mean annual temperature of 25.8°C. The canopy is 35-45 m high and it is dominated by the species *Brosimum utile* (Moraceae) and *Manilkara bidentata* (Sapotaceae). 0.92 hectares of the forest are accessible by the crane, which is 52 m high with a 54 m long arm. 22,400 trees and lianas belonging to more than 240 species with a minimum dbh of 1 cm have been censused and mapped in a 6-hectar-plot area surrounding the crane (STRI, 2013).

Maryland forest

The Maryland forest is located at 11 m above sea level at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland (38°53' 20"N, 76°33'32"W) (3,4). Mean annual rainfall is 1080 mm and mean annual temperature is 13.2°C. The site is dominated by mature secondary temperate deciduous forest ("tulip-poplar association" type), which is 120 years old, and it is bisected by a floodplain forest (which was not sampled for this study). The canopy is 30-40 m high, and the forest is dominated by the species *Liriodendron tulipifera* (Magnoliaceae), *Quercus* ssp. (Fagaceae), *Fagus grandifolia* (Fagaceae), *Carya* ssp. (Juglandaceae), *Acer rubrum* (Sapindaceae), *Nyssa sylvatica* (Cornaceae), *Carpinus caroliniana* (Betulaceae), *Lindera benzoin* (Lauraceae), and *Asimina triloba* (Annonaceae) (STRI 2013, SERC, 2013). Census data about this plot are not publicly available.

METHODS

Leaf sampling

In this study, only mature leaves were collected in order to reduce the possible bias in vein density estimate due to different developmental stages of the leaves. Sampling took place in two tropical primary rainforests in Panama and in a temperate secondary deciduous forest in Maryland.

Panama samples

Leaf sampling in Panama was carried out between January and March 2011. In both Panama forests, canopy leaves were collected by hand from the top of the tree crown (full sun leaves) using a canopy crane. A gondola (metal basket) is attached to the crane allowing sampling in different locations and heights within the forest. The crane sampling method presents several advantages, notably safe, easy and non-destructive access to the upper canopy. The maneuvers of the crane were coordinated with the crane operator through a walkie-talkie. Understorey leaves were collected at breast height or at any height reachable by hand.

119 canopy leaves (from 44 plants belonging to 30 species, 15 of which are trees, 10 lianas, 4 vines, 1 shrub, and 1 hemiepiphyte) and 39 understorey leaves (from 17 plants belonging to 7 species, 5 of which are trees, 2 lianas, and 1 shrub) were collected in PNM. 119 canopy leaves (from 46 plants belonging to 49 species, 30 of which are trees, 14 lianas, 3 hemiepiphyte, and 1 shrub), and 39 understorey leaves (from 23 plants belonging to 16 species, 12 of which are trees, 3 lianas, and 1 shrub) were collected in FTS. Because canopy tree species

tend to be sun-demanding species and are more abundant in the canopy, whereas understorey tree species tend to be shade adapted and more abundant in the understorey, only 15 species of the 83 collected were sampled in both strata. At least 3 leaves per individual and 1 to 3 individuals per species were sampled in both sites for D_V analysis. In order to keep the leaves hydrated, they were stored in a cooler and/or in a refrigerator before the clearing/staining process.

Maryland samples

Maryland leaf sampling was carried out in June 2012 over a period of 5 days. Understorey leaves in Maryland were collected following the same protocol used in Panama. As there is no crane on the site, I developed alternative methods for canopy leaf sampling. Leaves at the top of the crown of 5 tree species were reached from a meteorological tower and using a cherry picker. 10 species were collected using a new technique consisting of directing a balloon filled with helium and attached to a rope equipped with sharp blades. Pulling and relaxing the rope caused the blades to cut small branches or leaf fragments from the tree crown, which were picked up once they reached the forest floor. As previously done in Panama, at least 3 leaves per individual and 1 to 3 individuals per species were sampled, except for some canopy species for which the lack of time and the lack of precision of the new "balloon technique" did not allow an exhaustive sampling. 48 trees were sampled. A total of 137 canopy leaves belonging to 15 species (13 trees, and 1 woody vine) and 127 understorey leaves belonging to 19 species (12 trees, 6 shrubs, and 1 woody vine) were sampled for D_V analysis. Sampled leaves were stored in a cooler and/or in a refrigerator in order to keep them hydrated.

Leaf litter samples

Leaf litter sampling was carried out in Parque Natural Metropolitano in July 2012. An area of $1 \times 1 \text{ m}^2$ was chosen randomly in the forest. All the leaves covering the surface of the area as well as those deposited down to 2 cm of depth in the sediment were collected. The sampling surface chosen is similar to that used for sampling fossil floras. 173 leaves well enough preserved to allow morphotype classification were used for the study. 18 different morphotypes were identified. Samples were stored in a refrigerator to avoid putrefaction.

Laboratory protocol for leaf clearing, staining, and photographing

A 2 cm^2 section of leaf lamina was excised from each sample, cleared, stained, and photographed for vein density measurements. Although in temperate environments some

authors have not found significant differences in vein density across the blade of the same leaf (Uhl & Mosbrugger, 1999), others have observed a significant change in vein density across the blade of mature leaves from the top of the canopy (Zwieniecki *et al.*, 2004); for modern samples, in order to avoid any bias, leaf fragments were all cut from the same site on the blade. Furthermore, major veins were avoided because of their bigger thickness compared to other orders of veins. This was not always possible for litter sample due to the fragmented preservation of the leaves. For modern samples, three fragments (from three leaves of each tree) were stored in a 50 mL beaker where they were treated with around 25 ml of 10% NaOH for clearing. All the Panama litter samples (divided in morphotypes) were stored in 50 mL beakers and treated with around 35 mL of 10% NaOH for clearing. For modern species, the clearing time varied between species, depending on their leaf thickness and tannin content, and between sites (3 weeks to 2 months for Panama leaves, 3 to 10 days for Maryland leaves) because tropical leaves tended to be thicker and to have higher tannin content (personal observation). Therefore, when required (high thickness and/or tannin content), the NaOH solution was changed. For Panama litter samples the clearing time was between 2 and 3 weeks, and when required (high thickness and/or tannin content), the NaOH solution was changed. Subsequently, leaves were rinsed with distilled water 2 to 3 times. After a dehydration series with 50%, 75%, 95%, and 100% ethanol (1 minute for each concentration), leaves were stained in a Safranin (2%) – Ethanol (50%) solution for 1 hour minimum. The duration of the dehydration process was sometimes lengthened (with a supplementary Ethanol 100% step) because this facilitated further clearing of the specimens. The specimens were observed on a Petri dish using a stereoscope equipped with a camera (Nikon DXN1200C for the Panama samples; Leica DFC 480 for the Maryland samples), at a magnification of 20x. At least 3 photos were taken for each leaf fragment. Panama modern samples were processed and photographed at Carlos Jaramillo's lab at the CTPA (Center for Tropical Paleoecology and Archaeology) of the STRI (Smithsonian Tropical Research Institute) in Panama. Maryland samples were processed and photographed using the facilities of Kevin Boyce's laboratory at the University of Chicago (IL).

Leaf vein density measurements

Leaf vein density was estimated using a 2-dimensional method based on the measurement of the total vein length per unit leaf area. All the veins present in a known area (a) were drawn by hand and their total length (L) was measured using digital image analysis (Image J; National

Institute of Health, Bethesda, MD, USA) (fig. 2). Then, the leaf vein density (D_V) of each leaf was simply calculated as follow:

$$D_V = L/a$$

The area measured was around 10 mm² for Panama samples and 4 mm² for Maryland and litter samples. The choice of a smaller area for Panama-litter and Maryland samples is consistent with other studies published in the literature (Boyce *et al.*, 2009) and reduced the duration of the measurement phase by more than half the original time (15-30 minutes versus 30 minutes-1 hour per photo). It is important to note that this manual D_V estimation technique is extremely time-consuming. Therefore, reducing the time spent on measurements was considered a crucial point for the feasibility of this project. The effects of human error and variable measured areas on D_V estimations were also tested. The test showed that varying the area measured did not affect D_V estimation. Nonetheless, human error may occur for at especially at high D_V , and when the researcher has little experience with D_V measurement (although results are consistent from measurement to measurement) (SI table 1 and figure 3). 1 to 3 measurements were performed for each leaf, and averaged in order to obtain a single mean value. Then, the D_V for each species was calculated averaging the values obtained for the single leaves.

Statistical analyses

D_V values of canopy and understory leaves were compared among different ecological strategies and sites. D_V of the PNM standing forest was compared to the PNM leaf litter assemblage as well. The PNM litter was then compared to fossil data selected from Feild *et al.*'s (2011) Cretaceous-Paleocene dataset. These data include only morphotypes coming from a single formation per each time period. In order to test the effects of phylogeny on D_V , I also compared D_V among different large clades and between early- and late-diverging angiosperms. Wilcoxon rank-sum tests conducted in R 3.0.0 (R Development Core Team, 2013) were used for all comparisons because the data were not normally distributed (Shapiro-Wilk Normality test). All life forms together (trees, shrubs, hemiepiphyte, lianas, vines, and woody vines) were included in my analyses.

RESULTS

Vein density is higher in the canopy than in the understory in PNM (average D_V = 13.29±4.57 versus 8.98±2.75 mm/mm²), FTS (average D_V = 10.41±3.13 versus 5.98±1.63 mm/mm²), and SERC (average D_V = 10.87±2.49 versus 6.07±1.62 mm/mm²) forests ($p < 0.01$)

(fig.2). However the three sites present some differences: (1) canopy D_v is not significantly different between FTS and SERC ($p = 0.362$), and between PNM and SERC ($p = 0.069$) but it is different between FTS and PNM ($p < 0.01$); (2) understorey D_v is not significantly different between FTS and SERC ($p = 0.935$) but it is significantly different between PNM and the two other sites ($p < 0.05$); (3) when putting canopy and understorey data together, the overall D_v distribution of PNM (average $D_v = 12.47 \pm 4.58$) significantly differs from that of FTS (average $D_v = 9.32 \pm 3.41$) and SERC (average $D_v = 8.19 \pm 3.15$) ($p < 0.01$), whereas SERC and FTS D_v distributions are not significantly different ($p = 0.106$). Furthermore, the D_v curve of the PNM litter (average $D_v = 10.66 \pm 5.66 \text{ mm/mm}^2$) assemblage is not significantly different from that of the PNM standing forest (average $D_v = 12.47 \pm 4.58 \text{ mm/mm}^2$) ($p = 0.071$) and it is more similar to the PNM understorey ($p = 0.057$) than to the PNM canopy ($p < 0.05$) (fig. 2C).

D_v of canopy leaves is higher than D_v of understorey leaves regardless of being either a sun-demanding or shade-tolerant tree (Table 1). Lumping the data from all three sites, sun-established and shade-tolerant species have similar average canopy D_v values and similar average understorey D_v values. Average D_v values and p -values per site, ecology, and forest strata are reported in Table 1; the small sample size for some of these categories did not always allow me to test the hypothesis of a D_v difference between species ecologies at the site level.

D_v varies among clades, but in all clades canopy D_v values are significantly higher than understorey D_v values (fig. 3). Although D_v averages for early- and late-diverging angiosperms are similar (11.1 and 11.7 mm/mm^2 , respectively), the range for late-diverging angiosperms (max = 27.2 mm/mm^2 , min = 5.1 mm/mm^2) is higher than that of early-diverging angiosperms (max = 13.9 mm/mm^2 , min = 8.4 mm/mm^2).

The PNM litter D_v is significantly different ($p < 0.05$) from all fossil assemblages except for the Paleocene and Masstrichtian ones (fig. 4).

DISCUSSION

Canopy versus understorey trees

Vein density tends to be higher in the canopy independent of site, life form and ecology, suggesting that the location of the leaf within the forest is the main factor in determining D_v . Light irradiance may be one of the major factor driving D_v , as it is for many other leaf traits (Denslow, 1987; Rijkers et al., 2000), although other parameters such as the height of trees, relative humidity, and temperature may also play a role. Because all these factors and tree height

are strictly associated, my experimental design does not allow us to isolate these variables. However, a possible influence of all these factors at the same time does not affect my hypothesis that D_v is higher in the canopy than in the understorey, according to differential transpiration and metabolic needs at different forest strata. Furthermore this result suggests that high vein density is a unique character of emergent canopy trees. Hence, this trait can likely be used in the fossil record to characterize past ecosystems where angiosperm trees were a dominant component of the forest canopy.

Differences between sites

The difference in D_v distribution between sites is likely the effect of two interplaying factors: (1) a sampling bias - the ratio of canopy to understorey samples varies between PNM (~ 4.3), FTS (~ 3), and SERC (~ 0.7) - and (2) a significant difference in canopy and understorey average D_v among sites. The high canopy:understorey sample ratio at PNM compared to FTS and SERC may explain why PNM D_v distribution tends toward the high-values side of the D_v axis, and differs significantly from that of FTS and SERC. Despite these differences, higher D_v values in the forest canopy than in the understorey characterize all three study sites, reflecting closed-canopy environments dominated by angiosperm trees.

Sun-established versus shade-tolerant species

Different levels of light irradiation are thought to be the main control on variations in physiological traits throughout the forest. However, if light was the only control on D_v , I would expect sun-established trees to have significantly higher D_v than shade-tolerant species. The absence of an influence of tree ecological strategy on D_v , together with the fact that vein density is higher in the canopy than in the understorey in both sun-established and shade-tolerant species, indicate that the placement (not only light availability) of the leaf within the forest is the main driver of vein density variations. I suggest that other factors, such as tree height, also play an important role in modulating plant physiological adaptation including vein density. Rijkers et al. (2000) observed a positive relationship between tree height, leaf mass per area (LMA), and light-saturated rate of photosynthesis per unit area ($A_{\max}/\text{area}$). Cavaleri et al. (2010) related the LMA vertical gradient within a forest canopy to tree height, and hypothesized a direct effect of gravity on leaf water potential and turgor pressure, which in turn would affect LMA. I suggest that this hydraulic mechanism has similar effects on venation density.

Early-diverging versus late-diverging angiosperms

D_v varies largely among plant taxa. The higher range of D_v variation in late-diverging angiosperms suggests a higher plasticity, allowing them to explore different ecological niches within an ecosystem. The smaller range of D_v variation and the paucity of high D_v values in early-diverging angiosperms is consistent with Boyce *et al.*'s (2009) and Boyce and Leslie's (2012) observations of high vein density as a unique character of late-diverging angiosperms. Furthermore, the presence of high D_v values in late-diverging angiosperms at different taxonomic positions is in agreement with the Boyce *et al.* (2009) interpretation that increases in D_v occurred multiple times during angiosperms' diversification.

Leaf litter

The PNM litter assemblage does not significantly differ from the samples collected from living trees. Most leaves whose provenance (canopy or understorey) is not doubtful come from the canopy, confirming the hypothesis that canopy leaves are overrepresented in the fossil record due to their higher production, as traditionally assumed (Stebbins, 1965; Burnham *et al.*, 1992; Burnham, 1994). However, the data also indicate that understorey leaves contribute to the litter assemblage in a visible manner and that, in general, a litter assemblage is composed of leaves coming from different strata of the forest. This suggests that fossil flora assemblages may be more representative of an ecosystem than previously thought.

Vein density and the fossil record

The presence of the same D_v trend in both tropical and temperate regions suggests that this trait varies independent of climate, and it mainly reflects the occurrence of a highly competitive ecosystem where different species cohabit in different forest strata by modulating their physiological traits, including D_v . Hence, low D_v is associated with lower metabolic rates and transpiration in the understorey, whereas high D_v allows higher transpiration in the upper canopy. Consequently, D_v can be used in the fossil record to investigate the ecological strategies of angiosperms even in those time periods when climate is not well constrained. The vein density curve derived from the histograms of PNM litter assemblage is not significantly different from those obtained for the Paleocene and Maastrichtian floras, suggesting that the emergence of angiosperms as forest canopy members took place at that time. In fact, high vein density values only evolved by the end of the Maastrichtian, (Feild *et al.*, 2011); angiosperms metabolic capabilities were limited by lower transpiration and assimilation rates and as a consequence they

were unlikely able to attain and dominate the upper strata of the forest. The vein density curve of the Maastrichtian is not significantly different from that of PNM. Nevertheless, it lacks the lowest and highest modern D_v values, resulting in a smaller D_v value range for the Maastrichtian (7.33 - 15.42 mm/mm²) compared to the modern PNM litter assemblage (1.11 – 25.3 mm/mm²). Additional data are needed to verify whether this observation is the result of a small sample size or it reflects a different type of ecosystem, where angiosperms had not yet attained all forest layers.

CONCLUSION

Vein density variation within a modern angiosperm-dominated forest is mainly driven by the forest strata in which the leaf is located, and it is independent of plant ecological strategy and site. Different forest strata correspond to variable amounts of available light and different tree height, as well as other variable parameters like temperature, humidity, and CO₂ concentration. I suggest that tree height, not only light availability, is a major factor modulating D_v variation through forest strata. Because differences in D_v average values between sites are most likely due to a sampling bias rather than to any environmental or climatic differences, D_v can be used as a proxy to trace the emergence of angiosperm trees in the forest canopy in the fossil record even for those time periods whose climatic variables are uncertain.

Although leaves in a litter assemblage are more likely to come from the canopy than from the understorey, understorey leaves are more represented than previously thought. Assuming that a litter assemblage is similar in composition to a fossil leaf assemblage, I propose that fossil floras are representative of the D_v variation in the standing forest. Of the 8 fossil leaf assemblages analyzed in this study, the Paleocene flora has the most similar D_v density curve to modern tropical forest litter. Although the Maastrichtian flora is not significantly different from the tropical litter assemblage, more samples are needed for the Maastrichtian to strongly support any interpretation of the data. In conclusion, results suggest the occurrence of angiosperm as forest canopy members at least 58 Ma.

Section 2: The Mush Valley paleoflora: a preliminary case study of vein density as a proxy for canopy closure

INTRODUCTION

The two main objectives of this study were: 1) to explore the potential of fossil leaf cuticles for vein density measurements, and 2) to test vein density as a proxy for forest canopy coverage in the fossil record. The Mush Valley flora is an excellent candidate for this work because of its optimal state of preservation and because, as suggested by previous taxonomical studies, it represents a late stage successional forest, where trees were presumably tall enough to create a closed-canopy environment. In fact, taxa typically found in modern forest gaps and forest understorey are present in the Mush Valley flora (Currano et al. 2011; Pan, 2012; Pan et al., in prep).

SITE OF THE STUDY

The fossils used for this study come from Early Miocene sediments located in the Mush Valley, Ethiopia, approximately 160 km northeast of Addis Ababa in Debre Birhan Woreda. The sediments are mainly carbonaceous shales and mudstones where fossils are abundant and extremely well preserved. The site was interpreted as a lacustrine deposit (Pan et al., 2012). The age of the site is ~21.7 Ma (Pan et al., 2012), and it has been constrained using $^{239}\text{U}/^{206}\text{Pb}$ isotopes from zircons present in an ash layer.

METHODS

Thirty cuticle samples were selected for vein density measurements. Cuticle fragments (~0.5-1 mm²) were taken from each sample and soaked in a 0.1M solution of tetrasodium pyrophosphate decahydrate (Na₄P₂O₇) (Bates *et al.*, 1978) for a week in order to facilitate the separation of the cuticles from the rock matrix. Each cuticle was then put in a 48% HF solution to dissolve the silicate rock matrix (Barclay, 2011). Rock matrix dissolution generally took around 1 month. After isolation, the cuticles were stored in a slightly acidic distilled water solution to avoid fungal contamination. Venation density was measurable on 17 samples, belonging to 12 morphotypes. The area measured varies depending on the sample preservation and its available measurable surface (Table 2). Many treated samples were excluded from the analysis because they were too dark and, despite being present, veins were hardly visible. In addition several morphotypes had a very thin cuticle, which disintegrated during treatment.

Measured samples were plotted on a histogram and a density curve of D_v was obtained and compared to that of the PNM litter using R3.0.0. (R Development Core Team, 2013). A subsample of 12 morphotypes was extracted randomly 10,000 times from PNM litter using a bootstrap with replacement, and the histogram obtained was plotted together with the average D_v of Mush Valley flora.

RESULTS

Average vein density is $15.82 \pm 4.54 \text{ mm/mm}^2$, with a minimum of 9.85 mm/mm^2 and a maximum of 24.77 mm/mm^2 . Mush Valley D_v distribution is significantly different from that of PNM litter ($p < 0.01$) (fig. 5A). PNM litter average and minimum D_v (10.66 mm/mm^2 and 1.11 mm/mm^2) are lower than that of Mush Valley (15.82 mm/mm^2 and 9.85 mm/mm^2), whereas maximum D_v is very similar (25.29 mm/mm^2 for PNM litter, and 24.77 mm/mm^2 for Mush Valley). 11.56% of the PNM litter subsamples extracted with the bootstrap have an average equal or higher than that of Mush Valley. All other subsamples' (88.44%) averages are below that of Mush valley flora (fig. 5B).

DISCUSSION

Differences between the PNM litter assemblage and the Mush Valley fossil assemblage may be either the result of the low sample size of Mush Valley flora or they may be due to environmental differences between PNM modern tropical forest and Mush Valley paleoflora. Previous studies suggested that the Mush Valley flora represents a secondary succession forest, but also provided evidence for forest gaps and disturbed habitats (Currano et al. 2011; Pan, 2012; Pan et al., in prep). Assuming that the hypothesis that light is the main control on vein density is true, then gaps may account for the higher D_v values observed in the Mush Valley flora. Nonetheless, assuming that the main factor controlling D_v is tree height, high vein density values may reflect a forest dominated by relatively tall trees, plausibly creating dense canopy coverage. Hence, the absence of understorey-like D_v values may be simply due to a non-exhaustive sampling.

CONCLUSION

A more extensive sampling effort is required in order to make more definitive conclusions. Methods of cuticle treatment need to be improved. After the isolation treatment, cuticles could be treated using modern leaf clearing procedures. In order to eliminate the dark-colored material surrounding the veins, cuticles should be put into a NaOH solution for a few

hours/days. NaOH concentration should be low enough to avoid cuticle disintegration. Eventually, if the clearing is successful, cuticles could be stained using a Safranin solution, as done with modern leaves for morphological observation. Hence, more experimentation on clearing and staining methods is needed to determine precisely NaOH concentration, cuticle clearing time, and staining procedures.

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Figure 1: Photo of a leaf of *Miconia borealis* (Melastomataceae) for vein density estimation. Leaf vein density was calculated by drawing by hand all the veins present in a known area (a, in red). Both total vein length (L, in blue) and measured area were measured after having been drowned using digital image analysis (Image J; National Institute of Health, Bethesda, MD, USA). Vein density was calculates as (D_v) = L/a.

Figure 2. These graphics was obtained using the R function “*density*” and it represents the probability density function (pdf) or density of the continuous variable D_v . The pdf is a function that describes the relative likelihood for the variable D_v to fall within a particular region of an histogram. This probability is given by the integral of this variable’s density over the region. The algorithm used by this function disperses the mass of the empirical distribution function over a regular grid of at least 512 points, which represent a compromise between smoothing enough to eliminate insignificant bumps and smoothing too much so that real peaks are eliminated. Then, a fast Fourier transform is used to convolve this approximation with a discretized version of the kernel (a non-parametric test to estimate the probability density function), and a linear approximation is used to evaluate the density at the specified points.

Wilcoxon rank-sum tests on the data show significant differences ($p < 0.01$) between canopy (red) and understorey (blue) in: **A.** FTS, **B.** SERC, and **C.** PNM forests. D_v distribution does not significantly differ between FTS and SERC ($p > 0.05$) but is significantly different between SERC and PNM ($p < 0.01$) and between PNM and FTS ($p < 0.01$). The black line in C represents the litter D_v density curve, which is more similar to PNM understorey ($p > 0.05$) than to PNM canopy ($p < 0.05$). Red and blue colored areas under the litter curve correspond to D_v values respectively higher and lower than the maximum understorey and minimum canopy values encountered in PNM.

Canopy samples size (number of species) is 49 for FTS, 10 for SERC, and 30 for PNM. Understorey samples size is 16 for FTS, 19 for SERC, and 7 for PNM for the understorey.

Figure 3. D_v density curves (see figure 2 for more details) of 8 paleofloras (green) compared to the D_v density curve of the PNM litter (in black). p -values for Hautaverian, Barremian and Aptian are not provided because of the limited sample size. $p < 0.01$ for the Albian (3.99×10^{-5}), Cenomanian (0.0016), and Campanian (0.013). $p > 0.05$ for the Maastrichtian (0.1134) and the Paleocene (0.2583). * and ^{ns} indicate significant and not significant Wilcoxon rank-sum tests. The abbreviation “n” indicates the sample size (number of leaf morphotypes). For PNM litter, $n = 19$. Fossil D_v data were selected from Field et al.’s (2011) dataset and include only morphotypes coming from a single formation per each time period (Hautaverian: Chengzihe Formation, near Jixi, China; Barremian: Las Hoyas locality, La Huérguina Formation, Las Hoyas locality, Iberian Ranges, Spain; Aptian: Crato Formation, Brasil; Albian: Hoisington III, Dakota Formation, KS, USA; Cenomanian: Courtland, Dakota Formation, MN, USA; Campanian: Grunbach Formation, Austria; Maastrichtian: Guadas Formation, Colombia; Paleocene: Cerrejón Formation, Colombia).

Figure 4. Phylogenetic distribution of leaf vein density. The phylogeny was compiled using all species from this study (Angiosperm Phylogeny Groups, 2009). Group mean (dark red rectangles for canopy values, and dark blue rectangles for understorey values), and standard deviation (lighter rectangles) are provided when sampling is sufficient. Black lines indicate minimum – maximum ranges. The number of species corresponding to each value is indicated parenthetically (in red for canopy, and in blue for understorey values).

Figure 5. A. D_v density curve and histogram of Mush Valley floral assemblage (in orange, $n = 11$) and D_v density curve of the PNM litter assemblage (in black, $n = 18$) Left y axis (Density) refers to the density curves; right y axis (Frequency) refers to the histogram. **B.** Bootstrap histogram of PNM leaf litter average D_v , ($n = 11$; 10,000 repetitions); orange line represents Mush Valley D_v average.

Site	Average D_v sun-demanding		p -value	Average D_v shade-tolerant		p -value	n
	canopy	understorey		canopy	understorey		
PNM	13.81±3.85 (6)	8.67 (1)	NA	10.71±1.33 (3)	7.59 (1)	NA	11
FTS	12.59±4.14 (10)	8.19 (1)	NA	10.33±2.52 (15)	5.81±2.07 (7)	0.0011	33
SERC	10.03±2.71 (7)	5.09±0.72 (7)	0.0006	11.47±2.34 (7)	6.77±1.83 (10=	0.0019	31
TOTAL	12.11±3.81 (23)	5.83±1.6 (9)	9.62×10^{-6}	10.7±2.3 (25)	6.44±1.9 (18)	1.5×10^{-7}	75

Table 1. Average D_v values of sun-demanding and shade tolerant species in both canopy and understorey strata in PNM, FTS, SERC forests, and all forests together (TOTAL). Canopy versus understorey values were compared using Wilcoxon rank-sum tests, and p -values were indicated as “NA” when the sample size (in parenthesis) was too small to allow any statistical test. Ecological strategy was determined for all temperate but few tropical species because little knowledge on plant ecology has been acquired on tropical species, also due to their higher diversity.

Specimen	Morphotype	Area measured (mm ²)	Vein density (mm/mm ²)
MU33-19#2	Dinosaur footprint	1.18	13.96
MU27-38#1	Flaky Imposter	6.41	14.77
MU32-26#1	Herbie	0.75	18.8
MU23-26#3	Interrupt (Fabaceae)	15.56	9.56
MU32-20#2	Interrupt (Fabaceae)	10.14	10.14
MU18-17	InterruptC (Fabaceae)	1.42	20.09
MU7-35B#1	Legume 1 (Fabaceae)	16.3	13.59
MU16-27	Legume 4 (Fabaceae)	6.29	15.69
MUSH	Legume 4 (Fabaceae)	4.15	10.73
MU32-3B#2	Mushroom Trichomes	5.69	9.88
MU30-2	Pinnate Truncate (Fabaceae)	1.24	19.22
MU17- 28A#1	Short Drip Tip (Fabaceae)	2.11	18.69
MU18-13	Short Drip Tip (Fabaceae)	2.13	15.92
MU18-14A #2	Short Drip Tip (Fabaceae)	2.34	15.89
MU27-9	Short Drip Tip (Fabaceae)	3.98	13.18
MU31-16#1	Small-toothed Euphorbeaceae	3.54	23.53
MU31-30	Small-toothed Euphorbeaceae	1.71	26.01

Table 2. Table showing specimens names, corresponding morphotypes, area measured and vein densities.

SUPPLEMENTARY MATERIAL I – Figures and Tables

Figure1: Examples of vein density measurements of 3 different leaves. The area measured corresponds to the green square; area measured = 4 mm². **A.** *Coccoloba parimensis* (Polygonaceae), canopy leaf; **B.** *Tovomita longifolia* (Clusiaceae), understory leaf; **C.** *Marila laxiflora* (Clusiaceae), canopy leaf.

Species	Area (mm ²)	Dv1	Dv2	Dv2-Dv1
<i>Luehea seemanii</i>	1	24.98401598	29.06893107	4.08491509
<i>Luehea seemanii</i>	2	25.20586773	29.12829438	3.92242665
<i>Luehea seemanii</i>	3	25.09000332	28.94287612	3.8528728
<i>Luehea seemanii</i>	4	25.27222777	27.6471029	2.37487513
<i>Luehea seemanii</i>	5	24.56080542	27.93361244	3.37280702
<i>Luehea seemanii</i>	6	25.45454545	28.3997669	2.94522145
<i>Luehea seemanii</i>	7	NA	28.29217168	NA
<i>Luehea seemanii</i>	8	25.36318284	28.33574457	2.97256173
<i>Luehea seemanii</i>	9	NA	28.81218781	NA
<i>Luehea seemanii</i>	10	NA	28.3874	NA
Average		25.13294979	28.49480879	3.36081141
<i>Ocotea ira</i>	1	3.548707753	3.226640159	-
<i>Ocotea ira</i>	2	3.306387226	3.410678643	0.104291417
<i>Ocotea ira</i>	3	3.176353371	3.189637994	0.013284623
<i>Ocotea ira</i>	4	3.315027459	3.354717923	0.039690464
<i>Ocotea ira</i>	5	3.329802119	3.38776734	0.057965221
<i>Ocotea ira</i>	6	3.395934011	3.45325779	0.057323779
<i>Ocotea ira</i>	7	3.40076934	3.397919932	-
<i>Ocotea ira</i>	8	3.407633778	3.470250717	0.062616939
<i>Ocotea ira</i>	9	3.375333333	3.427222222	0.051888889
<i>Ocotea ira</i>	10	3.327606872	3.376648022	0.04904115
Average		3.358355526	3.369474074	0.011118548

Table 1: Table of vein density measurements of a high *Dv* canopy leaf of *Luehea seemanii* and an understorey leaf of *Ocotea ira*. The second column indicates the area measured. *Dv1* and *Dv2* are the vein density measurement obtained by two different people, using the same images and the same spots on each photo. *Dv1* was measured by an undergraduate with no prior experience performing vein density analyses, and *Dv2* was measured by the PI. The difference between *Dv2* and *Dv1* are reported on the last column. Data show that varying the area measured does not affect the accuracy of the vein density measurements. Although there is no significant difference between *Dv1* and *Dv2* for *Ocotea ira*, *Dv2* is consistently 3-4 mm/mm² higher than *Dv1* for *Luehea seemanii*. This is probably due to the higher chance of misidentifying veins at high densities, caused by different experience working with leaves. However, *Dv* measurements obtained by an individual researcher are consistent with each other, suggesting that the technique is well reproducible.

A **B** **C**

Figure 2: A. plot of Dv at different areas measured of a leaf of B. *Luehea seemanii* (Malvaceae) (upper points) and C. *Ocotea ira* (Lauraceae) (lowest points) by two different people (in pink and green). The x-axis corresponds to the area of the photo measured; the y-axis corresponds to vein density.

SUPPLEMENTARY MATERIAL II - R codes

Codes to open and charge the csv file on R

- **Standing forests**

```
data<-read.csv(file="Data  
species.csv",header=T,fill=T,na.strings="NA")  
attach(data)
```

- **Litter**

```
litter<-read.csv(file="litter.csv",header=T)  
attach(litter)
```

- **Cretaceous-Paleocene D_v**

```
paleo<-read.csv(file="paleo.csv",header=T,fill=T,na.strings="NA")  
attach(paleo)
```

- **Vein density of Mush Valley**

```
mush<-read.csv(file="mush.csv",header=T)  
attach(mush)
```

Codes to create vectors

- **Vein density of the canopy species of FTS**

```
CFTS<-dv[Site=="FTS"&Strata=="CANOPY"]
```

- **Vein density of the canopy species of SERC**

```
CSERC<-dv[Site=="SERC"&Strata=="CANOPY"]
```

- **Vein density of the canopy species of PNM**

```
CPNM<-dv[Site=="PNM"&Strata=="CANOPY"]
```

- **Vein density of the understorey species of FTS**

```
UFTS<-dv[Site=="FTS"&Strata=="UNDERSTOREY"]
```

- **Vein density of the understorey species of SERC**

```
USERC<-dv[Site=="SERC"&Strata=="UNDERSTOREY"]
```

- **Vein density of the understorey species of PNM**

```
UPNM<-dv[Site=="PNM"&Strata=="UNDERSTOREY"]
```

- **Vein density of canopy and understorey of FTS**

```
FTS<-c(CFTS,UFTS)
```


- **Vein density of canopy and understorey of SERC**

SERC = SERC canopy+understorey

- **Vein density of canopy and understorey of PNM**

PNM<-c(CPNM,UPNM)

- **Vector of vein density of all litter morphotypes**

DVlitter<-DV

- **Vector of all vein density of all fossil morphotypes**

dvp<-DVP

- **Vectors of fossil vein density for each age:**

Hautaverian<-dvp[1:2]

Barremian<-dvp[3:5]

Aptian<-dvp[6:11]

Albian<-dvp[12:39]

Cenomanian<-dvp[40:51]

Campanian<-dvp[52:62]

Maastrichtian<-dvp[63:74]

Paleocene<-dvp[75:105]

- **Vector of vein density of all Mush Valley morphotypes**

dvm=dvm

FIGURE 2: comparison of canopy and understorey at FTS, SERC, and PNM, and PNM litter.

Statistics

- **Mean Dv and standard deviation per site**

mean(FTS)

sd(FTS)

mean(SERC)

sd(SERC)

mean(PNM)

sd(PNM)

- **Mean canopy Dv and standard deviation per site**

```
mean(CFTS)
sd(CFTS)
mean(CSERC)
sd(CSERC)
mean(CPNM)
sd(CPNM)
```

- **Mean understorey Dv and standard deviation per site**

```
mean(UFTS)
sd(UFTS)
mean(USERC)
sd(USERC)
mean(UPNM)
sd(UPNM)
```

- **Wilcoxon rank-sum test between sites : CANOPY**

```
wilcox.test(CFTS,CSERC)
wilcox.test(CFTS,CPNM)
wilcox.test(CPNM,CSERC)
```

- **Wilcoxon rank-sum test between sites : understorey**

```
wilcox.test(UFTS,USERC)
wilcox.test(UFTS,UPNM)
wilcox.test(UPNM,USERC)
```

- **Wilcoxon rank-sum test between sites : canopy and understorey**

```
wilcox.test(FTS,SERC)
wilcox.test(FTS,PNM)
wilcox.test(PNM,SERC)
```

- **Wilcoxon rank-sum test between litter and PNM (whole sample, canopy, understorey)**

```
wilcox.test(DVlitter,PNM)
wilcox.test(DVlitter,CPNM)
wilcox.test(DVlitter,UPNM)
```

Graphics

- Code to make 3 histograms on the same graphic (3 lines, 1 column)

```
par(mfrow=c(3,1))
```

- Graphic A (FTS):

```
hist(UFTS,breaks=(1:28),freq=F,border=F,xlab="Dv")
lines(density(UFTS),type="l",lwd="1",col="blue")
hist(CFTS,breaks=(1: 28),freq=F,border=F,add=T)
lines(density(CFTS),type="l",lwd="1",col="red")
```

- Graphic B (SERC):

```
hist(UFTS,breaks=(1:28),freq=F,border=F,xlab="Dv")
hist(USERC,breaks=(1: 28),freq=F,border=F,add=T)
lines(density(USERC),type="l",lwd="1",col="blue")
hist(CSERC,breaks=(1: 28),freq=F,border=F,add=T)
lines(density(CSERC),type="l",lwd="1",col="red")
```

- Graphic C (PNM):

```
hist(UFTS,breaks=(1:28),freq=F,border=F,xlab="Dv")
hist(UPNM,breaks=(1: 28),freq=F,border=F,add=T)
lines(density(UPNM),type="l",lwd="1",col="blue")
hist(CPNM,breaks=(1: 28),freq=F,border=F,add=T)
lines(density(CPNM),type="l",lwd="1",col="red")
hist(DVlitter,breaks=(1:28),freq=F,border=F,xlab="Dv",add=T)
lines(density(DVlitter),type="l",lwd="1",col="black")
```

FIGURE 3: Comparisons of the PNM litter and Cretaceous-Paleocene fossil floras

Statistics

- Wilcoxon rank-sum test between the litter vein density (DV) and the vein density of each one of the 8 paleofloras

```
wilcox.test(Hautaverian,DVlitter)
wilcox.test(Barremian,DVlitter)
wilcox.test(Aptian,DVlitter)
```

```
wilcox.test(Albian,DVlitter)
wilcox.test(Cenomanian,DVlitter)
wilcox.test(Campanian,DVlitter)
wilcox.test(Maastrichtian,DVlitter)
wilcox.test(Paleocene,DVlitter)
```

Graphics

- Code to make 8 graphics on the same image (2 lines, 4 column)

```
par(mfrow=c(2,4))
```

- **Histogram of the Hautaverian + PNM modern litter**

```
hist(dvp[3],border=F,breaks=(1:28),freq=F, xlab="Dv",main=paste("
Hautaverian"),ylim=c(0,0.6))
lines(density(dvp[3]),type="p",pch="o",col="white")
hist(Hautaverian,border="darkgreen",breaks=(1:28),freq=F,
add=T,xlab="Dv")
lines(density(Hautaverian),type="p",pch="o",col="darkgreen")
hist(DVlitter,breaks=(1:28), border=F, freq=F ,add=TRUE)
lines(density(DVlitter),type="p",pch="o")
text(10,0.5,labels="n=2",col="darkgreen")
```

- **Histogram of the Barremian + PNM modern litter**

```
hist(dvp[3],border=F,breaks=(1:28),freq=F, xlab="Dv",main=paste("
Barremian"),ylim=c(0,0.6))
lines(density(dvp[3]),type="p",pch="o",col="white")
hist(Barremian,border="darkgreen",breaks=(1:28),freq=F,add=T)
lines(density(Barremian),type="p",pch="o",col="darkgreen")
hist(DVlitter,breaks=(1:28),border=F,freq=F ,add=TRUE)
lines(density(DVlitter),type="p",pch="o")
text(10,0.5,labels="n=3",col="darkgreen")
```

- **Histogram of the Aptian + PNM modern litter**

```
hist(dvp[3],border=F,breaks=(1:28),freq=F, xlab="Dv",main=paste("
Aptian"),ylim=c(0,0.6))
lines(density(dvp[3]),type="p",pch="o",col="white")
hist(Aptian,border="darkgreen",breaks=(1:28),freq=F,add=T)
```

```

lines(density(Aptian),type="p",pch="o",col="darkgreen")
hist(DVlitter,breaks=(1:28),border=F,freq=F ,add=TRUE)
lines(density(DVlitter),type="p",pch="o")
text(10,0.5,labels="n=6",col="darkgreen")

```

- **Histogram of the Albian + PNM modern litter**

```

hist(dvp[3],border=F,breaks=(1:28),freq=F, xlab="Dv",main=paste("
Albian"),ylim=c(0,0.6))
lines(density(dvp[3]),type="p",pch="o",col="white")
hist(Albian,border="darkgreen",breaks=(1:28),freq=F,add=T,
xlab="Dv")
lines(density(Albian),type="p",pch="o",col="darkgreen")
hist(DVlitter,breaks=(1:28),border=F,freq=F ,add=TRUE)
lines(density(DVlitter),type="p",pch="o")
text(10,0.5,labels="n=28",col="darkgreen")

```

- **Histogram of the Cenomanian + PNM modern litter**

```

hist(dvp[3],border=F,breaks=(1:28),freq=F,xlab="Dv",main=paste("C
enomanian"),ylim=c(0,0.6))
lines(density(dvp[3]),type="p",pch="o",col="white")
hist(Cenomanian,border="darkgreen",breaks=(1:28),freq=F,
add=T,xlab="Dv")
lines(density(Cenomanian),type="p",pch="o",col="darkgreen")
hist(DVlitter,breaks=(1:28),border=F,freq=F ,add=TRUE)
lines(density(DVlitter),type="p",pch="o")
text(10,0.5,labels="n=12",col="darkgreen")

```

- **Histogram of the Campanian + PNM modern litter**

```

hist(dvp[3],border=F,breaks=(1:28),freq=F, xlab="Dv",main=paste("
Campanian"),ylim=c(0,0.6))
lines(density(dvp[3]),type="p",pch="o",col="white")
hist(Campanian,border="darkgreen",breaks=(1:28),freq=F,add=T,
xlab="Dv")
lines(density(Campanian),type="p",pch="o",col="darkgreen")
hist(DVlitter,breaks=(1:28),border=F,freq=F ,add=TRUE)

```

```

lines(density(DVlitter),type="p",pch="o")
text(10,0.5,labels="n=11",col="darkgreen")
  • Histogram of the Maastrichtian + PNM modern litter
    hist(dvp[3],border=F,breaks=(1:28),freq=F,
xlab="Dv",main=paste(" Maastrichtian"),ylim=c(0,0.6))
lines(density(dvp[3]),type="p",pch="o",col="white")
hist(Maastrichtian,border="darkgreen",breaks=(1:28),freq=F,
add=T,xlab="Dv")
lines(density(Maastrichtian),type="p",pch="o",col="darkgreen")
hist(DVlitter,breaks=(1:28), border=F, freq=F ,add=TRUE)
lines(density(DVlitter),type="p",pch="o")
text(10,0.5,labels="n=12",col="darkgreen")
  • Histogram of the Paleocene + PNM modern litter
hist(dvp[3],border=F,breaks=(1:28),freq=F, xlab="Dv",main=paste("
Paleocene"),ylim=c(0,0.6))
lines(density(dvp[3]),type="p",pch="o",col="white")
hist(Paleocene,border="darkgreen",breaks=(1:28),freq=F,      add=T,
xlab="Dv")
lines(density(Paleocene),type="p",pch="o",col="darkgreen")
hist(DVlitter,breaks=(1:28),border=F,freq=F ,add=TRUE)
lines(density(DVlitter),type="p",pch="o")
text(10,0.5,labels="n=31",col="darkgreen")

```

FIGURE 4: Comparisons of the PNM litter and the Mush Valley fossil assemblage

Statistics

```
proba=(X)/sum(X)
```

proba = probability for each vein density value to be extracted randomly from the litter assemblage (X = number of leaves of the same morphotype)

- **Code for a Bootstrap with 10,000 repetitions of a subsample of 10 morphotypes, with replacement**

```
m=numeric()
```

```
d=numeric()
```

```
for(n in 1:10000){
  ls=sample(DVlitter,10,replace=T,prob=proba)
  m[n]=mean(ls)
  d[n]=sd(ls) }
```

- Percentage of mean vein density of the bootstrap equal or lower than Mush valley mean vein density:

```
minor<-length(which(m<=mean(dvm)))
minor/100
```

- Percentage of mean vein density of the bootstrap equal or higher than Mush valley mean vein density:

```
major<-length(which(m>=mean(dvm)))
major/100
```

Graphics

- Code to make 2 graphics on the same image (1 line, 2 columns)

```
par(mfrow=c(1,2))
```

- Histogram and density curve of Mush vein density + PNM modern litter density curve

```
par(mar=c(5,5,3,5))
hist(dvm,breaks=(1:28),border=T,col="orange",freq=F,axes=F,xaxt="n")
axis(2,col="black")
lines(density(dvm),col="darkorange",type="p",pch="o")
hist(DVlitter,border=F,breaks=(1:28),freq=F,
  xlab="Dv",ylim=c(0,0.6),add=T)
lines(density(DVlitter),type="p",pch="o",col="black")
par(new=T)
hist(dvm,breaks=(1:28),border=F,freq=T,axes=F,ylab="")
axis(4,col="black")
axis(1,col="black")
mtext("Frequency", side=4,line=3)
```

- Histogram of the bootstrap (means of subsamples)

```
par(mar=c(5,5,3,5))
```

```
hist(m)
a=mean(dvm)
  abline(v=a,col="darkorange")
```


SUPPLEMENTARY MATERIAL III – Row data

1) Species list.xlsx

Species mnemonic acronym	Genus	Species	Family	Ecology	Lifeform
ACEPS	Acer	pseudoplatanus	Sapindaceae	sun-demanding	tree
ALBG	Albizia	guachapele	Fabaceae	sun-demanding	understorey
AMPP	Amphilophium	paniculatum	Bignoniaceae		liana
ANAE	Anacardium	excelsum	Anacardiaceae		tree
ANNS	Annona	sparaguei	Annonaceae		midstorey
ANTT	Antirrhoea	trichanta	Rubiaceae	sun-demanding	tree
APEM	Apeiba	membranaceae	Tiliaceae	sun-demanding	tree
ARIM	Aristolochia	maxima	Aristolochicaceae		liana
ARRV	Arrabidea	verrucosa	Bignoniaceae		liana
ASITR	Asimina	triloba	Annonaceae	shade-tolerant	midstorey
ASTG	Astronium	graveolens	Anacardiaceae		tree
BERTH	Berberis	thunbergii	Berberidaceae	sun-demanding	shrub
BONM	Bonamia	maripoide	Convolvulaceae		vine
BROA	Brosimum	alicastrum	Moraceae	sun-demanding	tree
BROU	Brosimum	utile	Moraceae	shade-tolerant	tree
CAL2	Calophyllum	logifolium	Clusiaceae	shade-tolerant	tree
CARG	Carapa	guianensis	Meliaceae	shade-tolerant	tree
CARGL	Carya	glabra	Juglandaceae	shade-tolerant	understorey
CARP1	Carpinus	sp	Betulaceae	shade-tolerant	midstorey
CARTO	Carya	tomentosa	Juglandaceae	shade-tolerant	tree
CARY1	Carya	sp	Juglandaceae	shade-tolerant	tree
CAS4	Castilla	elastica	Moraceae	sun-demanding	midstorey
CECI	Cecropia	insignis	Cecropiaceae	sun-demanding	tree
CECL	Cecropia	longipes	Cecropiaceae	sun-demanding	midstorey
CES1	Cespedezia	macrophylla	Ochnaceae		tree
CHRC	Chrysophyllum	cainito	Sapotaceae		tree
CLUV	Clusia	valerioi	Clusiaceae		hemiepiphyte
COCP	Coccoloba	parimensis	Polygonaceae		liana
COMF	Combretum	fruticosum	Combretaceae		liana
CORB	Cordia	bicolor	Boraginaceae	sun-demanding	midstorey
CORFL	Cornus	florida	Cornaceae	shade-tolerant	midstorey
CYDA	Cydista	aequinoctalis	Bignoniaceae	sun-demanding	liana

DAVN	Davilla	nitida	Dilleniaceae		liana
DENA	Dendropanax	arboreus	Araliaceae		tree
DIOW	Dioclea	wilsonii	Fabaceae		liana
DOL1	Dolioscarpus	major	Dilleniaceae		liana
DOL2	Dolioscarpus	multiflorus	Dilleniaceae		liana
DUSM	Dussia	munda	Fabaceae		tree
ELAUM	Elaeagnus	umbellata	Elaeagnaceae	sun-demanding	shrub
FAGGR	Fagus	grandifolia	Fagaceae	shade-tolerant	tree
FIIN	Ficus	insipida	Moraceae	sun-demanding	tree
FORM	Forsteronia	myriantha	Apocynaceae		liana
FORS	Forsteronia	spicata	Apocynaceae		liana
FORV	Forsteronia	viridiscens	Apocynaceae		liana
FRAAM	Fraxinus	americana	Oleaceae	sun-demanding	tree
FRAPE	Fraxinus	pennsylvanica	Oleaceae	shade-tolerant	tree
FRAX1	Fraxinus	sp	Oleaceae		tree
GOUL	Gouania	lupuloides	Rhamnaceae		liana
GUAD	Guatteria	dumetorum	Annonaceae		tree
GUAK	Guarea	kunthiana	Meliaceae		tree
GUAU	Guazuma	ulmifolia	Sterculiaceae		midstorey
HAVF	Havetiopsis	flexilis	Clusiaceae		hemiepiphyte
HEIS	Heisteria	scadens	Olacaceae		liana
ILEOP	Ilex	opaca	Aquifoliaceae	shade-tolerant	midstorey
INGO	Inga	goldmanii	Cyperaceae	shade-tolerant	liana
LACP	Lacmella	panamensis	Chrysobalanaceae		tree
LINBE	Lindera	benzoi	Lauraceae	shade-tolerant	shrub
LIQST	Liquidambar	styraciflua	Altingiaceae	sun-demanding	tree
LIRTU	Liriodendron	tulipifera	Magnoliaceae	sun-demanding	tree
LONL	Lonchocarpus	longifolium	Fabaceae	shade-tolerant	tree
LUE1	Luehea	seemania	Tiliaceae		tree
MACR	Machaerium	riparum	Fabaceae		liana
MANB	Manilkara	bidentata	Sapotaceae	shade-tolerant	tree
MAR1	Marcgravia	nephentoides	Marcgraviaceae		hemiepiphyte
MAR3	Maranthes	panamensis	Chrysobalanaceae		tree
MARL	Marila	laxiflora	Clusiaceae		midstorey
MICB	Miconia	borealis	Melastomataceae	sun-demanding	shrub
MIKL	Mikania	leiostachya	Asteraceae		vine
NEC2	Nectandra	cuspidata	Lauraceae	shade-tolerant	midstorey
NECU	Nectandra	umbrosa	Lauraceae	shade-tolerant	midstorey

OCOI	Ocotea	ira	Lauraceae	shade-tolerant	midstorey
ODOP	Odontadenia	ponticulosa	Apocynaceae		liana
OMPD	Omphalea	diandra	Euphorbiaceae		liana
PASV	Passiflora	vitifolia	Passifloraceae		vine
PAUF	Paulinia	fibrigera	Sapindaceae		liana
PAUTO	Paulownia	tomentosa	Paulowniaceae	sun-demanding	tree
PERA	Pera	arborea	Euphorbiaceae	shade-tolerant	tree
PERX	Perebea	xanthocyma	Moraceae	shade-tolerant	understorey
PHI1	Philodendron	sp	Araceae		hemiepiphyte
PITC	Pithecoctenium	crucigerum	Bignoniaceae		liana
POUA	Poulsenia	armata	Moraceae	shade-tolerant	tree
POUB	Pouruma	bicolor	Cecropiaceae	sun-demanding	tree
PPRE	Piper	reticulatum	Piperaceae	shade-tolerant	shrub
PROP	Protium	panamense	Burseraceae	shade-tolerant	tree
PYSU	Psychotria	surrensis	Rubiaceae	shade-tolerant	shrub
QUEAL	Quercus	alba	Fagaceae	shade-tolerant	tree
QUER1	Quercus	sp	Fagaceae	shade-tolerant	tree
QUERU	Quercus	rubra	Fagaceae	shade-tolerant	tree
QUEVE	Quercus	velutina	Fagaceae	shade-tolerant	tree
SAPG	Sapium	glandulosum	Sapindaceae		tree
SERM	Serjania	mexicana	Sapindaceae		liana
SMIRO	Smilax	rotundifolia	Smilacaceae	sun-demanding	woody vine
SOCE	Socratea	exorrhiza	Arecacea	shade-tolerant	midstorey
SPNA1	NA	NA	na		na
STIR	Stizophyllum	riparium	Bignoniaceae		liana
SYMG	Symphonia	globulifera	Clusiaceae	shade-tolerant	tree
TACV	Tachigali	cersicolor	Fabaceae	shade-tolerant	tree
TOCP	Tocoyena	pittieri	Rubiaceae	shade-tolerant	understorey
TONO	Tontelea	ovalifolia	Hippocrateaceae		liana
TOVL	Tovomita	longifolia	Clusiaceae	shade-tolerant	understorey
TOXRA	Toxicodendron	radicans	Anacardiaceae	sun-demanding	shrub
TRIO	Trichostigma	octandrum	Phytolacaceae		liana
TYNC	Tynnanthus	croatianus	Bignoniaceae		liana
UREC	Urera	caracasana	Urticaceae	sun-demanding	tree
VAND	Vantanea	depleta	Humiriaceae		tree
VIBAC	Viburnum	acerifolium	Caprifoliaceae	shade-tolerant	shrub
VIBPR	Viburnum	prunifolium	Caprifoliaceae	shade-tolerant	understorey
VIRE	Virola	elongata	Myristicaceae	sun-demanding	tree

VIR2	Virola	surinamensis	Myristicaceae	shade-tolerant	tree
VITLA	Vitis	labrusca	Vitaceae	sun-demanding	woody vine
VITTT	Vitis	tilifolia	Vitaceae		vine
VOCF	Vochysia	ferruginea	Vichysiaceae	sun-demanding	tree

2) Data species.csv

Site	Species mnemonic acronym	Strata	Ecology	Vein density (mm/mm ²)	Mean squared error	n
SERC	ACEPS	CANOPY	SUN-DEMANDING	15.85516667	0.493520969	3
PNM	ALBG	CANOPY	SUN-DEMANDING	16.23907867	0.181558841	9
PNM	AMPP	CANOPY		8.028200011	0.237258042	2
PNM	ANAE	CANOPY		11.92410985	0.237569928	15
PNM	ANNS	CANOPY		13.45341447	0.355841247	6
PNM	ANTT	CANOPY	SUN-DEMANDING	18.89348751	0	1
FTS	APEM	CANOPY	SUN-DEMANDING	12.04709677	0.329209232	3
PNM	ARIM	CANOPY		11.22770545	0.395427696	6
PNM	ARRV	CANOPY		11.75693338	0.298445504	3
SERC	ASITR	UNDERSTOREY	SHADE-TOLERANT	4.820810824	0.10446418	3
PNM	ASTG	CANOPY		14.76282369	0.003561945	6
PNM	ASTG	UNDERSTOREY		10.47732004	0.637993855	3
SERC	BERTH	UNDERSTOREY	SUN-DEMANDING	4.13116786	0.374233244	3
PNM	BONM	CANOPY		9.751242524	0.105613042	6
FTS	BROA	CANOPY	SUN-DEMANDING	10.59397511	0.142960067	2
FTS	BROU	CANOPY	SHADE-TOLERANT	10.67997269	0.876610956	8
FTS	BROU	UNDERSTOREY		6.066229065	0.01565856	11
FTS	CAL2	CANOPY	SHADE-TOLERANT	8.04630473	0.074529037	3
FTS	CAL2	UNDERSTOREY		6.224753633	0.344402114	6
FTS	CARG	CANOPY	SHADE-TOLERANT	11.12706778	0.135936852	6
SERC	CARGL	UNDERSTOREY	SHADE-TOLERANT	7.416906455	0.844750506	2
SERC	CARP1	UNDERSTOREY	SHADE-TOLERANT	7.904658473	0.167262056	3
SERC	CARTO	CANOPY	SHADE-TOLERANT	10.57122222	0.460714565	3
SERC	CARY1	CANOPY	SHADE-TOLERANT	11.18477778	1.97837483	3
FTS	CAS4	CANOPY	SUN-DEMANDING	12.27578982	0.009363797	1
PNM	CAS4	UNDERSTOREY	SUN-DEMANDING	8.671992102	0.002168288	6
FTS	CECI	CANOPY	SUN-DEMANDING	19.34557664	0.731168381	3
PNM	CECL	CANOPY	SUN-DEMANDING	12.85331304	0.256306392	1
FTS	CES1	UNDERSTOREY		7.194697227	0.36239184	3
PNM	CHRC	UNDERSTOREY		7.0918191	0.018263216	6
FTS	CLUV	CANOPY		5.922601137	1.08432655	2
FTS	COCP	CANOPY		19.20944404	0.037605903	3
PNM	COMF	CANOPY		19.53771682	0.069992977	3

PNM	CORB	CANOPY	SUN-DEMANDING	15.65099533	0.996607594	2
SERC	CORFL	CANOPY	SHADE-TOLERANT	6.743888889	0.032968903	3
FST	CYDA	CANOPY	SUN-DEMANDING	7.594184641	0.226591097	2
FST	DAVN	CANOPY		9.052806221	0.150496753	3
FTS	DENA	UNDERSTOREY		4.288706437	0.038681486	3
FST	DIOW	CANOPY		10.28229908	0.064131727	3
FST	DOL1	CANOPY		7.766447049	1.13306341	3
PNM	DOL1	UNDERSTOREY		4.849754319	0.956370952	9
FTS	DOL2	UNDERSTOREY		4.711900962	0.109998414	3
FST	DUSM	CANOPY		11.07505811	0.181500404	9
SERC	ELAUM	UNDERSTOREY	SUN-DEMANDING	5.177048031	0.060688234	3
SERC	FAGGR	UNDERSTOREY	SHADE-TOLERANT	8.202155886	1.063181313	13
PNM	FIIN	CANOPY	SUN-DEMANDING	10.82849505	0.101548907	5
FTS	FORM	CANOPY		10.11473029	1.884400597	3
PNM	FORS	CANOPY		15.37860672	0.401523783	3
FTS	FORV	CANOPY		8.533244742	0.142960067	3
SERC	FRAAM	UNDERSTOREY	SUN-DEMANDING	5.613221162	0.270187453	6
SERC	FRAPE	CANOPY	SHADE-TOLERANT	13.43036727	0.104119958	8
SERC	FRAX1	UNDERSTOREY		7.082293748	0.105758918	3
PNM	GOUL	CANOPY		12.41565182	0.087658587	3
FTS	GUAD	CANOPY		10.50577752	0.336710603	6
FTS	GUAK	CANOPY		9.521106167	0.180440547	3
PNM	GUAU	CANOPY		15.25203174	1.424998594	3
FTS	HAVF	CANOPY		8.034049733	0.015231606	9
FTS	HEIS	CANOPY		9.860882964	0.059315639	3
FTS	HEIS	UNDERSTOREY		7.580771569	0.27755892	3
SERC	ILEOP	UNDERSTOREY	SHADE-TOLERANT	6.599277474	0.221732812	5
FTS	INGO	CANOPY	SHADE-TOLERANT	15.97155044	0.64382431	3
FTS	LACP	CANOPY		6.786839771	0.159407777	3
SERC	LINBE	UNDERSTOREY	SHADE-TOLERANT	5.56479653	0	3
SERC	LIQST	CANOPY	SUN-DEMANDING	9.930118056	0.245605722	1
SERC	LIQST	CANOPY	SUN-DEMANDING	8.40125	0.565192678	4
SERC	LIQST	UNDERSTOREY	SUN-DEMANDING	6.370232457	0.10036576	6
SERC	LIRTU	CANOPY	SUN-DEMANDING	8.616001775	0.354355473	8
SERC	LIRTU	CANOPY	SUN-DEMANDING	7.80226814	0.192803925	3
SERC	LIRTU	UNDERSTOREY	SUN-DEMANDING	4.819676214	0	1
PNM	LONL	CANOPY	SHADE-TOLERANT	11.53167323	0.178243623	3
PNM	LUE1	CANOPY		27.17881768	0.232288269	3

PNM	LUE1	UNDERSTOREY		12.8459288	0	3
FTS	MACR	CANOPY		13.57602998	0.104604076	3
FTS	MANB	CANOPY	SHADE-TOLERANT	8.563040252	0.244409029	12
FTS	MAR1	CANOPY		5.723590331	0.330251761	3
FTS	MAR3	CANOPY		13.04418719	0.040157542	3
FTS	MARL	CANOPY		8.728232247	0.183249116	3
FTS	MARL	UNDERSTOREY		5.601314664	0.24741691	6
FTS	MICB	CANOPY	SUN-DEMANDING	12.29072117	0.766695878	3
PNM	MIKL	CANOPY		7.20724056	0.072541578	6
PNM	NEC2	CANOPY	SHADE-TOLERANT	8.716798891	0.056735443	3
FTS	NECU	CANOPY	SHADE-TOLERANT	9.152810733	0.113923398	3
FTS	OCOI	CANOPY	SHADE-TOLERANT	8.775788833	0.016402727	3
FTS	OCOI	UNDERSTOREY	SHADE-TOLERANT	3.151005863	0.326333152	3
FTS	ODOP	CANOPY		9.684395566	0.582734288	3
FTS	OMPD	CANOPY		9.553638588	0.025929049	3
PNM	PASV	CANOPY		13.22322228	0.56350439	2
FTS	PAUF	CANOPY		8.5518328	2.186200663	3
SERC	PAUTO	CANOPY	SUN-DEMANDING	10.26930679	0.31657432	3
FTS	PERA	CANOPY	SHADE-TOLERANT	10.32122171	1.214468011	3
FTS	PERX	UNDERSTOREY	SHADE-TOLERANT	7.485640342	0.010951935	1
PNM	PHI1	CANOPY		24.77509487	0.100874432	3
PNM	PITC	CANOPY		11.28205944	0.004410546	3
FTS	POUA	CANOPY	SHADE-TOLERANT	12.42140147	0.303644592	3
FTS	POUA	UNDERSTOREY	SHADE-TOLERANT	4.619937243	1.938793594	3
FTS	POUB	CANOPY	SUN-DEMANDING	18.80018639	0.034074307	3
FTS	POUB	UNDERSTOREY	SUN-DEMANDING	8.181989633	0.772234933	3
PNM	PPRE	CANOPY	SHADE-TOLERANT	11.23899169	0.018212633	4
PNM	PPRE	UNDERSTOREY	SHADE-TOLERANT	11.36714661	0.204449633	9
FTS	PROP	CANOPY	SHADE-TOLERANT	13.25781456	1.52E-05	3
FTS	PROP	UNDERSTOREY	SHADE-TOLERANT	9.48496832	0.435765016	3
FTS	PYSU	UNDERSTOREY	SHADE-TOLERANT	5.538959067	0.033044101	3
SERC	QUEAL	CANOPY	SHADE-TOLERANT	13.28188889	0.172333571	3
SERC	QUEAL	UNDERSTOREY	SHADE-TOLERANT	9.744346673	0.022672052	6
SERC	QUER1	CANOPY	SHADE-TOLERANT	12.836125	0.362244986	2
SERC	QUERU	UNDERSTOREY	SHADE-TOLERANT	8.2995828	0.010715374	3
SERC	QUEVE	CANOPY	SHADE-TOLERANT	12.27866667	0.425811681	3
FTS	SAPG	CANOPY		10.56035533	0.596778724	6
PNM	SERM	UNDERSTOREY		7.586520626	1.378258183	7

SERC	SMIRO	UNDERSTOREY	SUN-DEMANDING	4.756640964	0.21038294	3
FTS	SOCE	CANOPY	SHADE-TOLERANT	9.580721274	0.00775835	3
FTS	SPNA1	CANOPY		10.53493949	0.082183275	3
SERC	SPNA2	CANOPY		12.53676389	0.228771784	3
SERC	SPNA2	UNDERSTOREY		4.955173944	0.151436142	3
PNM	STIR	CANOPY		10.85704441	0.041234725	3
FTS	SYMG	CANOPY	SHADE-TOLERANT	9.464458426	0.67559637	3
FTS	TACV	CANOPY	SHADE-TOLERANT	10.44015969	0.364234672	3
FTS	TACV	UNDERSTOREY	SHADE-TOLERANT	4.902106313	0.037481477	6
FTS	TOCP	CANOPY	SHADE-TOLERANT	12.05238431	0	1
FTS	TONO	CANOPY		6.442966801	0.173327755	3
FTS	TONO	UNDERSTOREY		5.206648411	0.152380935	3
FTS	TOVL	CANOPY	SHADE-TOLERANT	5.137194825	0.011651414	3
SERC	TOXRA	UNDERSTOREY	SUN-DEMANDING	4.74802019	0.075258044	2
PNM	TRIO	CANOPY		9.963486386	0.005384436	3
PNM	TYNC	CANOPY		8.882147379	0.231836374	3
PNM	UREC	CANOPY	SUN-DEMANDING	8.401182499	0	1
FTS	VAND	CANOPY		10.90956267	3.605209054	3
SERC	VIBAC	UNDERSTOREY	SHADE-TOLERANT	4.120487556	0.191974124	3
SERC	VIBPR	UNDERSTOREY	SHADE-TOLERANT	5.056225864	0.114797839	9
FTS	VIRE	CANOPY	SUN-DEMANDING	8.013553504	0.626993051	2
FTS	VIRE	UNDERSTOREY	SHADE-TOLERANT	5.520908679	0.117606353	3
FTS	VIRS	CANOPY	SUN-DEMANDING	7.347092406	0	1
SERC	VITLA	CANOPY	SUN-DEMANDING	9.361333333	0	1
PNM	VITT	CANOPY		13.58494121		1
FTS	VOCF	CANOPY	SUN-DEMANDING	12.65134581	0.809531367	3
FTS	TOVL	UNDERSTOREY	SHADE-TOLERANT	3.810767854	0.051554996	3

Site: FTS= Parque National San Lorenzo (Panama), PNM = Parque Natural Metropolitano

(Panama), SERC= Smithsonian Environmental Research Center (MD)

Species mnemonic acronym= 4 or 5 letter acronym of the genus and species

Strata: Canopy or understorey

Ecology: Ecological strategy of the species; sun-demanding or shade tolerant

dv : vein density (mm/mm²)

n: number of leaves measured per species

Mean squared error:
$$MSE = \frac{1}{n} \sum_{i=1}^n (\hat{Y}_i - Y_i)^2.$$

3) litter.csv

Morphotype	DV (mm/mm ²)	X
1	1.10743684	1
2	4.824953517	1
3	6.231539322	2
4	6.825159892	1
5	7.669427711	1
6	8.211364157	1
7	8.902658303	3
8	9.124082632	8
9	9.39452562	2
10	9.689252652	1
11	10.57745802	2
12	10.58878326	2
13	11.2505666	1
14	12.23157338	1
15	13.10902425	84
16	15.20372922	1
17	21.58700661	2
18	25.29665316	17

Morphotype: ID number of the morphotypes

DV: vein density

X: number of leaves collected of each morphotype

4) mush.csv

morphotype	Dvm (mm/mm²)	n
Dinosaur footprint	13.96317916	1
Flaky Imposter	14.76635813	1
Herbie	18.79840849	1
Interrupt	9.850056981	2
InterruptC	20.08796367	1
Legume 1	13.58529671	1
Legume 4	13.2109941	2
Mushroom Trichomes	9.879107363	1
Pinnate truncate	19.22375362	1
Short Drip Tip	15.92060103	4
Small-tooth Euphorb	24.76817674	1

morphotype: name of the morphotype

dvm: average vein density of each morphotype

n: number of specimens measured per morphotype

4) paleo.csv

Morphotype	DVP (mm/mm ²)	AGE1	AGE2	Formation
Asiatifolium elegans	3.67	132.35	Hauterivian-Early Barremian	Chengzihe Formation, near Jixi, China
Shenkuoa caloneura	5.23	132.35	Hauterivian-Early Barremian	Chengzihe Formation, near Jixi, China
eudicot-like leaf, chloranthoid teeth	2.45	127.5	Late Barremian	La HuŽrguina Formation, Las Hoyas locality, Iberian Ranges, Spain
Protoeaephyllum (nymphaeoid leaf)	4.28	127.5	Late Barremian	La HuŽrguina Formation, Las Hoyas locality, Iberian Ranges, Spain
Ficophyllum sp.	1.96	127.5	Late Barremian	La HuŽrguina Formation, Las Hoyas locality, Iberian Ranges, Spain
Endressinia brasiliana	5.23	119	Late Aptian	Crato Formation, Brasil
Araripia	4.12	119	Late Aptian	Crato Formation, Brasil
"broad" angiosperm	3.37	119	Late Aptian	Crato Formation, Brasil
"narrow" angiosperm	4.56	119	Late Aptian	Crato Formation, Brasil
Pluricarpellatia	2.39	119	Late Aptian	Crato Formation, Brasil
Nymphoid Crato Fossil	1.23	119	Late Aptian	Crato Formation, Brasil
Longstrethia aspera	3.654	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
Liriophyllum kansense	5.76	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
Nelumbintes crassinervum	3.12	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
Crassideniticulum decurrens	3.61	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
Wolffiophyllum pfaffiana	3.45	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
Rogersia potteri	3.46	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
Rogersia kansense	3.89	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
Credneria cyclophylla	7.84	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA

<i>Sapindopsis bagleyae</i>	7.12	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
<i>Sapindopsis retallackii</i>	7.75	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
<i>Anisodromum wolfei</i>	6.56	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
<i>Dicotylophyllum leptovena</i>	5.5	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
<i>Meiophyllum expansolobum</i>	7.5	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
<i>Meiophyllum kowalskiae</i>	6.47	102.7	Late Albian	Hoisington III, Dakota Formation, KS, USA
<i>Rogersia parlatorii</i>	3.27	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Crassidenticulum decurrens</i>	3.61	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Crassidenticulum landisae</i>	3.37	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Trochodendroides elliptica</i>	4.64	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Eoplatanus serrata</i>	7.84	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Credneria quadrata</i>	8.56	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Aspidiophyllum denticulatum</i>	8.46	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Hickeyphyllum imhofii</i>	3.36	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Dicotylophyllum braunii</i>	5.45	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Wolfiophyllum daphneoides</i>	4.23	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Dicotylophyllum huangi</i>	8.76	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Dicotylophyllum</i> sp.	4.88	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Wolfiophyllum heigii</i>	4.12	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Rogersia lottii</i>	4.65	102.7	Late Albian	Braun's Ranch, Dakota Formation, KS, USA
<i>Jarzenia kanbrasota</i>	7.84	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA

Dennsinervum kaulii	4.05	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Crassidenticulum cracendentis	4.61	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Manchesterii macrophylla	8.34	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Pandemophyllum attenuatum	6.51	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Setterholmia rotundifolia	6.54	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Wolffiophyllum pfaffiana	4.8	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Rogersia dakotensis	3.84	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Trochodendroides rhomboideus	5.6	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Credneria cyclophylla	7.89	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Dicotylophyllum coughlantia	8.45	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Setterholmia deleta	6.12	95.4	Cenomanian	Courtland, Dakota Formation, MN, USA
Lysichiton austriacus	3.45	77.05	Campanian	Grunbach Austria
Pandanites trinervis	4.51	77.05	Campanian	Grunbach Austria
Sabalites longirhachis	7.45	77.05	Campanian	Grunbach Austria
Monocotylophyllum sp. 1	5.65	77.05	Campanian	Grunbach Austria
Compositiphyllum serratum	8.12	77.05	Campanian	Grunbach Austria
Grebenkia eurpoea	6.68	77.05	Campanian	Grunbach Austria
Juglandiphyllites cretaceus	8.14	77.05	Campanian	Grunbach Austria
Brasenites krasseri	7.12	77.05	Campanian	Grunbach Austria
Dicotylophyllum proteodies	9.45	77.05	Campanian	Grunbach Austria
Dicotylophyllum species 5	7.91	77.05	Campanian	Grunbach Austria
Ettinghausenia gruenbachiana	7.8	77.05	Campanian	Grunbach Austria
GD01-20223-1	8.59	69	Maastrichtian	Guadas, Colombia
GD02-21092-1	11.72	69	Maastrichtian	Guadas, Colombia
GD06-20753-2	11.95	69	Maastrichtian	Guadas, Colombia

GD08-20956-1	12.34	69	Maastrichtian	Guadas, Colombia
GD08-20975-2	12.41	69	Maastrichtian	Guadas, Colombia
GD08-21266-2	14.74	69	Maastrichtian	Guadas, Colombia
GD23	13.21	69	Maastrichtian	Guadas, Colombia
GD35-20808-35	12.2	69	Maastrichtian	Guadas, Colombia
GD50	7.33	69	Maastrichtian	Guadas, Colombia
GD53-20353-1	11.5	69	Maastrichtian	Guadas, Colombia
GD54-20559-4	15.42	69	Maastrichtian	Guadas, Colombia
GD56	10.03	69	Maastrichtian	Guadas, Colombia
CJ10	7.45	58	Paleocene	Cerrejon Formation, Colombia
CJ20	9.87	58	Paleocene	Cerrejon Formation, Colombia
CJ12	8.63	58	Paleocene	Cerrejon Formation, Colombia
CJ13	8.18	58	Paleocene	Cerrejon Formation, Colombia
CJ6	12.56	58	Paleocene	Cerrejon Formation, Colombia
CJ3	7.88	58	Paleocene	Cerrejon Formation, Colombia
CJ19	10.15	58	Paleocene	Cerrejon Formation, Colombia
CJ20	7.34	58	Paleocene	Cerrejon Formation, Colombia
CJ30	7.15	58	Paleocene	Cerrejon Formation, Colombia
CJ58	6.66	58	Paleocene	Cerrejon Formation, Colombia
CJ40	13.9	58	Paleocene	Cerrejon Formation, Colombia
CJ22	10.26	58	Paleocene	Cerrejon Formation, Colombia
CJ23	2.34	58	Paleocene	Cerrejon Formation, Colombia
CJ24	6.67	58	Paleocene	Cerrejon Formation, Colombia
CJ25	10.3	58	Paleocene	Cerrejon Formation, Colombia
CJ27	10.8	58	Paleocene	Cerrejon Formation, Colombia

CJ28	10.56	58	Paleocene	Cerrejon Formation, Colombia
CJ32	8.23	58	Paleocene	Cerrejon Formation, Colombia
CJ43	8.62	58	Paleocene	Cerrejon Formation, Colombia
CJ49	4.04	58	Paleocene	Cerrejon Formation, Colombia
CJ58	6.5	58	Paleocene	Cerrejon Formation, Colombia
CJ53	10.44	58	Paleocene	Cerrejon Formation, Colombia
CJ82	15.65	58	Paleocene	Cerrejon Formation, Colombia
CJ84	10.27	58	Paleocene	Cerrejon Formation, Colombia
CJ55	14	58	Paleocene	Cerrejon Formation, Colombia
CJ82	15.71	58	Paleocene	Cerrejon Formation, Colombia
CJ84	10.27	58	Paleocene	Cerrejon Formation, Colombia
CJ62	4.7	58	Paleocene	Cerrejon Formation, Colombia
CJ63	4.2	58	Paleocene	Cerrejon Formation, Colombia
CJ65	5.3	58	Paleocene	Cerrejon Formation, Colombia
CJ108	3.81	58	Paleocene	Cerrejon Formation, Colombia

Morphotype: name or ID of each morphotypes

DVP: vein density

AGE1: Age in million years

AGE2: Geologic age (Cretaceous) or epoch (Paleocene), using the 2012 Geologic Time Scale

Formation: Name of the formation where the fossil comes from