



Plant Response to Environmental Gradient Mediated by Trait Through Ontogeny on Common Tree Species at Two Contrasting Habitats in Karst Forest of Southern Taiwan

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Abstract

One of central goal in ecology is to understand how plants respond to environment and what kind of attributes that can be obtained with an easy way to interpret the complexity of nature, especially on vegetation response. Ecologists use functional traits to understand how plants respond to environmental changes. Plant species may have experienced different environmental conditions during their ontogeny. Thus, they may show different patterns of ontogenetic trait variation (OTV) as their response to different environmental condition. In this study, the relationship between trait variation on different habitat and across ontogenetic stages both on community and population levels were investigated. Five selected leaves traits (leaf area, specific leaf area, leaf thickness, leaf dry matter content, and leaf succulence) were examined to look at plant response along soil water content and light gap interception gradient in Kenting forest dynamics plot (KFDP), Southern Taiwan. Leaf area was the most varied trait across habitat and ontogeny. Leaf thickness reveals an opposite pattern compare to leaf area. Leaf dry matter content (LDMC) showed less variation either between or within species and across ontogeny. Shift of community responses on environmental gradient by trait through ontogeny showed that intraspecific variation is important to be considered in ecological study. The other important finding in this study was by only using mean species we can misleading in understanding of plant responses to the environmental gradient in order to their adaptation both across different habitat and ontogenetic stages.

How to Cite

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INTRODUCTION

Over the past several decades, ecologists have been linking environmental condition to structure and species composition of plant communities. However, these studies have not been able to answer the big question about how a species can grow and thrive in a certain habitat while others could not. There is a stage in ecological process that missing when we try to make a link between environmental factors, plant performance (demographics), and plants distribution. This stage is about the process of how plants respond to environment and what kind of attributes that can be obtained with an easy way to interpret the complexity of nature, especially on vegetation response.

Trait-based approach in community ecology has been investigated increasingly in two decades recently. Functional trait is all the character of a plant that includes morphology, physiology, and phenology that give indirect effect on plant performance such as growth rate, reproduction and survivorship (Violle et al., 2007). It often measured at the individual level and usually used for comparisons between species (McGill et al., 2006).

Morphological and physiological adaptation may as the results of plants strategy in responding to different environmental factors. Thus, variation in morphological and physiological plants features maybe visible along environmental gradients (Schöb et al., 2013). Furthermore, based on functional trait possessed as a form of adaptation to the environment, plants can be grouped into several functional groups (Lavorel et al., 1997). For example, plant species are dominant in the resource-rich habitat, can be characterized by a short leaf life span with fast tissue turnover, high resource capture and fast growth abilities. Species are classified as exploitative plant which has a functional trait such as having a high specific leaf area (SLA) associated with photosynthetic capacity or have high leaf nitrogen content (LNC) correlated with rate of plant growth (Reich et al., 1997; Wright et al., 2004). The other group is conservative plant species, plants which have slower tissue turnover and longer leaf life span which is characterized by a low SLA and LNC. This plant group is also characterized by the large investment in high-density tissues, one of which is a high leaf dry matter content (LDMC) that can be used as a good estimator (Ryser & Urbas, 2000).

In most of previous studies, species mean value was wide be used for interpreting mechanisms and processes on ecology. It is based on the inter-specific variability or between species trait variation (BTV) and unconsidered intra-specific trait variability (ITV) properties (Albert et al., 2011). Plant traits are however variable within species, depending on genetic, developmental, and environmental factors (Coleman et al., 1994).

Plant species may have experienced different environmental conditions during their ontogeny. Thus, they may show different patterns of trait values as their response to different environmental conditions at different ontogenetic stages. Ontogenetic trait variation showed differences in resource use strategy on young and adult plants. Trait associated resource take and allocation showed contrasting patterns through ontogeny (Martin & Thomas, 2013). Moreover, ontogenetic trait variation is also strongly suspected role by showing the shift of the relative importance of different assembly mechanisms based on different patterns of functional diversity and community weighted mean trait across ontogenetic stages (Spasojevic, et al., 2014). The small plants tend to grow far from their large plants (Murdjoko et al., 2016).

Trait variation and its pattern in relation to how plants respond to environmental change become increasingly attractive for further investigation. Furthermore, shift of plant community of conservative traits at lower resource availability to opportunistic traits at higher resource availability (Reich et al., 1997, Wright et al., 2004) became one of essential pattern to be considered in study of plant ecology. The important thing is that strength of this shift in trait pattern may depend on ontogenetic. Therefore, assessing patterns of trait variation among ontogenetic stages across contrasting habitats become very important in seeing how plants respond to environmental changes.

Aim of this study was to answer the question about whether there is any difference trait values of communities and populations growth on different habitat and across ontogenetic stages. We predict that there are differences of trait value in plants that grow in different habitats, in this case on ridge and at valley. Trait across ontogenetic stages also will show the differences between groups of small, medium and big trees. Therefore, body size as a parameter of ontogeny can be considered as a function of trait variations.

METHODS

Study area

This study was conducted in the Kenting forest dynamics plot which is located in Kenting Uplifted Coral Reef Nature Reserve of Kenting national park, Hengchun peninsula, Pingtung, Southern Taiwan. The Kenting Karst Forest Dynamics Plot is located in an undisturbed forest in the northeastern part of the Reserve (East Longitude: 120°49'; North Latitude: 21°57'; elevation 250- 300 m). It is a 10-ha rectangle plot which runs 400 m long (east-west axis) and 250 m wide (north-south axis) with 1000 sub plots (Wu et al., 2011).



Figure 1. The location of study site (Kenting forest dynamics plot, Kenting national park, Hengchun peninsula, Pingtung, Southern Taiwan).

According to data from Hengchun Weather Station, Central Weather Bureau (in years 2000 – 2010), Kenting forest area has annual precipitation of 2,000 mm in average. About 87% rainfall occurs between June and November due to *Mei-Yu* season and typhoons, while from October to April are drier with strong northeast monsoon. The mean annual temperature is 25.4°C with a small difference between the average temperature of the coldest and hottest, from 20.9°C on January to 28.4°C on August. On average, 2.3 typhoons landed on the Hengchun Peninsula every year from 1897 to 2007 (Data source: Central Weather Bureau cited in Wu et al., 2011).

Sampling

Dominant tree species in Kenting forest dynamic plot which have abundance rank from 1-10 and it comprises more than 80% in total abundance in Kenting plot area (Wu et al., 2011) were chosen. Samples were taken from two different habitats (valley and ridge) by considering main paths at study area. The numbers of the collected samples were between 40-66 individuals for each species. Traits were measured on 5

leaves for each individual. For quantifying body size as function of trait, diameter on the breast high (DBH) of each tree were measured. Then we classified them into three different size classes: 1-5 cm DBH (small tree), 5.1-15 cm DBH (medium size tree) and bigger than 15 cm DBH (big tree).

There were 46 sub plots (10 x 10 m for each sub plots) selected to assess environmental factors. Soil water content, soil bulk density, soil porosity, soil particles, and leaf area index were collected from these sub plots.

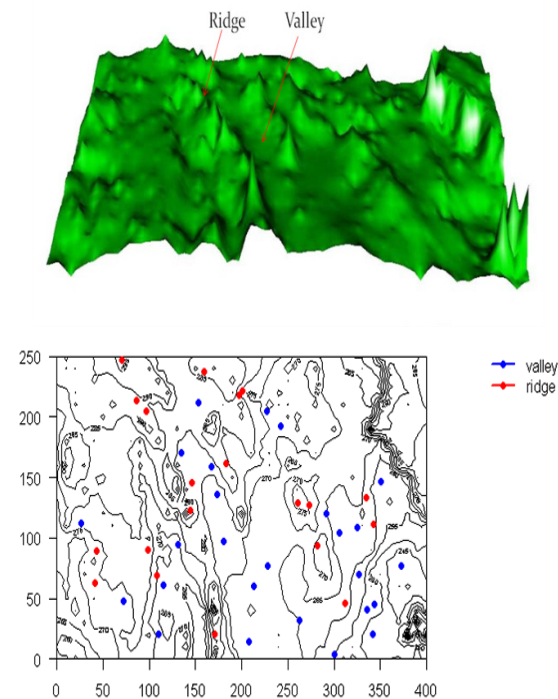


Figure 2. Topography and distribution of 46 sub plots for collecting samples of traits and environmental factor in Kenting plot.

Data collection

Environmental factor data

After careful removal of the dry litter layer from the top, random soil samples of the size (10x10x10 cm) were collected from the (0-10 cm) layer, at least from three different stands of each sub plot. Then samples were put in sealed plastic bag for preventing water loss. Fresh weight of samples soil was measured as soon as possible. After that, samples were put in paper bag and oven-dried for 3 days (72 hours) in 105 degree celcius. Dry mass of soil was measured every day until there was no difference weight. Soil water content was calculated by thermogravimetric method as (soil wet mass – soil dry mass)/ soil

dry mass multiplied by 100 to get value in percentage (ISO 1993 cited in Smith and Mullins 2005). Soil bulk density was calculated as the ratio of sample soil volume to oven-dried weight. Soil porosity was calculated by bulk density divided by particle density. Soil particles analysis was measured by calculating the percentage of sand, silt, and clay in the inorganic fraction using hydrometer method (Bouyoucos, 1962). Leaf area index was measured on each habitat using LAI 2200 plant canopy analyzer manufactured by LI-COR Bioscience based on its protocols.

Trait data

In this study, we used variables of leaf traits that included: leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness (L_{th}), and leaf succulence (LS). These traits were selected because they are widely used in trait-based ecology studies. Also, these traits are easy to collect and measured compared to other traits, such as root traits or whole plant traits.

The area of a leaf (also called leaf area, LA) is the most common metric for leaf size and is defined as the one-sided or projected area of an individual leaf. Leaf size has important consequences of the leaf energy and water balance (Cornelissen et al., 2003). Leaf size is a compromise between functional and resource-use efficiency. Specific leaf area (SLA), the ratio of leaf fresh surface area to dry mass, is a key component of the leaf economics spectrum (Wright et al., 2004), and reflects the tradeoff between rapid

resource uptake and resource conservation. Leaf dry matter content (LDMC), the ratio of leaf dry mass to fresh mass, is also related to the leaf economics spectrum and correlates positively with leaf lifespan, water use efficiency, and herbivore resistance (Cornelissen et al., 2003). Leaf thickness (L_{th}) plays a key role in determining the physical strength of leaves. In optimization theory, balancing photosynthetic benefits against C costs of respiration and transpiration, predicts that L_{th} should be higher in sunnier, drier and less fertile habitats, as well as in longer-lived leaves. Leaf succulence is often seen as an anatomical trait common to plants with a high development of a water storage tissue (Kluge & Ting, 2012). Succulence leads to high leaf water content (LWC) and leaf thickness (Cornelissen et al., 2003).

Leaf traits are measured according to handbook for standardised measurement of plant functional traits worldwide by Pérez-Harguindeguy et al. (2013). Fresh leaf weight was measured with an electronic balance to the nearest 0.1 mg. Leaf area (LA; cm^2) was measured with a flat-bed scanner directly within 12 hours of collection then was calculated using image-J software based on the scanned images. Leaves were then oven dried for 72–96 hours at 60 °C until a constant weight was reached. Specific leaf area (SLA; $cm^2 g^{-1}$) was calculated as leaf area per dry leaf mass. Leaf Dry Matter Content was measured from oven-dry mass (mg) of a leaf, divided by its water-saturated fresh mass (g), expressed in $mg g^{-1}$. Leaf thickness was measured using a dial thickness gauge with accuracy up to 0.01 mm.

Table 1. Ten common trees species and its abundance in Kenting forest dynamic plot (Wu et al., 2011). Relative density was calculated from species density divided by total density in Kenting FDP.

Species name	Family	Tag.Code	Density	Relative density (%)	Rank	Individual sampled
Diospyros maritima	Ebenaceae	DIOSMA	22079	56.48	1	66
Drypetes littoralis	Euphorbiaceae	DRYPLI	3456	8.84	2	61
Aglaia formosana	Meliaceae	AGLAFO	1648	4.22	3	55
Champereia manillana	Opiliaceae	CHAM-MA	970	2.48	4	48
Dendrocnide meyeniana	Urticaceae	DENDME	940	2.4	5	63
Cryptocarya concinna	Lauraceae	CRYPKO	759	1.94	6	41
Melanolepis multiglandulosa	Euphorbiaceae	MELAMU	758	1.94	7	46
Macaranga tanarius	Euphorbiaceae	MACATA	687	1.76	8	45
Palaquium formosanum	Sapotaceae	PALAFO	608	1.56	9	46
Diospyros philippensis	Ebenaceae	DIOSPH	569	1.46	10	55
Total			32474	83.08		

Leaf succulence was calculated as (leaf wet mass – leaf dry mass)/leaf area (gH₂O per cm⁻²) as proposed by Mantovani (1998).

Data analysis

All statistical data were analyzed by using “R” statistical program (R Core Team, 2015). We used coefficient of variation (CV) for quantifying intra-specific trait variability on each species. CV is the ratio of the standard deviation to the mean for calculating data dispersion. Variance decomposition was to investigate the structure of trait variation by using a restricted maximum likelihood (REML) method in the “varcomp” and “lme” function, I fitted a general linear mixed model which consist only random factors to the variance across different scales nested one into another. For community level the scales are: leaf, individual, ontogeny, species, and habitat. For population level (only ITV) the scales are: leaf, individual, ontogeny, and habitat. Habitat here is divided into two, ridge and valley in the study site. The code used in R to calculate the variance partitioning of the traits across ecological scales on community level for the full model on LA was: `varcomp.la<-varcomp(lme(log10(la)~1, random=~1|habitat/spname/size/tag, data=pft, na.action=na.omit),1)`.

Only LA and SLA were log transformed for normalized the data. The “ape” and “nlme” libraries are necessary to use the “varcomp” and “lme” commands. For calculating another trait, it only changes LA with the other trait in model. When calculating on species level, I remove “spname” from random factor. Then the result from variance decomposition was timed by 100 to get percentage values of all.

Two-way analysis of variance (ANOVA) was used to assess differences in trait values between communities, as well as across species ontogenetic stages. The F value and p value were used as the basis of whether there is difference between groups were compared. More specifically to determine trait variation through ontogeny, I used ordinary least squares (OLS) regression. This analysis is to investigate the trait patterns trough ontogeny. All bivariate relationships were log-transformed to meet the assumption of homogeneity of data, and fit with an ordinary least-square (OLS) regression slope, with DBH as the predictor variable. Coefficient of determination (R²), slope and the p value were used to describe the effect of high breast diameter (DBH) of trees to the trait variations through ontogeny.

RESULT AND DISCUSSION

Measurement of soil water was taken by mass-based. Data distribution of soil moisture (Figure 8) shows that there are significant differences between soil water content in the valley and ridge area (t = -5.6, p-value = <0.001). The average soil water content in the valley is 18% while in the ridge area is 24%.

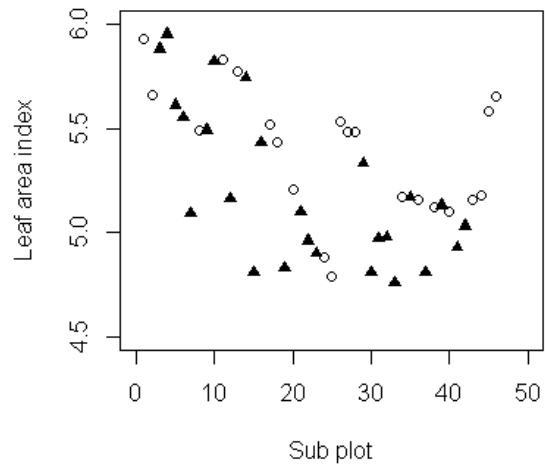


Figure 3. Leaf area index (LAI) values on different habitat (○: valley, ▲: ridge) of 46 sub plot. t = 1.7717, p-value = 0.08337

Based on the proportion of soil particles (clay, silt, and sand), we can classify the soil samples to different soil textures. Composition of soil texture that occurred on the ridge and the valley (Figure 9) shows that both habitats have similar type of soil, that is “loam” soil (55% of total samples on each habitat). What distinguished of these two habitats that approximately 35-40% of soil samples at the valley had “sandy loam” texture, whereas in the ridge area was “clay loam” soil.

Bulk density has a significant negative relationship to soil water content (figure S2). While soil water content increased significantly as increasing of soil porosity figure S2). Therefore, soil samples on ridge habitat that has lower bulk density and higher porosity than soil at valley habitat influence soil at ridge habitat has higher water content than valley. Furthermore, composition of soil texture on ridge habitat which has more clay soil than at valley also supports that soil water content on ridge habitat is higher than at valley habitat (Figure 5).

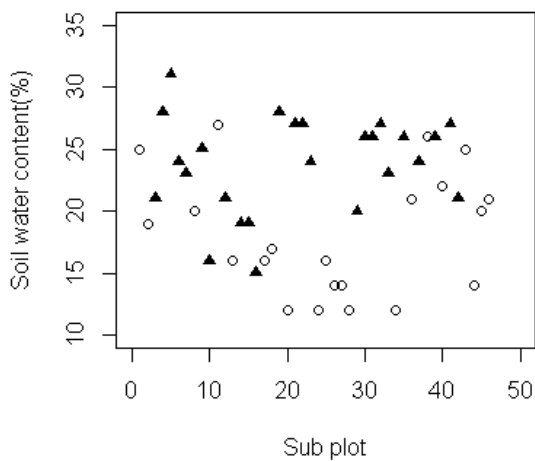


Figure 4. Soil moisture measured as soil water content by mass values on different habitat (○: valley, ▲: ridge) of 46 sub plot. $t = -4.1997$, $p\text{-value} = 0.0001556$

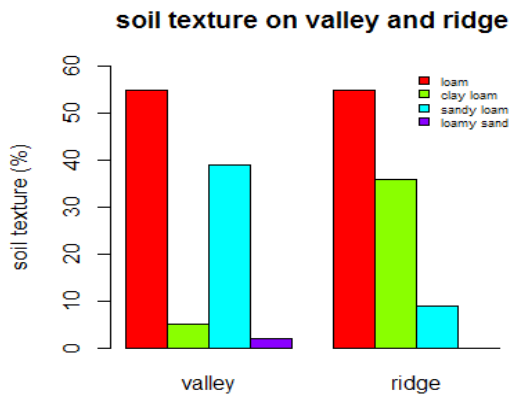


Figure 5. Percentage of each type of soil samples on two different habitat (at the bottom of valley and on the top of ridge). Soil texture by color (red: loam, green: clay loam, cyan: sandy loam, and blue: loamy sand).

Based on the average value for each species, it was found that inter-specific trait variation was very large (Table 2). For example in the leaf area, differences between species can up to 10-fold. For example, leaf area of CHAMMA was only 23.14 cm², but in MELAMU it reached to 236.28 cm², leaf thickness of MELAMU was only 0.09 mm compared to that of PALAFO which was 0.32 mm. Differences in SLA is also quite large, ranging from 81.69 cm²/g in DIOSPH to 256.49 cm²/g in MELAMU. Differences in LDMC and leaf succulence also relatively high. It ranged from 162.39 gH₂O/cm² to 391.4 gH₂O/cm² and 101.37 mg/g to 251.8 mg/g, respectively.

Based on coefficient of variation (CV), the largest intra-specific trait variation (ITV) was in

leaf area of AGLAFO which has the highest CV (0.57). In general, leaf area (LA) showed the largest ITV compared to other traits across species. CV range for LA was 0.39 - 0.57 followed by SLA (0.18-0.38) and leaf thickness (0.13-0.35) then leaf succulence (0.14-0.3) and LDMC which has smallest CV ranges from 0.06 - 0.19.

To determine the structure of variation in each trait measured, variance decomposition analysis was used based on the value of the trait resulting from sampling by hierarchical method. Measurements at the scale of the leaves, and then gradually to the next scales, that are individual (tree), ontogenetic, species, and sampling at two different habitats (on the top of ridge and at the bottom of valley). At the community level (Figure 6f.), trait variation structured mostly from inter-specific variation trait or between species trait variation (BTV). It was explained approximately 60% on a leaf thickness up to 80% for LDMC, while BTV for the other three traits (leaf area, SLA, and succulence) were 70% respectively. Other sources of variation derived from the intra-specific variation of trait (ITV) which is divided into several hierarchies. Ontogeny turns the greatest role in ITV for leaf area and leaf thickness, whereas for the SLA, LDMC, and leaf succulence variations were more explained by individual scale.

Variance partitioning (ITV) at the level of population showed a similar pattern with ITV at the community level. In general, the variation of the difference in size class explained more than 40% ITV for leaf area and leaf thickness respectively. While variation structures for SLA, LDMC and leaf succulence were most explained by individuals with almost has similar percentage (40% - 80% variations). At leaves scale, only a few species which have large variations, such as LDMC on CRYPCO and DIOSPH, or leaf succulence on MELAMU and PALAFO. There was no different trait variation coming from differences habitat (ridge and valley). Only leaf succulence in some species and LDMC on AGLAFO that have slightly different CV between two habitat and it only 5% - 15% variance explained from this scale.

Variance decomposition results from each trait (Figure 6) show that the role of BTV approximately 70%, while ITV 30% in contributions to trait variability. Similar results (comparison for 70% BTV and 30% ITV) were also reported by Albert et al. (2010) for SLA and LDMC on alpine ecosystems and Hulshof & Swenson (2010) for SLA and leaf water content on dry tropical forest. In accordance with the spatial variance partitioning (SVP) hypothesis (Albert et al., 2011)

Table 2. Mean, variance, and coefficient of variation (CV) trait values of ten common species in study area.

Trait	stat. desc	Aglaia formosana	Cham-pereia manilana	Cryp-tocarya con-cinna	Den-drocnide meyeniana	Dio-spyros mari-tima	Diospy-ros philip-pensis	Dry-petes littora-lis	Maca-ranga tanarius	Melanol-epis mul-tiglandu-losa	Pala-quium forma-num
Leaf Area	mean	64.22	23.14	25.23	166.81	43.01	130.91	29.09	174.22	236.28	84.86
	var	1320.66	110.50	172.98	5023.81	423.21	2336.79	238.03	9366.10	8428.61	2041.12
	cv	0.57	0.45	0.52	0.42	0.48	0.37	0.53	0.56	0.39	0.53
SLA	mean	113.14	113.35	108.19	241.54	126.96	81.69	79.87	158.70	256.49	86.29
	var	768.53	465.02	445.5	4359	842.96	988.58	284.97	773.21	7583.7	497.92
	cv	0.25	0.19	0.20	0.27	0.23	0.38	0.21	0.18	0.34	0.26
Leaf Thickness	mean	0.24	0.28	0.22	0.17	0.19	0.25	0.30	0.12	0.09	0.32
	var	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
	cv	0.27	0.25	0.24	0.22	0.20	0.23	0.22	0.13	0.35	0.24
LDMC	mean	365.11	281.80	410.1	162.39	385.2	435.63	389.7	391.40	275.51	323.36
	var	2069.5	824.59	2268.	963.13	1591.	1991.7	1720.	561.38	795.51	1652.8
	cv	0.12	0.10	0.12	0.19	0.10	0.10	0.11	0.06	0.10	0.13
Leaf Succulence	mean	161.82	235.70	138.2	227.36	131.5	176.72	203.9	101.37	110.42	251.80
	var	1171.3	2682.8	594.3	774.33	238.1	577.65	971.2	449.88	1115.4	1348.2
	cv	0.21	0.22	0.18	0.12	0.12	0.14	0.15	0.21	0.30	0.15

then the value of inter-specific variation trait or trait variation between species (BTV) is higher than the intra-specific variation of trait (ITV) at the broader scales.

Deeper study for understanding of variation pattern in different ecological scale of different traits will make us easier to take a decision to do ecological studies based on different questions. Messier et al. (2010) on the Figure 8, explain that variations at different scales are affected by different playing ecological and evolutionary processes. For example, water and nutrient status during leaf flushing will affect the variation of the trait on leaf scale. This is what might be able to explain that by partitioning variance in my research, traits related to water status (LDMC and leaf succulence) on a scale of leaves have a greater proportion of the percentage variation in contributing of ITV compared with ontogenetic scale. Even in some species, variations of these two traits are bigger than the individual scale.

Generally, plants on ridge habitat have smaller and thicker leaves with lower SLA and higher leaf succulence compare to plants that grow at valley. In addition, small trees tend to have larger and thinner leaves with higher SLA and lower leaf succulence then medium and big trees. Whereas LDMC on small and medium trees were relatively similar which have lower

values than big trees. Summary of analysis of variance (table 3) shows that at level of community, there are significantly different (p-value < 0.05) of trait values between habitats and across ontogenetic stages. However, only LDMC values between ridge and valley community was not significantly different. All leaves trait between group comparisons has very low p-value which means that in average, the variation of leaf trait between habitats and across ontogenetic stages was much larger than the variation of trait values within a habitat or in same stage of ontogeny.

At the population level, LDMC tend to have a stable value in most species either between or across ontogeny population, only on population AGLAFO, DIOSMA and PALAFO which showed a significant difference. Leaf area and leaf thickness is a trait with the greatest value variation across ontogenetic stages. This is shown by the significant differences across different species at all life stages, only on MACATA for leaf thickness were not significantly different.

Comparisons between populations of a certain size in a particular habitat did not show significant differences when compared to the size of the population in different habitats. The difference in value trait each leaf area on CRYPKO, SLA and leaf on PALAFO, leaf succulence on DIOSPH, and LDMC on CHAMMA, CRYPKO, and DENDME indicate a difference between the

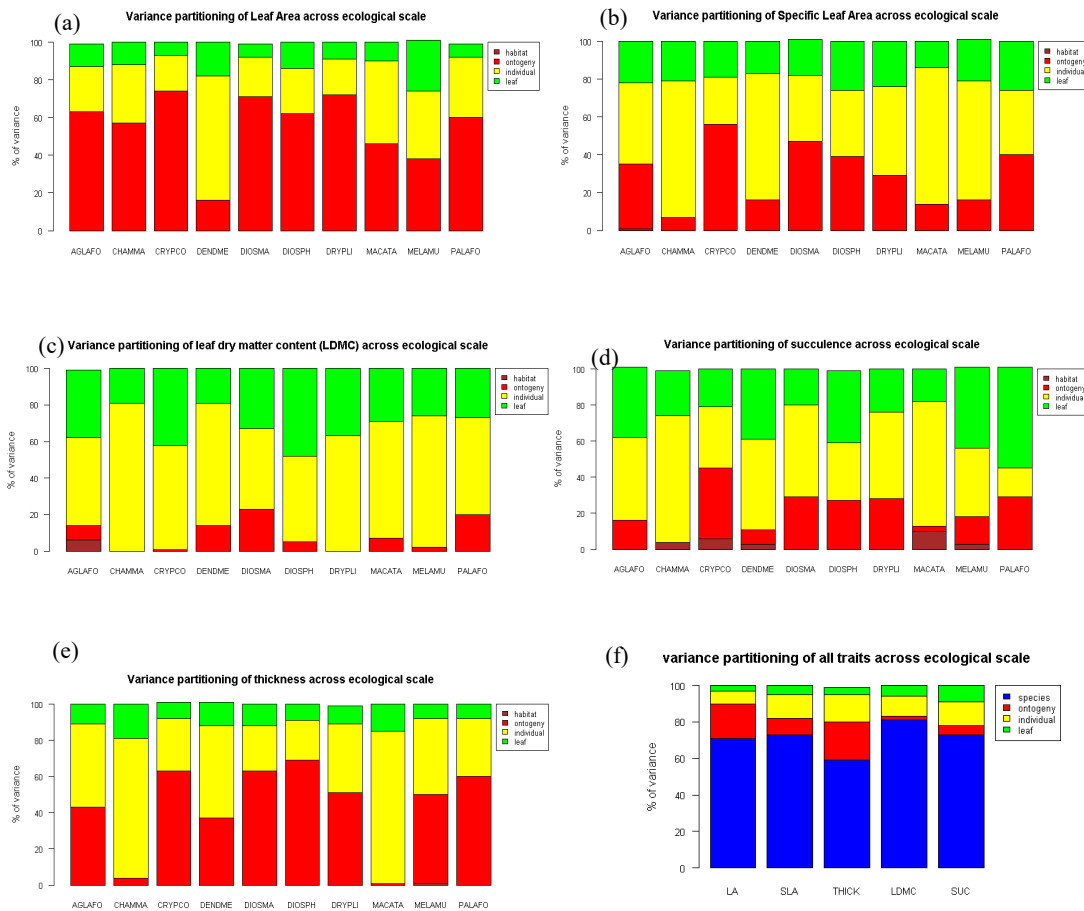


Figure 6. Composition of variations by variance partitioning on single trait across ecological scales. Relative variance decomposition at the population level for (a) leaf area (LA), (b) specific leaf area (SLA), (c) leaf dry matter content (LDMC), (d) leaf succulence, (e) leaf thickness, and community level for (f) all species. Species codes come from the Table 1.

size class on Certain habitats compare to other size classes or similar class on different habitat.

Since the ontogeny trait variation is matter in variance partitioning of ITV, here I try to explore more about body tree size related to trait variation. Ordinary least-squares (OLS) regression was used to examine the relationship between tree size with a functional trait for each species. Data of diameter breast high (DBH) tree was used as a predictor (x) to determine the value of a functional trait variation (y). All data were taken from the average value of each individual species with different DBH.

Trend lines represent leaf trait-DBH structural relationships based on regression analysis on a log-log transformed data (Figure 7). Overall, five leaf traits (leaf area, SLA, thickness, LDMC and succulence) has a significant relationship (p-value <0.001; table S2) to body size. But there are some species that do not have a significant relationship such as LDMC on CHAMMA, CRYPCO, DIOSPH, and DRYPLI, then SLA and suc-

culence in MACATA.

Leaf area and SLA negatively correlated to body size, while leaf thickness, succulence and LDMC has a positive correlation. The highest relationship was between leaf area and DBH in CRYPCO ($R^2 = 0.82$) and the lowest was thickness-DBH relationship on MACATA ($R^2 = 0.06$). The average values of R^2 for each trait are 0.62, 0.34, 0.45, 0.12, and 0.22 for leaf area, SLA, thickness, LDMC, and succulence respectively. Slope value, which represents the magnitude of the effect of body size on the trait measured, the highest (-0.665) on leaf area for MACATA and the lowest (0.043) on LDMC for MACATA. Therefore, based on R^2 and slope values it was known that body size (DBH) described the greatest to variation of leaf area, while the smallest relationship was with LDMC across ontogeny.

One of ecological scale in the study of Messier et al. (2010) is strata. This scale is important since most of leaf trait sampling in another study only taken on the leaves which get full sun

Table 3. ANOVA summary of trait values on community level between habitat and across size class

Trait	Parameter	F value	p value	signif.codes
Leaf Area	habitat	4.78	0.029	*
	size	13.67	0.0000016	***
	habitat:size	0.27	0.762	
SLA	habitat	20.95	0.0000059	***
	size	6.32	0.0019	**
	habitat:size	2.83	0.06	.
Leaf thickness	habitat	22.51	0.000002691	***
	size	21.54	0.000000001	***
	habitat:size	2.62	0.074	.
LDMC	habitat	2.46	0.1172	
	size	7.78	0.00046	***
	habitat:size	1.9	0.15024	
Leaf succulence	habitat	25.18	0.00000071	***
	size	9.18	0.00012	***
	habitat:size	0.57	0.56659	

Signif. codes: 0 '***' 0.001 '**'
0.01 '*' 0.05 '.' 0.1 ' ' 1

exposure. Yet the fact that most of the foliage there is contained in branching in under the canopy on the same individual at different foliage or individual with different body sizes (ontogenetic stage). The different strata that affect the acquisition of light availability and other resources may influence of ITV and can revive the ecological process that affected the plant's performance.

In this study, ontogenetic stage occupied the similar scale as the strata in term of light resource availability. Small trees would get less light in small gap of light interception (high LAI) area compared to medium and bigger size trees. There are two environmental conditions and ecological process that influence the trait variation in addition to water and nutrient status on this scale, namely humidity and wind; and resource allocation (Figure 8). Environmental conditions associated with humidity and winds are often associated with the response of plants in order to self-defense, while resource allocation strategy is closely related to plants in selecting of which resources are more to be a priority than others. Secondly, it is consistent with the findings that the trait variation on ontogenetic stage has a great

proportion trait that plays a role in self-defense and resource allocation strategy (leaf thickness, leaf size, and SLA).

A very significant influence of the body size to trait variation through ontogeny and a substantial contribution from ontogenetic stages of the trait variability both at the level of populations and communities (Figure 7) strengthen our assumptions for the important to consider ontogenetic trait variation (OTV) in the study of ITV and trait-based community ecology. Further OTV role is increasingly clear to explain species and community response to environmental gradient mediated by trait.

To become dominant species (high abundance and high frequency), plants should adapt to different environmental conditions and respond to environmental changes in such habitat. Therefore, the dominant species should have adaptive traits, responsive traits or both in order to be abundant in large distribution at the study site. When species are only able to adapt to particular environmental conditions, they could have a high abundance in certain habitat types in accordance with its adaptive trait but less common

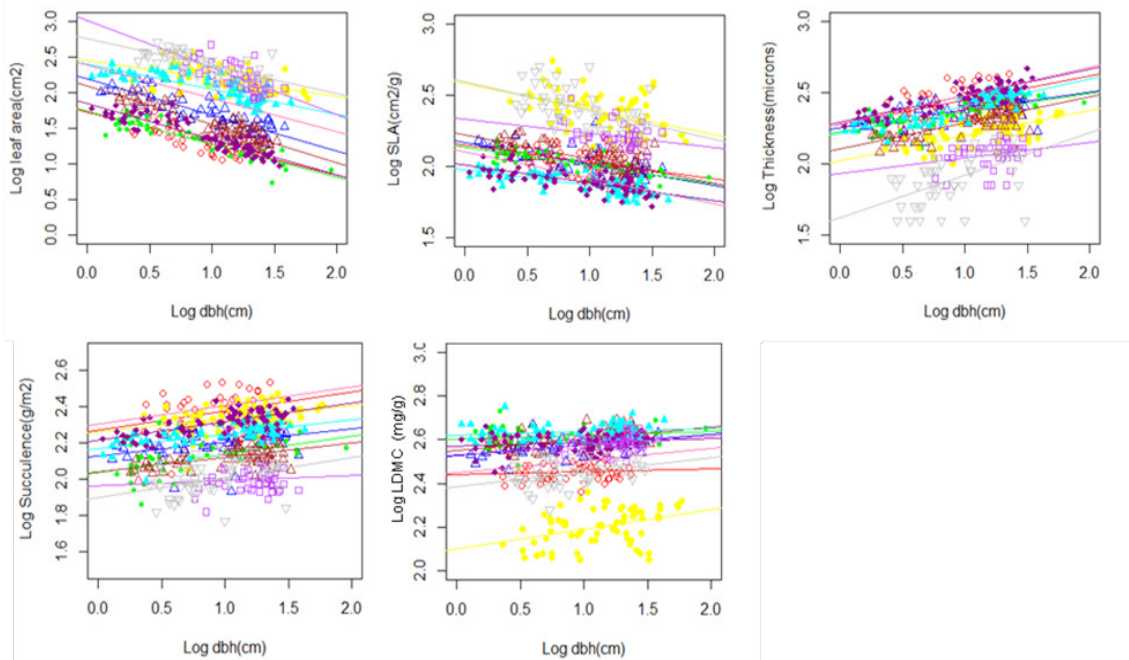


Figure 7. Trait (Leaf area, SLA, Thickness, Succulence, and LDMC) as a function of DBH across common tree species in Kenting karst forest (species code; AGLAFO(blue), CHAMMA(red), CRYPCO(green), DENDME(yellow), DIOSMA(brown), DIOSPH(cyan), DRYPLI(dark magenta), MACATA(darkorchid), MELAMU(gray), PALAFO(hotpink)).

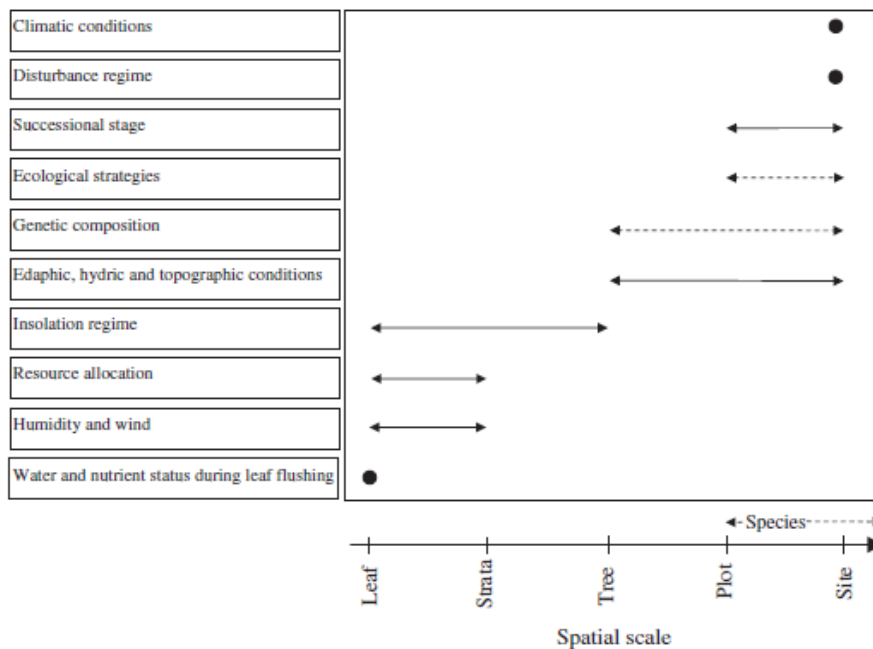


Figure 8. Processes affecting trait variation on different ecological scales. The abscissa represents the spatial scale and the ordinate lists the processes. The scale of species is drawn using a dashed line and overlaps the plot and site levels. The processes affecting a spatial scale via its effects on species are also drawn using a dashed line (Messier et al., 2010).

in other habitat types. In my case, dominant species could be able to grow in both habitats (valley and ridge) or abundant only in one habitat type (valley or ridge).

At valley habitat, plants exposed to conditions of less light availability, especially for small and medium trees. Various types of soil texture are quite diverse (loam, sandy loam, clay loam, and loamy sand), allowing soil water gradient on this habitat. Furthermore, proportion of sand particle in soil sample is relatively higher than ridge soil, allowing soil conditions at valley habitat has lower soil water content than ridge habitat. In contrast, on ridge habitat, LAI values tend to be lower than valley habitat. This allows for more light availability. In addition, ridge area condition that tends to be more exposed and has higher altitude than the valley, allows for getting higher solar radiation and hotter air temperature. This condition can cause evapotranspiration process will be faster, so plants that grow on the ridge habitat should be adapt for changing status of soil water content. Unfortunately, in this study I did not measure soil water content at different times so we could not see fluctuations of soil water content status at study site.

Occurrence of dominant species on different environmental conditions of both habitat (valley and ridge) was probably as result of local adaptation process at a study site for long time periods. Whether because of plasticity response, evolutionary changes, or both, there is plenty of evidence for local adaptation in plants (Franks et al., 2014). Local adaptation is defined as a dynamic process that applies in the population to maintain or increase the frequency of traits that increase survival or reproductive success of individuals with the trait and value of an adaptive trait for an individual is measured relative to other individuals with properties (Taylor, 1991).

Among dominant species showed a similar pattern of trait values on contrasting habitats. On the ridge habitat, leaves tend to have lower SLA, higher leaf thickness, and higher leaf succulence compare to valley habitat. These three traits (SLA, leaf thickness and leaf succulence) may be used as a candidate as both adaptive and responsive traits. As an adaptive trait, it was known that SLA is one of key traits in plant functional grouping involved conservative versus opportunistic plants (Reich et al., 1997, Wright et al., 2004). While leaf thickness and leaf succulence, both have a strong relationship in strategies for optimizing water use efficiency and allocation of capacity to water storage in leaf organs (Smith, 1978). Lower SLA (due to thicker and/or denser

leaves) contribute to long leaf survival, nutrient retention and protecting from desiccation (Mooney & Dunn 1970). Higher SLA (due to larger and thinner leaves) tend to have high leaf nitrogen content (LNC) reflected a faster potential rate of return on investment in leaves (Wright et al., 2004). Also, reviews of these three traits have significant relationships along both environmental gradients. Furthermore, these traits have relatively high CV as a form of adaptation to changes in environmental factors within habitat.

The last trait is leaf dry matter content (LDMC). This trait is proposed as one of the potential adaptive traits. In addition, its value was relatively stable at individuals within and among species, LDMC was less variation trait both between habitat and across ontogenetic stage. LDMC is also known as less sensitive trait to soil resources variation in different types of sand dunes (Yulin et al., 2005). No significant different of LDMC in two different habitats indicate that plant is able to adapt to different environments, probably through certain investment values in leaf tissue density (Chaves et al., 2002) or adjust to adapt from similar physical hazards such as herbivory and the wind (Cornellisen et al., 2003) at the study site.

CONCLUSIONS

This research reveals trait variability across ecological and ontogenetic stages scales between contrasting habitats on community and population levels. There are fundamental finding that has important contribution to trait-based plant ecological study; inter-specific trait variation was higher than intra-specific trait variation on dominant species community in tropical karst forest, body size had remarkable effect to trait variation through ontogeny, and plants that grow on ridge habitat tend to have smaller and thicker leaves, lower SLA and higher leaf succulence compare to plants at valley. The important finding in this study was by only using mean species we can misleading in understanding of plant responses to the environmental gradient in order to their adaptation both across different habitat and ontogenetic stages.

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