SAURASHTRA UNIVERSITY

FUNCTIONAL TRAIT VARIATION WITHIN AND ACROSS WOODY PLANT SPECIES ALONG AN ELEVATION GRADIENT

Submitted by

Ashish Nambiar

For the award of the Degree of

Master's Degree in Wildlife Science

Under the Supervision of

Dr. Navendu Page

Dr. Meghna Krishnadas

Dr. Sathish BN

July, 2021

भारतीय वन्यजीव संस्थान
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DECLARATION

I, **Ashish Nambiar**, hereby declare that the research work titled **" Functional trait variation within and across woody plant species along an elevation gradient",** carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of research work. This research work was carried out under the supervision of **Dr. Navendu Page**, at the Wildlife Institute of India from January 2021 to June 2021. I hereby declare that this work has not been submitted for any other degree of any university.

Ashish

Date: June 16, 2021
Place: Dehra Dun

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CERTIFICATE

This is to certify that **Mr. Ashish Nambiar** has carried out an original piece of research in partial fulfilment of Master's Degree in Wildlife Science of the Saurashtra University, Rajkot, Gujarat. The topic of his dissertation is **"Functional trait variation within and across species along an elevation gradient".** The study was carried out under our supervision from January 2021 to June 2021. We hereby certify that this work has not been submitted for any degree to any university

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CERTIFICATE OF PLAGIARISM CHECK

It is certified that the MSc thesis titled "**Functional trait variation within and across woody plant species along an elevation gradient**" submitted by Mr. Ashish Nambiar has been examined by us for plagiarism check as per UGC (Promotion of Academic Integrity and Prevention of Plagiarism in Higher Educational Institutions) Regulations. The following inferences are drawn from this check:

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Contents

1.1 Acknowledgments

First of all, I am eternally thankful to my parents for having supported me emotionally and financially throughout my Masters. It’s with their constant support that I see myself inching towards what I always dreamed I would do with my life.

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It would be an absolute shame to not acknowledge the role that Lucy has played in guiding my thoughts and showing me how beautiful and intriguing the natural world can be. Because of its multidimensional and multi-layered nature, scientific investigation in the wild can be a challenging endeavor. However, it has become clear that with a little work, the appropriate guidance, and a lot of patience, the various layers of natural phenomena can be peeled away, bringing us closer and closer to the truth.

I thank the Director, WII, and Dean WII for their support and feedback through my entire MSc.

Lastly, I would like to thank my guides Dr. Navendu Page and Dr. Meghna Krishnadas for having guided me throughout my dissertation and having supported me through the entire process of conducting a planned and systematic scientific study. Both Meghna and Navendu have been very patient with me through the course of this study and I am in awe of the clarity with which they approach questions and subsequently data. If I were to peer into the future when I first joined the institute I would never have believed that I’d be so much in love with plants, for which I almost entirely credit Navendu. Navendu is the coolest teacher I have had the pleasure of observing and learning from. His curiosity and almost viral love for plants rubbed off on a plant hater like me and it has been an absolute privilege having a mentor like him. I am excited for the life after WII and I hope to dedicate more of my time unraveling the secrets that our plant friends keep from us.

Summary

Plant phenotypes are defined by a set of traits that have been theorized to be closely linked to the fitness of individuals. These traits have an impact on their ability to grow and compete given the local environment. Variability (intra-specific or inter-specific) in the values of these functional traits is thought to be associated with the ability of an individual to survive in highly variable environments or a wide range of environments. Elevation gradients represent a change in environmental factors within a short spatial scale and hence offers the ideal context to examine functional trait variation.

This study seeks to understand the extent of intraspecific trait variation and theorize the drivers of this variation in five woody plant species in response to a change in elevation in a tropical evergreen forest. I focussed on three different functional traits i.e Specific leaf area (SLA), leaf dry matter content (LDMC), and Stem specific density (SSD) which represent leaf resource acquisition as wells as stem differentiation. When examining the trends of functional trait values for the entire data set irrespective of species identity, it was seen that differences in mean trait values drove the across-species trends. This highlights the role of the environment in selecting for species with specific mean trait values. Contrary to this, intra-specific trait values did not show directional selection in response to elevation, however, the percentage of the total variation associated with the intra-specific scale was significant. This indicates the occurrence of simultaneous counter gradients which may be leading to there being a lack of signal in functional trait values in response to elevation. I failed to establish a correlation between intra-specific trait variation and the elevation range

of occurrence. The results highlight the high functional trait variation seen at the intra-specific scale and emphasizes the importance of considering intra-specific trait variation especially at the scales of high environmental heterogeneity.

2 Introduction

Plant species have different environmental requirements for successful establishment and survival. Due to this, variation in environmental factors across space and time is thought to limit the occurrence of different species, making the distribution non-random (Violle et al. 2007). These limits on the occurrence and distribution of species are largely mediated through selection on functional traits (Lebrija-Trejos et al. 2010; Kraft, Godoy, and Levine 2015; Muscarella and Uriarte 2016). Violle et al. 2007 define functional traits as 'morpho-physio-phenological traits' which impact fitness indirectly via their effects on growth, reproduction, and survival. Thus, functional traits can be interpreted as strategies that plants develop to cope with locally prevalent environmental regimes (Westoby and Wright 2006).

At scales where the environmental constraints are relatively homogenous, species in plant communities converge in their functional trait values, in response to common environmental constraints (Ackerly and Cornwell 2007). In contrast, at scales with high environmental heterogeneity, it is expected that community composition will change as a result of a change in the environmental variables selecting for different functional traits among individuals. This shift in community composition is accompanied by a change in weighted trait means result from both intra-specific and inter-specific (due to species turnover) functional trait variation (Messier, McGill, and Lechowicz 2010; Kichenin et al. 2013; Fajardo and Siefert 2019). Examining functional trait variation within and across species of varying ranges of occurrence across different environments could offer insights into the mechanisms that govern patterns of species range of occurrence and community assembly.

2.1 Relevance of Intra-specific functional trait variation (ISTV)

While the environment selects for species based on their functional trait values, many plant species are known to span across a wide range of environments, intra-specific trait variation (ISTV) of species could indicate their ability to tolerate a varying environment. Hence, greater intra-specific trait variation in populations may allow a species to occupy a larger range of environmental conditions than species with narrow intraspecific trait variation. Consequently, the niche breadth of plant species is expected to show a positive correlation with intraspecific trait variation (Fajardo and Siefert 2019; Violle et al. 2012). Sides et al. (2014) arrived at a similar conclusion when investigating the relationship between ISTV and local elevation ranges of 21 different species. While it seems intuitive that a wider ISTV would be related to the ability of species to survive and persist in widely different environments, so far there isn’t conclusive support for this expectation. Umaña and Swenson (2019) highlight that studies based on trait-based analyses have assumed intra-specific trait variation to be negligible in comparison to interspecific trait variation and this may probably be the case since these studies were conducted at scales with a largely homogenous environment. It is expected that broadly distributed species found across different environments will have greater intra-specific trait variability than previously expected, in response to changing environmental constraints across its range of occurrence. This may even be comparable to the magnitude of the interspecific trait variation seen among different plant species. Alternately, if the environmental constraints do not adequately impose selection pressures on functional trait values or if plant species have strong biophysical constraints, one would expect even broadly distributed species to have low intra-specific trait variation (Umaña and Swenson 2019).

2.2 Elevation gradients as natural laboratories

Environmental gradients offer the opportunity to study the relationship between functional trait variation and the distributional range of species across a heterogeneous environment on a relatively small spatial scale. Elevation gradients offer a proxy for change in several environmental factors such as temperature and precipitation to detect changes in the structure and functional composition of plant communities. Temperature can strongly co-vary with elevation wherein a decrease in temperature has been linked with increasing altitude (Körner 2007). Other abiotic factors such as wind velocity, precipitation, solar radiation, and soil fertility are also known to change with an increase in elevation (Macek, Macková, and Bello 2009; Fisher et al. 2012; Daws et al. 2002). Given the climatic variation observed along elevation gradients, Sides et al. (2014) demonstrated that wide-ranging species are characterized by high intra-specific trait variation, implying that individuals responded to varying environmental pressures along the elevation gradient. Comparing functional trait variation within and across species, and exploring its link with species range of occurrence will provide insights into the processes associated with observed patterns of species distribution.

2.3 The functional trait economic spectrum

To cope with locally prevalent environmental regimes plants develop strategies in the form of functional traits (Westoby and Wright 2006). At the local scale, however, a set of common environmental constraints result in convergent functional trait values across different plant species (Ackerly and Cornwell 2007). Simultaneously, to avoid competition at the neighborhood scale, species will tend to diverge in their functional trait values (Kraft, Valencia, and Ackerly 2008). These measurable attributes of plants in the form of functional traits are representative of strategies that have evolved with underlying trade-offs which form the crux of plant resource economics.

Resource economic traits are closely linked with the life history of plant species since it influences growth vs survival trade-offs. This, in turn, impacts the performance spectrum of low to high levels of resources (Reich 2014). The traits chosen for this study are those closely related to the ability to acquire limiting resources since this would reflect ecological strategies in response to the various biotic and abiotic constraints, e.g., resource acquisition traits related to wood economics, leaf economics, structure (X. Liu et al. 2016) which are distinctly seen to vary along elevation gradients. Higher elevations are expected to favor resource conservative strategies because of reduced competition due to unfavorable environmental conditions specifically low temperatures while lower elevations favour resource acquisitive strategies due to high competition associated with a favourable environment i.e. high temperature and resource abundance (Pfennigwerth, Bailey, and Schweitzer 2017; Read et al. 2014). I briefly discuss the traits relevant to this study which are broadly classified as leaf or wood traits -

Leaf traits

The leaf economic spectrum (LES) described by (Wright et al. 2004) is based on the productivity-persistence trade-off in a range of successful strategies with inexpensive short-lived leaves with a rapid return on C and nutrients (N, P) i.e. acquisitive traits on one extreme and costly long-lived leaves with slow returns on C and nutrients (N, P) on the other end of the spectrum (Reich 2014). The specific leaf area (SLA) is the light intercepting leaf area per unit of leaf dry mass invested. This is representative of the leaf nutrient concentration and the rate of photosynthesis and respiration. Lower values of SLA, Nitrogen content, Phosphorous content, and high carbon content are associated with low leaf nutrient concentrations, low rates of photosynthesis and respiration, and longleaf lifespan.

Individuals of the same species have been seen to have lower leaf area and lower SLA in response to lower temperatures at higher elevations (Midolo et al. 2019; Poorter et al. 2009).

The link between SLA and elevation may be driven by limited cell expansion at lower temperatures resulting in larger numbers of small cells per unit area. This consequently leads to there being a greater density of cells (leaf density (LD)) and more cell layers (leaf volume per area(LVA)). Since SLA can be expressed as the inverse of the product of LD and LVA, an increase in LD and LVA associated with low temperatures will result in lower SLA values. This increase in LD and LVA and consequently the decrease in SLA values with low temperatures can reduce the severity of cold stress by slowing down rates of freezing (Poorter et al. 2009).

Another important leaf functional trait closely related to the leaf economic spectrum is the leaf dry matter content (LDMC). LDMC is defined as the ratio of dry leaf mass and the water-saturated fresh leaf mass. LDMC is hence representative of the cost of leaf construction.

Similar to SLA, LDMC values have been strongly associated with rates of resource acquisition and productivity (Smart et al. 2017; Hodgson et al. 2011). LDMC is closely related to leaf density (LD) such that high values of LDMC is associated with dense leaf tissues, low photosynthetic rates and low growth rates (conservative trait value) and low values of LDMC correspond with low-density leaf tissues and higher growth rates (acquisitive trait value)(Albert et al. 2010). Since it is expected that conservative trait values are associated with lower temperatures, higher elevations would be associated with higher values of LDMC due to relatively lower temperatures.

Wood traits

Stem-specific density (SSD) is the oven-dry mass of a section of the stem of the tree divided by the volume of the same section. It reflects a trade-off between growth potential and mortality risk from biomechanical or hydraulic failure (Díaz et al. 2016). The wood economics spectrum proposed by Chave et al. (2009) links wood density with hydraulic and mechanical failure. High wood density (acquisitive strategy) is associated with a ‘slower’ potential to move water i.e. low stem hydraulic conductivity but with stronger and more flexible mechanical properties and greater protection from drought stress (and hence freezing). We suspect that higher elevations will tend to have individuals with higher wood density since higher elevations are thought to be more conducive for the survival and persistence of individuals with conservative traits while lower elevations are expected to individuals with acquisitive traits.

Species with a wide range of occurrences cover a variety of environments and studying functional trait variability within and across species scales could give greater insights into the processes governing species' ecological niche breadth (Ackerly and Cornwell 2007). Umaña and Swenson (2019) compare functional trait variation at both, within and across species levels and report that the magnitude of within species functional trait variation across an elevation gradient is comparable to the magnitude functional trait variation across species. This observation suggests that individuals adjust to local environmental conditions across the elevation gradient, highlighting the role of environmental constraints in shaping trait distributions.

2.4 Objectives and questions

The following objectives and questions have been addressed in this study:

Objective 1: To examine the link between intra-specific functional trait values and elevation.

1) Do functional traits move towards conservative functional trait values with an increase in elevation? Is this directional change in trait values unique for each species?

I hypothesized that if elevation affects functional trait values of individuals, with an increase in elevation the functional traits will tend to assume values representative of more conservative strategies. This means that one can expect a decrease in SLA, increase in LDMC and increase in SSD with increasing elevation.

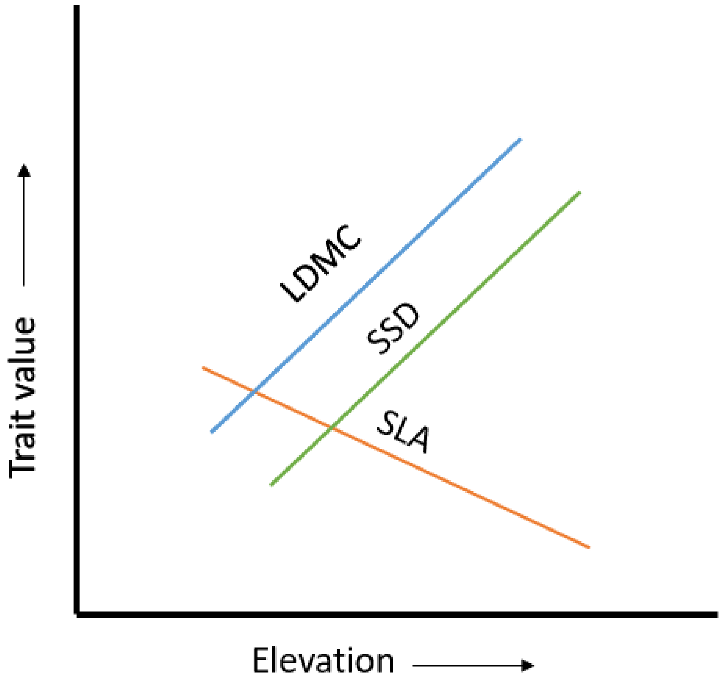

Figure 1 Schematic representation of hypothesis 1. Functional trait values are expected to shift towards more conservative values with an increase in elevation. LDMC and SSD are expected to increase with elevation while SLA is expected to decrease with elevation.

Objective 2: To estimate the proportion of variance explained by the four nested levels of organization, namely elevation, species, populations, and individuals.

To address this objective, the total variance of the functional trait values is assumed to be explained across four nested levels that are structured hierarchically i.e. Elevation, Species, Population, Individual:

Elevation: Comparison of variance between different elevation bands. The identity of individual species is not taken into consideration.

Species: Comparison of variance between species irrespective of elevation.

Populations: Comparison of variance between populations (individuals of a species in one elevation band) of a species from different elevation bands

Individuals: Comparison of variance between all individuals of the same species.

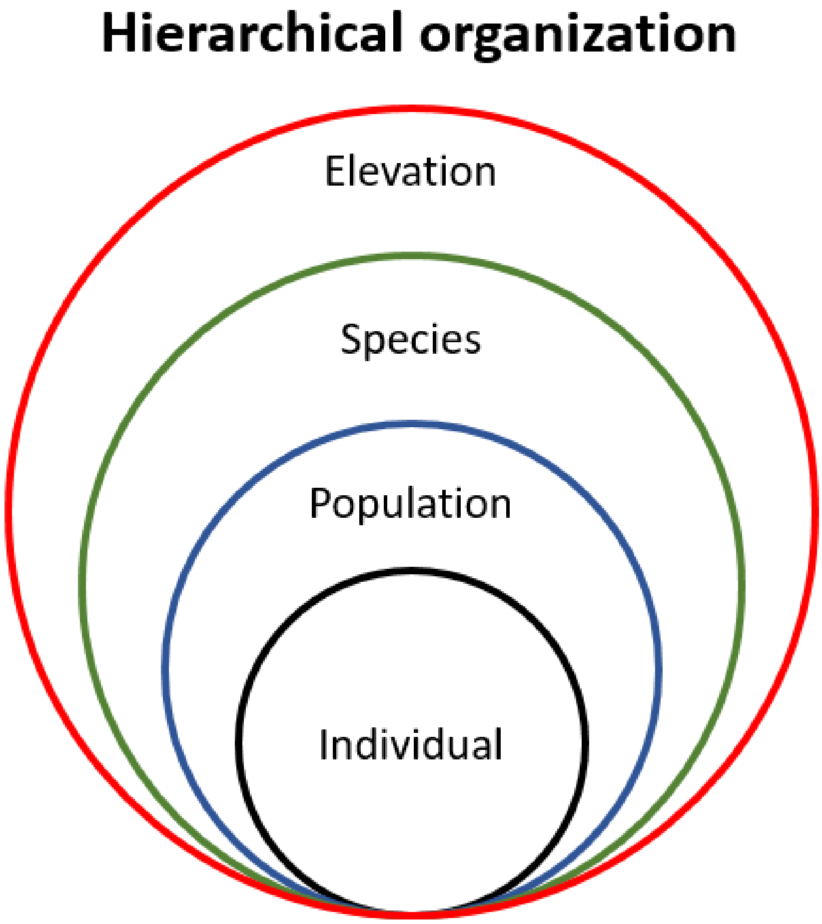

Figure 2 Schematic representation of the four nested levels – Elevation, Species, Population, Individuals. The total variance is associated with these four levels.

1) Is the proportion of variance attributed to the population level (across individuals of a species that are broadly distributed) comparable to the proportion of variance at the species level (across species).

I hypothesized that if environmental constraints across the gradient are sufficiently strong and species adapt to local conditions, the proportion of variance explained at the population level will be comparable to the proportion of variance explained at the species level. Alternatively, if there are biophysical constraints to functional trait variation or if the environmental filters do not select for traits strongly enough, the proportion of variance explained at the population level will be lower than the proportion of variance explained at the species level.

Objective 3: To study the link between intra-specific trait variation and the elevation range of occurrence of plant species.

1) Do species with wider elevation ranges show greater intra-specific trait variability?

   I hypothesized that intra-specific trait variability and the range of occurrence will be positively correlated. This means that plant species with a restricted/narrow range of occurrence along the elevation gradient would have low intra-specific trait variability since they would be more phenotypically constrained in their ability to survive and reproduce given the variation in environmental conditions along the elevation gradient. Similarly, plant species with a wide distribution range along an elevation gradient would have high intra-specific trait variability since they would be more flexible in their phenotypes and their ability to survive and reproduce given the variation in environmental conditions along the elevation gradient.

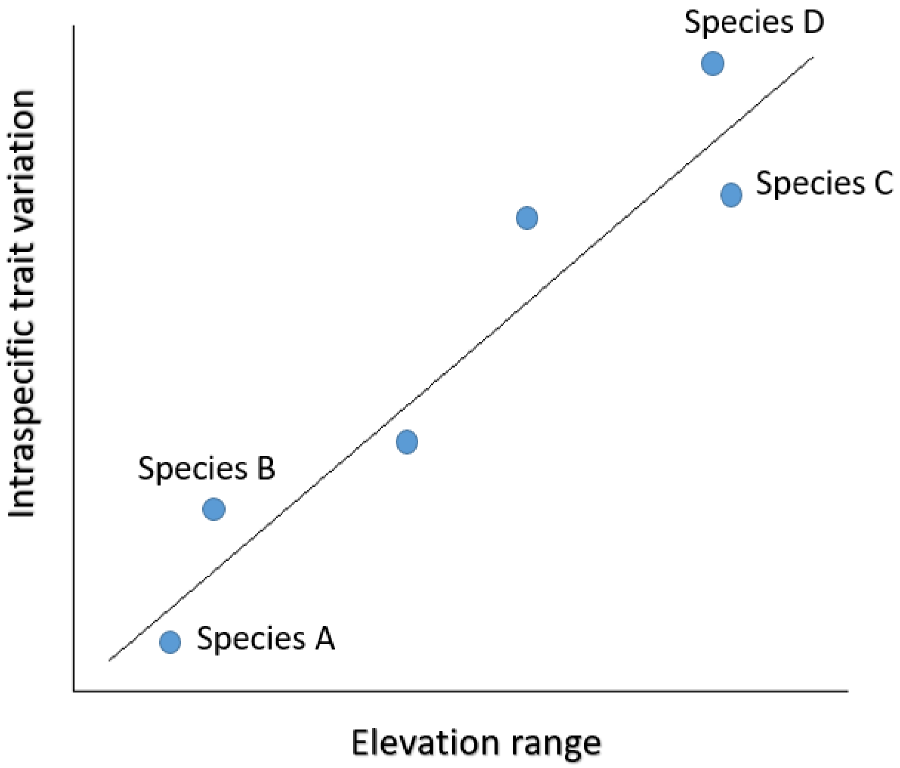

Figure 3 Schematic representation of hypothesis 3. Intraspecific trait variation is expected to be positively correlated to species elevation range. Species A and B have a narrow elevation range and are hence expected to have low intraspecific functional trait variation.

3 Study area

3.1 Western Ghats

The Western Ghats is a continuous mountain range running alongside the Western coast of the Indian peninsula of an approximate area of 160,000 Km^2 and a length of 1600 Km, extending from 8°- 20° N latitudes and 73°- 77° E longitudes. This stretch is largely contiguous except at the Palakkad gap which is approximately 30 km in width. This particular region has been designated as one of the 25 global biodiversity hotspots due to the high level of species richness, endemism, and loss of primary vegetation (Myers et al. 2000).

3.2 Kodagu

The district of Kodagu is located on the Western Ghats' eastern slopes. The district's altitude ranges from 175 m to 1734 m above sea level, with Tadiandamol, the district's highest mountain, located on the district's western border, forming a natural barrier between Kodagu and the low-lying coastal districts (Pascal, Ramesh, and Franceschi. 2004).

The district is a mosaic of tropical forests (4106 sq km) and coffee and pepper plantations. Because of a sharp gradient in environmental factors across the district such as temperature, annual precipitation, and duration of monsoon along with variation in topographical features such as aspect and altitude. Based on these factors Pascal and Meher-Homji (1986) broadly classified the forest types into the following vegetation types :

Wet Evergreen forests: These are mostly found in the district's western border and on the western aspect of the Western Ghats. This forest type has a short dry season and receives a lot of rain. They are also known for their high species diversity and are divided into three vegetation categories based on elevation and species composition.

1. Low elevation (up to 750 m altitude) - *Dipterocarpus indicus – Kingiodendron pinnatum – Humboldtia brunonis* type.
2. Mid elevation (750 – 1400 m) - *Mesua ferrea – Palaquium ellipticum* type
3. High elevation (above 1400m altitude) - *Schefflera spp. – Gordonia obtuse – Meliosma arnottiana* type.

Moist deciduous forests: These are located in the Kodagu district's central-eastern plains. These areas receive lower rainfall (1500-2000m) and have a long dry season. *Alstonia scholaris, Vitex altissima, Dillenia pentagyna, and Stereospermum personatum* are the dominant species in these forests. Dry Deciduous forests: With an annual rainfall of 750- 1500 mm and a dry season of 5-8 months, this forest type is mostly found on the district's eastern side. Tectona grandis, Terminalia spp., Anogeissus latifolia, and other species can be found in these forests.

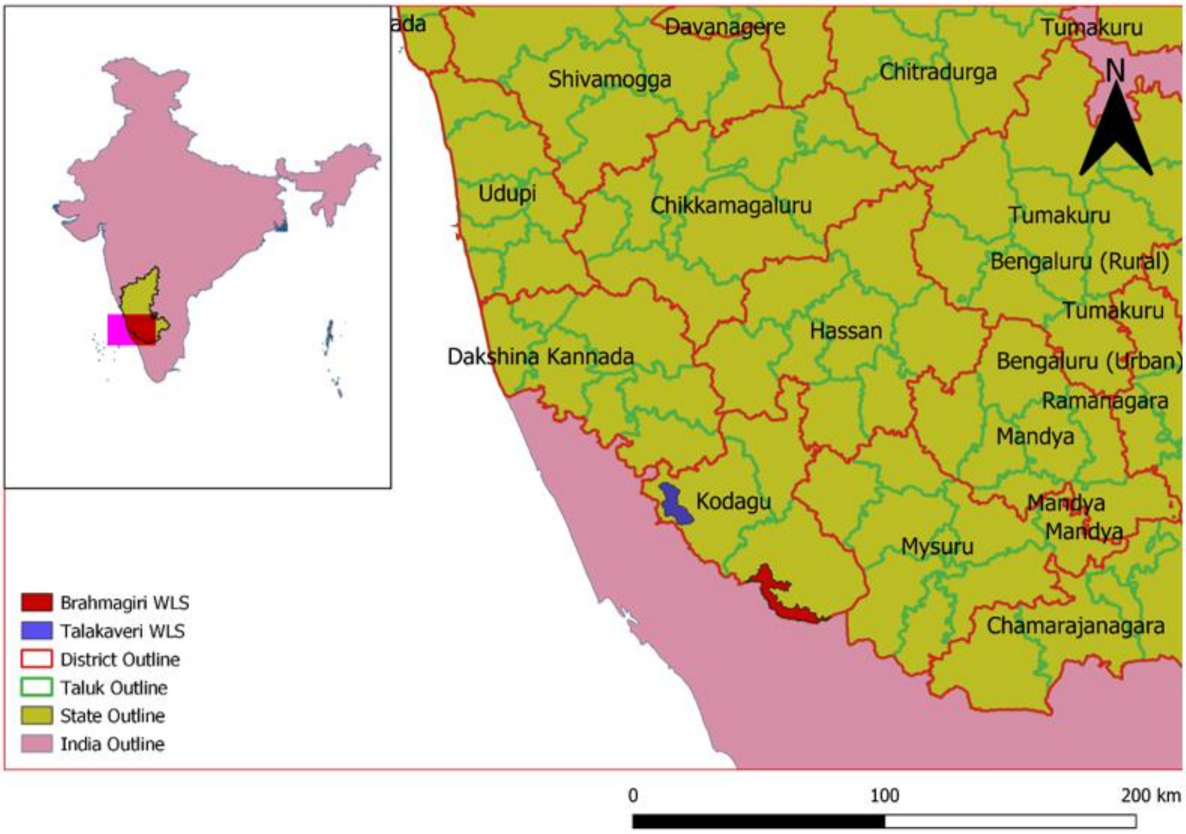

Fig. 1 Map of Kodagu district showing the three taluks. The study area is within the Madikeri and Virajpet Taluk.

3.3 Sampling sites

The sites that were chosen for sampling spanned an elevation gradient from 200 m to 1600 m above sea level. Since there was no single site that spanned the entire gradient, different sites of evergreen forests had to be sampled that covered different portions of the entire gradient -

1. **Brahmagiri Wildlife Sanctuary (Makutta Range)**: This particular region spanned an elevation range of 200 m – 700 m above sea level. This region was characterized by trees with a thick canopy and dense understory vegetation. Some of the common woody plant species were *Dimocarpus longan,*

Canarium strictum, Hydnocarpus pentandra, Garcinia morella. Sampling took place inside the forest along previously established patrolling paths by the forest department. A route frequently visited was the Narayana beat along which several patches of *Humboldtia brunonis* were encountered. Apart from walking on trails inside the forest, sampling of *Dimocarpus longan* was largely carried out along the Makutta – Kerala highway since it passed through the Brahmagiri wildlife sanctuary. The highway was apt for the collection of samples of *Dimocarpus longan* since it was found in great abundance along the road and leaf samples were easily accessible along the road.

2. **Chelavara – Udumbe range:** This particular region represents an overlap of the Virajpet reserve forests (Chelavara) and the Brahmagiri Wildlife Sanctuary (Udumbe range). This site spanned an elevation range of 450 m – 1200 m above sea level with shola type patches of evergreen forest at the higher elevation and a contiguous forest below 1100 m a.s.l similar to that found in Makutta. Samples of the species *Litsea floribunda* and *Symplocos cochinchinensis* were collected from the upper limits of this site while several samples of *Humboldtia brunonis* were collected from elevations below 800 m. A few samples of *Dimocarpus longan* were also obtained at the lower stretches of this site.
3. **Tadiandamol:** The highest point in Kodagu at a maximum elevation of 1734 m a.s.l which is a part of the reserve forests in the Madikeri territorial division. The elevation range for which the collection of samples took place was 1200 m – 1600 m a.s.l. This site is largely characterized by shola type patches of evergreen forests with species like *Vernonia monosa*, *Holligarna nigra*,

Symplocos cochinchinensis, *Litsea floribunda*, *Eudia lunu-ankenda*. The species for which samples were collected from here were *litsea floribunda* and *Symplocos cochinchinensis*.

4. **Iruppu falls (Brahmagiri range):** This site spans an elevation range of 1200 m -1600 m and is located in the Brahmagiri range of the Brahmagiri Wildlife Sanctuary. This site has shola type evergreen forests and species composition of vegetation similar to Tadiandamol. Samples for the species *Litsea floribunda*, *Symplocos cochinchinensis*, and *Symplococs macrophylla* was collected from here.

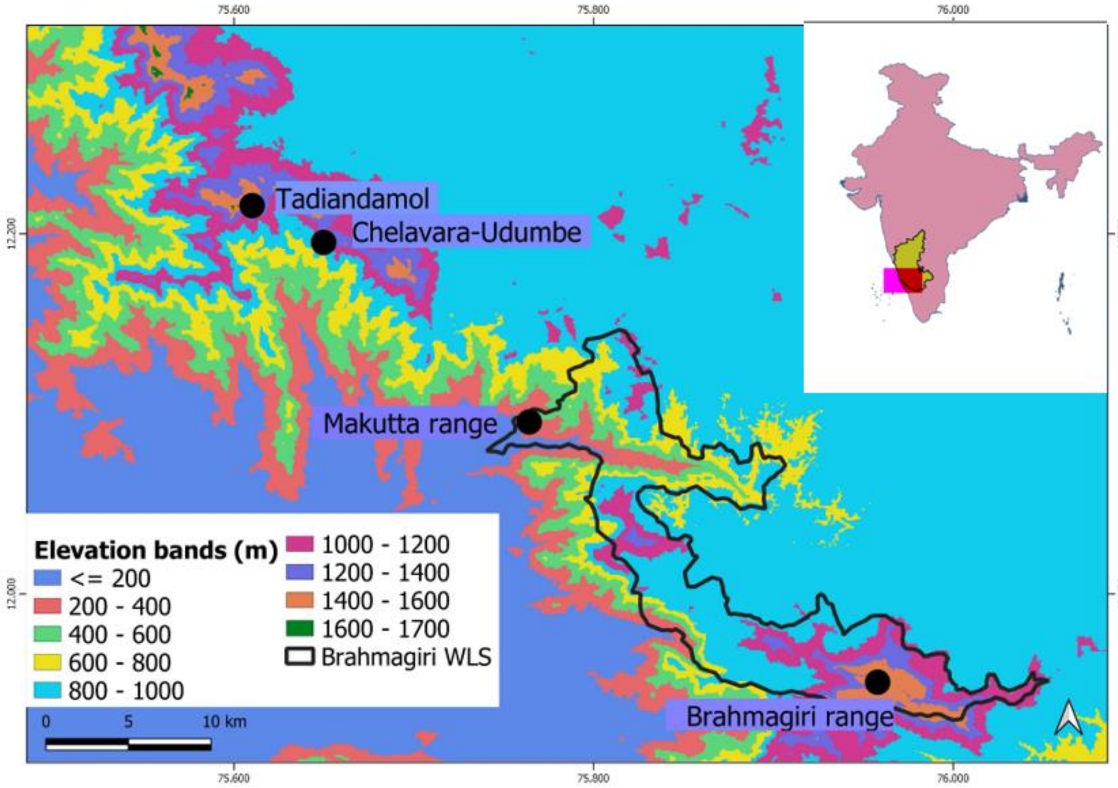

Figure 4 Map of all the sampling sites in Kodagu. Sites marked are – Brahmagiri range (yellow), Makutta range (Green), Chelavara-Udumbe (Brown), Tadiandamol (Blue), Brahmagiri Wildlife Sanctuary (Red).

4 Methods

This study was conducted in the evergreen forests of Kodagu district, covering an elevation gradient of 100 m to 1740 m above sea level. Leaf and wood core samples were collected for a select group of woody plant species across their respective elevation ranges of occurrence in the landscape. To measure functional trait values of the leaf and wood core samples, standardized methods described by (Pérez-Harguindeguy et al. 2013) were followed. The collected data was analyzed further using the appropriate techniques to understand the patterns of intra-specific trait variation.

Since no single study site represented all 7 elevational zones, data was collected across 4 different study sites spanning the district of Kodagu (Fig. 4). The study sites were finally chosen from the Brahmagiri Wildlife Sanctuary and the reserve forests of Virajpet and Madikeri in Coorg. These field sites were finalized since together they spanned across the 7 elevational zones that were chosen a-priori. Logistic feasibility was another critical factor for the choice of these field sites. The chosen field sites were also within a few hours of travel from our host institution, College of Forestry, Ponnampet since it was imperative to measure the functional trait values from the leaf and wood core samples within 24 hours of collection.

Species	**Elevation range (m)**	**Elevation band**	**SSD**	**SLA**	**LDMC**
***Dimocarpus longan* (DIMLO)**	200-1000 (800 m)	200-400	20	20	20
		400-600	17	17	17
		600-800	20	20	20
		800-1000	15	13	13
***Humboldtia brunonis* (HUBRU)**	275 – 935 (660 m)	200-400	22	22	22
		400-600	21	19	19
		600-800	27	27	27
		800-1000	28	28	28
***Litsea floribunda* (LIFLO)**	830 - 1615 (785)	800-1000	6	6	6
		1000-1200	10	9	9
		1200-1400	27	27	27
		1400-1600	21	21	21
***Symplocos cochinchinensis* (SYMCO)**	1250 - 1600 (350 m)	1000-1200	10	9	9
		1200-1400	27	27	27
		1400-1600	21	21	21
***Symplocos macrophylla* (SYMMA)**	1600 - 1450 (450 m)	1200-1400	24	24	24
		1400-1600	20	20	20

Table 1 Selected species along with their respective elevation range and sample size per elevation band.

4.1 Selection of study sites and species

I collected samples over a 1400 m elevation gradient (200 m – 1600 m a.s.l) in the Kodagu district. A total of 7 elevational zones, each spanning 200 m in elevation were delineated. Since no single study site represented all 7 elevational zones, data was collected across 4 different study sites spanning the district of Kodagu. The study sites were finally chosen from the Brahmagiri Wildlife Sanctuary and the reserve forests of Virajpet and Madikeri in Coorg. These field sites were finalized since together they spanned across the 7 elevational zones that were chosen a-priori. Logistic feasibility was another critical factor for the choice of these field sites. The chosen field sites were also within a few hours of travel from our host institution, College of Forestry, Ponnampet since it was imperative to measure the functional trait values from the leaf and wood core samples within 24 hours of collection.

The primary criterion for the selection of species for the study was that they must span a minimum of the 2 previously delineated elevation zones. The species were also required to have adequate abundance to get a minimum sample size of 10 individuals per species in each elevation zone. A preliminary assessment of candidate species for the study was done using data from Page et al. (2010). A group of candidate species was chosen based on the elevation and abundance criteria mentioned previously. A final list of species was formalized after conducting field surveys to determine whether a sufficient number of individuals per species can be sampled alongside trekking routes in the selected study sites. Ease of accessing leaves was another factor that was considered for the selection of the final list of species. 5 species were selected which were of differing elevation ranges: *Dimocarpus longan* (Sapindaceae) (referred to as

DIMLO henceforth), *Humboldtia brunonis* (Fabaceae) (referred to as **HUBRU** henceforth), *Litsea floribunda* (Lauraceae) (referred to as **LIFLO** henceforth), *Symplocos cochinchinensis* (Symplocaceae) (referred to as **SYMCO** henceforth), *Symplocos macrophylla* (Symplocaceae) (referred to as **SYMMA** henceforth). *Dimocarpus longan* (**DIMLO)** and *Humboldtia brunonis* (**HUBRU)** are species spanning the lower to the mid-elevation range. *Litsea floribunda* (**LIFLO)** spanned the mid-elevations to the upper elevations while *Symplocos cochinchinensis* (**SYMCO)** and *Symplocos macrophylla* (**SYMMA)** spanned the upper elevations. The elevation ranges of each species along with the number of individuals sampled are shown in Table 1.

4.2 Selecting individuals

To access individuals of the selected species across the elevation gradient, trekking paths used by the forest department staff were used. However, due to the forest being largely inaccessible because of the terrain and thick understory, the method of sampling was arbitrary where individuals were sampled arbitrarily whenever they were encountered while walking along the trekking routes. An effort was made to sample individuals at a minimum distance of 10 - 15 m from each other, however, this could not be strictly followed in some cases where individuals were distributed in a clustered manner and were found in close proximity to each other. To ensure that healthy adult individuals were sampled, the girth cutoff for each species was decided using by calculating the 75th percentile value of girth data from Page et al. (2010).

Individuals that were flowering and fruiting were also considered as adults and were sampled.

4.3 Collection and measurement of functional traits

Data on specific leaf area (SLA), leaf dry matter content (LDMC), stem specific density (SSD), height, and the girth at breast height (GBH) was collected for each individual. The collection of samples and the measurement of the functional traits was done using standardized methods as described by (Pérez-Harguindeguy et al. 2013).

I chose relatively young but fully expanded and hardened leaves for the measurement of SLA and LDMC. A minimum of 5 leaves was taken from each individual. On average, leaves with symptoms of pathogen or herbivore attacks were avoided as much as possible. Since SLA is strongly affected by the light intensity to standardize the type of leaves collected only outer canopy leaves were collected. In the case of compound leaves of *Dimocarpus longan* and *Humboldtia brunonis*, the rachis and all veins were considered to be part of the leaf. Whole twigs along with the leaves were procured either by using an extendable tree pruner or an arborist throw line. This was then stored in plastic zip-lock bags with water to keep it hydrated until the samples were measured at the end of the day. The leaves were later on scanned for leaf area by using a flat-bed scanner (CANON LIDE 300). Leaf areas of the scanned leaves were estimated using the BLACKSPOT software (Varma and Osuri 2013). The wet weight of the leaves was also determined using a sensitive weighing balance following which the leaves were packed in brown paper bags and oven-dried for 72 hours at 60 °C. The samples were again weighed after oven drying to determine the dry weight. The SLA of each leaf was calculated as the one-sided leaf area per unit dry weight. The LDMC for each leaf was calculated as the oven-dry mass of a leaf divided by its water-saturated fresh mass. The functional trait values of each leaf were averaged to obtain a value for each individual.

Wood cores were obtained using an increment borer that extracted a sliver of the wood core from each individual, which was later used to obtain its density and weight. The fresh wood volume was determined using the water displacement method and then stored in the brown paper bags along with the leaves. The wood cores after being oven-dried along with the leaves were weighed using the sensitive weighing balance. Finally, the SSD was calculated as the oven-dried weight per unit fresh volume. Tree height was estimated by using either a clinometer or a laser range finder. GBH was measured using a measuring tape at a height of 1.5 m from the ground.

4.4 Analytical methods

4.4.1 Directionality of functional traits

All the trait values were log-transformed to reduce the skewness of the data. Following this, all the functional trait values were standardized to a mean of 0 and a standard deviation of 1 before analysis for ease of comparison and interpretation of results (Yang et al. 2020).

To explore directional change in the functional trait values in response to elevation, each trait was independently analyzed in a linear regression framework and this was done for each species. The functional trait values were taken as the response variables while the elevation was considered as an explanatory variable. Assumptions of homoscedasticity, normality of residuals, and independence of observations were not found to be violated.

Functional trait data for all the species were pooled and simple linear models of varying complexity were used to check if there was an overall trend of the functional trait values in response to elevation. I produced three models where Model 1 is a linear regression with only one predictor variable, elevation. Model 2 and model 3 are models with the categorical predictor Species, which takes into account the species identity. Model 2 is an additive model while model 3 is an interaction model. These models were run for SLA, LDMC, and SSD.

4.4.2 Variance partitioning

To partition trait variance across ecological scales in the dataset, variance partitioning analysis as described by Messier, McGill, and Lechowicz (2010) was conducted. This involved fitting the data into a linear mixed-effects model to explain the variance in the data across the 4 different hierarchical ecological scales. The random effects were nested in increasing order: individuals, populations, species, elevation bands. A variance component analysis was conducted on this model to estimate the contribution of each random effect to the total variance of the response.

4.4.3 Correlation between CV and elevation range

I have used the coefficient of variance (CV) as a measure to estimate the ISTV for each species and functional trait per species by following the guidelines discussed by Yang et al. (2020). This has been traditionally used by several studies to quantify the absolute extent of ISTV since it is dimensionless. This allows for the comparison of ISTV between functional traits with vastly different trait means and also between species with different abundances (Helsen et al. 2017). According to Yang et al. (2020), the most commonly used ISTV estimator ($CV = \sigma_{sample}/\mu_{sample}$) to a great extent underestimates the magnitude of functional trait variation, which varies among traits as well as species. This bias in estimation is largely dependent on the sample size, skewness, and kurtosis of the trait value distribution. It has been proposed that the data be log-transformed and scaled following which the usage of alternate CV estimators has been prescribed. The Bao's CV estimator along with log data normalization was attempted to estimate the ISTV since this exhibits the lowest bias and can reach ± 5% accuracy with samples greater than 20.

To test for a correlation between the functional trait CVs and the elevation range of occurrence a non-parametric test for correlation, Kendall's rank test for correlation was conducted. A non-parametric method was employed to test for correlation between the functional trait CV and elevation range of occurrence due to the low number of species because of which we could not make assumptions on the underlying distribution of the dataset.

5 Results

5.1 Variation of functional traits in response to elevation

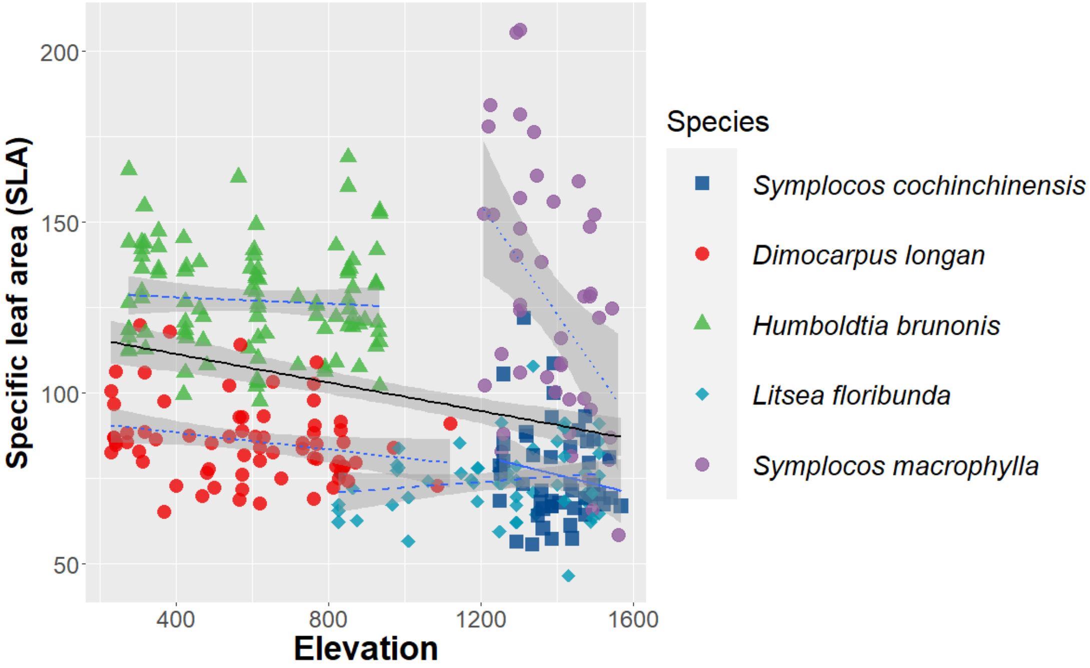

Figure 5. Relationship of specific leaf area (SLA) to elevation. The blue lines represent per species smoothened regression lines, while the black line is an overall smoothened regression line for the entire dataset.

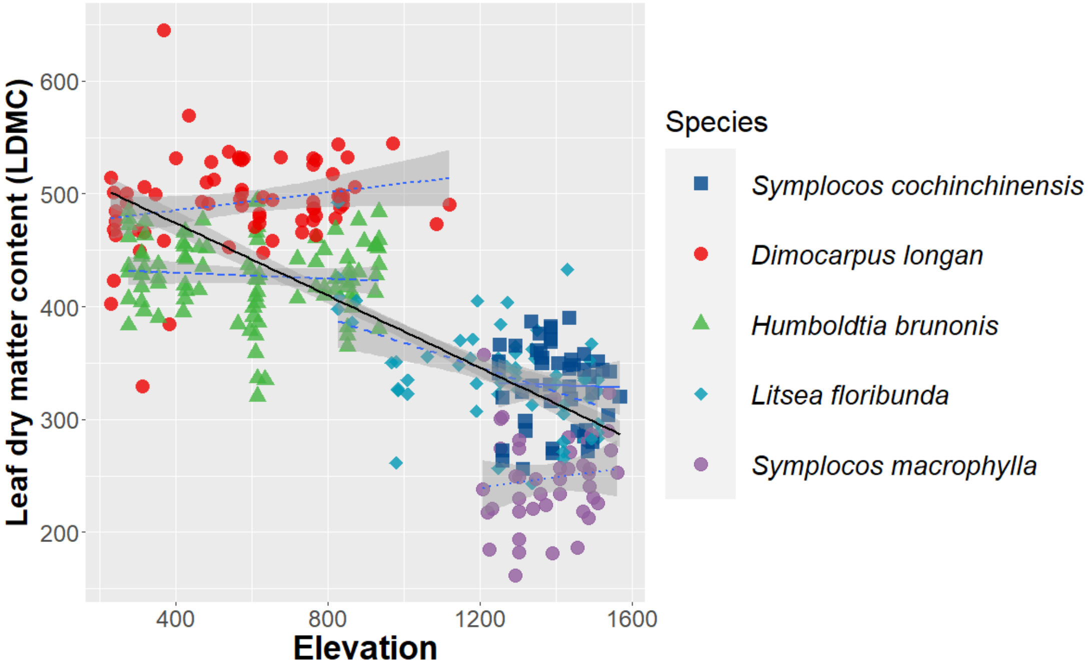

Figure 6. Relationship of leaf dry matter content (LDMC) to elevation. The blue lines represent per species smoothened regression lines, while the black line is an overall smoothened regression line for the entire dataset.

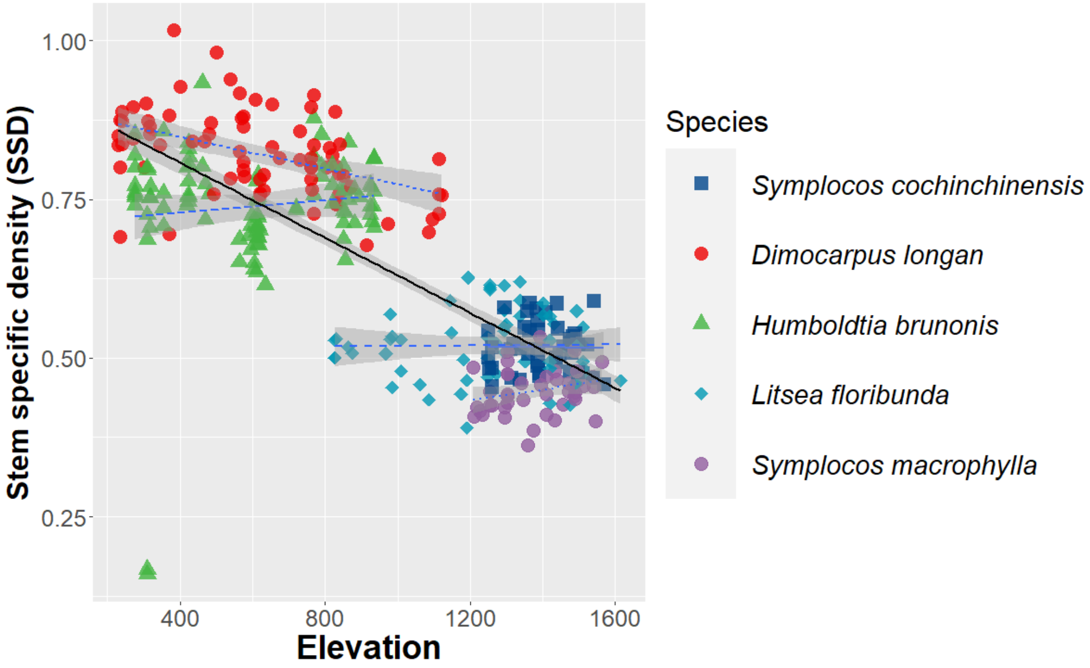

Figure 7. Relationship of stem specific density (SSD) to elevation. The blue lines represent per species smoothened regression lines, while the black line is an overall smoothened regression line for the entire dataset.

A simple model for SLA (Simple model, Table 2) was built to predict SLA as a response to change in elevation with no additional complexity. Elevation is seen to have a significant effect with an adjusted R^2 of 0.11.

To run multiple regression models for all three functional traits (SLA, LDMC, and SSD) with elevation (continuous) and species (categorical) as predictors as baseline level was taken. All other estimates were values expressed in relation to the baseline estimate (of both slope and log average value).

Accounting for species identity improved the amount of variation explained in SLA. When species identity was explicitly accounted for in the additive model (Table 2) it was seen that elevation continued to remain a significant predictor of SLA even when controlling for species identity. The log average values of SLA for each species are mentioned in the table of coefficients (Table 2). The additive model also demonstrates that the average values of *Symplocos macrophylla* and *Humboldtia brunonis* are significantly different from the average value of *Symplocos cochinchinensis* (marked as the intercept). The adjusted R^2 for this model is 0.65 (ANOVA : F(4, 318) = 139.24, p < .001)

An interaction model (Model 3) with the same predictor variables gave an adjusted R^2 of 0.68 65 (ANOVA : F(4, 314) = 8.15, p < .001) . Upon examining model 3 it is seen that elevation controlled for species identity does not remain a significant predictor of SLA. However, the effect of elevation on SLA for the species *Symplocos macrophylla* is the only interaction predictor that is significantly different from the baseline estimate i.e. interaction between species identity of *Symplocos cochinchinensis* and elevation.

	Simple model			Additive model			Interaction model		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	-0.00	-0.10 – 0.10	0.982	-0.70	-0.92 – -0.47	**<0.001**	-0.39	-1.24 – 0.47	0.373
Elevation	-0.33	-0.44 – -0.23	**<0.001**	-0.14	-0.28 – -0.00	**0.045**	-0.43	-1.21 – 0.35	0.275
SYMCO	*Reference*			*Reference*			*Reference*		
SpeciesDIMLO:Elevation							0.24	-0.58 – 1.05	0.565
DIMLO				0.17	-0.18 – 0.52	0.338	-0.19	-1.07 – 0.70	0.678
SpeciesHUBRU:Elevation							0.38	-0.43 – 1.19	0.357
HUBRU				1.52	1.19 – 1.86	**<0.001**	1.29	0.41 – 2.16	**0.004**
SpeciesLIFLO:Elevation							0.57	-0.26 – 1.40	0.177
LIFLO				-0.11	-0.34 – 0.12	0.350	-0.62	-1.51 – 0.27	0.169
SYMMA				1.64	1.39 – 1.88	**<0.001**	3.15	2.05 – 4.25	**<0.001**
SpeciesSYMMA:Elevation							-1.47	-2.49 – -0.45	**0.005**
Observations	321			321			321		
R^2 / R^2 adjusted	0.113 / 0.110			0.663 / 0.657			0.695 / 0.686		

Table 2 Coefficients for linear models with SLA as the response variable. The simple model has one predictor (elevation). The additive model has species identity (categorical variable) added as a predictor along with elevation. The interaction model represents an interaction between species identity and elevation.

The Simple model (Table 3) with LDMC as a response to elevation with no additional complexity had an adjusted R^2 value of 0.52 where elevation is a significant predictor.

Accounting for species identity improved the amount of variation explained in LDMC. Upon running the additive model (Model 2, Table 3) it is seen that elevation controlled for species identity does not remain a significant predictor. The log average values of LDMC for each species are mentioned in the table of coefficients (table 3) The adjusted R^2 for this model is 0.79 (ANOVA : F(4, 318) = 85.67, $p < .001$). In Model 2 for LDMC (additive model), the log average value of *Litsea floribunda* is the only predictor that is not significantly different from the log average value of *Symplocos cochinchinensis*.

Accounting for species identity improved the amount of variation explained in SSD. Just like in the case of LDMC, for SSD model 1 elevation is seen to be a significant predictor of SSD with an adjusted R^2 of 0.54. Upon running the additive model (Table 4) it is seen that elevation controlled for species identity does not remain a significant predictor. The log average values of SSD for each species are mentioned in the table of coefficients (Table 4). In Model 2 for SSD (additive model), the average value of *Litsea floribunda* is the only predictor that is not significantly different from the average value of *Symplocos cochinchinensis*. The adjusted R^2 for this model is 0.69 (ANOVA : F (4, 318) = 65.15, $p<.001$).

	Simple model			**Additive model**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.04	-0.00 – 0.09	0.067	-0.23	-0.33 – -0.12	**<0.001**
Elevation	-0.44	-0.48 – -0.39	**<0.001**	-0.04	-0.11 – 0.02	0.218
SYMCO	*Reference*			*Reference*		
DIMLO				0.89	0.72 – 1.05	**<0.001**
HUBRU				0.55	0.39 – 0.70	**<0.001**
LIFLO				0.05	-0.05 – 0.16	0.322
SYMMA				-0.71	-0.82 – -0.60	**<0.001**
Observations	321			321		
R^2 / R^2 adjusted	0.528 / 0.527			0.799 / 0.795		

Table 2 Coefficients for linear models with LDMC as the response variable. The simple model has one predictor (elevation). The additive model has species identity (categorical variable) added as a predictor along with elevation.

	Simple model			**Additive model**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.01	-0.07 – 0.08	0.891	-0.65	-0.85 – -0.44	**<0.001**
Elevation	-0.71	-0.78 – -0.64	**<0.001**	-0.05	-0.18 – 0.08	0.448
SYMCO	*Reference*			*Reference*		
DIMLO				1.60	1.28 – 1.92	**<0.001**
HUBRU				1.20	0.89 – 1.51	**<0.001**
LIFLO				0.01	-0.20 – 0.22	0.905
SYMMA				-0.44	-0.66 – -0.22	**<0.001**
Observations	321			321		
R^2 / R^2 adjusted	0.541 / 0.540			0.701 / 0.696		

Table 3 Coefficients for linear models with SSD as the response variable. The simple model has one predictor (elevation). The additive model has species identity (categorical variable) added as a predictor along with elevation

5.2 Proportion of variance explained by the nested levels

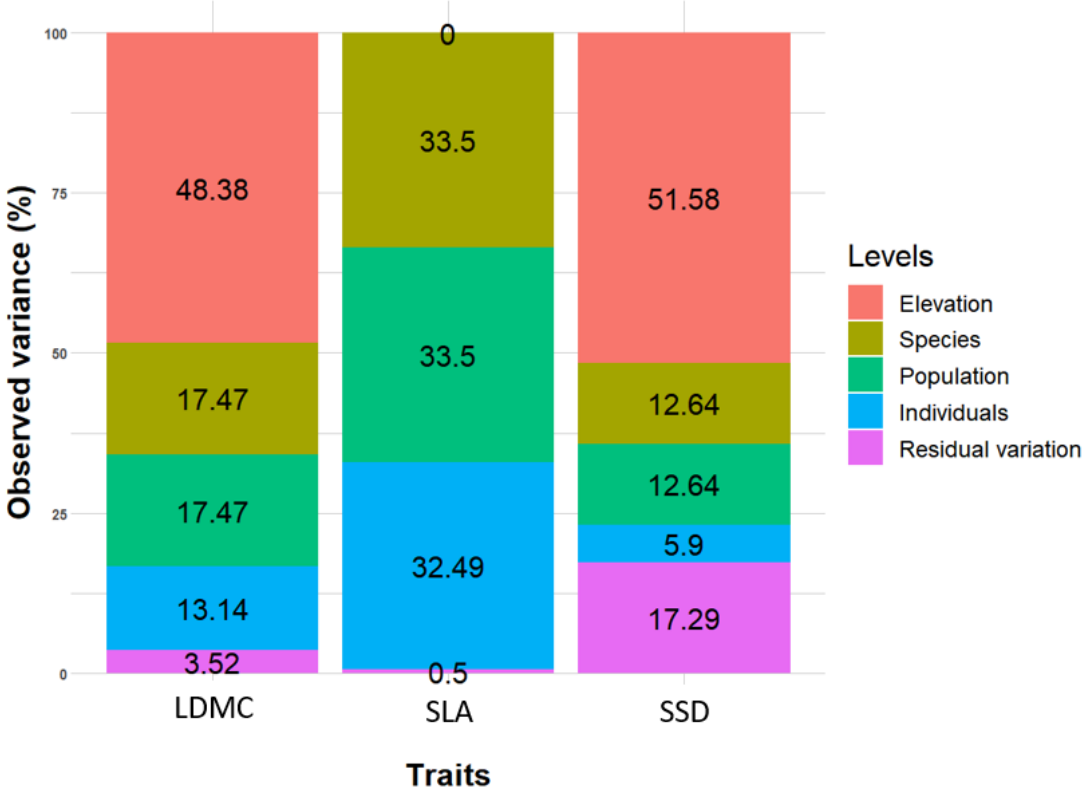

Table 4. A visual representation of the percentage of variance associated with different hierarchical levels - Elevation, Species, Populations, and the individual level following the variance components analysis. The functional traits are SLA (Specific leaf area), LDMC (Leaf dry matter content), SSD (Stem specific density).

The variance partitioning analysis highlights the amount of variation distributed across each of the nested levels of organization. The trait variation for all three traits ranged from 33.50 % to 12.64 % for the species level as well as the population level. The variation in trait values explained across individuals ranged from 33% to 23.23%, while the variation explained at the elevation level was 0 %, 48.38%, and 51.58% for SLA, LDMC, and SSD.

From the perspective of the variance partitioning analyses, the variance explained by species and population levels was found to be almost similar for all three functional traits. Elevation was seen to explain nearly half the variance for LDMC and SSD, while the variance explained for SLA was negligible.

Trait	Total variance explained (%)	Elevation (%)	Species (%)	Population (%)	Individual (%)	Residual (%)
SLA	99.5	0.0	33.50	33.50	32.49	0.5
LDMC	96.4	48.38	17.47	17.47	13.14	3.52
SSD	82.8	51.58	12.64	12.64	5.9	17.29

Table 5. Percentage of variance explained across Elevation, Species, Populations, and the individual level following the variance components analysis.

5.3 Correlation between CV and elevation range

The intra-specific variability in the three functional traits (SLA, LDMC, and SSD) differed for all the species and each of the traits. CV of SLA varied from 0.13 to 0.29, CV of LDMC varied from 0.11 to 0.15 and CV of SSD varied from 0.07 to 0.18. The CV for neither of the three traits was found to be significantly correlated with the elevation ranges of the plant species.

Species	SLA	LDMC	SSD
Dimocarpus longan	0.13	0.15	0.18
Humboldtia brunonis	0.12	0.12	0.13
Litsea floribunda	0.13	0.13	0.10
Symplocos macrophylla	0.29	0.16	0.08
Symcplocos cochinchinensis	0.19	0.11	0.07

Table 6 CV values computed for all the species per functional trait (SLA, LDMC, SSD).

Upon running a Kendall's ranked test for correlation it was seen that none of the functional trait CVs was seen to be significantly correlated to the elevation range of occurrence (Fig 8)

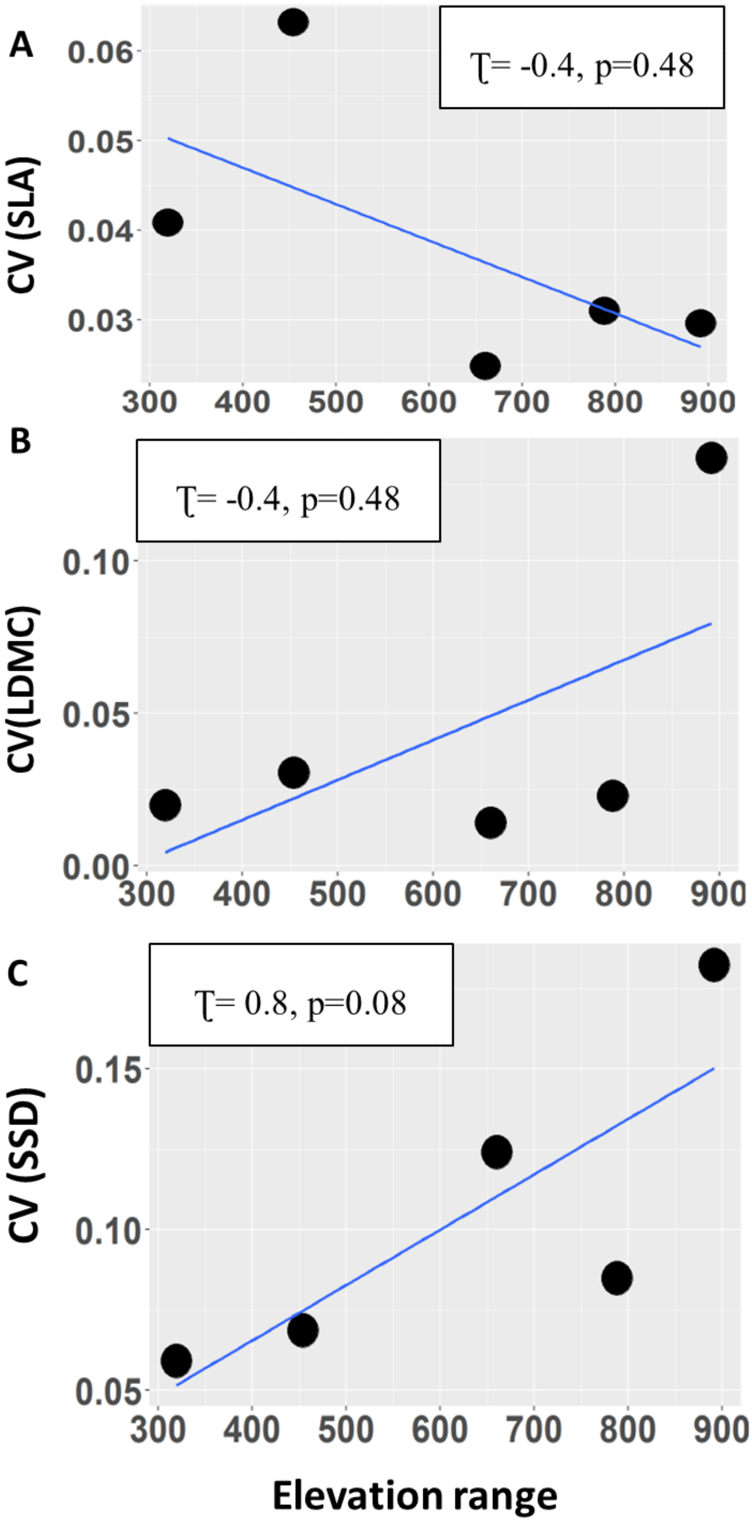

Figure 8. Results of Kendall's rank correlation test between CV of functional traits – SLA (A), LDMC (B), SSD (C), and the elevation range of species. The Tau (ꞇ) and p values have been shown in the graphs above.

6 Discussion

This study attempts to examine trends in the variation of the three functional traits, namely specific leaf area (SLA), leaf dry matter content (LDMC), and stem specific density (SSD) for 5 woody plant species with varying ranges of distribution along an elevation gradient. Since the environment is known to have a significant impact on the plant phenotype through selection, elevation gradients provide an opportunity to examine the response of functional traits to a changing environment as well as how this influences within and across species functional trait variation.

Trends across species

The entire dataset was pooled to examine the response of each of the functional traits to variation in elevation across all the species. This was done with the understanding that if natural selection were to operate at the level of the individual, trends would emerge for the entire dataset as opposed to when examining individual species trends. Such a theory would be true only if the different species are functionally identical and similarly respond to a changing environment. All three functional traits exhibited a decrease in value with an increase in elevation, the strength of this however was variable for each functional trait. A decrease in functional trait values in response to elevation seems to be primarily driven by interspecific differences in the mean values of the functional traits between species as opposed to being driven by intra-specific differences in functional traits along the elevation gradient. The exception to this, however, is *Symplocos macrophylla* (SYMA), in the case of SLA, where there is a strong relationship between SLA and elevation, potentially influencing the overall trend of SLA in response to elevation.

The significantly different mean trait values that might be driving across-species trends of functional traits are indicative of the fact that change in environmental constraints selects for species with specific mean trait values. This in turn may be driving community-wide trends of functional trait values in response to environmental gradients (Kichenin et al. 2013).

Trends within species

Species-specific trends of functional traits in response to elevation paint a different picture as opposed to the across-species trends. Functional trait values did not appear to change in response to elevation in most cases. Only in the case *Symplocos macrophylla* (SYMA), SLA is seen to vary in response to elevation. For the other species, there does not appear to be any trend observed in any of the functional traits.

The lack of an observed shift in intra-specific functional trait values along the elevation gradient for four of the five species might be because of other abiotic counter gradients operating across the elevation gradient (Umaña and Swenson 2019). Alternatively, species may also confer tolerance towards changing environments without changing functional trait values due to biophysical constraints, which could lead to a lack of response of functional traits to changing elevation. To explore these alternate reasons it might be required to measure variation in fine-scale abiotic factors along the elevation gradient.

Proportion of variance contributed by different ecological levels

The variance components analysis highlights the similarity in the percentage of variance associated with the species level and the percentage of variance associated with the populations level. The high trait variation at within-species scales (population and individual scales) in comparison to the level of species is a pattern observed from previous studies conducted at the community level (Albert et al. 2010; Messier, McGill, and Lechowicz 2010; Umaña and Swenson 2019). This observation is particularly relevant since it indicates that functional trait variation within species could be higher than previously expected, especially when environmentally heterogeneous scales are considered in the study. The high trait variation observed at the population scale is indicative of adjustment to a changing environment at within species scales along the elevation gradient. There however is a lack of an observed signal at within species levels for LDMC and SSD in response to elevation for the pooled data models (Table 3, Table 4) which may be because of counter gradients operating simultaneously along the elevation influencing functional trait values. It is also seen that the proportion of variance associated with the elevation, species, and population levels are comparable in the case of SLA.

It is seen that, unlike SSD and LDMC which have a substantial proportion of the total variance associated with the elevation level, for SLA, the proportion of total variance associated with the level of elevation is negligible. The SSD and LDMC high proportion of variance at the elevation level highlights the selection of functional trait values, independent of species identity. The high proportion of variance associated with the SSD and LDMC indicates that there appears to be a strong selection for these traits along the gradient when species identity is not taken into consideration. The variation at within species levels (populations and individuals) is seen to be much greater than the other traits which are congruent with other studies that highlight the high intra-specific variation of SLA along environmental gradients (Albert et al. 2010; Messier, McGill, and Lechowicz 2010; Umaña and Swenson 2019). This supports the idea that SLA is more variable than other functional traits at within-species scales (Albert et al. 2010; Messier, McGill, and Lechowicz 2010).

At the level of individuals, it is seen that SLA has the highest proportion of total variance in comparison to LDMC and SSD. This could potentially be because this trait is relatively more sensitive to the micro-environmental variability at local scales (Albert et al. 2010). Due to the link between SLA and light intensity (Liu et al. 2016) SLA may also have a greater magnitude of explained variance associated with the level of individuals because of the variation in the intensity of sunlight that individuals are exposed to in the wet-evergreen forests of Kodagu. In contrast for SSD, the proportion of variance explained at the level of individuals is relatively lower than SLA and LDMC. Similarly, the high trait variation for SLA at the population level is indicative of the selection of different SLA values within species, across the elevation gradient. However, the lack of a significant relationship between SLA and elevation for three of the five species might suggest the operation of counter gradients.

7 Conclusion

From this study, it becomes apparent that species that are distributed across an elevation gradient have the potential to exhibit substantial levels of functional trait variation across the different levels of organization, especially at within-species scales. This observation is particularly relevant since it emphasizes the importance of considering within-species functional trait variation in functional trait studies especially at scales where environmental factors are highly variable. This is contrary to the traditional practice of assuming intra-specific trait variation to be negligible in comparison to inter-specific trait variation. It is also seen that traits are highly variable across elevations as well as populations, however, there doesn't appear to be a directional selection of functional trait values in response to changing elevation in most cases. This implies the existence of multiple environmental gradients operating simultaneously which will require further investigation. Future studies exploring trait variation would benefit from measuring variation in other abiotic factors that vary along an elevation gradient.

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9 Appendix

Figure 9 A telescopic tree pruner of maximum 5.5 m in length being used to collected sun-exposed leaves.

Figure 10. Scanning and weighing of leaf samples using a flatbed scanner and sensitive weighing balance.

Figure 11. An increment wood borer being used to extract a wood core sample.

Figure 12. Oven drying of leaf and wood core samples in brown paper covers inside a hot air oven .